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Key words: elevated [CO₂], glacial maxima, global change, methane (CH₄), peatlands, wetlands.

Delivering resistance to a major constraint for rain-fed rice production

At a time when we are considering new ways to increase food security in developing countries, and not least sub-Saharan Africa, we have important research that will be of immense value, specifically for small-scale farmer production of upland or rain-fed nonirrigated rice. These studies will lead to increased sustainability by reducing external inputs because the traits being developed are for crop protection against parasitic weeds (Scholes & Press, 2008) and will be delivered via the seed. For the first time, we see a rigorous investigation of upland rice cultivars in terms of post-attachment resistance to the parasitic weeds, *Striga hermonthica* and *S. asiatica* (Cissoko *et al.*, pp. 952–963) and pre-attachment resistance to the parasitic weed, *S. hermonthica* (Jamil *et al.*, pp. 964–975) in this issue of *New Phytologist*. The New Rice for Africa (NERICA) rice cultivars and some of their ancestry have been chosen because of their importance in Africa for upland cultivation, and it is the major constraints on yield, the parasitic weeds known also as witchweeds, *S. hermonthica* and *S. asiatica*, to which the work is directed (Fig. 1).

‘... because this new type of weed resistance will be delivered via the seed, the approach is sustainable and could be managed even via farmer collected seed ...’



Fig. 1 Rain-fed rice (NERICA) in Kenya highly infested with the parasitic weed *Striga hermonthica*. Courtesy of Professor Zeyaur Khan, International Centre of Insect Physiology and Ecology (ICIPE).

Understanding and exploiting differences in post-attachment to rice by parasitic weeds

Cissoko *et al.* demonstrate pronounced differences in post-attachment resistance to the two parasite species in the NERICA cultivars and their ancestors, some (CG14, NERICA 1 and 10) showing substantial resistance effects. This is the primary discovery made in this paper and will serve further investigations into the molecular mechanisms underpinning this type of resistance and will, even while such studies take place, provide the basis for new breeding programmes. However, the study continues to investigate the phenotype of post-attachment *Striga hermonthica* and *S. asiatica* resistance in the NERICA cultivars. Thus necrosis in the host, at the site of attempted attachment, is observed when parasites fail to develop. This has been observed before with the *Oryza sativa* cultivar, Nipponbare infected by *S. hermonthica* and also with sorghum cultivars infected by *S. asiatica*. However, most interesting is the similarity with resistance in cowpea cultivars to *S. gesnerioides* reported by Timko in 2009 (Li & Timko, 2009), the significance being that in the cowpea–*S. gesnerioides* system, this phenotype was linked to the classical gene-for-gene resistance mechanism further elaborated in the Timko reference and relating to previous work by some of this team (Gurney *et al.*, 2006). This will provide further opportunities and impetus for determining the specific mechanisms for the resistance traits discovered here. By studying the two parasitic species *S. hermonthica* and *S. asiatica*, there was an indication that the resistance discovered here is a relatively broad spectrum and effective against a number of ecotypes of *S. hermonthica* and *S. asiatica*. The final section of the work deals with the issue of damage caused by those parasites that develop even on

the resistant plants, it having been demonstrated clearly at the outset that although highly resistant cultivars are identified here, none of the resistance was complete. However, these final studies show clearly that the biomass of the host improved in resistant compared with susceptible cultivars.

The authors refer variously to the need for the types of resistant traits discovered here being used in an integrated programme with other forms of resistance. In this respect they specifically recommend integration with pre-attachment resistance and refer to such a study: Jamil *et al.*

Low strigolactone production lowers pre-attachment to rice of parasitic weeds

The work by Jamil *et al.* demonstrates that levels, from root exudation, of the germination stimulants, strigolactones, by this cereal negatively correlate with resistance at this stage of parasite development, that is, the lower strigolactone levels exuded by rice roots the greater is the resistance because of the role of these compounds as germination stimulants for *Striga hermonthica* (Matusova *et al.*, 2005). Although critics would immediately respond by pointing out that the strigolactones play an important role in the plants' regulation of rhizosphere interactions (Lopez-Raez *et al.*, 2008), the authors acknowledge this and clearly demonstrate that some structural types within the strigolactones are more stimulatory to *S. hermonthica* than others. Thus, they suggest selective reduction in the amount of, for example, the methoxy-5-deoxystrigol isomers 2 and 3 could raise resistance to *S. hermonthica* whereas other strigolactones such as 5-deoxystrigol and orobanchol could be allowed to remain for the benefit of rhizosphere interactions (Fig. 2). This would avoid creating NERICA cultivars resistant to *S. hermonthica* that would lack positive effects on arbuscular mycorrhizal fungi (AMF), which indeed is now well understood (Akiyama *et al.*, 2010) as are other advantageous effects known as a consequence of pioneering work by the senior author of this paper, H. J. Bouwmeester, (Kohlen *et al.*, 2011). In addition, they also report a negative correlation between tillering, and the strigolactone exudation level and *S. hermonthica* infestation, thereby suggesting that

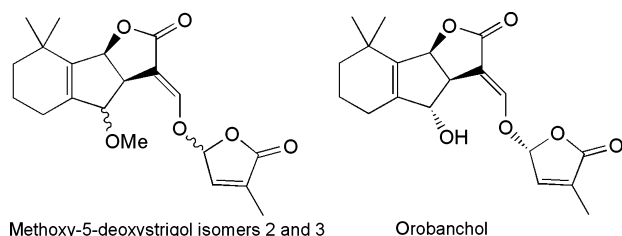


Fig. 2 The structure of strigolactones may provide selectivity between high *Striga* germination stimulation (left) and promotion of arbuscular mycorrhizal association (right).

higher tillering cultivars will have greater pre-attachment resistance.

The work is entirely laboratory based, but the authors prominently acknowledge the need for field testing and even extend to providing valuable advice for such work to be done in extension of the discoveries made here. The authors also explain that, where using a reduction in certain strigolactones for pre-attachment resistance to *Striga hermonthica*, this must be done in integration with other approaches. In this they specifically stipulate the potential value for integrating with the use of cultivars showing post-germination resistance and indeed Jamil *et al.* appears together with another paper dealing with post-attachment resistance and to which they refer: Cissoko *et al.*

In conclusion, as a consequence of the two studies cited initially here (Cissoko *et al.* and Jamil *et al.*), we have discoveries that present a real breakthrough in defining breeding opportunities for new rain-fed rice varieties, particularly for resource poor farming systems, to overcome constraints on yield by parasitic weeds. To date only cultural approaches to controlling these weeds are compatible with the low cost inputs available to the bulk of the affected farming systems (Pickett *et al.*, 2010). However, because this new type of weed resistance will be delivered via the seed, the approach is sustainable and could be managed even via farmer collected seed thereby avoiding subsequent seasonal inputs – a lesson also for Northern agriculture?

John A. Pickett* and Antony M. Hooper

Department of Biological Chemistry, Rothamsted Research, Harpenden, Hertfordshire, AL5 2JQ, UK
(*Author for correspondence: tel +44 (0)1582 763133;
email john.pickett@rothamsted.ac.uk)

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Key words: plant breeding, parasitic weeds, rice, *Striga*, strigolactone, weed resistance.

Letters

Estimation of the *Glomus intraradices* nuclear DNA content

The arbuscular mycorrhizal fungi (AMF) are able to establish a symbiotic relationship with 70–90% of land plant species including Angiosperms, Gymnosperms, Pteridophytes and some Bryophytes (Smith & Read, 2008). In plants, AMF improve the uptake of phosphorus and nitrogen (Bücking & Shachar-Hill, 2005; Govindarajulu *et al.*, 2005), provide protection from root pathogens (Newsham *et al.*, 1994; Liu *et al.*, 2007; Hata *et al.*, 2010), improve salt and drought tolerance (Marulanda *et al.*, 2006, 2007; Evelin *et al.*, 2009) and potentially contributes heavy metal tolerance (Ricken & Hofner, 1996; Zhang *et al.*, 2005).

Despite the positive impact of AMF fungi on plant nutrition and stress tolerance, only a small number of studies have been performed on AMF genetics. Basic information, such as a genome sequence, ploidy level, the number of chromosomes or the origin of genetic material in spore is currently not available; this lack of knowledge hampers investigations on genetic exchanges, recombination and segregation in the AMF.

The aim of this study was to determine the nuclear DNA content of the *Glomus intraradices* (syn.: *G. irregulare*) industrial strain produced by AMYkor GmbH (Germany) with *G. intraradices* DAOM197198 isolate (Pont Rouge, Canada) used as the reference. The decision to use *G. intraradices* DAOM197198 Schenck & Smith DAOM 197198 (recently reassigned to *Rhizophagus irregularis* (Blaszk., Wubet, Render & Buscot) C. Walker & A. Schüßler comb. nov.) isolate as the reference organism was based on the fact that both isolates are closely related (data not shown), and the genome size and ploidy level of

DAOM197198 isolate has already been determined by Hijri & Sanders (2004). *G. intraradices* DAOM197198 was also chosen for the first complete genome sequencing project on AMF (Martin *et al.*, 2008). Unfortunately, despite a large amount of sequencing data, sequence assembly is complicated by the high degree of polymorphism among nuclei (F. Martin, pers. comm.).

There are only a few reports on the nuclear DNA content of AMF. The average genome size of AMF seems to be highly variable and ranges from *c.* 15.7 Mb in *Glomus intraradices* (DAOM197198, Hijri & Sanders, 2004) and *c.* 37 Mb in *Glomus etunicatum* (Hijri & Sanders, 2005), up to *c.* 250 Mb in *Glomus versiforme* (Bianciotto & Bonfante, 1992) and *c.* 740 Mb in *Gigaspora margarita* (Hosny *et al.*, 1998). In most of these reports the DNA content was estimated by means of flow cytometry (FC).

In this study, we present data on the nuclear DNA content of *Glomus intraradices* AMYkor isolate and a reference, DAOM197198 isolate, measured by FC and Feulgen DNA image densitometry.

Estimation of the nuclear DNA content

The nuclear DNA content of *in-vitro* monoxenic cultures from both *Glomus intraradices* isolates (AMYkor and DAOM197198) was determined by FC on six independent nuclei isolations using *Arabidopsis thaliana* as an internal reference standard (Fig. 1). The nuclei of *A. thaliana* were isolated from differentiated leaf tissue, which is characterized by distinct endopolyploidization resulting in a mixture of polyploid cells (Galbraith *et al.*, 1991). Nuclei suspensions from endopolyploid cells are consequently composed of nuclei with different DNA content (2C, 4C, 8C and so on). Accordingly, FC histograms, representing the relative fluorescence intensities of stained nuclei, are comprised of the 2C peak used for the genome size estimation and additional peaks of the higher ploidy level (Fig. 1).