Studying the mutual interaction between rice and the parasitic weed *Rhamphicarpa fistulosa*: the role of host size at the moment of parasite infection.

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Contents

1. Introduction

Rice (*Oryza sativa)* is an important cereal crop commonly grown in Africa. It is a traditional staple food to increase food security in most parts of Africa. Rice can be very productive and sustainable and be produced in areas where other crops cannot be grown (Balasubramanian et al., 2007; Rodenburg and Meinke). Worldwide, rice (*Oryza spp*) has the second highest production after maize (FAOSTAT, 2009; Pflug, 2013). Currently demand for rice consumption is increasing in sub Saharan Africa (SSA) more than anywhere in the world. The increased demand for rice is as a result of a continuing population growth and a change in consumer preference for rice, specifically in the urban area. Annual per capita milled rice consumption in sub-Sahara Africa has increased from 11 kg in 1961 to 22 kg 2003 (Balasubramanian et al., 2007). In current years rice production has been expanding at the rate of 6% per annuum, with 70% of production increases due to land expansion and only 30% being attributed to an increase in productivity (Balasubramanian et al., 2007).

Rice production in SSA cannot meet the demand for rice consumption. This is due to production constraints such as out-dated production techniques, poor soil fertility, diseases, insects and weeds. Weeds are one of the major constraints, hampering a further increase in rice production in SSA, mainly due to competition for light, water and nutrients (Bastiaans et al., 1997) and attract disease causing organisms (Atera et al., 2011). Parasitic weeds are found among the more severe weed problems. Rice is susceptible to different parasitic weeds such as *Striga asiatica*, *Striga hermonthica*, *Striga aspera* and *Rhamphicarpa fistulosa*. *R. fistulosa* from *Orobanchaceae* family is found as a newly arising problem that causes considerable yield loss in rice production, specifically in rain fed low land sub-Saharan Africa (Rodenburg et al., 2011). Yield loss due to *R. fistulosa* infestation can be varying based on agronomic practice, but the damage can be as high as complete crop loss (Rao et al., 2007). More than 60 % yield loss was encountered in Benin (Rodenburg et al., 2011). Similarly, yield losses of 30 to 100 % were reported in Tanzania (Kayeke et al., 2010). Yield loss due to R. fistulosa infestation can be varying based on agronomic practice, but the damage can be as high as complete crop loss (Rao et al., 2007). More than 60 % yield loss was encountered in Benin (Rodenburg et al., 2011). Similarly, yield losses of 30 to 100 % were reported in Tanzania (Kayeke et al., 2010)

Nowadays the damaging impact of *R. fistulosa* is increasingly becoming a serious production problem due to the lack of appropriate control options (Raynal-Roques.,1994; Rodenburg et al., 2010). Lack of a proper control method is related to the limited knowledge regarding the mutual interaction between *R. fistulosa* and its host.

Based on experience from *Striga spp*. farmers use hand weeding, resistant rice cultivars and soil fertility management as *R. fistulosa* control options. Application of more fertilizers can also reduce the negative impact of *R. fistulosa* on rice as the application of more fertilizer can increase the soil fertility and improve the competition of the crop against the weed (Rodenburg et al., 2011). Some of the mentioned control methods are not feasible for economically poor farmers in SSA where *R. fistulosa* problem is relatively high. Therefore a consistent and practical integrated control method needs to be developed. In order to develop sustainable control strategies the mutual interaction between the parasite and the host plant needs to be understood well.

R. fistulosa occurs naturally in hydromorphic and rain fed lowland areas, where soil is wet (Rodenburg et al., 2011). It grows on a wide range of soils such as sand, clay, loam soil and even on rocks. *R. fistulosa* occurs in natural vegetation, however the parasitizing effect of *R. fistulosa* in natural vegetation is not reported yet. This might be due to the higher competition of natural vegetation against the parasite. Age difference between natural vegetation and the annual parasite can also play a role (Ouedraogo et al., 1999).

R. fistulosa is an annual facultative root parasite. Being a facultative parasite, *R. fistulosa* is able to complete its life cycle in the absence of a host plant. Seeds of *R. fistulosa* can stay dormant for about six months. Germination of *R. fistulosa* needs sufficient moisture and light, but does not require the presence of root exudates from a host as is the case for *Striga spp* (Ouedraogo et al., 1999). Under suitable conditions seeds of *R. fistulosa* germinate within four days and start to develop a transparent radicle. Infection of the host root starts with the development of haustoria on the root of the parasite. The first stage of haustoria development is characterized by the propagation of papillae in the region of haustoria formation. Up on attachment, *R. fistulosa* forms un interrupted connection with host root vessel elements. *R. fistulosa* connected to a host grows fast and produces more flowers and branches while growth of the host plant is reduced compared to those that are not infected (Ouédraogo et al., 1999; Rodenburg et al., 2010).

R. fistulosa harms its host rice, through withdrawal of assimilates, distortion of host physiological processes (i.e. increased respiration as well as a decline in net photosynthesis) and an altered allocation of biomass (Pflug, 2013). The negative effect on host biomass allocation involves accumulation of more dry matter in the root system that in turn decreases growth of the shoot system. This leads to a lower number of tillers produced per plant, a lower number of leaves and therefore a low dry matter. Development stage or host size during first parasite infection might be an important factor determining the level of host damage and further host performance. Particularly if the host plant is still in its exponential growth phase, a distortion of its growth might have more serious implications for its further growth.

In the mutual interaction between *R. fistulosa* and its host rice the factors determining growth of the parasite are not clear yet. Host size can be considered as an important factor, but various hypotheses regarding the influence of host plant size can be formulated. A small host plant might not be a good host, since less assimilates are available to the parasite. At the same time, the ability of the parasite to withdraw assimilates from the host can also play a significant role. With a relatively smaller host size the parasite might be regarded a relatively stronger sink, that can more easily withdraw assimilates from its host and grows faster. Yet another hypothesis is that attachment of the parasite to the host root might be relatively early in older rice plants, because of well-developed root system in case of older rice plants. In this case the relatively larger host size results in a faster connection between host and parasite and therefore growth of *R. fistulosa* can be faster.

The aim of this study was to determine the role of host size at the time of parasite infection on a. growth of *R. fistulosa* and b. on the effect of *R. fistulosa* attachment on growth of the rice plant. To achieve this objective, a pot experiment was conducted in which rice plants of three different ages were grown with and without the presence of the parasite *R. fistulosa.* To reveal the role of host plant size on the mutual interaction between the rice plant and its parasite *R. fistulosa* the following research questions were addressed. How and to what level does *R. fistulosa* negatively affect growth and dry matter allocation of rice plant? At which developmental stage of the host does *R. fistulosa* grow taller and produce more biomass? The above questions will be addressed in the current study.

2. Material and Methods

A pot experiment was conducted under greenhouse conditions at Radix Serre, Wageningen University, the Netherlands (51°59'19" N and 5° 39, 49" E). The experiment was conducted from April 15 to August, 2013.

2.2. Growth conditions

The average temperature during growth period was ± 26 °C at day time and 23°C during night. Day length was artificially adjusted to short day for 12 hours starting from 20:00 pm to 8:00 am. Plants were provided with supplemental (artificial) light using lamps (SON-T Agro, 400 W, Philips) during day in the absence of sun light. The lamps automatically switched on when photosynthetically active radiation (PAR) was below 910 µmol m^{-2} s^{-1}. The average air relative humidity was between 65 % to 70 %.

Mixture of arable soil and white sand (1:1 ratio by volume) was used as growth substrate. The mixed soil was filled into bottom sealed five litre pots (diameter of 0.29 m at the rim, 0.23 m at the bottom and 0.28 m height) to a total weight of 8 kg per pot.

At the beginning of the experiment the pots were watered with 2 litres of water until saturation level. Later on, the pots were watered daily. After rice plants were grown bigger the pots were watered according to the size of the plants, i.e. larger plants were given more water. During the experiment, no fertilizer application was used. Small weeds grown on the pots were removed manually.

2.3. Plant material

Rice (*Oryza sativa*) cultivar IR 64 and *Rhamphicarpa fistulosa* were used to assess the interaction between *R. fistulosa* and its host rice in relation to host age. Both rice seeds and *R. fistulosa* were obtained from Tanzania and were collected in 2012.

Rice seeds were pre-germinated for 72 hours in an incubator with illumination of fluorescent light at 33 ° C. Before planting, the germinated seeds were selected for uniformity of germination initiation. One pre-germinated rice seed was planted at the centre of pot at depth of approximately 1.2 cm. The remaining germinated seeds were planted in an extra pot as a reserve. Seeds that did not emerge were replaced within 4 to 6 days.

2.4. Experimental design

The experimental design was a randomized complete block design with five replicates. The experiment contained 7 treatments which consisted of three host parasite interactions, three rice monocultures (control) and one *R.fistulosa* monoculture (control). Treatments for the host-parasite interaction and rice monocultures contained rice plants of three different ages. The three different rice ages were obtained by sowing the pre-germinated rice seeds at different sowing dates to which seeds of the parasitic weed *R. fistulosa* were added at the same moment in time. Age of the rice plants at the time of inoculation of *R.fistulosa* were 40 days, 21 days and 0 days and in the remainder these are referred to as D40, D21 and D0, respectively. Approximately 100 seeds of *R. fistulosa* were mixed with about 10 g of white sand and then dispersed on the upper soil surface (i.e. 100 seeds per pot). After inoculation of *R. fistulosa,* the pots were moistened with fine water spray. At 17 to 19 days after inoculation of the parasite, the seedlings of *R. fistulosa* were thinned to 20 plants per pot. Eight harvests were set-up for the entire experiment. This report only deals with the first four harvests, including the time period until .. days after inoculation (DAI)..

2.5. Data collection

The effect on growth of rice and *R.fistulosa* when *R.fistulosa* seeds were inoculated to rice plants at different ages were evaluated based on data obtained from morphology and biomass production of rice plant, height of *R.fistulosa* plants per size class and biomass production. Growth of *R. fistulosa* and its rice host was measured destructively and non-destructively. The entire experiment contained 8 harvests. This report was written using the first four harvests, which took place at 19, 26, 33 and 40 DAI of *R. fistulosa*.

Rice Morphology and biomass production

Morphology and biomass production of rice plant was determined through non-destructive and destructive measurements. Number of tillers and total leaf number were counted. The main stem was cut at the soil level and then height was measured from the base of stem to the growing point (youngest ligule). Above ground parts of rice plants were harvested and separated into stem, green leaves, dead leaves, panicle (if existent), and roots. Green leaf blades were removed from the stem by cutting them at the base of ligule. Leaf area of green leaf blades was measured immediately after harvest using leaf area meter (Li-Cor, Lincoln, NE, USA). Roots were harvested by washing the root system under running water. For treatments combining *R. fistulosa* and rice, the cleaned roots were frozen at -20 ^{o}C for 24h, to be able to separate roots of rice and *R. fistulosa* based on colour change after freezing, i.e *R. fistulosa* roots turn purple while rice roots remain white. The harvested samples were dried at 70 ^{o}C for 24 hours to determine root dry weight (g plant^{-1}), leaf dry weight (g plant^{-1}) and stem dry weight (g plant^{-1}). Panicle and dead leaves dry weight were determined if present. Specific leaf area (SLA) was calculated by dividing leaf area with green leaf dry weight. Total dry weight (g plant^{-1}) was calculated as the sum of leaves, stem, roots, panicle and dead leaves dry weight. Total dry weight per pot was calculated as sum of total dry weight of rice and that of *R. fistulosa***.** For statistical analysis dead leaves and panicle was included in the leaf and stem part respectively.

R. fistulosa height and biomass production

Growth and biomass production of *R. fistulosa* were assessed destructively and non-destructively. Numbers of germinated *R. fistulosa* plants per pot were counted in pots with and without rice, twice per week starting 7 days after inoculation to the host plant. Height of individual *R. fistulosa* plants per pot was measured based on height classes of 1 cm width (i.e. 0.1 – 1 cm, 1.2. – 2 cm, 2.1 – 3 cm, 3.1 – 4 cm etc.) during each harvest. Root dry weight and shoot dry weight were measured destructively after drying plant material at 70 ^{o}C for 24 h.

2.6. Statistical analysis

Statistical evaluations of the data were done by using Genstat 15th edition. For the analysis of variance randomized complete block design with *P* value < 0.05 was used to detect differences between individual treatment means.

3. Result

Number of emerged R.fistulosa plants per pot

The first emergence of *R.fistulosa* seedlings were noticed 7 days after sowing. A strong significant effect of presence of the rice plants was noticed ($P < 0.001$) on the emergence of *R.fistulosa* plants per pot. The effect of host size on the emergence of *R.fistulosa* was not differed among the three rice ages.

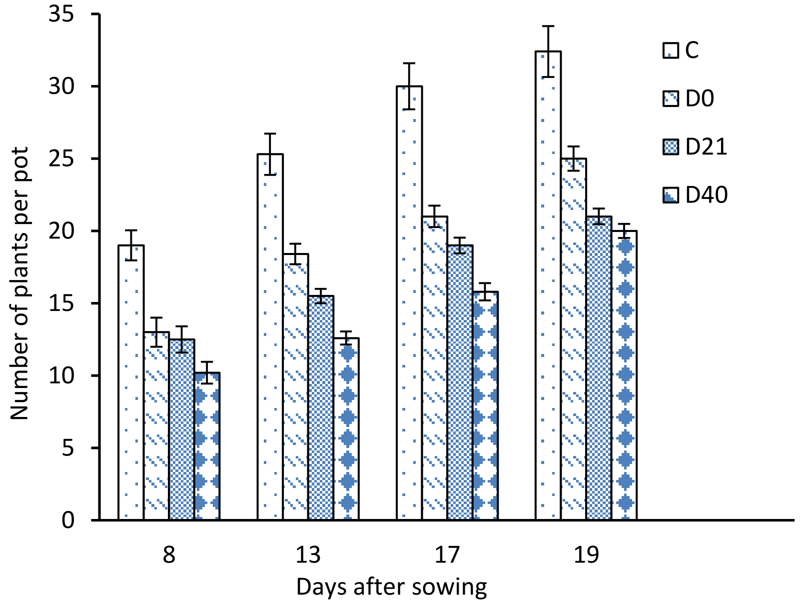


Fig. 1. Emergence of *R.fistulosa* plants over time for monoculture *R.fistulosa* (C) and for the three combinations with rice plants on which *R.fistulosa* was added at different developmental stages of rice plant. D0 represents the rice plant to which *R.fistulosa* was added at the moment of sowing the rice seed, D21 and D40 indicate rice plants that were 21 days and 40 days old respectively at the moment of adding *R.fistulosa* seed.

Significant effect of host size on total dry weight of *R.fistulosa* plants was noticed at 33 DAS (P = 0.004) and at 40 DAS (P = 0.013). At 33 DAS significant differences in total dry weight was noticed between *R.fistulosa* grown as monoculture and *R.fistulosa* grown with rice plants ($LSD_{0.05}$ = 0.00646). At 40 DAS total dry weight for *R.fistulosa* grown in association with D0 and D21 rice plants were significantly increased. At 40 DAS total dry weight of *R.fistulosa* monoculture and *R.fistulosa* plants grown with D40 rice plants were not significantly differed according to LSD test at 5 % level ($LSD_{0.05}$ = 0.0592). However, total dry weight of *R.fistulosa* grown with D0 and D21 rice plants were significantly increased compared to *R.fistulosa* grown as monoculture.

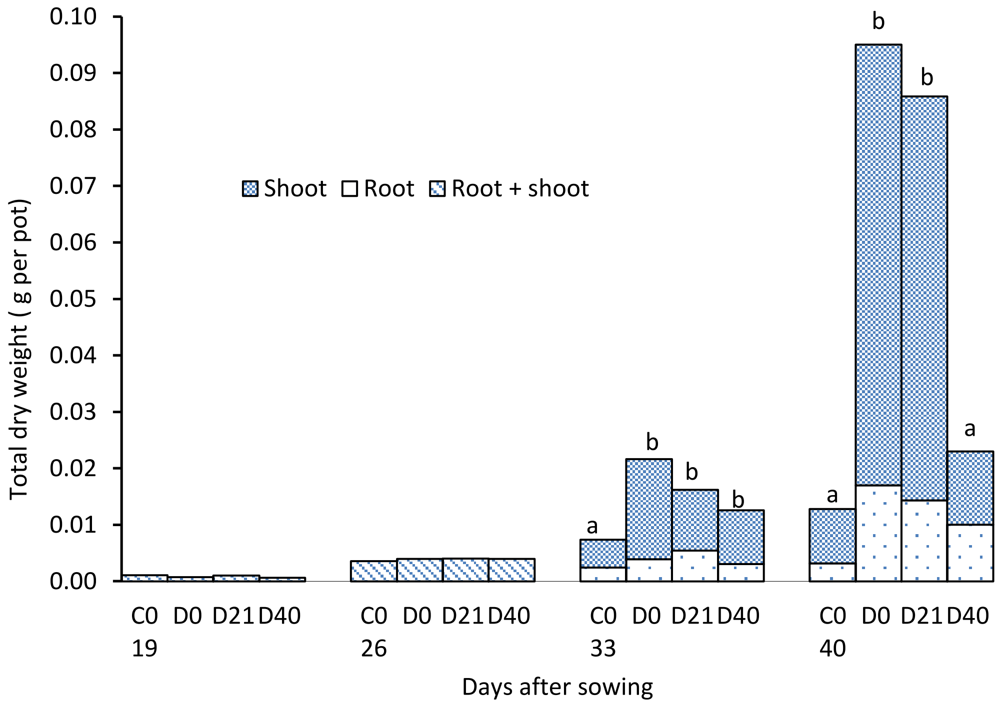


Fig. 2. Total dry weight for *R.fistulosa* plants over time for monoculture (C) and for the three combinations with rice plants to which *R.fistulosa* was added at different developmental stages of the rice plant. D0 represents rice plants to which *R.fistulosa* was added at the moment of sowing of rice seed, D21 and D40 indicate rice plants that were 21 days and 40 days old respectively at the moment of adding *R.fistulosa* seed. At harvest days 19 and 26, only total dry weight of *R.fistulosa* plants was determined, while at day 33 and 40 dry weights of shoot and root of *R.fistulosa* plants was determined. Different letters indicate significant difference between treatment means according to LSD test at 5 % level.

Rice total dry weight

Seeds of *R. fistulosa* were introduced in pots with rice plants of 0, 21 and 40 days old. Nineteen days after inoculation clear differences in plant size between these plant ages were still present. Over the next three weeks plants continued to increase in size, but the differences in plant dry weight between plant ages were maintained (P < 0.001, for all sampling times). More interesting was however to determine whether the presence of *R. fistulosa* did have an effect on the dry matter accumulation of the host plant. For all three rice ages, the presence of the parasitic weed *R. fistulosa* did not significantly affect the total dry weight of the rice plants for none of the sampling dates (P = 0.326, P=0.594, P = 0.343 and P = 0.199 for 19, 26, 33 and 40 DAS, respectively). Although not significant, rice plants grown in combination with *R. fistulosa* gradually seemed to produce less total dry weight compared to their respective control plants. This trend was most clear at the last sampling date in D0 and D21 rice plants.

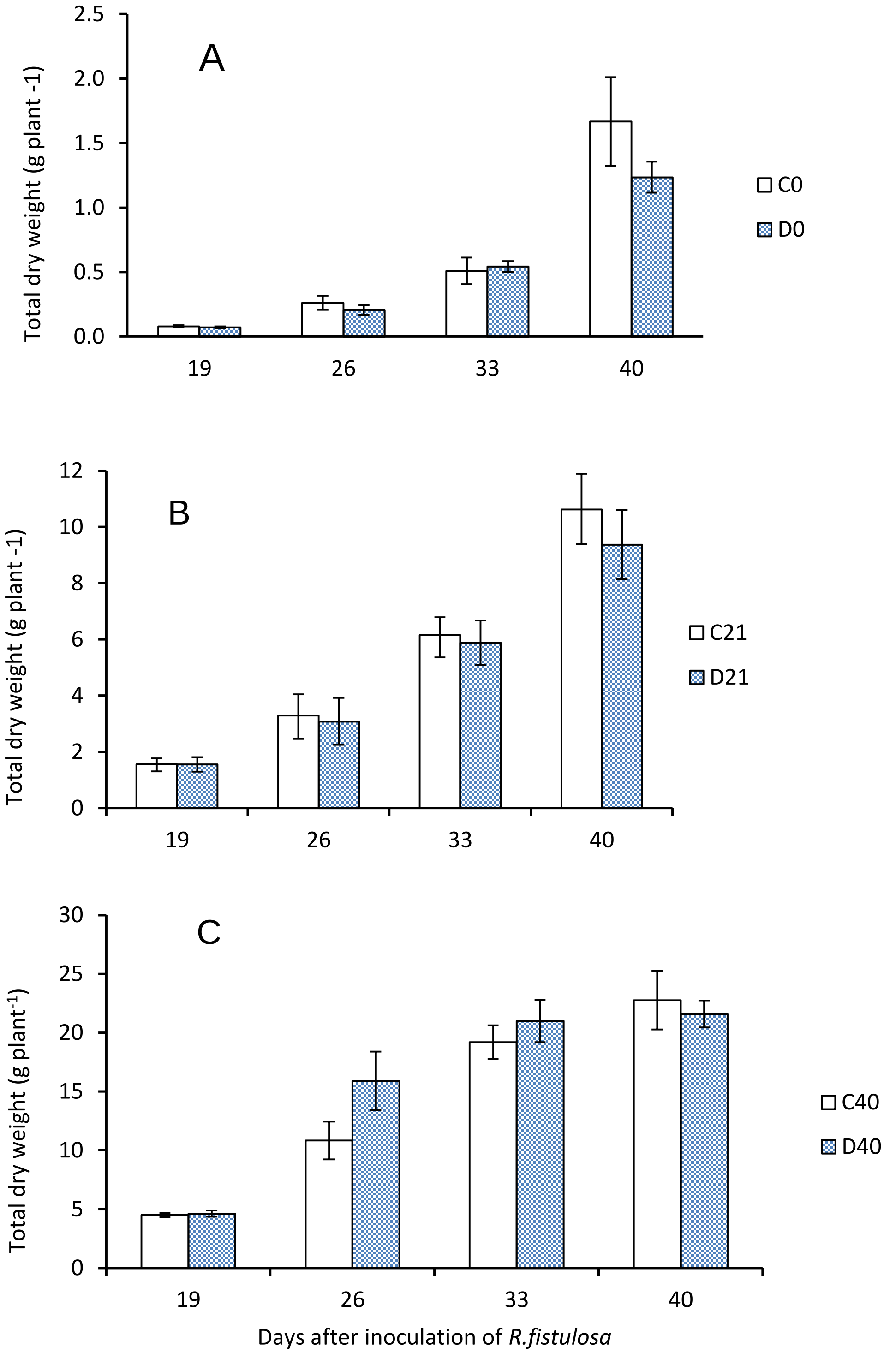
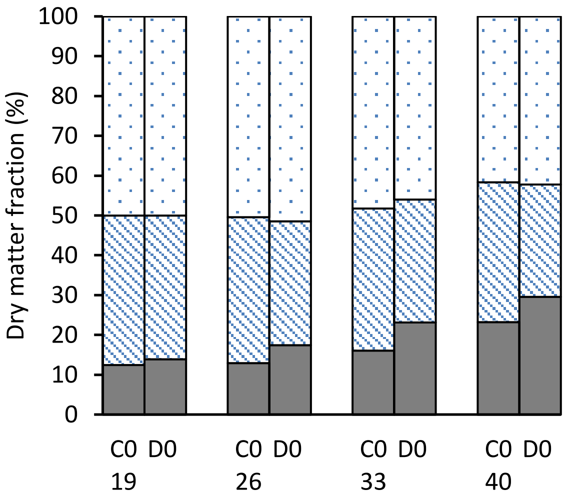


Fig. 3. Total dry weight of rice (g plant^{-1}) over time for rice monocultures (C0 (A), C21 (B) and C40 (C)) and rice plants grown in combination with *R. fistulosa* (D0 (A), D21 (B) and D40 (C)). D0 represents rice plants into which *R. fistulosa* was inoculated at the moment of sowing the pre-germinated rice seed; D21 and D40 indicate rice plants that were 21 days and 40 days old at the moment of introducing *R. fistulosa*, respectively. Error bars represent ± SEM in which N = 5.

Dry matter partitioning in rice

Dry matter distribution differed between rice age classes ($P < 0.001$ for all sampling dates) and gradually changed over time. An interaction effect between presence of *R.fistulosa* and age of rice plants on root dry matter allocation was found significant ($P = 0.018$) only at 33 DAS. No significant differences were noticed between infected D21 and D40 rice plants compared to their respective control treatments according to LSD test at 5 % level ($LSD_{0.05} = 0.042$). Only for infected D0 plants the fraction dry matter allocated to the roots was significantly increased compared to the control plants. Significant effect of *R.fistulosa* on stem dry matter allocation of infected rice plants was noticed at 33 DAS ($P = 0.009$) and at 40 DAS ($P = 0.013$). Both at 33 DAS ($LSD_{0.05} = 0.01766$) and 40 DAS ($LSD_{0.05} = 0.02843$) dry matter allocated to the stem fraction of the infected rice plants was significantly reduced compared to their respective control treatments. During none of the harvests a significant effect of *R.fistulosa* infection on fraction leaf dry matter was noticed.



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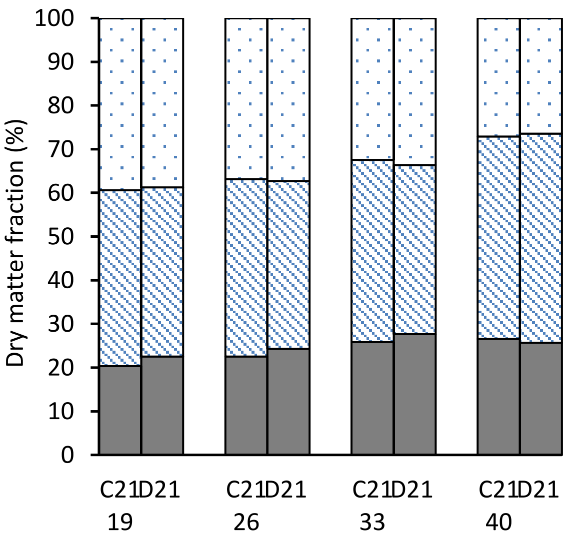

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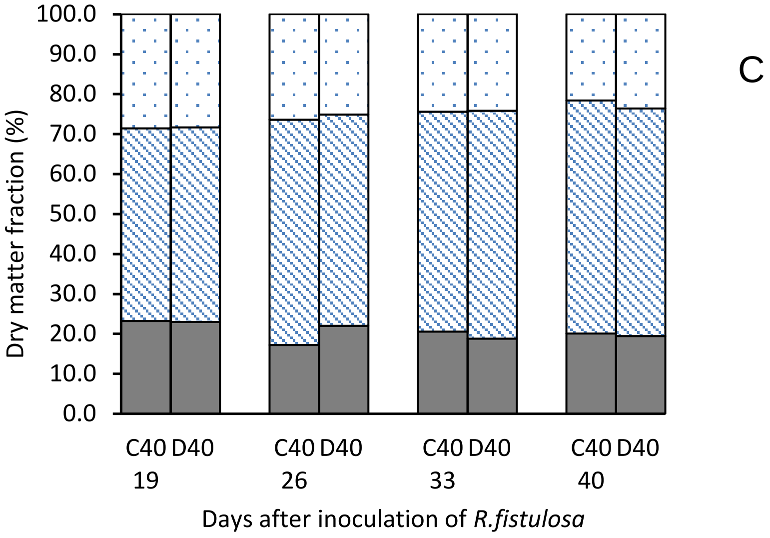

Fig. 4. Distribution of biomass (%) over time for rice monocultures (C0, C21 and C40) and rice plants grown in combination with *R.fistulosa* (D0, D21 and D40). D0 represent rice plant into which *R. fistulosa* was inoculated at the moment of sowing the pregerminated rice seed; D21 and D40 indicates rice plants that were 21 and 40 days old at the moment of introducing *R.fistulosa*, respectively. The bottom, middle and upper part of each bar represents fraction of dry matter that was allocated to roots, stem and leaves, respectively.

Morphological changes in rice

Height of the main stem was measured during each sampling date. Total numbers of leaves were counted including leaves produced per tiller. On each sampling date, a highly significant effect of rice age was observed. However, no significant effect of *R.fistulosa* infection was noticed on height, leaf number, tiller number or specific leaf area of rice plants on any of the sampling date.

Table 1. Average height (cm) for rice plants monoculture (C0, C21 and C40) and rice plants grown in combination with R.fistulosa (D0, D21 and D40).

	Mean		Mean		Mean		*P*	
DAS	C0	D0	C21	D21	C40	D40	Rice age	*R.fistulosa*
19	8.8	9.4	22.1	21.1	26.0	25.1	<.001	0.468
26	14.7	14.0	24.7	23.8	30.7	29.8	<.001	0.366
33	16.7	18.0	26.3	28.7	35.0	37.6	<.001	0.177
40	21.5	19.0	30.0	29.3	53.0	51.5	<.001	0.721

Table 2. Number of tillers per plant for rice plants monoculture (C0, C21 and C40) and rice plants grown in combination with R.fistulosa (D0, D21 and D40).

	Mean		Mean		Mean		*P*	
DAS	C0	D0	C21	D21	C40	D40	Rice age	*R.fistulosa*
19	0.0	0.0	3.0	3.0	4.0	3.8	<.001	1.000
26	1.0	1.0	5.0	6.0	6.4	9.8	<.001	0.052
33	1.8	1.6	6.0	6.0	8.8	9.4	<.001	0.920
40	3.4	2.4	7.0	7.0	8.6	8.6	<.001	0.721

Table 3. Total number of leaves for rice plants monoculture (C0, C21 and C40) and rice plants grown in combination with R.fistulosa (D0, D21 and D40).

	Mean		Mean		Mean		*P*	
DAS	C0	D0	C21	D21	C40	D40	Rice age	R.fistulosa
19	4.2	4.4	16.0	18.0	24.0	23.0	<.001	0.941
26	7.0	8.0	25.0	27.0	36.0	48.0	<.001	0.172
33	11.0	9.0	32.0	27.0	39.0	45.0	<.001	0.986
40	20.0	16.0	33.0	41.0	44.0	44.0	<.001	0.634

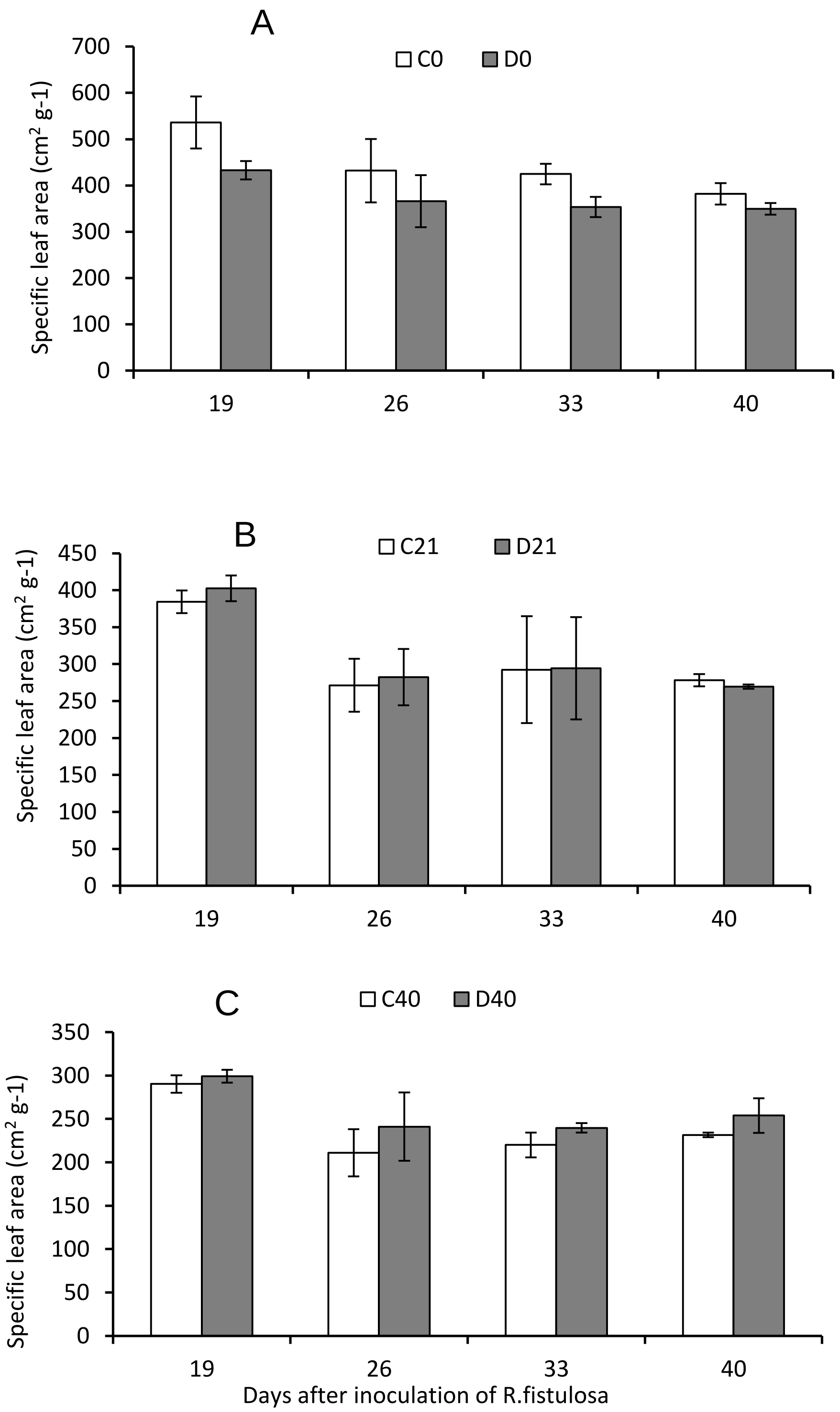

Fig. 5. Specific leaf area (cm^2 g^{-1}) over time for rice monoculture (white bar) and rice grown in combination with rice plant (black bar). D0, D21 and D40 at the top of the figures represent rice plant into which R.fistulosa was inoculated at the moment of sowing the pregerminated rice seed, D21 and D40 indicates rice plants that were 21 days and 40 days older at the moment of introducing *R.fistulosa* respectively. C0, C21 and C40 represents control plants for D0, D21 and D40 respectively. Error bars represent ± SEM in which N = 5.

4. Discussion

The aim of this study was to determine the role of host plant size on growth of parasitic weed *R. fistulosa* and to determine the effect of *R. fistulosa* infection time on growth of the host. To achieve this objective, a pot experiment was conducted in which rice seeds were sown at three different dates and *R. fistulosa* was inoculated to all rice plants at the same moment in time. Due to time constraints, this report only contains the first four sampling times of an experiment that contained a total of six sampling times. The other two harvests were conducted, but could not be included in the report anymore.

At 40 DAI the only effect of the parasitic weed on rice was a change in the dry matter distribution of the host plant. In fact this effect was first noticed at 33 DAI. At that date, a significant increase in the fraction root was noticed, resulting from parasite infection. At the same time, the fraction stem was reduced. At 40 DAS only a significant reduction in stem dry weight was observed. The response of the host plant on parasite infection was similar for the rice plants of all three ages. Also Pflug (2013) observed that a reduction in dry matter allocated to the stem to the benefit of the root was the first symptom after parasite infection. Later on, a significant reduction in dry matter production was observed. It was also only in this stage that a difference in the response of differently aged rice plants was observed. The reduction in dry matter was stronger for younger rice plants. Similarly in sorghum the disruption of host dry matter distribution as a strong indication of the negative effects of the parasite on total dry weight and therefore growth of the host plant has been reported (Van Ast, 2006).

Based on visual observation it was clear however that rice growth was negatively affected by *R.fistulosa* infection. It was also obvious that this effect was stronger on younger host plants. The higher effects of *R.fistulosa* infection on the younger rice plants might be because of age related resistance against root penetration during infection with the parasite. Age related resistance against infection with *S.hermonthica* have been reported in sorghum (Rolando et al., 1992) and in maize (Oswald et al., 2001). Rolando et al., (1992) suggested that the older host plant is less affected by *S.hermonthica* infection because of developments of substances such as phenols, lipids, suberin and lignin in the older host root cells. From this point of view the higher effects of *R.fistulosa* infection in the current study might be therefore because of less development of phenols and lignin substances in the root cell. Moreover further the further effects of *R. fistulosa* on the leaf level were reported by Stefanie (2013) and Rodenberg et al (2011) mainly due to pathological effects on the host plant such as declining leaf photosynthesis, increasing respiration and transpiration rate (Rodenburg et al., 2011 and Stefanie 2013 unpublished). No effect was noticed on plant height as it was also reported by Rodenburg et al (2011). No effect of R. fistulosa infection was noticed on leaf number, leaf area and tiller number. The absence of effects of *R. fistulosa* infection on numbers of tillers was also reported by Pflug (2013).

Apart from the effects of *R. fistulosa* infection on the host plant, the effects of host size on growth of the parasitic weed *R. fistulosa* was investigated. The previous study has been reported that a higher growth of *R. fistulosa* plants in the presence of host plant is an indication of connection of the parasite to the host root (Klaren and Jansenn 1978). Similarly in the current study the increased height of *R.fistulosa* was considered as an indication of attachment to the host root.

It was noticed that *R. fistulosa* grew better in connection with a host plant and also grew more profound when connected with younger host plants remained visible. The higher growth and the increased accumulation of total dry weight in the connected *R. fistulosa* with the younger host might be due to withdrawal of assimilates from the host root. As it might be argued the larger host size might be better guarantee for faster and better growth of the parasite. However in the current experiment a higher growth of *R. fistulosa* in combination with the younger rice plants might be because of *R. fistulosa* is better able to easily withdraw assimilates from the smaller and often weakened host plant. At the same time less canopy formation in the smaller host plant might create good light situation for the hemi-parasitic *R. fistulosa* to produce its own assimilates. The increased biomass production of *R. fistulosa* grown in combination with rice plants were originated from the increased shoot dry weight of the parasite. During each harvest shoot dry weight of *R. fistulosa* grown in association with rice plants was largely increased than that of root dry weight. This showed that parasitism of *R. fistulosa* in the mutual interaction with its host rice has resulted in the increased shoot to root ration in *R. fistulosa* as it was also reported by Pflug (2013).

5. Conclusion

The study has shown that the effect of host plant on growth of *R. fistulosa* was not determined by host size, but related to host presence. This indicate that growth of *R. fistulosa* is therefore determined by its ability to withdraw assimilates from the host root (strong sink). D0 and D21 rice plants were suitable host. Host presence increased total biomass production, height of *R. fistulosa* plants and shoot root ration. Host size at the moment of infection determine the level of host damage. Infection with *R. fistulosa* altered distribution of dry matter allocation.

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