

**BRIEF REPORT**

# Differences in the ecology of witchweed and vampireweed: Implications for rice farming in Africa

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**Societal Impact Statement**

Parasitic weeds in African rice systems threaten household-level food security and income generation. Most affected farmers are smallholders with limited capacities to address these pests. Obligate parasites *Striga asiatica* and *Striga hermonthica* (witchweed) are problematic in rainfed upland rice, affecting approximately 312,000 households. Facultative parasite *Rhaphicarpa fistulosa* (rice vampireweed) has more recently become problematic in rainfed lowland rice, affecting approximately 133,000 households. A better appreciation of differences in biology, ecology and host–parasite interactions between these weeds, and the implications for species-specific management, will inform awareness and preparedness among regional actors.

**KEYWORDS**Africa, *Rhaphicarpa*, rice vampireweed, *Striga*, weed management, witchweed

## 1 | INTRODUCTION

Parasitic plants occur in 270–275 genera and 28 families of flowering plants (Heide-Jørgensen, 2013). About 60% of parasitic plants are root parasites, several species of which are known as weeds in crop production systems, all within the Orobanchaceae family (Parker, 2013). Root parasites are subdivided in holo- or hemiparasites. Holoparasites have no chlorophyll and therefore rely fully on their host for their carbon needs. Prime examples of weedy root holoparasites are the broomrapes (*Orobanche* and *Phelipanche*). Other major root parasitic weeds are hemiparasites. They have chlorophyll enabling them to assimilate at least part of their own carbon needs (DePamphilis & Palmer, 1990). Two genera impact cereal production, that is, *Striga* and *Rhaphicarpa*. *Striga asiatica*, *Striga hermonthica* and *Rhaphicarpa fistulosa* (Figure 1) are particularly widespread and impactful and all are common in rainfed rice production environments in Africa (Rodenburg, Demont, et al., 2016). The main difference between them is that *Striga* species are obligate parasites, whereas *Rhaphicarpa* species are facultative parasites. Obligate hemiparasites require a host connection soon after seed germination,

in order to survive (Riopel & Timko, 1995), while for facultative parasites such connection is beneficial but optional (Matthies, 1997). Various aspects of parasitic weeds in rice production systems have been intensively studied in the past decade, and differences and similarities are specified here (Table 1). This synthesis is then used for defining a species-specific outlook for effective management, based on the observed differences in biology and ecology.

## 2 | BIOLOGY AND ECOLOGY

The host range of *S. asiatica* and *S. hermonthica* and that of *R. fistulosa* encompasses (potentially all) cereal crop species grown in Africa (Ouédraogo et al., 1999) (Table 1). However whereas the host range of these *Striga* species is restricted to grasses, *R. fistulosa* can also parasitise legumes (Houngbedji & Gibot-Leclerc, 2015). *Rhaphicarpa fistulosa* favours waterlogged soils and is therefore mostly found in the lower parts of the landscape, that is, the rainfed lowlands. *S. asiatica* and *S. hermonthica* are associated with drier, free-draining soils and therefore, next to other major cereal crops such as maize

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**FIGURE 1** Photos of the obligate parasitic weeds *Striga asiatica*, red witchweed (left), *Striga hermonthica*, purple witchweed (middle) and the facultative parasitic weed *Rhamphicarpa fistulosa*, rice vampireweed (right), parasitising on rice (*Oryza sativa*) in Africa. Photos by J. Rodenburg.

and sorghum, primarily found on rice grown at higher parts of the landscape, that is, the rainfed uplands. Field and experimental observations on *S. asiatica* and *R. fistulosa* indeed demonstrate this clear ecological demarcation (Kabiri et al., 2015).

Both *Striga* spp. (Botanga et al., 2002; Unachukwu et al., 2017) and *R. fistulosa* (Zossou et al., 2016) are genetically highly diverse, both within and between geographical locations. Both genera are prolific seed producers. *R. fistulosa* can produce more than 2000 seeds per plant (Kabiri et al., 2016), and average production per *S. hermonthica* plant ranges between 6700 and 26,500 seeds (Rodenburg et al., 2006). Seeds of *Striga* spp. are often reported to maintain viability for more than 10 years, but a recent study on *S. hermonthica* suggests a significant loss of germination rate and viability to occur within a timespan of 5 years (Brun et al., 2023). Seed viability of *S. asiatica* in soils is estimated between 5 and 9 years (Bebawi et al., 1984). Seed longevity of *R. fistulosa* is approximately only 1 year (Gbehounou & Assigbé, 2004).

Apart from sufficient soil moisture, seed germination of *Striga* spp. and *R. fistulosa*, have rather different requirements. A direct consequence of the parasitic nature is that seeds of obligate *Striga* species require a biochemical cue (e.g. strigolactones) from nearby roots of potential host plants to germinate, facilitating the required prompt host connection after germination. This requirement in turn is associated with the small seed sizes (3.7–4.5 µg; Parker & Riches, 1993; Rodenburg et al., 2006) and hence growth reserves of *Striga* spp. Failing establishment of a host connection within 3–4 days after germination leads to death of the *Striga* seedling. This is referred to as suicidal germination. Connection with the host roots is made by means of terminal haustoria, followed by lateral haustoria (Joel, 2013). Germination of the larger seeds (11.5 µg) of facultative *R. fistulosa*, in contrast, only requires light, and host plant presence has no effect on their germination rate (Kabiri et al., 2016). *R. fistulosa* connects to a host by means of lateral haustoria, and this occurs no earlier than 3–4 weeks after germination (Neumann et al., 1998).

### 3 | IMPACT

Both *Striga* spp. and *R. fistulosa* are distributed across Africa. *S. asiatica* is found mostly south of the equator, *S. hermonthica* mostly north of the equator, and *R. fistulosa* is observed both in the southern and northern hemisphere but mostly south of the Sahara (Table 1). The main cereal crops impacted by *Striga* spp., in decreasing order of economic importance, are maize, sorghum, millet and (upland) rice. The main crop impacted by *R. fistulosa* is (lowland) rice. In terms of infested area, grain production and economic losses in rice systems in Africa, *Striga* spp. and *R. fistulosa* are similar (Table 1). The rainfed upland rice area infested by *Striga* spp. is estimated at 388,000 ha, 12% of the total; the area of rainfed lowland rice infested by *R. fistulosa* is estimated at 214,000 ha, equating to 5.7% of the total (Rodenburg, Demont, et al., 2016). Grain production and economic losses to rice were estimated at 293,000 t, worth US \$117 M, caused by *Striga* spp. and 204,000 t, worth US \$81.7 M, caused by *R. fistulosa* (Rodenburg, Demont, et al., 2016).

The facultative parasitic plant *R. fistulosa* has a similar effect on their host as the obligate parasitic plants *S. asiatica* or *S. hermonthica* (Table 1). Both genera cause severe reductions in CO<sub>2</sub> assimilation, through a combination of reduced stomatal conductance, leaf chlorophyll concentrations and functionality of the photosystem, leading to chlorosis, wilting and stunting of the host (Kabiri et al., 2021; Rodenburg et al., 2017). Perhaps the main difference is that effects of the obligate parasites (*Striga* spp.) start long before parasite emergence aboveground, whereas plants of the facultative *R. fistulosa* usually develop autonomously 4 weeks before they parasitise and impact the host (Kabiri et al., 2017). The result in terms of host plant damage is nevertheless similar, that is, stunted growth, decreased leaf area, delayed phenological development and severely reduced grain production (Kabiri et al., 2017; Kaewchumnong & Price, 2008). At the crop level, the range of reported rice yield losses is also similar, that is, 21%–80% (*Striga* spp.) and 21%–73% (*R. fistulosa*) (Rodenburg, Cissoko, et al., 2016; Rodenburg, Demont, et al., 2016).

**TABLE 1** Similarities (green) and differences (red) between the obligate parasitic weed *Striga* (*Striga hermonthica* or *Striga asiatica*) and the facultative parasitic weed *Rhamphicarpa* (*Rhamphicarpa fistulosa*) in rice production systems in Africa. Comparisons across three main categories, that is, (1) biology and ecology, (2) host interaction and impact and (3) management.

|                     |                               | <i>Striga asiatica</i> (Sa), <i>Striga hermonthica</i> (Sh)  | <i>Rhamphicarpa fistulosa</i>   | Sources   |
|---------------------|-------------------------------|--|---|---|
| Biology and ecology | Parasitism                    | <ul style="list-style-type: none"> <li>• Root hemi-parasite</li> <li>• Obligat parasite</li> </ul>   | <ul style="list-style-type: none"> <li>• Root hemi-parasite</li> <li>• Facultative parasite</li> </ul>  | Musselman and Rodenburg (2023)  |
|                     | Host range                    | <ul style="list-style-type: none"> <li>• Grasses, including cereal crops</li> </ul>  | <ul style="list-style-type: none"> <li>• Grasses, including cereals</li> <li>• Legumes</li> </ul>   | Houngbedji and Gibot-Leclerc (2015); Ouédraogo et al. (1999)  |
|                     | Seed biology                  | <ul style="list-style-type: none"> <li>• Seed weight: 3.7 µg (Sa) to 4.5 µg (Sh)</li> <li>• in situ seed viability 5–9 years</li> <li>• Longevity favoured by (free-draining) environment</li> </ul>             | <ul style="list-style-type: none"> <li>• Seed weight: 11.5 µg</li> <li>• In situ seed viability &lt;1 year</li> <li>• Longevity shortened by (waterlogged) environment</li> </ul>   | Bebawi et al. (1984); Gbehounou and Assigbé (2004); Kabiri et al. (2016); Parker and Riches (1993); Rodenburg et al. (2006) |
|                     | Seed germination requirements | <ul style="list-style-type: none"> <li>• Soil moisture</li> <li>• Biochemical cues</li> </ul>  | <ul style="list-style-type: none"> <li>• Soil moisture</li> <li>• Light</li> </ul>  | Kabiri et al. (2016)  |
|                     | Haustorium formation          | <ul style="list-style-type: none"> <li>• Terminal and lateral</li> <li>• Within days after germination</li> </ul>  | <ul style="list-style-type: none"> <li>• Lateral</li> <li>• 3–4 weeks after germination</li> </ul>  | Joel (2013); Neumann et al. (1998)  |
|                     | Environments                  | <ul style="list-style-type: none"> <li>• Free-draining soils (rainfed upland)</li> </ul>   | <ul style="list-style-type: none"> <li>• Waterlogged soils (rainfed lowland)</li> </ul>   | Kabiri et al. (2015); Ouédraogo et al. (1999)   |
|                     | Impact                        | Regional spread  | <ul style="list-style-type: none"> <li>• Across Africa</li> <li>• Sh: 32 countries, mostly sub-Saharan northern hemisphere</li> <li>• Sa: 44 countries, mostly southern hemisphere</li> </ul>                             | <ul style="list-style-type: none"> <li>• Across Africa</li> <li>• 37 countries, mostly sub-Saharan</li> </ul>               |
| Economic impact     |                               | <ul style="list-style-type: none"> <li>• 388,000 ha infested (upland rice)</li> <li>• 293,000 t (milled) rice grain losses</li> <li>• US\$117 M losses</li> </ul>  | <ul style="list-style-type: none"> <li>• 214,000 ha infested (lowland rice)</li> <li>• 204,000 t (milled) rice grain losses</li> <li>• US\$82 million losses</li> </ul>   | Musselman and Rodenburg (2023); Rodenburg, Demont, et al. (2016)  |
| Main crops          |                               | <ul style="list-style-type: none"> <li>• Rice</li> <li>• Maize, sorghum, millet</li> </ul>   | <ul style="list-style-type: none"> <li>• Rice</li> </ul>  | Musselman and Rodenburg (2023)  |
| Host effects        |                               | <ul style="list-style-type: none"> <li>• Reduced CO<sub>2</sub> assimilation</li> <li>• Stunted growth, delayed phenology</li> <li>• Reduced reproduction</li> <li>• Starts before parasite emergence</li> </ul> | <ul style="list-style-type: none"> <li>• Reduced CO<sub>2</sub> assimilation</li> <li>• Stunted growth, delayed phenology</li> <li>• Reduced reproduction</li> <li>• Starts 4–5 weeks after parasite emergence</li> </ul> | Kabiri et al. (2017, 2021); Kaewchumngong and Price (2008); Rodenburg et al. (2017)   |
| Yield losses        |                               | <ul style="list-style-type: none"> <li>• 21%–80% (rice)</li> </ul>   | <ul style="list-style-type: none"> <li>• 21%–73% (rice)</li> </ul>  | Rodenburg, Cissoko, et al. (2016); Rodenburg, Demont, et al. (2016)   |
| Management          | Preventive weed management    | <ul style="list-style-type: none"> <li>• No-till</li> <li>• Cover-/intercropping, crop rotation</li> <li>• Fertilisers</li> <li>• Delayed sowing</li> <li>• Resistant and tolerant varieties</li> </ul>          | <ul style="list-style-type: none"> <li>• Early sowing</li> <li>• Resistant and tolerant varieties</li> </ul>  | Randrianjafazanaka et al. (2018); Rodenburg et al. (2017); Rodenburg, Cissoko, et al. (2016); Tippe et al. (2017, 2020)     |
|                     | Curative weed management      |  | <ul style="list-style-type: none"> <li>• Post-emergence (chemical) weed control</li> </ul>  | Ouédraogo et al. (2017); Tippe et al. (2020)  |

## 4 | MANAGEMENT

Here, we present a synthesis of published field research to identify how biology, ecology and host interactions can inform the effective management of witchweed and vampireweed in rice systems in Africa.

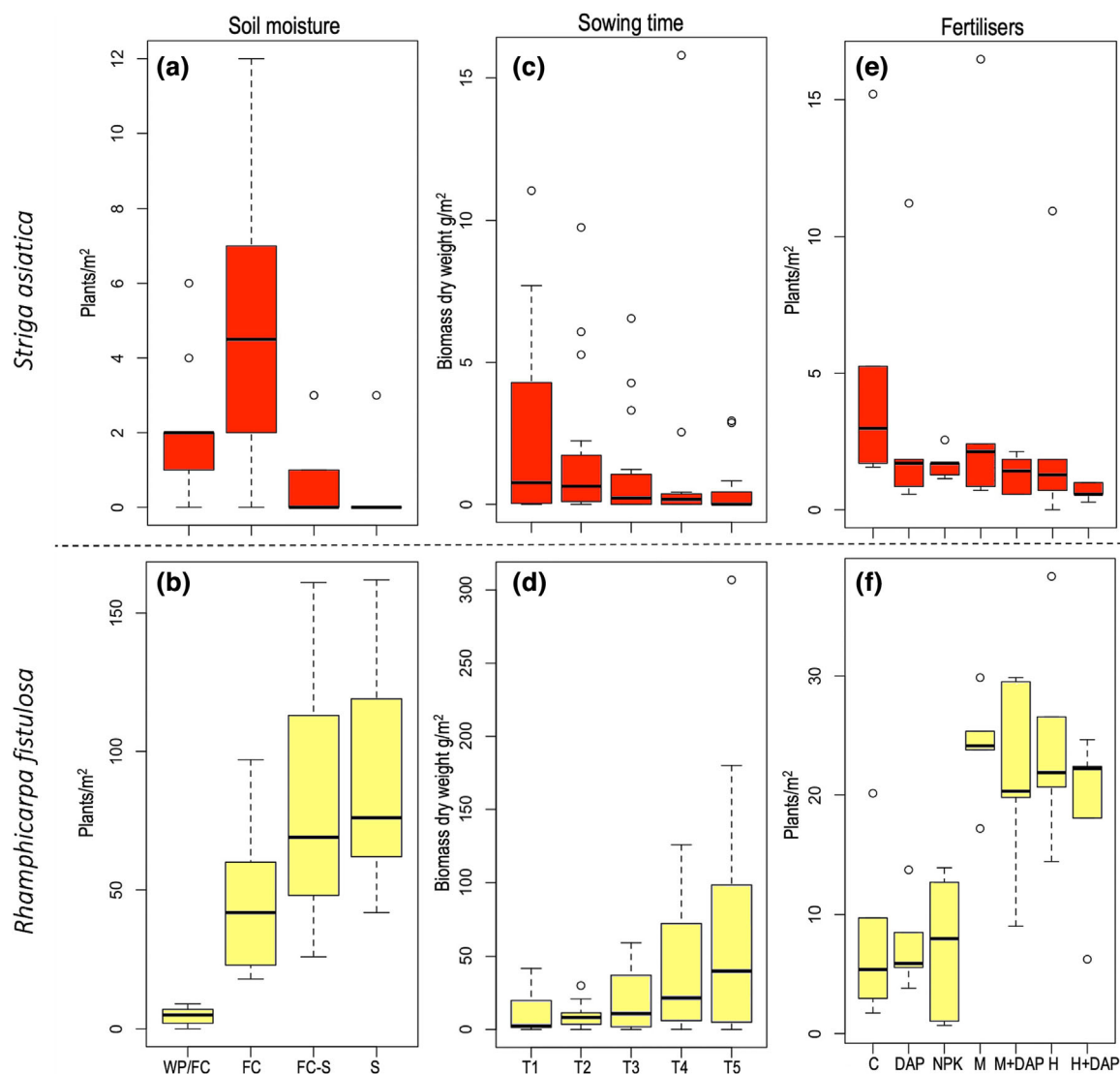
Aforementioned yield losses vary from year to year and are a function of infestation levels and varietal resistance and tolerance.

Rice varieties with increased resistance, tolerance or a combination of both are identified in field trials and comprise one of the main preventive weed management practices against *Striga* spp. (Rodenburg et al., 2017) as well as *R. fistulosa* (Rodenburg, Cissoko, et al., 2016). Resistance against *Striga* is based on pre-attachment mechanisms (i.e. low germination stimulant production) or post-attachment mechanisms (e.g. hypersensitivity or mechanical barriers in host-root tissue) as shown in rice (Cissoko et al., 2011; Jamil, Rodenburg, et al., 2011).

Resistance against *R. fistulosa* is not yet characterised but due to independence on germination stimulants, logically based on post-attachment mechanisms only.

Effectiveness of other preventive weed management options is largely determined by the biological and ecological traits of the parasites. There are more options for *Striga* spp. than for *R. fistulosa* (Table 1). For instance, the use of trap crops (i.e. non-host crops that cause suicidal germination of parasitic weed seeds) through crop rotations or intercropping is an effective management practice against *Striga* spp. on upland soils (Randrianjafizana et al., 2018) but of little use against *R. fistulosa*. The waterlogged conditions in which rice and

*R. fistulosa* thrive are unsuitable for growing most other crops. Furthermore, *R. fistulosa* seed germination is independent of a host plant and therefore the presence of a trap crop will not cause suicidal germination. Avoiding pre-season soil tillage (i.e. no-till), or practising shallow tillage only, is another example that works against *Striga* spp. (Randrianjafizana et al., 2018; van Ast et al., 2005) as it circumvents *Striga* seeds from reaching sufficient depths for host root contact. For *R. fistulosa*, we postulate that inversion tillage is more likely to be effective, as the light requirement for germination combined with the short seed longevity would minimise the success rate of these seeds. In addition, *R. fistulosa* emerges several weeks before parasitism,



**FIGURE 2** Responses to environmental conditions and agronomic practices observed with the obligate parasite *Striga asiatica* (top, red boxes) and the facultative parasite *Rhamphicarpa fistulosa* (bottom, yellow boxes), based on published greenhouse trials, and field trials in Africa, conducted between 2012 and 2014. (a,b) Soil moisture levels (WP = wilting point; FC = field capacity; S = saturation), (c,d) sowing times (T1–T5 with 14-day intervals between each time) and (e,f) fertilisers (C = no-fertiliser control; DAP = diammonium phosphate; NPK = nitrogen–phosphorus–potassium; M = cattle manure; H = rice husks; M + DAP: cattle manure + 1/2 DAP; H + DAP: rice husks + 1/2 DAP). Sources: soil moisture (greenhouse pot data of experiment 2-2012-2013; 10 replicates; *Rhamphicarpa fistulosa* grown without a host; Kabiri et al., 2015), sowing time (field data of 3 years—2012, 2013, 2014; 1 rice cultivar: Supa India; five replicates; Tippe et al., 2017), fertilisers (field data of third experimental year—2014; five replicates; Tippe et al., 2020). All treatment effects were significant ( $P < 0.05$ ).

which allows time for post-emergence control of the weed by herbicides (e.g. Ouédraogo et al., 2017) or mechanical weeding. For *Striga* spp., severe damage is incurred before emergence of the parasites, making curative control inappropriate for avoiding crop losses.

Based on aforementioned differences in the relation between hydrology and species presence (Kabiri et al., 2015), managing the soil water levels is another consideration. Compared to soils at field capacity, *S. asiatica* infection levels are reduced when soils are wetter (Figure 2a). Plant numbers of *R. fistulosa* show the exact opposite response (Figure 2b). Irrigation or drainage as parasitic weed management is unfortunately not a feasible preventive weed management practice as affected farmers often lack the required infrastructure or access to water.

Crop establishment timing and fertiliser application are two potential preventive management options farmers can consider. Delayed sowing of rice decreases *S. asiatica* in upland rice (Figure 2c), but increases *R. fistulosa* infection (Figure 2d; Tippe et al., 2017). *Striga* seed dormancy is broken after 7–10 days of moist conditions, after which the seeds will germinate if they are triggered by cues indicating host root presence. In absence of a host the seeds return to secondary dormancy after a few weeks (Mohamed et al., 1998). This explains why delayed sowing is a potential preventive measure against *Striga* spp. Under lowland conditions, advanced sowing of rice reduces the severity of *R. fistulosa* infection. Typically, sowing before soil conditions are optimal for *R. fistulosa* germination and growth will give the host plant a head start, as *R. fistulosa* seed germination depends on environmental rather than host plant cues (Kabiri et al., 2016). The shading potential of a bigger rice plant, following from the head start of the crop, will act as a contributing weed management factor.

Application of fertilisers has been observed to reduce *Striga* spp. infection (e.g. Jamil et al., 2012) but to stimulate *R. fistulosa* (Rodenburg et al., 2023). Field tests in rice confirm this. Compared to a no-fertiliser control the application of mineral fertilisers (DAP, NPK), locally sourced organic amendments (cattle manure, rice husks) or combinations of mineral and organic supplements, decrease *S. asiatica* infection (Figure 2e), but increase *R. fistulosa* infection (Figure 2f; Tippe et al., 2020). Application of fertilisers, in particular N and P, reduces the host-plant production of strigolactones known as potent *Striga* seed germination stimulants (Jamil, Charnikhova, et al., 2011), which partly explains reduced *Striga* infection levels. *R. fistulosa* germination does not depend on these host-derived germination stimulants.

Based on the above assessments of germination biology, host-parasite interactions, ecology and control, there are several options for *preventive* weed management of the obligate *Striga* spp., that is, (1) no-till, (2) crop diversification, (3) fertilisers, (4) delayed sowing and (5) resistant and tolerant varieties. Fewer *preventive* strategies are available against the facultative *R. fistulosa*, that is, (1) early sowing, (2) resistant and tolerant varieties. On the other hand, *curative* weed management options are lacking against *Striga* spp., whereas *R. fistulosa* can still be controlled through post-emergence (chemical) interventions in the window between emergence and parasitism.

## 5 | CONCLUSION

The differences in biology and ecology of parasitic witchweeds and vampireweeds in Africa drive the need for different weed management strategies in rice production systems. Delayed crop establishment reduces *Striga* spp. infection in upland rice because of the secondary dormancy of their seeds. The reverse, that is, earlier crop establishment before soil conditions are optimal for the germination of *R. fistulosa*, reduces infection of this parasite in lowland rice. No-till (avoiding seeds entering the crop rooting zone), fertilisers (reducing host plant production of germination stimulants) and the use of non-host intercrops or rotation crops (acting as trap crops) can be applied as preventive management options against *Striga* spp. because of their obligate nature of parasitism. These strategies are unsuitable against the facultative *R. fistulosa* as this weed requires light rather than host-derived stimulants for seed germination. The lowland environment and wider host range of *R. fistulosa* also limit companion or rotation crop choice. Curative weed management, applied after weed emergence, can be effective against *R. fistulosa* because of the window between emergence and the start of parasitism, but not against *Striga* spp. that impact their host well before their plants emerge aboveground.

## AUTHOR CONTRIBUTIONS

Funds enabling the research reported here were won by Jonne Rodenburg and Lammert Bastiaans. Manuscript was initiated and drafted by Jonne Rodenburg and co-written and edited by Lammert Bastiaans. Figures were made by Jonne Rodenburg.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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