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Stored rice varietal resistance towards *Sitophilus oryzae*

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ABSTRACT

Previous research has demonstrated that varieties of rice are differentially susceptible to stored rice pests, but modern varieties are lacking evaluation. Thirteen varieties of rice, *Oryza sativa* (L.), were tested for their susceptibility to the rice weevil, *Sitophilus oryzae* (L.). *Sitophilus oryzae* adults were placed into vials containing one of 13 USA commercial rice varieties. Adult damage, larval damage, days to eclosion, total progeny, and progeny mass were recorded over a period of six weeks. Subsequently, varietal mixes of the resistant and susceptible varieties were evaluated for associational resistance or susceptibility using the same methodology. Rice variety impacted adult damage, larval damage, progeny counts, progeny mass, and development time. The rice variety most susceptible to adult damage had 11-fold greater damage than the rice variety most resistant to adults. Similarly, the rice variety most susceptible to larval damage received 10-fold more damage than the most resistant. Progeny had the shortest development time and greatest adult mass feeding on high protein, low-glycemic rice variety, Frontière. Varietal mixes often resulted in associational susceptibility, where mixes of two rice varieties resulted in damage equal to or greater than that of the most susceptible variety in the mix. Blends created similar changes in the numbers of progeny, progeny mass, and development time. These results demonstrate the importance of stored rice varietal susceptibility, blend susceptibility, and their impact on stored rice pest management.

1. Introduction

Grain loss to pests is a global problem, with 5–30% of postharvest grain destroyed by insects (Neupane, 1995; Deshpande and Singh, 2001; USDA, 2005; Santos, 2006; Yigezu et al., 2010; Jiang and HS, 2013; Sharon et al., 2014; Zhang et al., 2021). Rice (*Oryza sativa* (L.)) value can be reduced through weight loss, designation as animal feed, or requirements for additional insect control. The rice weevil, *Sitophilus oryzae* (L.) (Coleoptera: Curculionidae), is among the most damaging pests of stored grains, feeding on rice, corn, wheat, and many other cereals (Cogburn, 1977; Padín et al., 2002; USDA, 2016; Vijay and Bhuvaneswari, 2018; Charles Kasozi et al., 2018). It occurs within grain in all regions of the world and is particularly abundant in warmer climates. *Sitophilus oryzae* is a primary pest of grains, meaning that it attacks sound, undamaged grain. Once damaged, the grain then becomes more susceptible to secondary pests, exacerbating problems further.

Both *S. oryzae* adults and larvae feed on grain. Adults commonly feed upon the endosperm under the husk, while larvae will also eat the germ in the grain interior (Gvozdenac et al., 2020). Adult females bore holes into kernels to oviposit an egg within, laying as many as 400 eggs in their

lifetime (USDA, 2016). Once hatched, *S. oryzae* larvae remain feeding within the grain, until they emerge as adults. Their average lifespan is 4–5 months over which a single weevil can consume 10–25 g of grain (Padín et al., 2002).

Presently, phosphine fumigation is the primary form of stored grain pest management in many regions. While fumigation can quickly and reactively rid stored grain of pests, concerns over phosphine resistance are growing, particularly because there is not a suitable substitute fumigant (Hagstrum et al., 2012; Nayak et al., 2020). Thus, the development of other pest management tools, such as host resistance, is of great importance to sustainable grain storage.

Varietal host resistance to *S. oryzae* has been identified in numerous stored grains. In wheat (*Triticum aestivum* L.), Chaudhary et al. (2021) found large differences in damage and weight loss due to *S. oryzae* between varieties. Sorghum (*Sorghum* spp.) has also been studied for varietal resistance, and physical characteristics like grain size have been shown to affect *S. oryzae* choice and development (Russell, 1962). In rice, differential varietal resistance and susceptibility to stored grain pests has also been previously studied. Cogburn (1977) demonstrated the value in stored rice varietal resistance, finding that varieties had

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large differences in damage due to *S. oryzae* as well as the Angoumois grain moth, *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae), and the lesser grain borer, *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae). Further studies have made similar findings about the effects of rice variety upon damage and pest biology (Cogburn and Bollich, 1990; Chanbang et al., 2008); however, none of the varieties tested in these studies are commonly grown any longer.

More recently, research efforts have been made to examine susceptibility of rice on modern varieties. In Nepal, Pal et al. (2021) found that susceptible rice varieties had twice as much weight loss as resistant rice varieties. In Benin, Santos et al. (2015) found rice variety was responsible for over 7-fold differences in the number of damaged kernels. In the USA, *S. cerealella* have been found to produce over 7-fold differences in progeny produced between rice varieties, while *R. dominica* produce over 28-fold differences in progeny between varieties (Arthur et al., 2013). However, no published studies have examined *S. oryzae* varietal susceptibility among the modern inbred and hybrid lines commercially produced in the USA. Recently developed specialty rice such as the high protein, low-glycemic rice, Frontière (Boyd, 2021), likely also differ in pest susceptibility from conventional rice. Further, modern producers frequently store rice of multiple varieties together in the same grain silos, but the influence of these mixtures on pest susceptibility is unknown.

In some cropping and urban landscape systems, intraspecific diversity has been shown to produce effects which reduce herbivore fitness beyond what it would be in a monoculture (Tooker and Frank, 2012; Grettenberger and Tooker, 2016; Doherty et al., 2019). For example, in St. Augustinegrass, *Stenotaphrum secundatum* (Walt.) Kuntz, genotypic diversity has been shown affect to *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) development time, larval weight, and herbivory (Doherty et al., 2019). Similarly, in wheat (*Triticum aestivum* L.), genotypic diversity affected *Rhopalosiphum padi* L. (Hemiptera: Aphididae) resulting in smaller reproductive individuals and fewer progeny (Grettenberger and Tooker, 2016). These effects may be a result of associational resistance, whereby a neighboring plant confers resistance to a target plant (Tahvanainen and Root, 1972). However, intraspecific diversity may also result in associational susceptibility, whereby a neighboring plant confers susceptibility to a target. Mixes of stored rice varieties principles may also influence pests in stored grain systems, but it has yet to be investigated.

Here, we aim to reexamine influences of rice variety on *S. oryzae* biology. Our specific objectives are to (1) compare *S. oryzae* development and reproduction on modern USA rice varieties, and to (2) examine *S. oryzae* development and reproduction on varietal mixes.

2. Methods and materials

2.1. Varietal resistance

We acquired freshly harvested rough rice of 13 varieties from the LSU Rice Research Station, including: three imidazolinone herbicide-resistant inbred varieties (CL111, CL151, and CL153), two imidazolinone herbicide-resistant hybrids (CLXL745 and Gemini 214CL), a conventional hybrid (XP753), two conventional long grain inbred varieties (Mermentau and Cheniere), two conventional medium grain inbred varieties (Jupiter and Caffey), a quizalofop-*p*-ethyl (QPE)-resistant long grain (PVL02), an aromatic Jasmine-type variety (Jazzman 2), and the high protein, low-glycemic variety, Frontière (Harrell et al., 2021). These rice varieties represent a diverse genetic background of commercial varieties that are widely grown in the USA Midsouth. Rice varieties were refrigerated at 4 °C until needed. Before use, rice was sieved and tempered to 12% moisture content (MC) according to the following equation (AACC, 2009):

$$\text{mL water} = ((100 - \text{original moisture} (\%)) / (100 - \text{desired moisture} (\%)) - 1) * \text{sample mass}$$

We then added 24 g of rice to 10-dram plastic vials. Ten mixed sex *S. oryzae* adults from a laboratory colony reared on wheat were then added to each vial, and vials were kept in a growth chamber (27 ± 1 °C, continual darkness). The sex ratio of introduced beetles was assumed to be 1:1 based on prior samples of our colony and published literature (Holloway, 1985). Adults were given 2 weeks to feed and reproduce, then were removed from the vials to allow for quantification of larval feeding. After removal, adults were counted as alive or dead, and sexed. The rice of each vial was sieved (#12 mesh) and adult feeding damage was assessed by weighing rice fragments and frass. The intact rice was then returned to the vials and placed into the growth chamber for another 8 weeks.

During the 8-week period, vials were checked every two days for emerging progeny. Any adult progeny that emerged were removed from the vials. We recorded their time until emergence, weight, and sex. Sex was determined using morphological characteristics, predominantly the width and length of the rostrum and abdomen (Halstead, 1963; Lum and Baker, 1975). At the end of 8 weeks, we sieved the rice, weighing the broken grains and frass to assess larval damage. There were 6 replicates of each rice variety in an experimental trial in a completely randomized design, and 4 experimental trials which were done at different times (n = 24 vials/variety).

Unfortunately, some data was lost, including: adult damage data from the third trial, larval damage data from the second trial, and larval damage data for some samples in the third and fourth trials. Additionally, Frontière was not included in the first trial and no larval damage for this rice variety are reported. However, there was still sufficient replication for all measures, except for larval damage in Frontière.

All statistics were performed in JMP Pro 16, with α set at 0.05. We performed chi-squared analyses to examine the effect of rice variety on progeny sex ratio. Additionally, we ran an analysis of variance examining factors that influenced days to eclosion and adult progeny mass, with sex, variety, and variety × sex as fixed effects, while random effects included experimental trial and trial × variety × replicate. Analyses of variance were also run for adult mortality, introduced sex ratio, total progeny, larval damage, and adult damage using variety as a fixed effect and experimental trial as a random effect. Tukey's HSD were used for post-hoc analysis between treatments.

2.2. Associational resistance

Two susceptible (XP753 and PVL02) and two resistant rice varieties (Mermentau and Caffey) from the varietal resistance study were chosen for this experiment. Rice varieties were tempered to 12% MC before use. There were ten total treatments. Six treatments were created from every unique mixture of the four rice varieties, and an additional four treatments were made from each individual rice variety. Mixtures of two rice varieties were created by stirring 12 g of each variety together. Mixes of rice varieties were referred to by the initials of their component varieties (ex. Caffey and Mermentau is labeled as C + M). Single variety treatments were created with 24 g of the one rice variety. These treatments then underwent the same methods as the rice of the varietal resistance experiment. There were 6 replicates of each treatment in a single experimental trial, and 3 experimental trials (n = 18 vials/treatment). Statistical analyses were identical to those of the previous experiment, but replacing variety with treatment.

3. Results

3.1. Varietal resistance

Over the course of this experiment over 2650 beetles were produced, sexed, and weighed. We saw no differences in adult mortality ($F_{12,226} = 1.29$, $P = 0.220$). Sex ratio of introduced adults was 1.00:1.12 (male:female), and it did not differ among rice varieties ($F_{12,154} = 0.50$, $P = 0.914$). We also did not see differences in progeny sex ratio due to rice

variety, which was 1.00:0.76 (male:female) ($\chi^2 = 16.65, P = 0.163$). There was an effect of sex on adult mass ($F_{1,2606} = 44.23, P < 0.001$), where males weighed 1.66 ± 0.14 mg (LSM \pm MSE), and females weighed 1.81 ± 0.14 mg. However, there was no interaction effect of variety \times sex ($F_{1,2604} = 1.33, P = 0.195$). There was also no effect of sex on developmental time ($F_{1,2599} = 0.48, P = 0.489$), which averaged 41.25 ± 1.70 days across sexes and rice varieties. Additionally, there was no interaction effect of variety \times sex ($F_{12,2578} = 0.91, P = 0.537$).

Adult damage, larval damage, total progeny, development time, and progeny adult mass were influenced by rice variety (Table 1). Adult damage (weight of frass and broken grains) in PVL02 was approximately 2-fold greater than the rice variety with the second highest damage, Frontière, and 11-fold greater than the least susceptible rice variety, Jupiter. Larval damage was greatest in XP753, followed by CL111, which were 10.2- and 6.5-fold greater, respectively, than the least susceptible rice variety, Mermentau.

XP753 produced the most progeny, nearly 2-fold more than the rice variety with the second most, PVL02, and nearly 18-fold more than Caffey which produced the fewest emerged adults per vial. Gemini had the longest development time, which was 11% longer than that of the fastest development occurring in Frontière. The progeny in Frontière were also the largest and were 16% greater in mass than the smallest (CLXL745).

3.2. Associational resistance and susceptibility

During this experiment another 1000 beetles were produced, sexed, and weighed. There were no differences in sex ratio among treatments ($\chi^2 = 4.13, P = 0.903$). However, the effect of sex on mass, seen in the previous experiment, was also demonstrated here ($F_{1,988} = 17.24, P < 0.001$). Males weighed 1.59 ± 0.04 mg (LSM \pm MSE), and females weighed 1.76 ± 0.04 mg. There was no effect of treatment \times sex on mass ($F_{9,985} = 0.84, P = 0.582$). Also consistent with the previous experiment, there was no effect of sex ($F_{1,988} = 2.43, P = 0.119$) or sex \times treatment ($F_{9,975} = 0.51, P = 0.865$) on days to eclosion, which was 40.36 ± 1.68 across sexes and treatments.

Similar to the previous experiment, adult damage, larval damage, total progeny, development time, and progeny adult mass were influenced by treatment (Table 2). The mass of damage by adults in C + P was >3-fold greater than Caffey; damage weight in M + P was >2-fold more than Mermentau; damage weight in X + P was almost 2-fold more than XP753. However, none of these mixes were different from their more susceptible component rice variety, PVL02. Conversely, adult damage to

Table 1

Sitophilus oryzae adult damage, larval damage, progeny counts, days to eclosion, and progeny mass by rice variety.

Rice Variety	Adult Damage (mg)/vial	Larval Damage (mg)/vial	Total Progeny/vial	Days to Eclosion	Progeny Adult Mass (mg)
PVL02	43.37a	27.79bc	12.47b	40.65cde	1.63b
Frontière	24.19b	NA	12.33b	38.97e	1.84a
CLXL745	15.03bc	14.23bc	3.47cd	41.32abcd	1.59b
CL153	14.67bc	39.00abc	11.34b	41.04bcd	1.70ab
XP753	13.37bc	62.19a	23.75a	40.20de	1.70ab
Jazzman 2	11.52bc	24.67bc	9.78b	40.69cde	1.79a
Gemini	11.48bc	22.68bc	3.27d	43.24a	1.71ab
CL111	9.71c	39.53ab	10.31b	41.92abc	1.81a
CL151	9.42c	23.20bc	11.59b	40.94cd	1.74ab
Chenièrè	8.34c	10.65c	8.15bc	40.76cde	1.81a
Mermentau	8.14c	5.88bc	1.80d	41.31abcde	1.62ab
Caffey	5.73c	8.03bc	1.56d	42.61abcd	1.81ab
Jupiter	3.79c	11.21bc	4.15cd	42.91ab	1.81a
<i>F</i> =	15.89	6.31	35.25	6.48	4.95
<i>df</i> =	12, 225	11, 107	12, 281	12, 236	12, 273
<i>P</i> =	<0.001	<0.001	<0.001	<0.001	<0.001
<i>SE</i> =	2.42	2.24	0.92	1.73	0.14

NA: Not available due to data loss.

Table 2

Sitophilus oryzae adult damage, larval damage, progeny counts, days to eclosion, and progeny mass by rice variety or mix.

Treatment	Adult Damage (mg)/vial	Larval Damage (mg)/vial	Total Progeny/vial	Days to Eclosion	Progeny Adult Mass (mg)
C + P	26.67a	11.56bc	4.44de	40.96abc	1.57bcd
X + P	26.41a	27.98a	9.28ab	40.21bc	1.58cd
PVL02	24.97a	14.02bc	7.94bc	41.74 ab	1.66abc
M + P	21.41ab	10.78bc	4.28def	41.47abc	1.40d
X + C	20.37ab	19.66ab	6.50bcd	40.52bc	1.77ab
M + X	17.01bc	12.67bc	5.00cd	40.22bc	1.59cd
XP753	14.48bcd	28.37a	12.28a	39.28c	1.75ab
Mermentau	10.91cde	3.55c	0.78g	38.63bc	1.82abc
C + M	8.14de	3.49c	0.94fg	41.01abc	1.97a
Caffey	7.34e	6.68c	1.06efg	44.51a	1.65abcd
<i>F</i> =	22.06	14.34	25.98	4.19	8.03
<i>df</i> =	9, 167	9, 167	9, 168	9, 131	9, 141
<i>P</i> =	<0.001	<0.001	<0.001	<0.001	0.002
<i>SE</i> =	0.93	5.44	1.44	1.60	0.04

C + M was not different from Caffey or Mermentau. Stored rice treatment also had significant effects on larval damage. Larval damage in X + P was 2-fold greater than that of PVL02; larval damage in X + C was 3-fold greater than Caffey; however, larval damage in those mixes was not significantly different than that of the more susceptible component rice variety, XP753.

Progeny development to adulthood in Caffey took 5 days longer on average than in X + C. Progeny masses in Mermentau and PVL02 were 30% and 18% larger, respectively, than in M + P. Additionally, progeny mass in XP753 was 10% greater than in X + M and X + P.

4. Discussion

This study is the first to document differential susceptibility to *S. oryzae* among a diverse assemblage of modern commercial rice cultivars produced in the USA. Varieties of stored rice showed differential resistance through our measures of adult damage, larval damage, progeny count, progeny development, and progeny weight. These findings agree with previous studies, in that rice varietal differences create differential resistances when stored (Cogburn and Bollich, 1990; Rizwana et al., 2011; Arthur et al., 2013; Chaudhary et al., 2021). However, unlike past studies, resistance toward adults was not necessarily the same as resistance towards larvae. Resistance based on life-stage has not been demonstrated in stored grain, but it is seen in other systems. For example, *Melitaea cinxia* (L.) (Lepidoptera: Nymphalidae) larvae prefer drought-exposed host plants, while adult females preferred to oviposit upon well-watered host plants (Salgado and Saastamoinen, 2019). Insects with life stage-dependent resistances may require additional consideration to effectively manage. In our study, XP753 and CL111 were intermediately susceptible to adult *S. oryzae* but were heavily damaged by larvae, which may be important for management. Control of initial adult infestations is of less priority than controlling subsequent larval generations in these rice varieties.

The susceptible rice varieties identified in this study may require additional monitoring and management inputs. The heavier damage seen in PVL02 and XP753 reported herein suggests growers will need to be more aggressive with insecticides or other management techniques. Although our larval damage data were lost for Frontière, the high number of progeny, high progeny mass, and low days to eclosion suggest this rice variety is highly suitable for larval development. Which is to say, it is another susceptible rice variety that may require more aggressive monitoring and management than other varieties of stored rice. The conventional inbred lines Mermentau, Jupiter, Caffey, Chenièrè were among the most resistant rice varieties overall suggesting the similar genetic backgrounds of these rice varieties may impart some resistance to *S. oryzae*, and that they likely will require less intensive

pest management. Other groups of rice varieties, including Clearfield lines (CL111, CL151, CL153) and hybrids (CLXL745, Gemini – 214CL, and XP753), had more varied responses.

Progeny mass is not strictly an indicator of rice susceptibility, nor is it necessarily an indicator of increased fitness, though it is commonly used as such (Honěk, 1993). Many of the stored rice varieties we studied that are relatively resistant in other measures produced some of the largest adults in our dataset. For instance, the *S. oryzae* adults produced in Jupiter and Caffey are the second and third leading rice varieties for high progeny mass. Sex is a large factor influencing *S. oryzae* size. Previous research has found that female *S. oryzae* are larger than males (Kiritani, 1965), and our own results agree with that literature. However, this is unlikely to be the cause of the size differentiation we have seen across rice varieties, as we found no evidence of rice variety influencing sex ratio, and no effect of sex \times variety on mass. Alternatively, nutritional content may provide an explanation for the discrepancies in beetle mass. Frontière's susceptibility is likely the result of enhanced nutritional content relative to other rice varieties, as it is a high protein rice developed to help combat malnutrition in the developing world (Boyd, 2021). Protein is a key nutrient for insect growth and development and is especially sought after for herbivorous insects given its variable availability in plants (Behmer, 2009; Le Gall and Behmer, 2014).

Development time was also affected by rice variety, but like mass, it is difficult to say if changes in developmental rate are indicators of host resistance. A shorter development time could mean less time to acquire nutrients; however, some research has demonstrated that a focus on efficient nutrient utilization can be unnecessary or even harmful to fitness, i.e., reproductive output (Miller et al., 2009; Zehnder and Hunter, 2009). Moreover, Frontière had the shortest developmental time, and rice varieties that were commonly susceptible in other measures also produced adults with shorter developmental cycles. These findings suggest that shorter developmental cycles are not harmful to *S. oryzae*, and thus, a longer developmental cycle is an indicator of host resistance in this system. In terms of management, over an extended storage period, the difference between a 39-day and a 43-day generation time can add up to another generation. Additionally, understanding a generation time in a particular rice variety can also assist growers with some control applications, like timing the application of insecticides.

Looking at the overall development time, *S. oryzae* eclosion occurred within its expected range of 5–6 weeks (Okram and Hath, 2019). Our finding that sex did not affect development time is in contrast to the findings of the existing literature. Some studies have found that male *S. oryzae* develop more quickly than females at 20 °C and 25 °C (Kiritani, 1965). While other studies have found the opposite to be true at 30 °C (Nishigaki, 1958). Our experiments were run at 27 °C, and we found no differences in development based on sex. Being between the temperatures at which males develop more quickly (25 °C), and the temperature at which females develop more quickly (30 °C), 27 °C may be the inflection point where males and females develop at the same rate.

In our experiment mixing varieties, mixes of two varieties of rice usually resulted in associational susceptibility, or no effect, as the susceptibility of the mix was between its two component effects. Our finding that susceptible rice varieties imparted associational susceptibility suggests these may require enhanced management even when stored with less susceptible rice. We could not distinguish which rice varieties the adults fed on because adults had the freedom to choose between rice varieties within a vial. Thus, the associational susceptibility may be the result of adults preferentially feeding on the susceptible rice in the mixes. In other studies diet choice has allowed herbivores to optimize their diets thereby minimizing negative effects of diet mixing or maximizing its positive effects (Waldbauer and Friedman, 1991; Mody et al., 2007; Wetzal and Thaler, 2018). In a mixed diet, if one food source is poor in a particular nutrient, it can be supplemented by another, allowing for an improved nutritional balanced and fitness (Waldbauer and Friedman, 1991; Mody et al., 2007). Additionally, a

harmful substance can be avoided if insects have the option to feed on other food sources (Waldbauer and Friedman, 1991; Wetzal and Thaler, 2018). The ability to choose could then produce results where any mix is as susceptible as its most susceptible rice variety. Only the mix of two resistant rice varieties did not result in associational susceptibility.

Larval damage and progeny counts were most often between the levels expected for individual rice varieties, suggesting that while adults chose where to feed, they may not have used the same decision-making process during oviposition. Thus, larvae may have been evenly distributed amongst the grain, which is unusual given that several studies have demonstrated that *S. oryzae* oviposition choice can be influenced by physical characteristics like grain hardness and texture (Russell, 1962; Salunkhe and Jadhav, 1982; Akhter et al., 2017). Those findings were done within stored sorghum systems, so it remains unclear if physical characteristics affect *S. oryzae* oviposition behavior in stored rice. It is worth noting that there were some minor instances of associational resistance among our findings, but further research is needed before it can be of use to growers. Overall, our results suggest that there are very few pest management applications for mixes of resistant and susceptible rice varieties where *S. oryzae* is concerned.

While our results provide some new information, they also raise new questions. For instance, the mechanisms that confer rice resistances to adults and larvae are poorly understood. The role of nutritional and physical characteristics in resistance are still unknown. It is also unknown if these rice resistance mechanisms are specific to *S. oryzae*, or also confer resistance to other pests. Some grain pest beetles, like *R. dominica*, lead similar life histories to *S. oryzae*, living inside the grain as larvae, only emerging as adults, while others have larval stages that are in whole or in part spent outside the grain, like *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) and *T. confusum* Jacquelin du Val (Coleoptera: Tenebrionidae) (USDA, 2016). These life histories may interact with resistance mechanisms in different ways or completely circumvent them. The practical implications for growers have also not yet been studied. While growers are unlikely to select their rice varieties based upon its resistance towards stored grain insects, resistance information can be used to inform a grower's post-harvest pest management practices. These studies aim to improve incorporation of varietal resistance into stored grain IPM programs.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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