PEST MANAGEMENT





How Do *Collaria oleosa* and *Brachiaria* spp. Respond to Increase in Carbon Dioxide Levels?

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Keywords

Mirid bug, congo grass, forage, climate change

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Edited by Leandro P Ribeiro - EPAGRI

Received 8 June 2018 and accepted 28 September 2018 Published online: 29 October 2018

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Abstract

The current study determines the indirect effect of CO₂ level increase on Collaria oleosa (Distant, 1863) (Hemiptera: Miridae) fed on Brachiaria spp. (Poaceae), at two trophic levels, and evaluates resistance to these forages against the insect pest. Mirid bug nymphs and host plant were maintained under four climate environments: (1) nymphs and plants kept at 400 ppm CO_2 level; (2) nymphs kept at 400 ppm CO_2 level and fed on plants grown at 700 ppm CO_2 level; (3) nymphs kept at 700 ppm CO_2 level and fed on plants grown at 400 ppm CO_2 level; (4) nymphs and plants kept at 700 ppm CO₂ level. A totally randomized design was employed with 50 replications. Mean duration and survival of each instar and nymphal phase of insect, subjected to different climate scenarios and food sources, were evaluated. High CO₂ levels promote changes in the plant, which trigger changes in the biology of C. oleosa, especially when the insects are kept at the current CO₂ level. Moreover, since longer developmental period and shorter survival rates will induce the reduction of the number of generations and number of specimens, it may be underscored that B. brizantha species resistance will be maintained in future climate scenarios. Similarly, genotypes of B. ruziziensis demonstrated that they will be resistant at current and future CO₂ levels.

Introduction

Brazil is a major meat and milk producer, sporting a livestock herd of approximately 215.2 million heads raised on pasture (IBGE 2016). In 2016, 29.67 million cattle were slaughtered to meet the demands of domestic and international markets (IBGE 2017). Forage is the most practical and economical way for feeding cattle, ensuring low production costs (Alencar *et al* 2010, Dias-Filho 2014). However, the production and quality of forage is compromised by attacks from *Collaria oleosa* (Distant 1863). Mirid bugs, at the nymphal and adult phase, cause damage by inserting their stylet in the leaf epidermis, through the stomata. The leaves lose pigmentation by a drain out of cell contents. Leaves are directly injured through impairment of active photosynthesis, with a subsequent decrease in plant yield and nutritional contents (Auad *et al* 2011) and, consequently, reduction in meat and milk production.

It is a well-known fact that CO_2 concentrations increased since the Industrial Revolution, it almost reached 410 ppm in 2018 (CO2.Earth 2018), and climate scenarios indicate that the concentration of the gas may double by the end of the century (IPCC 2007). According to Hunter (2001) and Yadugiri (2010), due to increasing CO_2 rates, climate changes will have a significant impact on crop yields. Further, increasing temperature rates may influence several plant-insect interactions. Response to herbivory triggered by rising CO_2 could be dependent on the host plant and on herbivores (Bezemer *et al* 1998).

Since CO_2 is the primary substrate for photosynthesis (Taiz & Zeiger 2004), high concentrations of atmospheric CO_2 increase plants' growth rates. Plants with C_3 metabolism



Fig 1 Indirect effect on duration (days) and survival (%) of *Collaria* oleosa fed on *Brachiaria* spp. Insects kept at 400 ppm CO_2 level and fed on plants grown at 400 ppm (current CO_2 level) or at 700 ppm (CO_2 level expected in the future). Bars with the same lowercase letters for the comparison of duration and bars with uppercase letters for the comparison of survival rates do not differ by Dunn's test (P < 0.05).

benefit more by an increase in atmospheric CO₂ concentration than plants with C_4 metabolism (Tubiello *et al* 2000, Streck 2005), such as Brachiaria sp. In Brazil, the latter forage is of greatest economic importance, known for its perenniality, with great leaf mass production and the ability to adapt to different environmental conditions and pasture managements (Kissmann 1997). According to Amiri-Jami et al (2012), knowledge on the effects of the host plant on the insect pest life cycle foregrounds studies on population dynamics and pest management programs, assessed by variations of insect performance on the host plant. Studies have shown that CO₂ induces changes in leaf nutrients and secondary substances that alter plant quality and define the adaptation capacity or resistance of the host plant associated to the herbivore (Agrell et al 2000, Zavala et al 2013, Guo et al 2014). They also indicate that the indirect effect of CO₂ increase via plants is often regarded as responsible for the impact on insect performance (Chen et al 2005, Wu et al 2006, Yin et al 2010) and insect consumption rates (Yin et al 2009, Sun et al 2010, 2015, Guo et al 2017).

Since time immemorial, plants have been selected because of their resistance to insect pests, frequently by improved varieties containing resistance genes that occur naturally or that have been transferred to the plant (Maxwell & Jennings 1980). Recent evidence suggests that global climate change may interrupt insect resistance in specific crops, with serious implications for food security (Gregory *et al* 2009, Guo *et al* 2014, Sun *et al* 2015, Guo *et al* 2017).

Our hypothesis is that physiological changes in forages and changes in *Brachiaria* resistance against the mirid bug, triggered by increasing CO_2 , will alter certain biological aspects of *C. oleosa* that will take to the exacerbation of the issue with the insect pest in a future climate scenario. The current study determines the indirect effects of increasing CO_2 levels on *C. oleosa* biology, when fed with two species of *Brachiaria*, both (plants and insects) subjected to different CO_2 levels, and evaluates the forages' resistance against the mirid bug.

Material and Methods

Obtaining and maintaining C. oleosa and forage

The mirid bug, *C. oleosa*, was retrieved from the Experimental Station of the Embrapa Dairy Cattle, in

Coronel Pacheco, Minas Gerais State, Brazil. The insects were placed in acrylic cages ($60 \times 30 \times 30$ cm) in the entomology laboratory, together with a *Brachiaria decumbens* plant as a substrate for oviposition and feeding. The eggs were extracted from the leaf sheath by a fine-tip brush and placed in a petri dish (5-cm diameter) with agar layer deposited on *Brachiaria* leaf disks on which the newly hatched nymphs could feed. The petri plates were covered with an organza-type fabric and kept in a climatic chamber at 25 ± 2°C, RH 70 ± 10%, and 12-h photoperiod.

The plants were grown in plastic pots (5 L) with soil substrate and manure (2:1 w/w) and maintained in a greenhouse for 30 days. Two genotypes of *Brachiaria ruziziensis* (CNPGL BR150 and BR1765 CNPGL) were used in all tests since the genotypes are resistant to the main forage pest: the spittlebug (Hemiptera, Cercopidae). *Brachiaria brizantha* is the resistance standard to the same insect pest (Souza Sobrinho *et al* 2010) and *C. oleosa* (Silva *et al* 2013a). The authors expected to obtain forage that, besides being resistant to the main pasture pest (spittlebug), was also resistant to *C. oleosa*.

Experiment

Eggs, nymphs, and plants were maintained under the same environment at different CO_2 levels. CO_2 concentrations were kept close to current levels (400 ppm) or to levels expected for the year 2100 (700 ppm) by the Intergovernmental Panel on Climate Change (IPCC 2007).

The indirect effect of rising CO_2 levels on *C. oleosa* biology was studied in a phytotron-type controlled environment (2.5 × 2.20 × 2.80 m), featuring the following conditions: *C. oleosa* nymphs and plants were kept at 400 ppm CO_2 level (scenario 1); nymphs kept at 400 ppm CO_2 level were fed on plants grown at 700 ppm CO_2 level (scenario 2); nymphs kept at a 700 ppm CO_2 level were fed on plants grown at 400 ppm CO_2 level (scenario 3); nymphs and plants were kept at 700 ppm CO_2 level (scenario 4). Temperature (25 ± 2°C), relative humidity (70 ± 10%), and photoperiod (12 h) were constant in all treatments.

Conditions in the CO_2 chamber were maintained constant by an automatic control system (COEL model HW 4200, Manaus-Amazonia, Brazil), and an injection system with a CO_2 cylinder to maintain the required CO_2 concentration. Nymphs up to 12 h old were used to evaluate CO_2 on *C. oleosa* biology. The nymphs were kept individually on petri dishes (5-cm diameter) containing a *Brachiaria* leaf disk extracted from plants submitted to different CO_2 levels, conditioned on a 1% agar layer. Rearing units were covered with organza-type cloth and fastened with elastic band. Each leaf disk was evaluated daily; leaves with a yellowish color were removed to avoid degradation of the food resource.



Fig 2 Indirect effect on duration (days) and survival (%) of *Collaria* oleosa fed on *Brachiaria* spp. Insects kept at 700 ppm CO_2 level and fed on plants grown at 400 ppm (current CO_2 level) or at 700 ppm (CO_2 level expected in the future). Bars with the same lowercase letters for the comparison of duration and bars with uppercase letters for the comparison of survival rates do not differ by Dunn's test (p < 0.05).

The study of the indirect effect of elevated CO_2 on *C. oleosa* biology was conducted in a completely randomized design, with 50 replications per treatment. Mean duration (days) and survival (%) of each instar and of the nymphal phase (from the first to the fifth instar) of *C. oleosa* were evaluated.

So that the indirect effect on *C. oleosa* duration and survival among climate scenarios could be assessed, climate scenarios 1 and 2 (insect at the current CO_2 level) were compared, likewise 3 and 4 (insect at future CO_2 level), with sole alteration of the CO_2 level to which the plant was subjected. Moreover, the resistance of forages against mirid bugs was verified within each climate scenario.

Survival data of *C. oleosa* (%) were transformed by calculating arc sine $(x + 1)^{0.5}/100$ prior to analysis. Non-parametric Kruskal-Wallis test, followed by Dunn's test, was applied at p < 0.05 significance. Statistical analysis was carried out with SigmaPlot 13.0.

Results

Insects kept at the current CO₂ level

No significant alteration occurred in the duration of C. oleosa at the first and second instar, fed on B. brizantha, when insects were maintained always under current weather status and fed on plants submitted to current or future types of weather (Fig 1). There was no comparison from the third instar neither for forage species B. brizantha nor for B. ruziziensis genotype CNPGL BR150, from the first instar, due to the deleterious effects on plants submitted to a future climate scenario and offered to the insect maintained under current weather conditions. B. ruziziensis genotype CNPGL BR1765, subjected to high CO₂ concentrations, decreased duration in the third and fourth instar and, consequently, in the nymphal phase of the insect pest (Fig 1). Forages also reduced the survival of C. oleosa, when plants were subjected to high CO₂ levels. There was a 100% mortality rate in insects from the third instar in B. brizantha and from the first instar in B. ruziziensis genotype CNPGL BR150. In the case of CNPGL1765 genotype, although no difference was observed from the first to the fifth instar, there was a survival increase during the nymphal phase when kept at 700 ppm (Fig 1).

Insect kept at a future CO₂ level

When insects subjected to 700 ppm CO_2 were fed on plants submitted to 400 ppm or 700 ppm CO_2 , significant reductions occurred in the duration of *C. oleosa* at the second and fourth instars when fed on *B. brizantha*, and in *C. oleosa* duration of the fourth instar in *B. ruziziensis* genotype CNPGL BR150, when mirid bugs were fed on plants kept within a future scenario (Fig 2). *B. ruziziensis* genotype CNPGL BR1765 enhanced a significant increase in the *C. oleosa* duration of the first and fourth instars and, consequently, in the nymphal phase (Fig 2). Insect pest survival increased only in the first instar when fed on *B. brizantha* kept at 700 ppm; no difference occurred in the other forages (Fig 2).

Resistance evaluation of forage within each climate scenario

The duration of the first and fifth instars in CNPGL BR1765 genotype only did not differ from standard resistance (*B. brizantha*) in the scenario in which insect and plants were kept at 400 ppm CO₂ (climate scenario 1). In the case of the second instar, no difference was registered among the forages offered (Fig 3). Therefore, CNPGL BR1765 and BR150 CNPGL genotypes provided significantly higher mirid bug duration in the third and fourth instars when compared to *B. brizantha*. In future climatic conditions in which plants and insects would be subjected to high CO₂ levels (climate scenario 4), the CNPGL BR150 genotype for the first to fourth instars of *C. oleosa*, and the CNPGL 1765 genotype, only in the fourth instar, will cause significantly higher *C. oleosa* durations when compared to standard resistance (Fig 3).

In the case of treatments where insects and plants were subjected to different CO_2 levels, no alteration in the *C. oleosa* duration at the first and second was registered to forage *B. brizantha* and CNPGL BR 1765 supply, when insects were exposed to 400 ppm CO_2 and plants to 700 ppm. There was no comparison from the third instar neither for forage species nor for *B. ruziziensis* CNPGL BR150, from the first instar (climate scenario 2). When insects were subjected to high CO_2 and plants were grown at 400 ppm conditions (scenario 3), CNPGL BR150 genotype triggered significantly longer *C. oleosa* duration in the first and third instars. For the second instar, a shorter duration occurred in CNPGL BR1765 compared to *B.brizantha* (scenario 3) (Fig 3).

The survival of *C. oleosa* was not significantly different for *Brachiaria* sp. in the current scenario (scenario 1), except for CNPGL BR 1765 genotype that was higher in the fifth instar. In a future scenario (scenario 4), CNPGL BR150 genotype reduced the survival of *C. oleosa* for the second and fifth instars when compared to that of *B. brizantha* (Fig. 3). In climate scenario 2 in which insects were exposed to 400 ppm CO_2 and plants to 700 ppm, the survival of *C. oleosa* fed on



Fig 3 Effect on duration (days) and survival of *Collaria oleosa* fed on *Brachiaria* spp. *Collaria oleosa* nymphs and plants kept at 400 ppm CO_2 level (scenario 1); nymphs kept at 400 ppm CO_2 level and fed on plants grown at 700 ppm CO_2 level (scenario 2); nymphs kept at 700 ppm CO_2 level and fed on plants grown at 400 ppm CO_2 level (scenario 3); and nymphs and plants kept at 700 ppm CO_2 level (scenario 4). Bars with the same lowercase letters that compare *Collaria oleosa* duration in the forage within each climate scenario do not differ by Dunn's test (p < 0.05).

B. ruziziensis genotype CNPGL BR1765 was greater than that on standard resistance from the first to the third instar. Posterior to the latter instar, total mortality of bugs occurred when fed on *B. brizantha*. CNPGL BR150 genotype had already caused total mortality to the first instar (Fig 3). In the case of insects subjected to elevated CO_2 and to plants grown at 400 ppm CO_2 (scenario 3), CNPGL BR150 genotype caused a similar or lower survival rate than that by *B. brizantha*. Insects fed on CNPGL BR1765 genotype have higher survival rates than resistance standard, but only in the first instar.

The nymphal phase of *C. oleosa* fed on CNPGL BR1765 genotype was significantly superior when compared to insects fed on *B. brizantha* in scenarios 1 and 4 (Fig 3). In the case of scenarios in which plants and insects were kept under different conditions (scenarios 2 and 3), the nymphal phase was identical to that of *B. brizantha* and CNPGL BR 1765 genotype in scenario 3. Within this scenario and scenario 2, other comparisons of the nymphal phase could not be performed, due to high *C. oleosa* mortality. CNPGL BR1765 genotype provided a higher survival rate in all scenarios, except when insects and plants were kept at 400 ppm, where the genotype proved to have the same resistance standard as the others.

Discussion

In the current study, we demonstrated the response to herbivory promoted by quality change in forage submitted to the current and future CO_2 levels with regard to duration and survival of *C. oleosa*, and forage responses to their resistance against mirid bugs. Effects on plant characteristics and on herbivore response mediated by high CO_2 concentrations have been researched for other insect species (Goverde & Erhardt 2003, Sun *et al* 2015, 2016, Guo *et al* 2017). This is the first study to determine the indirect effect of rising CO_2 levels on *C. oleosa* biology when fed on two *Brachiaria* species. Plants and insects were both subjected to different CO_2 levels.

Herbivorous insects are commonly affected by changes in the chemical components of their host plants (Yin *et al* 2010, Zavala *et al* 2013). Research has suggested that the CO_2 decreased protein concentration and increased carbohydrate

content of some plants (Barbehenn 2005, Taub *et al* 2008). High levels of the two macronutrients characterize the host plants as more nutritious (Mattson 1980, Lee *et al* 2002, Barbehenn 2005). The current study suggests that CO_2 altered the nutritional quality of *Brachiaria* genotypes since it provided variations in the duration and survival of *C. oleosa* instars, especially when the insect was maintained at the current CO_2 level (400 ppm) and fed on plants submitted in a future CO_2 level (700 ppm).

Alterations in certain plants with different CO₂ levels may change photosynthesis and reduce stomatal conductance due to the stomata's decreasing number (Bettarini et al 1998, Fraks & Beerling 2009) or pore size (Herrick et al 2004, Ainsworth & Rogers 2007). The decrease of the stomatal apertures appears to be a common response of plants to high CO₂ levels in Medicago truncatula Gaertn infested by the aphid Acyrthosiphon pisum (Harris) (Sun et al 2015) and Nicotiana attenuata Torr Ex Wats wild-type infested by Myzus persicae (Sulzer) (Guo et al 2017). In these cases, stomatal closure has been considered as responsible for maintaining the water potential of the host plant improving the feed efficiency of aphids under high CO2 levels. However, in the current work, this may explain the high mortality of nymphs in the genotypes evaluated in this study, when submitted to high CO₂ levels. In fact, the closing of the stomata may hinder the feeding of C. oleosa since the insects insert their stylet into the plants' stomata (Auad et al 2011).

Exposure to high CO₂ alters the plants' chemical components and their nutritional value to herbivores, especially by reducing nitrogen content and increasing the C:N ratio (Chen et al 2004, Robinson et al 2012, Zavala et al 2013). Reduced nitrogen availability, the main constituent of proteins, may reduce protein contents in plant tissues. Consequently, the amount of food ingested by insects increases (Bezemer et al 1998, Sun & Ge 2011). However, the abovementioned indirect effect of the plant on the survival of the nymphs has not been observed when the insects were kept in future climate conditions (700 ppm) and fed on plants grown under current (400 ppm) and future (700 ppm) scenarios. Insect species depend on the plants' nutritional quality and interact with the host plants, with different responses to high CO₂ levels (Hunter 2001, Hattenschwiler & Schafellner 2004, Barbehenn 2005, Guo et al 2014, Sun et al 2016). In some cases, herbivorous insects have reduced growth, lower survival and density, and compensatory increases in food intake caused by alterations in their host plant (Bezemer et al 1998, Coviella et al 2002, Knepp et al 2005, 2014, Sun et al 2015, Guo et al 2017, Trębicki et al 2017).

The resistance of plants to insects is a strategy that the former use to limit biotic stress. Abiotic factors, including the level of atmospheric CO₂, also affect insects (Guo *et al.* 2012, Trębicki *et al* 2017). According to Silva *et al* (2013a, b), *B. brizantha* fails to combine with *C. oleosa* biology.

Current results showed that the forage was resistant to the current scenario (scenario 1) and maintained resistance when insects and plants were subjected to high CO_2 levels (scenario 4).

Mirid bugs fed on genotypes CNPGL BR 150 and CNPGL BR 1765 of *B. ruziziensis* normally presented the same *C. oleosa* duration and survival when compared to *B. brizantha* in current and future scenarios (scenarios 1 and 2), confirming the forages' resistance when insect and plants were kept at 400 ppm CO_2 .

In climate scenario 2, in which insects were exposed to 400 ppm CO₂ and plants to 700 ppm CO₂, total mortality of mirid bugs occurred when fed on B. brizantha and CNPGL BR150 genotype in the third or first instar respectively. The insect completed the immature phase only when fed on CNPGL 1765 genotype in this climatic scenario. Although plants contain all nutritional requirements for the development of herbivores, the absolute and relative amounts of nutrients may be highly variable (Schoonhoven et al 2005). Nutrient variation occurs among the different plant species, but occurs also within the same species, as a result of genotypic differences and environmental conditions (Behmer 2009). Current results show that C. oleosa nymphs may be affected by food subjected to higher CO₂ levels, with consequences on the duration of the insect pests' life cycle and survival.

Based on results for the survival of C. oleosa nymphs maintained in environments 700 ppm CO₂ and plant 400 ppm CO₂ levels (scenario 3), the non-variation of B. brizantha with regard C. oleosa resistance was evident. B. ruziziensis genotypes demonstrated the same behavior to insect developmental period and survival. Martin & Johnson (2011) reported that raspberry cultivars with genes highly susceptible and resistant to the aphid Amphorophora idaei (Borner) maintained their levels of susceptibility and resistance when subjected to high CO₂ concentrations (700 ppm). However, high CO₂ levels reduced resistance only of the cultivar with a moderate resistant gene. Ferreira et al (2013) did not detect any change in the resistance and susceptibility patterns of B. decumbens and B. brizantha cultivars to the spittlebugs when subjected to high CO₂ levels. Contrastingly, an increase in CO₂ reduces resistance by decreasing jasmonic acid levels, an important hormone defense, lipoxygenase activity of proteinase inhibitors, and polyphenol oxidase in wild-type tomato plants infested with Helicoverpa armigera Hübner (Guo et al 2012). Similarly, an increase of soybean susceptibility to Popillia japonica Newman and Diabrotica virgifera LeConte by regulating the pathway of jasmonic acid (JA) expression has been registered (Zavala et al 2008). Further, the synthesis of phenols, terpenes, and other secondary plant metabolites may also be altered (Bezemer et al 2000, Sun et al 2010). Robinson et al (2012) report that plants grown in an environment with high CO_2 increased total phenol (19%), condensed tannin (22%), and flavonoids (27%). They are actually secondary compounds that induce plant resistance to insect pests. Moreover, according to Guo *et al* (2014), elevated CO_2 suppresses the ethylene signaling pathway in *M. truncatula*, which results in the decrease in plant resistance against aphids.

High CO_2 levels promote quality changes in the plant, which trigger changes in the biology of *C. oleosa*, especially when the insects are kept at current CO_2 level. Moreover, since longer developmental period and shorter survival rates will induce the reduction of the number of generations and number of specimens, it may be underscored that *B. brizantha* species resistance will be maintained in future climate scenarios. Similarly, genotypes of *B. ruziziensis* demonstrated that they will be resistant at current and future CO_2 levels. CNPGL BR150 genotype is the most indicated for regions where *C. oleosa* is an important pest in pasturelands.

Acknowledgments We thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Brazil) and Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG, Brazil) for supporting our research.

Authors' Contribution DMS and AMA planned and designed experimental work; DMS performed the experiments; DMS, AMA, and JCM analyzed the data; DMS, AMA, JCM, and SEBS wrote the manuscript.

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