



Impact of the gall-inducing fly *Polymorphomyia basilica* Snow (Diptera: Tephritidae) on the growth and reproduction of *Chromolaena odorata* (L.) R.M.King & H.Rob (*Asteraceae*) in the laboratory

Thandeka Mahlobo¹ · Nontembeko Dube^{1,3} · Costas Zachariades^{1,2} · Thinandavha Caswell Munyai¹

Received: 26 April 2022 / Accepted: 8 June 2023 / Published online: 21 June 2023
© The Author(s) 2023

Abstract

Gall-inducing insects are a classic example of how insects can impact the morphology and physiology of their host plants by forming galls which act as nutrient sinks. An 8-months laboratory study was conducted to determine the impact of the galls induced by *Polymorphomyia basilica* oviposition and or the subsequent larval feeding on the growth and reproduction of *Chromolaena odorata*. Three treatment levels were used, viz. control: 0% of the shoots were exposed, low infestation: 50% of shoots were exposed, and high infestation, where 100% of the shoots were exposed for *P. basilica* to oviposit for 48 h each month. Results showed that *P. basilica* oviposition and or the subsequent feeding by larvae reduced the height and flower production of *C. odorata* plants but promoted lateral growth by increasing the number of shoot tips. Basal stem diameter was not affected by the presence of the galls. The presence of galls also decreased the leaf and root dry biomass on the treated plants but had no significant impact on stem biomass. The difference between the low- and high-infestation treatments was only significant for root biomass, suggesting that more galls are required for the roots to be affected. Overall, the study showed that *P. basilica* meets the requirements of an effective biocontrol agent against *C. odorata* in South Africa. Its release should complement the already released agents in reducing the fitness and productivity of *C. odorata*.

Keywords Galls · Efficacy · Biocontrol · Biomass

Introduction

Insect herbivores are known to adversely impact the growth, reproduction, and competitive ability of their host plants (Myers and Sarfraz 2017), resulting in a top-down limitation or regulation of the population of these plants. Biological control takes advantage of this by introducing specialist natural enemies such as insects from the native range into areas where the host plant has naturalised (Uyi and Igbinsosa

2010; Schwarzländer et al. 2018). Prior to introducing natural enemies to the adventive range, biological control programmes use various approaches to evaluate the potential efficacy of insect agents, including the assessment of the life history traits, the impact of agents on their host plant and the taxonomic placement of the insect (McClay and Balciunas 2005; Cripps et al. 2020). Life history characteristics such as fecundity, voltinism and dispersal capabilities determine how the agent responds to the environment and thus, aid in predicting range and abundance (McClay and Balciunas 2005). Taxa with a narrow host range are essential, as a wide host range indicates a risk to economically and ecologically significant non-target species (Sands and van Driesche 2000).

The Order Diptera is one of the most successful taxa used for biological control (Dube et al. 2020). Within the Diptera, fruit flies (Family Tephritidae) are often gall inducers that rarely attack non-target species (Harris and Shorthouse 1996). Thus, they are selected for the detrimental effect on their host plants and their limited host range. For these reasons, tephritids have been successfully used in

Handling Editor: Makoto Tokuda.

✉ Thandeka Mahlobo
Thandekatee99@gmail.com

¹ School of Life Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville 3209, South Africa

² Agricultural Research Council, Plant Health and Protection, P.O. Box 1055, Hilton 3245, South Africa

³ Department of Zoology and Entomology, University of the Free State, P.O. Box 339, Bloemfontein 9300, South Africa

various biological control programmes (Woodburn 1993; Cruz et al. 2006; Barton et al. 2007; Aigbedion-Atalor et al. 2019). Most gall-inducing insects, including tephritids, have an intimate relationship with their host plants (Shorthouse et al. 2005; Florentine et al. 2005; Hardy and Cook 2010). Usually, an insect will spend one or several parts of its life-cycle inside the gall (Florentine et al. 2005; Blanche 2012).

Galls are an outgrowth of plant tissue; their formation is stimulated by the presence of foreign bodies (insects, mites, fungi, nematodes) in the plant (Prade et al. 2016; Miller and Raman 2019). Gall induction has evolved in about 13,000 described insect species (Stone and Schönrogge 2003; Hardy and Cook 2010), representing only about 2% of herbivorous insects (Harris and Shorthouse 1996). Galls demonstrate a perfect example of plant manipulation by insects (Giron et al. 2016). Feeding by gall-inducing insects reprogrammes the plant genome's expression and hijacks the plant's cellular machinery to create these novel structures (Giron et al. 2016). These galls alter their host plants' life-history traits and performance. The relationship of the insect with its host is generally parasitic (Florentine et al. 2005; Prade et al. 2016). This is another characteristic that allows gall-forming insects to have a negative effect on the host plant, hence their successful use as biocontrol agents (Dennill 1988; Erasmus et al. 1992; Florentine et al. 2005; Prade et al. 2016).

Galls sometimes become metabolic sinks, rendering nutrients unavailable for adjacent cells and other plant parts (Harris and Shorthouse 1996; Cruz et al. 2006). They reduce photosynthetic and transpiration efficiency in their host plants, affecting stomatal conductance and water potential, eventually leaving the plant stressed (Florentine et al. 2005). When plant tissue is subjected to prolonged stress, growth and reproduction are disrupted, and the plant may die (Harris and Shorthouse 1996).

A gall protects its inducer from abiotic and biotic stressors such as dehydration and predation while also providing nutrients for the insect (Shorthouse et al. 2005; Giron et al. 2016; Prade et al. 2016). Compared to their free-living counterparts, gall-inducers show unique nutritional physiology and population dynamics (Miller and Raman 2019). Most tephritid gall-inducers use *Asteraceae* as their preferred host (Miller and Raman 2019), for example a stem gall-inducing fly *Cecidochares connexa* (Macquart) (Diptera: Tephritidae) significantly reduced the lengths of the shoots of *Chromolaena odorata* (L.) R.M.King & H.Rob (*Asteraceae*) plants in Guam (Cruz et al. 2006).

Chromolaena odorata is a notorious weed originating from the Neotropics (Zachariades et al. 2011). The southern African biotype (SAB) invading South Africa has a Jamaican/Cuban origin (Zachariades et al. 1999; Pateron and Zachariades 2013). Thus, natural enemies such as *Pareuchaetes pseudoinsulata* Rego Barros (Lepidoptera: Erebidae: Arctiinae) and *C. connexa* which were effective

in countries invaded by the Asian/West African biotype (AWAB), proved ineffective on the SAB due to incompatibility between the plant and the herbivore (Muniappan et al. 2005). The SAB has caused a significant decline in the populations of some native plant and animal species. For example, Mgobozi et al. (2008) showed that *C. odorata* significantly reduced the spider diversity in Hluhluwe-iMfolozi Park, in northern KwaZulu-Natal province, South Africa.

After mechanical and chemical control methods proved unsustainable, a biological control programme for *C. odorata* was initiated in 1988 (Zachariades et al. 1999). Between 1999 and 2010, 16 potential agents were imported into quarantine in South Africa (Zachariades et al. 2011), and two have been established, viz. *Calycomyza eupatorivora* Spencer (Diptera: Agromyzidae) and *Pareuchaetes insulata* Walker (Lepidoptera: Erebidae: Arctiinae). Dube et al. (2019) reported that *P. insulata* reduced the reproductive potential and plant vigour of *C. odorata* where it established and persisted. However, the impact of *C. eupatorivora* is generally negligible (Nzama et al. 2014). Despite the presence of two biocontrol agents in the field, *C. odorata* remains a significant threat in the country, especially in drier inland habitats, where both *C. eupatorivora* and *P. insulata* have failed to establish (Dube et al. 2020; Zachariades et al. 2021). Both these agents depend on *C. odorata* leaves for their survival, and the plant loses its leaves in winter in these climatically more extreme inland habitats. Thus, more species are being tested as potential agents.

Polymorphomyia basilica Snow (Diptera: Tephritidae) is a gall-inducing fly imported from Jamaica (Zachariades et al. 2011) and has recently been approved for release in South Africa as an agent against *C. odorata*. This fly exhibited a high level of host specificity (Dube et al. 2020). Clearance from the authorities for releasing a biocontrol agent is based on adequate host specificity to protect the native biodiversity and agriculturally important crops. Although pre-release impact studies are not mandatory, they are advisable to help limit the costs and risks involved in releasing inefficient agents (McClay and Balciunas 2005; Myers and Sarfraz 2017; Dube et al. 2019).

This study aims to determine the impact of *P. basilica* on the growth and reproduction of *C. odorata* in the laboratory. In earlier laboratory studies on the biology of *P. basilica*, pupae seemed more tolerant to dry conditions, its survival did not depend on the presence of the leaves. Dry galls were not predated, and lower mortality was observed on them (Dube et al. 2020). This means the agent may survive in the climatically more extreme inland parts of the invasive range of *C. odorata*, unlike *C. eupatorivora* and *P. insulata* whose distribution is limited to the moister regions where humidity is high, and temperatures are not extreme (Zachariades et al. 2011).

Materials and methods

Culturing methods and quarantine conditions

Both culturing of, and trials on, *P. basilica* were conducted in the glasshouse and quarantine laboratory at the Agricultural Research Council, Plant Health and Protection (ARC-PHP), Cedara, KwaZulu-Natal province, South Africa. The laboratory and glasshouse are kept at a temperature of 25 ± 3 °C and relative humidity of 40% to 70%. *Polymorphyia basilica* was cultured in steel-framed insect breeding cages of $0.9 \times 0.5 \times 0.5$ m with gauze panels and a transparent plastic curtain to prevent adults from flying out.

Four potted plants of the SAB *C. odorata* were placed into each cage, together with ten pairs of *P. basilica* and a small container with enzymatic yeast hydrolase and sugar mixed at a ratio of 1:3. The nutrients contained in the mixture may help develop the ovules of females and increase their fecundity (Wang et al. 2018; Dube et al. 2020). Mated females inserted their eggs into growing shoot tips of the *C. odorata* plants. The resulting larvae bored down inside the shoot tip and a gall was initiated, usually on the first stem internode. After two weeks, plants with galls were placed in a large walk-in cage ($2 \times 4 \times 2$ m) (referred to as the culturing cage throughout) to allow further larval development and pupation. Eclosing adults were captured using glass vials and used for further culturing and experiments.

Impact trial

The trial to determine the impact of *P. basilica* on *C. odorata* was initiated in January 2021 in order to include both the growing and flowering season of *C. odorata*. *Chromolaena odorata* plants begin growing at the start of the rainy austral summer season (October/November) and continue until autumn (April). They produced flower buds, with flowering and seed-set occurring during winter, in June and August, respectively. Plants used in these trials were propagated from about 100 similar-sized *C. odorata* shoot-tip cuttings field collected from the city of Pietermaritzburg in South Africa and rooted in a heated mist-bed using Seradix® No.1 rooting hormone. Rooted plants were placed in 18 cm pots containing a 1:1 ratio mixture of Umgeni River sand and Gromor® potting medium and placed in the greenhouse tunnel. Plants were watered daily and fertilized using a fertigation dripper system or Multicote® for about 2 months before being used in the trials.

Once plants had grown, a total of 48 small plants of a similar size (≤ 25 cm) and in good condition were selected

and randomly assigned to three groups. All 48 plants were moved to the quarantine glasshouse, watered accordingly, and kept in a large walk-in cage to prevent attack by *P. basilica* or other insects. A week prior to that, 40 *P. basilica* adults (20 pairs of unknown age) were collected from the culturing walk-in cage and exposed to SAB plants in three standard breeding cages ($0.5 \times 0.5 \times 0.9$ m). The adults were divided between the three cages, seven pairs were placed in the first two cages, and the last cage had six pairs. The cages were containing four plants and enzymatic yeast hydrolase for a week to optimize the likelihood of using ovipositing adults in the impact trial.

Three treatment levels (of 0, 50 and 100%) were used. Sixteen plants were subjected to low infestation, in which 50% of their shoots were covered with a piece of pantyhose throughout the experiment to prevent the biocontrol agent from ovipositing on them, while another 50% were exposed to *P. basilica* adults. The other set of 16 plants were subjected to high infestation, in which 100% of their shoots were exposed to other *P. basilica* adults, and the last 16 plants served as the control group and were not exposed to *P. basilica*. Control plants were kept in the walk-in cage for the duration of the trial.

Individual plants from the treatments were exposed to *P. basilica* adults in a standard insect breeding cage for 48 h monthly. After 48 h, plants were moved into a walk-in cage where they were placed randomly. Prior to the experiment, three growth parameters were measured for each plant viz plant height and basal stem diameter (measured at 1 cm above the soil surface) and the number of shoots longer than 1 cm (i.e., suitable for galling) were counted. Galled shoot tips were included in the count to obtain the total number of shoots per individual plant before exposing them to adults again. Plants were re-exposed to adults again after a month, and this continued until the flowering season (June to August). This was to determine the impact that each damage level had on the different phenological stages of potted *C. odorata*, including the impact on reproduction. Initially, three pairs of *P. basilica* were used per cage, but the number was adjusted accordingly in all the cages as the number of shoots increased and plants grew taller, by the end of the trial, ten pairs were used per cage.

Growth parameters were measured monthly before the re-exposure. Initially, plants were watered daily with 500 ml of tap water. This was later (~3 months) increased accordingly as they grew. At 2 months, plants were treated with Multicote™ fertilizer to help with recovery after the larvae of a lepidopteran pest attacked them. As a consequence of overheating in the quarantine glasshouse due to a technical problem, and an attack by mealybugs, of the 48 plants at the start of the experiment, only 29 had survived by the end of it (control: 10 plants, low: 10 plants, and high: nine (9) plants). At the end of the trial, surviving

plants were measured again for growth parameters (plant height, basal stem diameter and the number of shoots) before they were destructively sampled to measure the total biomass. The leaves, stems, and roots were separated and dried in the oven at 105 °C for 24 h (Matthews 2010). Emerging adult flies were collected and placed back into the culture as soon as they eclosed.

Table 1 The monthly average number of galls induced on *Chromolaena odorata* shoots exposed to varying levels of *Polymorphomyia basilica*

Month	Low	High
1	0 ± 0	0 ± 0
2	2.06 ± 2.18	5.94 ± 1.77
3	2.68 ± 2.21	8 ± 2.78
4	4.67 ± 2.02	12.13 ± 2.68
5	7.62 ± 1.66	15.38 ± 4.03
6	8.67 ± 2.71	15.81 ± 3.28
7	7.9 ± 2.42	14.75 ± 4.12
8	5.78 ± 2.82	10.85 ± 3.16

Low-treatment plants had 50% of their shoots exposed, and high-treatment had 100% of their shoots exposed to the agent. SEM indicated after the mean

Data analysis

The relationships between *C. odorata* growth parameters (number of shoot tips, stem diameter and plant height) and plant growth stage (months) for the different treatments were determined using multiple regression analysis. For the multiple regression, monthly averages of the growth parameters from all the plants were used as the dependent variables, and growth stage (month) and treatment were the independent variables. A Kruskal–Wallis test was performed to determine the effect of *P. basilica* oviposition levels on gall formation between the low- and high-treatment plants. The growth parameters, reproduction (flowers) and the total dry biomass of the leaves, roots and stems of *C. odorata* after 8 months were also analysed this way. If results were significant ($P \leq 0.05$), the differences among treatments were compared using a Mann–Whitney pairwise test, and the P-values were all corrected using sequential Bonferroni. Apart from the multiple regression analysis that was performed using Microsoft Excel 365, all other analyses were performed using PAST Version 4.03 software (Hammer et al. 2001).

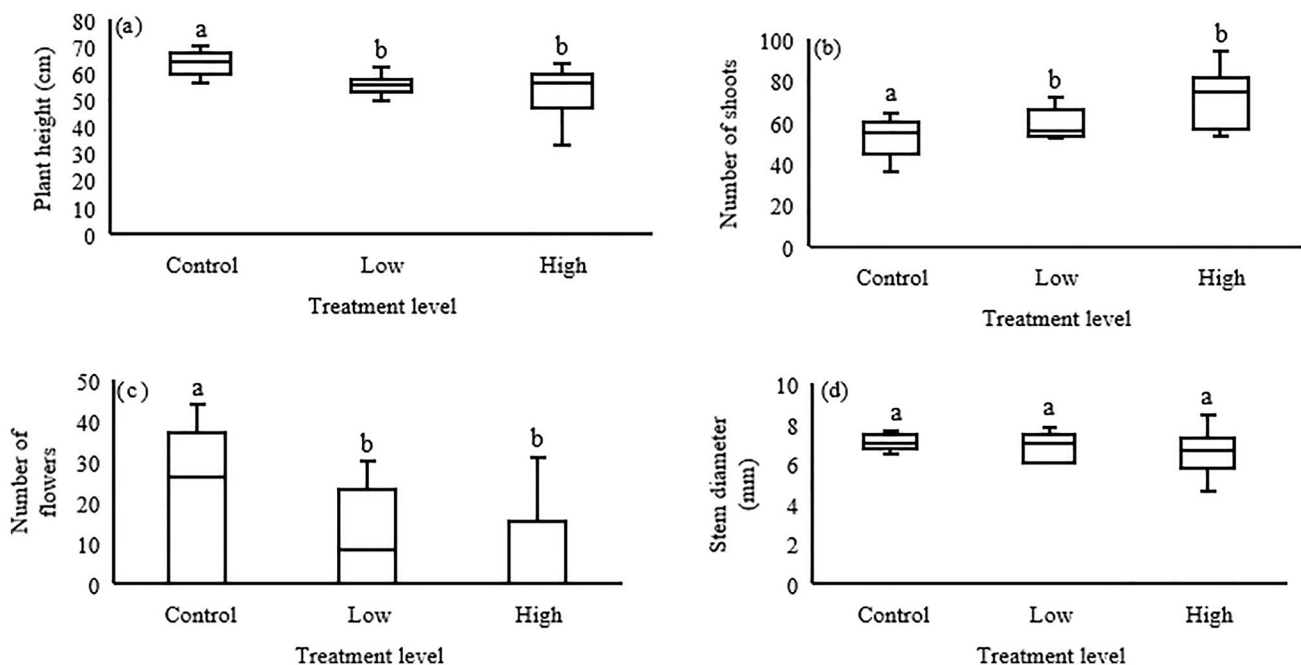


Fig. 1 Effect of *Polymorphomyia basilica* oviposition levels on the plant height (a), number of shoots (b), the number of flowers (c) and the basal stem diameter (d) of *Chromolaena odorata* plants after 8 months of monthly oviposition with varying percentages of shoots

exposed to *P. basilica*. Control ($N=10$): 0%, low ($N=10$): 50% shoots exposed, high ($N=9$): 100% shoots exposed. On the figures, different letters denote a significant difference between the treatments within each plant trait

Results

On average, the high-treatment plants had significantly more galls (per month) than the low-treatment plants ($P = 0.0355$, $H = 4.365$) (Table 1). The galled plants were significantly shorter than the ungalled plants ($P = 0.002$, $H = 12.59$). However, the height difference was not significant between the low and high treatments (Fig. 1a). The galled plants also had significantly more shoot tips than the ungalled plants ($P = 0.017$, $H = 8.105$). The number of *C. odorata* shoot increased with an increase in *P. basilica* oviposition and gall formation, but the difference was not significant between the low and high treatments (Fig. 1b). The results indicated that flower production was affected by *P. basilica* oviposition and gall formation ($P = 0.023$, $H = 7.518$). Control plants produced significantly more flowers per plant (Fig. 1c) and more plants (seven) produced flowers compared to the low- and high-treatment plants in which only five and three plants produced flowers. There was no significant difference in the basal stem diameter between the treatments ($P = 0.616$, $H = 0.970$) (Fig. 1d).

Leaf and root biomass were significantly influenced by *P. basilica* feeding and oviposition, both the leaf ($P = 0.004$, $H = 10.831$) and root ($P = 0.012$, $H = 8.774$) biomass decreased with an increase in *P. basilica* oviposition percentage (Fig. 2). Plants from the high infestation treatment had leaf and root biomasses which were significantly lower from plants on the control and low infestation treatments. However, plants from the latter treatments were not significantly different from each other. There was no significant difference in the stem biomass between the treatments ($P = 0.090$, $H = 4.825$).

Multiple regression analysis showed significant positive relationships between the duration (months) and all the

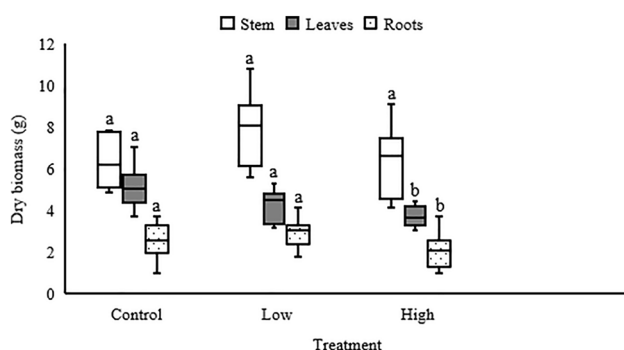


Fig. 2 Effect of *Polymorphomyia basilica* on the total dry biomass of the stems, leaves and roots of *Chromolaena odorata* after 8 months of ovipositing on varying percentages of plant shoots. Control ($N = 10$): 0%, low ($N = 10$): 50% shoots exposed, high ($N = 9$): 100% shoots exposed. On the figures, different letters denote a significant difference between the treatments within each trait

Table 2 Multiple regression analysis of the relationship between the plant growth parameters and the duration (months) of *Chromolaena odorata* plants with varying levels of shoots exposed to *Polymorphomyia basilica* (control: 0%, low: 50%, high: 100%)

Growth parameter	R ²	F _(3;23)	P
Plant height	0.978	307.108	<0.0001
Stem diameter	0.984	418.238	<0.0001
Number of shoots	0.958	153.875	<0.0001

measured plant growth parameters. Irrespective of the treatment level, the number of shoots, stem diameter, and plant height increased with plant growth duration. However, *P. basilica* oviposition and larval feeding significantly affected the increase rates of all the tested parameters. The average monthly increase of both the low and high treatments was lower than those of the control treatment plants in all the growth parameters (Table 2 and Fig. 3).

Discussion

In this study, we demonstrated that the actions of *P. basilica* which result in gall formation reduced plant height, root and leaf biomass and the number of flowers produced by *C. odorata* in the laboratory. A reduction in plant height due to insect activity has been observed in several studies (Cruz et al. 2006; Stephens and Westoby 2015; Prade et al. 2016; Dube et al. 2019). The reduction of plant height changes the architecture, thus decreasing the plant's overall fitness and competitive ability (Schierenbeck et al. 1994). A plant's architecture determines the amount of light intercepted for photosynthesis (Schierenbeck et al. 1994) and aids in seed dispersal (Stephens and Westoby 2015). Dube et al. (2019) demonstrated that the shoot-tip borer *Dichrorampha odorata* Brown and Zachariades (Lepidoptera: Tortricidae) increased lateral growth of *C. odorata*, similarly to the current study. This also changes the architecture and can impact the plant's performance (Stephens and Westoby 2015). In regions where it is invasive, *C. odorata* gains much of its competitive advantage over other plant species by rapid vertical growth from the start to the end of the rainy season. Reducing the rate of this vertical growth through feeding and oviposition by *P. basilica* can be expected to reduce the competitiveness of *C. odorata*.

Galls induced by *P. basilica* also decreased the leaf biomass of *C. odorata* plants; this will have a negative effect on the photosynthetic rate. Gall induction can decrease the host plant's metabolic functions (e.g., water potential, photosynthesis, stomatal conductance, and transpiration) (Florentine et al. 2005; Cruz et al. 2006). The negative effect of galling on photosynthesis has been observed in other systems. For example, Florentine et al. (2005) found that galls formed

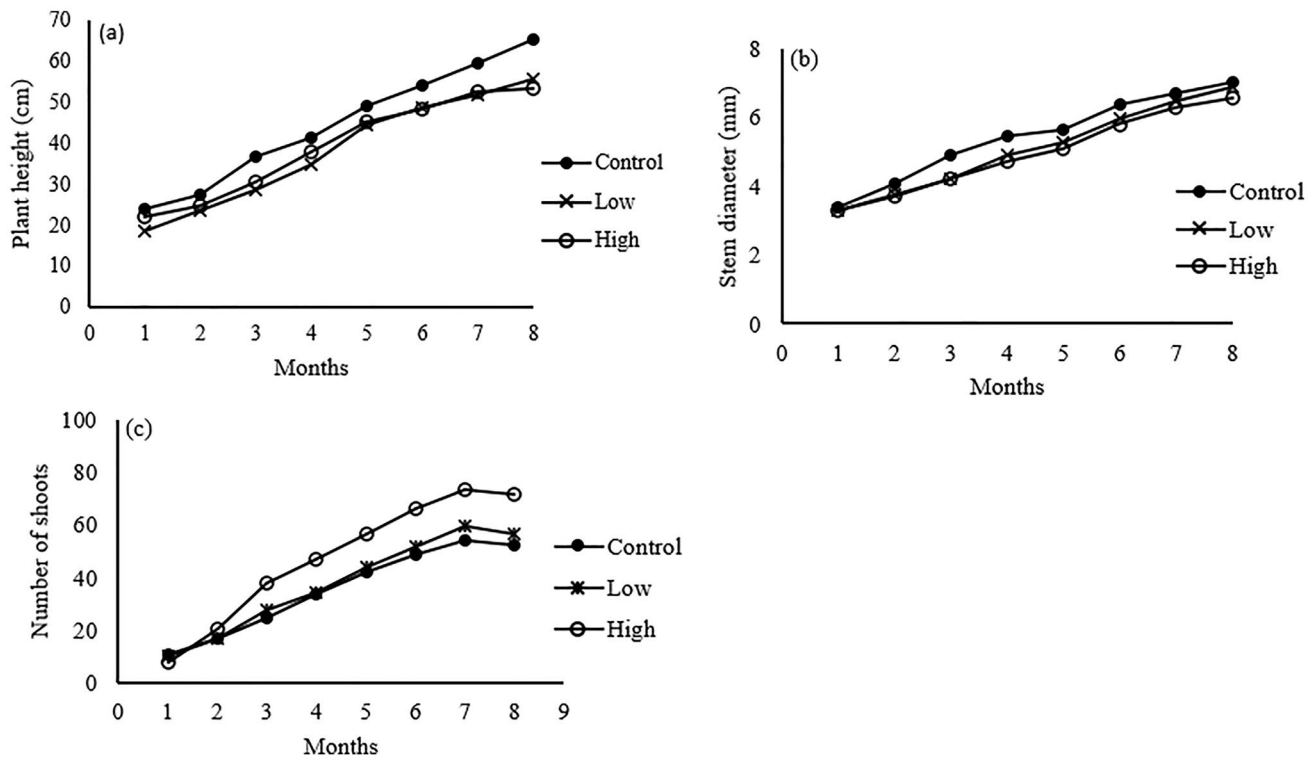


Fig. 3 Relationship between the growth parameters [plant height (a), basal stem diameter (b) and the number of shoots (c)] of *Chromolaena odorata* and the duration (in months) of growth in plants with

varying percentages of shoots exposed to *Polymorphomyia basilica* (control: 0%, low: 50%, high: 100%)

by the actions of *Epiblema strenuana* Walker (Lepidoptera: Tortricidae) caused an 80% and 87% decrease in the photosynthetic rate of the rosette and pre-flowering stages of *Parthenium hysterophorus* L. (Asteraceae) respectively.

During herbivory, roots are used to store photo-assimilates for future regrowth and synthesize secondary metabolites for defence (Nalam et al. 2013). This may be why studies such as those of Schat and Blossey (2005), Nalam et al. (2013) and Dube et al. (2019) reported an increase in root biomass after herbivory. In contrast to the studies mentioned above, root biomass was reduced in the current study. Galls sometimes function as metabolic sinks, taking photo-assimilates and other nutrients from adjacent cells and other parts of the plant (Harris and Shorthouse 1996; Cripps et al. 2020). Consequently, it is possible for other parts of the plant that were not oviposited on to be affected by the galls.

Although this was not explicitly tested for, *P. basilica* galls may have made the plants more susceptible to the observed attacks by mealybugs. There were more mealybugs, *Phenacoccus madeirensis* Green (Hemiptera: Pseudococcidae), near the galls than there were on the ungalled shoots of the control plants. Gallers are known to decrease plant defence to maximize the fitness of the gall (Giron et al. 2016). An example of this was reported by Nyman and Julkunen-Tiitto (2000). They found the concentration

of defensive phenolics to be lower in the galls and tissues located closer to the galls of sawflies, *Pontania* species (Hymenoptera: Tenthredinidae), laid on willow trees. Attack from opportunistic arthropods will also negatively affect the performance of *C. odorata* in the field.

Reproduction (flower production) was reduced in treated plants similar to results from other studies. For example, flower production of *C. odorata* was reduced by *D. odorata* larvae in a study by Dube et al. (2019), while gall damage by *Epiblema strenuana* Walker (Lepidoptera: Tortricidae) reduced flower production in *Parthenium hysterophorus* L. (Asteraceae) (Dhileepan and McFadyen 2001). Adverse impact on the reproduction of target weeds is one of the desired results in biocontrol programmes.

Except for root biomass, the difference between the low (50%) and high (100%) treatments was not significant, suggesting that *P. basilica* will affect the growth and reproduction of *C. odorata* plants even if galls are produced in only half of the shoots. However, the impact of the fly will be greater when more galls are present on the plant.

Despite the negative effect on the overall performance, the positive relationship between duration of growth (months) and plant growth parameters viz. number of shoots, stem diameter and plant height, suggests that on its own, *P. basilica* may not be able to kill *C. odorata* plants, at least

not in 8 months which was the duration of our experiment. In the field however, the effect of *P. basilica* will be complemented by the presence of other agents (*P. insulata* and *C. eupatorivora*), opportunistic arthropods such as *Zonocerus elegans* (Thunberg) (Orthoptera: Pyrgomorphidae) and other biotic and abiotic stress factors. *Zonocerus elegans* and its congener *Zonocerus variegatus* (L.) are known to be attracted to plants containing pyrrolizidine alkaloids, such as *C. odorata* (Fischer and Boppré 1997; Housecroft 2018; Dube et al. 2021).

In conclusion, this study showed that the actions of *P. basilica* reduce the plant height and flower production of *C. odorata*, it also decreases the leaf and root biomass, which will negatively affect the overall productivity of the weed. The actions of multiple agent species together could enable the threshold where *C. odorata* is no longer a problem. The release of *P. basilica* in South Africa will not have detrimental effects on the already established agents as they operate in different niches.

Acknowledgements The research was financially supported by the DST-NRF Centre of Excellence for Invasion Biology (C-I-B). The Agricultural Research Council-Plant Health and Protection is thanked for the access to the facilities and materials needed to complete these trials. ARC-PHP Cedara staff are also thanked for assistance in breeding the fly and for watering plants whenever the first author was unavailable.

Funding Open access funding provided by University of KwaZulu-Natal. DST-NRF Centre of Excellence for Invasion Biology

Data Availability Data is available from the corresponding author upon request.

Declarations

Conflict of interest All authors report that they have no conflict of interest.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Aigbedion-Atalor PO, Day MD, Idemudia I, Paterson WDD, ID, (2019) With or without you: stem-galling of a tephritid fly reduces the vegetative and reproductive performance of the invasive plant *Chromolaena odorata* (Asteraceae) both alone and in combination with another agent. *Biocontrol* 64:103–114. <https://doi.org/10.1007/s10526-018-09917-x>
- Barton J, Fowler SV, Gianotti AF, Winks CJ, de Beurs M, Arnold GC, Forrester G (2007) Successful biological control of mist flower (*Ageratina riparia*) in New Zealand: agent establishment, impact and benefits to the native flora. *Biol Control* 40:370–385. <https://doi.org/10.1016/j.biocontrol.2006.09.010>
- Blanche R (2012) Life in a gall: the biology and ecology of insects that live in plant galls. CSIRO Publishing, Clayton
- Cripps M, Navukula J, Casonato S, van Koten C (2020) Impact of the gall fly, *Urophora stylata*, on the pasture weed, *Cirsium vulgare*, in New Zealand. *Biocontrol* 65:501–513. <https://doi.org/10.1007/s10526-020-10007-0>
- Cruz ZT, Muniappan R, Reddy GVP (2006) Establishment of *Cecidochares connexa* (Diptera: Tephritidae) in Guam and its effect on the growth of *Chromolaena odorata* (Asteraceae). *Ann Entomol Soc Am* 99:845–850. [https://doi.org/10.1603/0013-8746\(2006\)99\[845:EOCCDT\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2006)99[845:EOCCDT]2.0.CO;2)
- Dennill GB (1988) Why a gall former can be a good biocontrol agent: the gall wasp *Trichilogaster acaciaelongifoliae* and the weed *Acacia longifolia*. *Ecol Entomol* 13:1–9. <https://doi.org/10.1111/j.1365-2311.1988.tb00327.x>
- Dhileepan K, McFadyen REC (2001) Effects of gall damage by the introduced biocontrol agent *Epiblema strenuana* (Lep., Tortricidae) on the weed *Parthenium hysterophorus* (Asteraceae). *J Appl Entomol* 125:1–8. <https://doi.org/10.1111/j.1439-0418.2001.00494.x>
- Dube N, Uyi O, Zachariades C, Munyai TC, Whitwell M (2019) Impact of the shoot-boring moth *Dichrorampha odorata* (Lepidoptera: Tortricidae) on growth and reproductive potential of *Chromolaena odorata* (Asteraceae) in the laboratory. *Biocontrol Sci Technol* 29:350–364. <https://doi.org/10.1080/09583157.2018.1562038>
- Dube N, Zachariades C, Uyi O, Munyai TC (2020) Life history traits and host suitability of a gall-forming fly, *Polymorphyia basilica* (Diptera: Tephritidae), for the biological control of *Chromolaena odorata* (Asteraceae) in South Africa. *Arthropod Plant Interact* 14:237–250. <https://doi.org/10.1007/s11829-019-09731-x>
- Dube N, van Heerden FR, Zachariades C, Uyi OO, Munyai TC (2021) First record of pyrrolizidine alkaloids in the southern African biotype of *Chromolaena odorata* (Asteraceae). *S Afr J Bot* 139:19–25. <https://doi.org/10.1016/j.sajb.2021.01.026>
- Erasmus DJ, Bennett PH, Staden JV (1992) The effect of galls induced by the gall fly *Procecidochares utilis* on vegetative growth and reproductive potential of crofton weed, *Ageratina adenophora*. *Ann Appl Biol* 120:173–181. <https://doi.org/10.1111/j.1744-7348.1992.tb03414.x>
- Fischer OW, Boppré M (1997) Chemoecological studies reveal causes for increased population densities of *Zonocerus* (Orth.: Pyrgomorphidae) and offer new means for management. In: Krall S, Peveling R, Ba Diallo D (eds) *New Strategies in Locust Control*. Basel, Birkhäuser, pp 267–281. https://doi.org/10.1007/978-3-0348-9202-5_43
- Florentine SK, Raman A, Dhileepan K (2005) Effects of gall induction by *Epiblema strenuana* on gas exchange, nutrients, and energetics in *Parthenium hysterophorus*. *Biocontrol* 50:787–801. <https://doi.org/10.1007/s10526-004-5525-3>
- Giron D, Hugué E, Stone GN, Body M (2016) Insect-induced effects on plants and possible effectors used by galling and leaf-mining insects to manipulate their host-plant. *J Insect Physiol* 84:70–89. <https://doi.org/10.1016/j.jinsphys.2015.12.009>
- Hammer Ø, Harper DA, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. *Palaeontol Electron* 4:1–9

- Hardy NB, Cook LG (2010) Gall-induction in insects: evolutionary dead-end or speciation driver? *BMC Evol Biol* 10:257–265. <https://doi.org/10.1186/1471-2148-10-257>
- Harris P, Shorthouse JD (1996) Effectiveness of gall inducers in weed biological control. *Can Entomol* 128:1021–1055. <https://doi.org/10.4039/Ent1281021-6>
- Housecroft CE (2018) Tolerating toxins: grasshoppers that feast on pyrrolizidine alkaloids. *Chimia* 72:156–157. <https://doi.org/10.2533/chimia.2018.156>
- Matthews S (2010) Effect of drying temperature on fuel moisture content measurements. *Int J Wildl and Fire* 19:800–802. <https://doi.org/10.1071/WF08188>
- McClay AS, Balciunas JK (2005) The role of pre-release efficacy assessment in selecting classical biological control agents for weeds—applying the Anna Karenina principle. *Biol Control* 35:197–207. <https://doi.org/10.1016/j.biocontrol.2005.05.018>
- Mgobozi MP, Somers MJ, Dippenaar-Schoeman AS (2008) Spider responses to alien plant invasion: the effect of short-and long-term *Chromolaena odorata* invasion and management. *J Appl Ecol* 45:189–197. <https://doi.org/10.1111/j.1365-2664.2008.01486.x>
- Miller DG III, Raman A (2019) Host–plant relations of gall-inducing insects. *Ann Entomol Soc* 112:1–19. <https://doi.org/10.1093/aesa/say034>
- Muniappan R, Reddy GVP, Lai PY (2005) Distribution and biological control of *Chromolaena odorata*. In: Inderjit S (ed) *Invasive plants: ecological and agricultural aspects*. Birkhäuser, Basel, pp 223–233. https://doi.org/10.1007/3-7643-7380-6_14
- Myers JH, Sarfraz RM (2017) Impact of insect herbivores on plant populations. *Annu Rev Entomol* 62:207–230. <https://doi.org/10.1146/annurev-ento-010715-023826>
- Nalam VJ, Shah J, Nachappa P (2013) Emerging role of roots in plant responses to aboveground insect herbivory. *Insect Sci* 20:286–296. <https://doi.org/10.1111/1744-7917.12004>
- Nyman T, Julkunen-Tiitto R (2000) Manipulation of the phenolic chemistry of willows by gall-inducing sawflies. *PNAS* 97:13184–13187. <https://doi.org/10.1073/pnas.230294097>
- Nzama S, Olckers T, Zachariades C (2014) Seasonal activity, habitat preferences and larval mortality of the leaf-mining fly *Calycomyza eupatoriavora* (Agromyzidae), a biological control agent established on *Chromolaena odorata* (Asteraceae) in South Africa. *Biocontrol Sci Technol* 24:1297–1307. <https://doi.org/10.1080/09583157.2014.935293>
- Paterson ID, Zachariades C (2013) ISSRs indicate that *Chromolaena odorata* invading southern Africa originates in Jamaica or Cuba. *Biol Control* 66:132–139. <https://doi.org/10.1016/j.biocontrol.2013.04.005>
- Prade P, Diaz R, Vitorino MD, Cuda JP, Kumar P, Gruber B, Overholt WA (2016) Galls induced by *Calophya latiforceps* (Hemiptera: Calophyidae) reduce leaf performance and growth of Brazilian peppertree. *Biocontrol Sci Technol* 26:23–34. <https://doi.org/10.1080/09583157.2015.1072131>
- Sands DPA, van Driesche RG (2000) Evaluating the host range of agents for biological control of arthropods: rationale, methodology and interpretation. In: van Driesche RG, Heard TA, McClay AS, Reardon R (eds.) *Proceedings: Host Specificity Testing of Exotic Arthropod Biological Control Agents: The Biological Basis for Improvement in Safety*. Forest Health Technology Enterprise Team 1999–01, USDA Forest Service, Morgantown, West Virginia pp 69–83.
- Schat M, Blossey B (2005) Influence of natural and simulated leaf beetle herbivory on biomass allocation and plant architecture of purple loosestrife *Lythrum salicaria* L. *Environ Entomol* 34:906–914. <https://doi.org/10.1603/0046-225X-34.4.906>
- Schierenbeck KA, Mack RN, Sharitz RR (1994) Effects of herbivory on growth and biomass allocation in native and introduced species of *Lonicera*. *Ecol* 75:1661–1672. <https://doi.org/10.2307/1939626>
- Schwarzländer M, Hinz HL, Winston RL, Day MD (2018) Biological control of weeds: an analysis of introductions, rates of establishment and estimates of success, worldwide. *Biocontrol* 63:319–331. <https://doi.org/10.1007/s10526-018-9890-8>
- Shorthouse JD, Wool D, Raman A (2005) Gall-inducing insects—Nature’s most sophisticated herbivores. *Basic Appl Ecol* 6:407–411. <https://doi.org/10.1016/j.baae.2005.07.001>
- Stephens AE, Westoby M (2015) Effects of insect attack to stems on plant survival, growth, reproduction and photosynthesis. *Oikos* 124:266–273. <https://doi.org/10.1111/oik.01809>
- Stone GN, Schönrogge K (2003) The adaptive significance of insect gall morphology. *Trends Ecol Evol* 18:512–522. [https://doi.org/10.1016/S0169-5347\(03\)00247-7](https://doi.org/10.1016/S0169-5347(03)00247-7)
- Uyi OO, Igbinosa IB (2010) The status of *Chromolaena odorata* and its biocontrol in West Africa. In: Zachariades C, Strathie L.W, Day MD, Muniappan R (eds) *Proceedings of the eighth international workshop on biological control and management of Chromolaena odorata and other Eupatorieae*, Nairobi. ARC-PPRI, Pretoria, pp 1–2
- Woodburn TL (1993) Host specificity testing, release and establishment of *Urophora solstitialis* (L.) (Diptera: Tephritidae), a potential biological control agent for *Carduus nutans* L., in Australia. *Biocontrol Sci Technol* 3:419–426. <https://doi.org/10.1080/09583159309355296>
- Zachariades C, Strathie-Korubel LW, Kluge RL (1999) The South African programme on the biological control of *Chromolaena odorata* (L.) King and Robinson (Asteraceae) using insects. In: Olckers T, Hill MP (eds) *Biological control of weeds in South Africa: African Entomology Memoir 1*. Entomological Society of Southern Africa, Hatfield, South Africa, pp 89–102
- Zachariades C, Strathie LW, Retief E, Dube N (2011) Progress towards the biological control of *Chromolaena odorata* (L.) R.M. King & H.Rob. (Asteraceae) in South Africa. *Afr Entomol* 19:282–302. <https://doi.org/10.4001/003.019.0229>
- Zachariades C, van der Westhuizen L, Heystek F, Dube N, McConachie AJ, Nqayi SB, Dlomo SI, Mpodi P, Kistensamy Y (2021) Biological control of three Eupatorieae weeds in South Africa: 2011–2020. *Afr Entomol* 29:742–767. <https://doi.org/10.4001/003.029.0742>
- Wang F, Chambi C, Li Z, Huang C, Ma Y, Li C, Tian X, Sangjia F, Ntambo MS, Kankonda OM, Hafeez S (2018) Influence of Supplemental Protein on the Life Expectancy and Reproduction of the Chinese Citrus Fruit Fly *Bactrocera minax* (Enderlein) (*Tetracus minax*) (Diptera: Tephritidae). *J Insect Sci* 18:5–32. <https://doi.org/10.1093/jisesa/iey008>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.