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SUPPRESSION OF PHOTOSYNTHETIC CAPACITY, BIOMASS AND RELATIVE CHLOROPHYLL CONTENT OF SELECTED HOST SPECIES AFFECTED BY PARASITIC PLANT *Cassytha filiformis* L.

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ABSTRACT

Cassytha filiformis infected its host through haustorium to absorb nutrients. Due to its parasitic property and growth habit with extensive coverage, *C. filiformis* has a great potential as cover crops in oil palm plantation. The extensive establishment is able to control weed encroachment and suppress its aggressiveness on crops. A study was conducted to determine the suppression of photosynthetic capacity, biomass and relative chlorophyll content of seven crop species infected by *C. filiformis*. The seven species included *Asystasia intrusa* Bl., *Colocasia esculenta* (L.) Schott, *Ipomoea aquatica* Forsk., *Ischaemum muticum* L., *Manihot esculenta* Crantz, *Merremia umbellata* (L.) Hall, and *Mikania micrantha* H.B.K. The photosynthetic rate of *M. micrantha* was suppressed by 95.62 % while *A. intrusa*, *I. aquatica, M. esculenta*, C. *esculenta* and *M. umbellata* were suppressed at 94.29 %, 84.00 %, 80.81 %, 67.55 % and 67.07 %, respectively. The lowest suppression of the photosynthetic rate was for *I. muticum* which was 43.06 %. The rate of suppression of all species by *C. filiformis* could probably be related to the morphological and physiological characteristics of the species. A strong relationship between photosynthesis and stomatal conductance of 0.92 for infected and 0.97 for uninfected species were recorded. Similarly, the biomass and chlorophyll content reduction were positively correlated with photosynthetic rate depending on the level of infection by *C. filiformis* with values of 0.82 and 0.95, respectively. Therefore, *C. filiformis* has the potential to be an effective biological control agent.

Keywords: Parasitic plant, hemiparasite, photosynthetic capacity, biomass, relative chlorophyll content

INTRODUCTION

Cassytha filiformis (L.) is a hemiparasite from the family of Lauraceae with some common names such as laurel dodder, woe and love vine. It is a perennial vine with small scales as a replacement of the leaves (Nelson 2008). The individual stems that are copiously branched have a diameter of 1 to 3 mm in diameter and can attain a maximum length of 10 to 20 m (Mythili et al. 2011). The stems which are filiform and glabrous are green to orange in color with extensive branches which twine around each other or over one to several host plants with haustoria that penetrate the epidermis of the other plants (Prider et al. 2009; Mythili et al. 2011). A haustorium is the bridge of swollen mass of both the host and parasite tissue, which is a specialized hypha that can penetrate the tissues of the hosts (Parker and Riches 1993). When mature, it provides a vascular conduit of water and nutrients from hosts to parasite (Press and Graves 1995).

The purpose of *C. filiformis* connecting with the host plants is to obtain nutrients and water without interfering with their activities. The parasitic plant does not create immediate, fatal damage to host cells and their metabolic processes. Rather, through intimidate membrane-to-membrane contact with its host and itself, it extracts what is required for it to grow, flower and produce seeds for its future generations, and the host plants eventually die a long, protracted death by starvation and desiccation. *C. filiformis* clings to woody plants for physical support, nutrition, and water (Nelson 2008). In addition, the parasitic plant is known to survive with unlimited number of host species to be parasitized in obtaining the necessary food and water (Reece 2011).

Hemiparasites attack the host xylem, in contrast with holoparasites that infect both phloem and xylem, and as a consequence, hemiparasitic plants have access to water and mineral nutrients but little carbon (Těšitel et al. 2010). Due to their reduced or non-existing root networks, hemiparasitic plants acquire virtually all mineral nutrients and water from the host while organic carbon is provided, at least in part, by their own photosynthetic activity (Těšitel et al. 2010).

Photosynthetic rate, stomatal conductance and water use efficiency (WUE) of plants infected by parasites can be altered significantly thus affecting the overall plant growth performance. Parasitic plants have significant, deleterious effects on their host in terms of photosynthetic rate and/or total canopy photosynthesis over the life of the plant (Watling and Press 2001). In response to infection with the holoparasite *Orobanche cernua*, *Nicotiana tabacum* exhibited suppressed leaf senescence, with the net effect of increasing canopy photosynthesis over the life of the host by 20%, although in the study it did not completely compensate for the carbon lost to the parasite (Hibberd et al. 1998).

In contrast, in the *Striga hermonthica – Zea mays* association, only 20 % of the host biomass reduction affected by the parasite was attributable to the direct effects of resource abstraction with the remainder associated with parasite-induced suppression of host photosynthesis (Graves et al. 1989). Xylem sap is drawn through the haustorium, the organ of attachment providing vascular continuity between *Striga* and its host, and into the parasite via cohesion due to elevated parasite transpiration (Press and Graves 1995).

A reduction in host stomatal conductance (Frost et al. 1998) was found to increase the effective sink strength of the parasite by reducing competition with the host for xylem sap (Taylor et al. 1996; Watling and Press 2001). The other study found that the influence of arbuscular mycorrhizal infection on plant WUE has received comparatively little attention, and the studies addressing this aspect have produced contradictory results (Querejeta et al. 2003). Knowledge of water requirements by crops and their WUE are important for assessing crop water balance and water resources (Zobiole et al. 2010). It is anticipated that increased CO_2 and temperature may increase transpiration by plants to impact the input of water required for crop production (Zobiole et al. 2010).

Measurement of photosynthetic activity in hemiparasites tells us little about the extent to which these plants rely on the host(s) to supplement their carbon supply (Press and Graves 1995). The extent to which hemiparasites are dependent on host carbon varies widely between species, and also within species, again as a function of nitrogen application (Press and Graves 1995). Therefore, photosynthesis of the host tree is often found to be reduced as a result of infection (Parker and Riches 1993).

The purpose of this study was to provide information about the photosynthetic capacity, biomass and relative chlorophyll content of seven selected plant species infected by *C. filiformis*. The seven selected species in this study were *Asystasia intrusa* from the Acanthaceae family, *Colocasia esculenta* which belongs to Araceae family, *Ischaemum muticum* which comes from the Poaceae family, *Manihot esculenta* from Euphorbiaceae family, and *Mikania micrantha* from the Asteraceae family. Meanwhile both *Ipomoea aquatica* and *Merremia umbellata* belong to the family of Convolvulaceae.

MATERIALS AND METHODS

Plant materials and experimental location

The study was carried out at Universiti Malaysia Sarawak, Kota Samarahan, Sarawak (N01^{o} 27.274’, E110^{o} 26.422’). Five plots of the size 1 m x 1 m were established in an open field beside a roadside namely Jalan Datuk Mohammad Musa with abundance of parasite infecting the area near Kota Samarahan. Seven host plants namely *Asystasia intrusa* Bl., *Colocasia esculenta* (L.) Schott, *Ipomoea aquatica* Forsk., *Ischaemum muticum* L., *Manihot esculenta* Crantz, *Merremia umbellata* (L.) Hall, and *Mikania micrantha* H.B.K. were chosen for the study as the host to be infected by *C. filiformis*.

Photosynthetic Capacity Measurement

The photosynthetic capacity was measured on the newly matured leaf using a portable photosynthetic system, Model LI-6400 (LI-COR Inc., USA). Measurements of photosynthetic capacity of the selected host plants were conducted for both infected plants which were detected by their yellow colored leaves with the presence of the parasite filiform through stem of plants, and uninfected plants which were undisturbed by *C. filiformis*. Each treatment comprised five replicates where each leaf represented one replication. The measurement was conducted from 8.00 am and stopped before 12.00 noon. The data were subjected to analysis of paired samples t-test SPSS ($P<0.05$) where significant differences were detected. The statistical analysis was performed using SPSS 18.0. WUE was calculated by dividing photosynthetic rate to transpiration. All identified weeds were separated based on species and quadrates. The samples were oven-dried for at least seven days at 60^{o}C for accurate measurement of biomass and carbon stock (Syahrinudin 2005). After seven days, samples were taken out from the oven and measurement of biomass was performed using electronic weighing scale.

Chlorophyll Content Determination

SPAD-502 Chlorophyll Meter (Konica Minolta Co. Ltd., Japan) was used to determine the relative chlorophyll content of leaves. Ten measurements of newly matured leaves for all species were taken for plants uninfected and infected by *C. filiformis*. Each leaf represented one chlorophyll reading. Measurements were taken by simply inserting a leaf by avoiding the main vein and closing the measuring head. The data were subjected to analysis of paired samples t-test SPSS ($P<0.05$) where a significant difference was detected. The statistical analysis was performed using SPSS 18.0.

RESULTS AND DISCUSSION

The botanical name, family and life forms from the seven selected plant species were recorded (Table 1). Two species were recorded for shrub, herb and climber life forms. Only one species was recorded for grass life form (Table 1). The life cycles of all species recorded were perennial.

Table 1. Botanical name, family and life forms of species

Species	Family	Life forms
A. intrusa	Acanthaceae	Shrub
C. esculenta	Araceae	Herb
I. aquatica	Convolvulaceae	Herb
I. muticum	Poaceae	Grass
M. esculenta	Euphorbiaceae	Shrub
M. micrantha	Asteraceae	Climber
M. umbellata	Convolvulaceae	Climber

The highest suppression of photosynthetic rate by *C. filiformis* was recorded in *M. micrantha* at 95.62% (Table 2). Lower reductions of photosynthetic rates were recorded for *A. intrusa, I. aquatica*, *M. esculenta* and *C. esculenta* with the values of 94.29%, 84.00%, 80.81% and 67.55%, respectively. *M. umbellata and I. muticum* recorded reduction of photosynthesis rates of only 67.07% and 43.06%, respectively (Table 2).

Mature haustoria often appear as swollen, round structures firmly attached to or clasping the host surface (Press and Graves 1995). Similarly, the haustoria in the present study were found to be swollen on the host stem after successful contact with the host plants. Different species had different morphological and physiological characters and therefore differed in the degree of infection.

The highest species being suppressed by *C. filiformis* was *M. micrantha*. *Mikania* genus has a multi–branched and glabrous stems (Tripathi et al. 2012) which has phototoxic activity acting as plant defense mechanism (Pérez et al. 2010). However, these compounds were absent in *M. micrantha* (Pérez et al. 2010) and hence were being suppressed most vigorously by *C. filiformis* at 95.62%. Based on previous study by Chak et al. (2010), *M. micrantha* was identified as potential true host species where *Cuscuta* has managed to successfully establish effective haustoria to obtain xylem- and phloem-derived nutrients from their respective hosts. Thus, this was probably because *M. micrantha* was one of the species favored the most by *C. filiformis* as host. The second highest species infected was *A. intrusa* which has been known to be a consistently weaker competitor (Samedani et al. 2012).

Meanwhile average photosynthetic rate reductions were recorded for *I. aquatica* (84.00%) and *M. esculenta* (80.81%), which had been listed as true host–plants similar to *M. micrantha* (Chak et al. 2010). Both plants come from the same family of Convolvulaceae. However, earlier both plants were found to belong to one genus namely *Ipomoea* but advanced members of this family were placed in separate genus *Merremia* on the basis of morphological differences (Ganjir et al. 2013). Therefore, this would probably be the reason for the differences in percentage of suppression by the parasite for both species. *M. umbellata* was suppressed by *C. filiformis* at 67.07%. The presence of cytotoxicity of *M. umbellata* was probably the reason that hinders the penetration of haustoria of *C. filiformis* giving a lower suppression of photosynthesis (Ganjir et al. 2013).

Finally, the lowest suppression of photosynthesis by *C. filiformis* was for *I. muticum* with only 43.06%. The penetration of haustorial tissue into the xylem and phloem tissues of the host to successfully establish the intimate connections for the host to derive solute uptake could probably be hindered due to the presence of course, thick and hairy epidermal tissues of *I. muticum* (Chak et al. 2010). Most of the pseudo–host species studied by Chak et al. (2010), came from the family of Poaceae and Cyperaceae. Since *I. muticum* came from the family of Poaceae, it could probably share the same structure through the presence of course, thick and hairy epidermal tissues with other species of Poaceae. The results concurred with previous report where for both host species, plants infected by the parasite had significantly lower photosynthetic rates than uninfected plants (Prider et al. 2009). Similar results have been reported where photosynthesis in the host tree was often found to be reduced as a result of infection (Balasubramanian et al. 2014). Previous study by Shen et al. (2011) also found that infection significantly reduced net photosynthetic rates (P_n) of mature *M. micrantha* leaves at all infection densities, compared to P_n of the uninfected leaves.

The stomatal conductance varied for all species with the highest reduction of 90.48% for *A. intrusa*, followed by *I. aquatica* with 76.92% (Table 2). Meanwhile, values for *M. esculenta*, *M. micrantha*, *M. umbellata*, *C. esculenta* and *I muticum* were all reduced at 73.68%, 72.00%, 62.50%, 53.33% and 20.00%, respectively. For transpiration, the highest decrease was 89.88% for *M. micrantha* followed by 77.53% for *I. aquatica*. *A. intrusa, M. esculenta*, *M. umbellata*, *C. esculenta*, *I. muticum* values were decreased by 70.85%, 69.97%, 44.44%, 42.75% and 27.38%, respectively (Table 2). Loss of water may lead to a decrease in the host stomatal conductance and consequently a fall in the rate of host photosynthesis (Press and Graves 1995). Parasites can reduce host carbon fixation by lowering host stomatal conductance, impacting host photosynthetic metabolism or changing host biomass, biomass allocation or architecture (Press and Graves 1995; Press et al. 1999; Watling and Press 2001). Similarly, in the present study, photosynthesis, transpiration, and survival were significantly reduced in infected plants (Prider et al. 2009).

WUE of the infected plants showed significant variations among species with *A. intrusa* showing the highest reduction of 80.32% followed by *M. micrantha* with 57.19%. Lower WUE readings were observed from *C. esculenta*, *M. umbellata*, *M. esculenta*, and *I. aquatica* with reductions ranging from 42.62% to 27.79% (Table 2). *I. muticum* showed the lowest reduction of 21.99% of WUE. Values for WUE also showed relatively small differences between parasite and associated hosts, but there was some evidence of better WUE of the host than the parasite (Radomiljac et al. 1999). The transfer of solutes occurs as a passive mass flow driven by a water potential gradient between the host and the parasite. The hemiparasite maintains more negative water potential than its host, which is generated by substantially elevated transpiration rates and abnormal behaviour of stomata which do not close even in dark or under water stress conditions (Těšitel et al. 2010).

Diurnal profiles of gas exchange and leaf water potential of hosts and parasites indicated closely coordinated diurnal stomatal responses of the parasite water relations to its host, thus resulting in transpiration rates of the parasite generating leaf water potential gradients favouring continuous abstraction of water and nutrients from a host (Radomiljac et al. 1999).

A strong correlation between P_n and g_s was observed for all seven selected plants species with correlation coefficient of 0.92 ($P<0.05$) for infected and 0.97 ($P<0.05$) for uninfected species (Figure 1). The results for the relationship between P_n and g_s showed that species infected by *C. filiformis* was lower compared to uninfected by *C. filiformis*. This was probably due to the reason that uninfected plants have always shown higher assimilation rates for a given stomatal conductance compared to infected plants (Shen et al. 2011). These associations have indicated the reduced g_s results in the suppression of photosynthesis in the host (Shen et al. 2007). The parasite had a significantly negative effect on the stomatal conductance (g_s) of host plants, and there was a linear relationship between the decline in P_n and g_s (Shen et al. 2011).

The biomass (Table 3) and photosynthetic rate reduction of the host species (Table 2) concurred with one another. The relationships between the species biomass to the P_n value was at correlation coefficient of 0.82 (Figure 2). The highest percentage in biomass was for *M. micrantha* at 91.52 %. Meanwhile, *A. intrusa*, *I. aquatica*, *M. esculenta*, *C. esculenta*, *M. umbellata* and *I. muticum* were reduced by 90.97 %, 90.10 %, 89.80 %, 61.47 %, 59.77 % and 55.19 %, respectively (Table 3). Therefore, in this study, *C. filiformis* infection formed linear R^2 correlation at 0.82 for photosynthesis rate and biomass (Figure 2). Similar results have been reported previously where the total biomass of the *C. campestris–M. micrantha* association was significantly less than the control at all infection densities. This is probably due to the fact that at high infection densities, the growth of the host is severely reduced, and this in turn would reduce its ability to generate resources and support the growth of the parasite (Shen et al. 2011).

Table 2. Photosynthesis, transpiration, water use efficiency and stomatal conductance of plants infected and uninfected with *C. filiformis*

Species	Treatments	Photosynthesis (P_n) (µmol CO_2 $m^{-2}s^{-1}$)	Stomatal Conductance (g_s) (mol H_2O_2 $m^{-2}s^{-1}$)	Transpiration (E) (mol H_2O_2 $m^{-2}s^{-1}$)	Water use efficiency (WUE)
A. intrusa	Infected	1.75 ± 0.02^{a}	0.02 ± 0.0008^{a}	0.65 ± 0.03^{b}	2.71 ± 0.11^{a}
	Uninfected	30.66 ± 0.30^{b}	0.21 ± 0.0013^{b}	2.23 ± 0.15^{a}	13.77 ± 0.91^{b}
C. esculenta	Infected	6.62 ± 0.27^{a}	0.07 ± 0.0021^{a}	3.20 ± 0.50^{a}	2.10 ± 0.28^{a}
	Uninfected	20.40 ± 0.19^{b}	0.15 ± 0.0011^{b}	5.59 ± 0.34^{b}	3.66 ± 0.25^{b}
I. aquatica	Infected	5.71 ± 0.29^{a}	0.06 ± 0.0036^{a}	1.69 ± 0.27^{a}	3.43 ± 0.39^{a}
	Uninfected	35.68 ± 0.25^{b}	0.26 ± 0.0024^{b}	7.52 ± 0.32^{b}	4.75 ± 0.19^{b}
I. muticum	Infected	11.53 ± 0.31^{a}	0.12 ± 0.0003^{a}	1.91 ± 0.01^{a}	6.03 ± 0.16^{a}
	Uninfected	20.25 ± 0.31^{b}	0.15 ± 0.0034^{b}	2.63 ± 0.22^{b}	7.73 ± 0.73^{b}
M. esculenta	Infected	5.48 ± 0.38^{a}	0.05 ± 0.0086^{a}	1.15 ± 0.12^{a}	4.83 ± 0.80^{a}
	Uninfected	28.56 ± 0.09^{b}	0.19 ± 0.0022^{b}	3.83 ± 0.13^{b}	7.47 ± 0.27^{b}
M. umbellata	Infected	6.56 ± 0.33^{a}	0.06 ± 0.0085^{a}	1.95 ± 0.03^{a}	3.36 ± 0.13^{a}
	Uninfected	19.92 ± 0.43^{b}	0.16 ± 0.0052^{b}	3.51 ± 0.24^{b}	5.69 ± 0.30^{b}
M. micrantha	Infected	1.55 ± 0.41^{a}	0.07 ± 0.0077^{a}	0.43 ± 0.08^{a}	3.57 ± 0.48^{a}
	Uninfected	35.41 ± 0.31^{b}	0.25 ± 0.0025^{b}	4.25 ± 0.15^{b}	8.34 ± 0.30^{b}

Note: Readings for selected species recorded for infected and uninfected plants (mean ± S.D; n=5). Means with same letter superscript within columns are not statistically different using Paired sample t-test at $P < 0.05$ probability level.

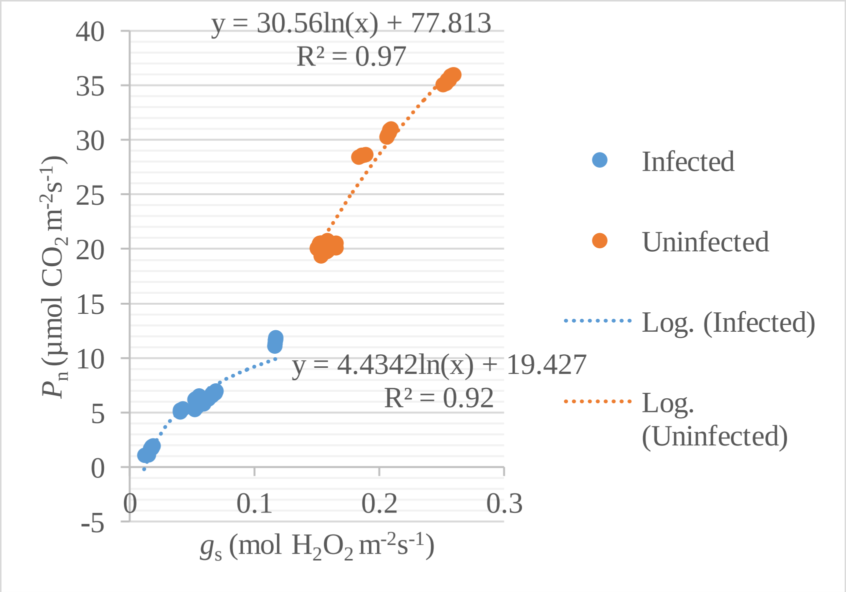

Figure 1. The relationship between photosynthesis and stomatal conductance for *C. filiformis* infection

Table 3. Biomass of plants infected and uninfected with *C. filiformis*

Species	Biomass (g)	
	Infected	Uninfected
M. micrantha	28	330
A. intrusa	25	277
I. aquatica	30	303
M. esculenta	15	147
C. esculenta	42	109
M. umbellata	35	187
I. muticum	82	183

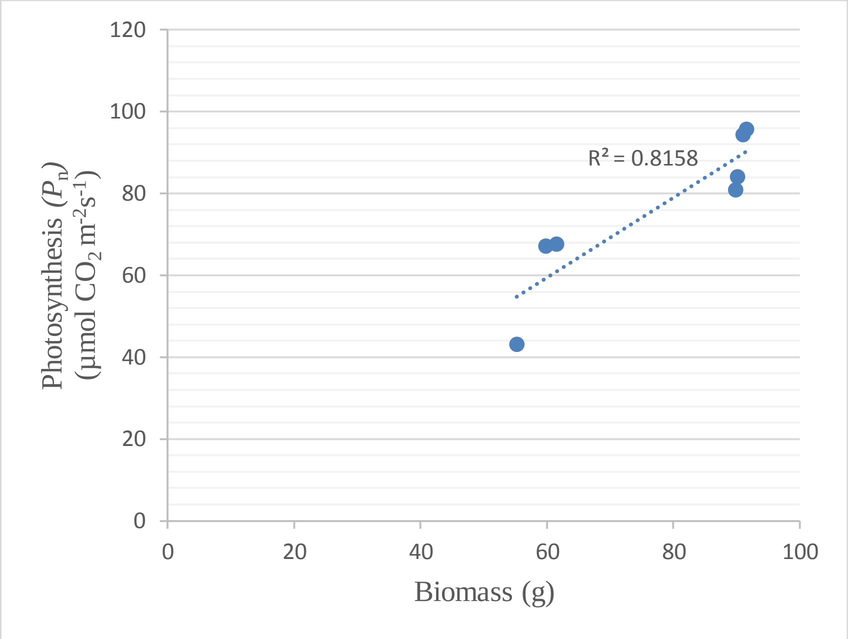

Figure 2. Relationship between photosynthesis and biomass for species infected by *C. filiformis*

The relative chlorophyll content of species infected and uninfected (control) by *C. filiformis* were coherent from higher to lower amount of infection based on species (Table 4). *M. micrantha* recorded the highest relative chlorophyll content reduction of 92.12% while *I. muticum* showed a reduction of only 66.66%. Likewise, a strong relationship between photosynthesis (P_n) and relative chlorophyll content was observed with correlation coefficient of 0.95 (Figure 3).

A decrease in chlorophyll concentration can result in a decrease in antenna size, reducing light capture and lowering photosynthesis rate (Cameron et al. 2005). A strong relationship between photosynthesis (P_n) and chlorophyll content was observed with correlation coefficient of 0.95. Lower photosynthesis rate may also result in light stress and photo damage for the infected host. The parasite significantly reduced the host chlorophyll content at all infection densities. Thus, the decreased chlorophyll content also explains the decline in P_n of host plants (Shen et al. 2011).

CONCLUSION

The result from this study provided information on photosynthesis capacity, biomass and relative chlorophyll content. The photosynthesis capacity consisted of photosynthetic rate, transpiration, water use efficiency and stomatal conductance. Significant differences were found for all seven selected plants species either infected or uninfected by *C. filiformis*. The impacts which *C. filiformis* can have on the hosts conducted is exhibited in the declines of photosynthesis capacity probably due to the result of suppression by the *C. filiformis*. However, the level of infection between all plants species conducted varies from one another probably due to the differences in morphological as well as the physiological aspects depending on the family of the plant species. The relationship between photosynthesis and stomatal conductance showed lower level of correlation coefficient for infected plants species while higher for the uninfected one. Meanwhile, the biomass and chlorophyll content reductions were concomitantly reduced from a high to low level depending on the increasing level of infection by *C. filiformis* on the plants. Introduction of parasitic plant to function themselves as cover crop is probably another alternative to overcome the problem which has occurred through the usage of traditional combination cover crops. Thus, *C. filiformis* will probably control the encroachment and invasion of weeds in oil palm plantation. Therefore, *C. filiformis* has the potential to be used as a biological control agent.

Table 4. Relative chlorophyll content, chlorophyll content reduction and photosynthetic reduction for species infected by *C. filiformis*

Species	Treatment	Relative chlorophyll content	Relative chlorophyll content reduction (%)
M. micrantha	Infected	4.20 ± 2.59	92.12
	Uninfected	53.31 ± 5.24	
A. intrusa	Infected	5.03 ± 4.33	89.51
	Uninfected	47.97 ± 3.51	
I. aquatica	Infected	6.57 ± 3.57	89.08
	Uninfected	60.17 ± 2.35	
M. esculenta	Infected	7.20 ± 3.32	83.30
	Uninfected	43.11 ± 3.49	
C. esculenta	Infected	8.36 ± 3.82	81.61
	Uninfected	45.46 ± 6.38	
M. umbellata	Infected	8.33 ± 3.15	77.38
	Uninfected	36.83 ± 4.05	
I. muticum	Infected	13.26 ± 1.37	66.66
	Uninfected	39.77 ± 4.16	

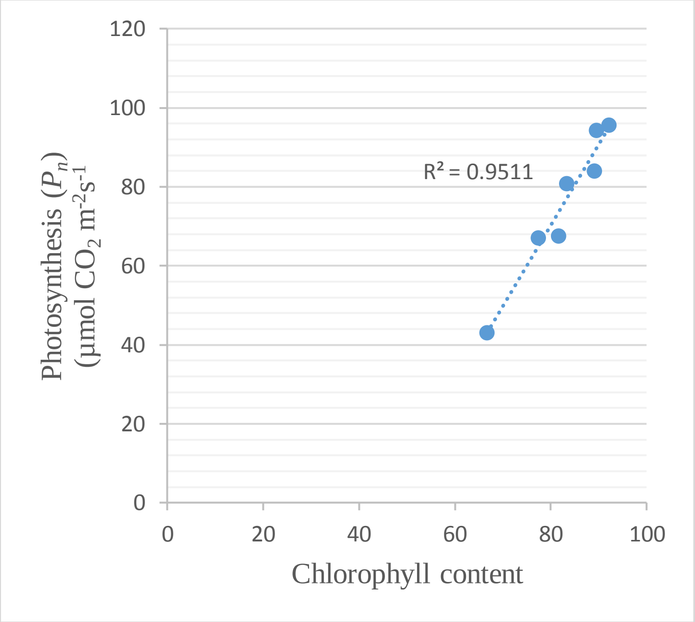

Figure 3. Relationship between photosynthesis (P_n) and relative chlorophyll content within species infected by *C. filiformis*

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