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Guy Smagghe
other

Su Wang
Institue of plant and environment protection, Beijing academy of agriculture and …

L.-S. Zang
Guizhou University

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Dead-end trap plants as an environment-friendly IPM tool: A case study of the successful use of vetiver grass in China

Liang-De Tang[1], Guy Smagghe[2], Su Wang[3,*], Zhong-Xian Lü[4], Lian-Sheng Zang[1,*]

[1] National Key Laboratory of Green Pesticide, Key Laboratory of Green Pesticide and Agricultural Bioengineering, Ministry of Education, Guizhou University, Guiyang 550025, China
[2] Guizhou Provincial Key Laboratory for Agricultural Pest Management of the Mountainous Region, Institute of Entomology, Guizhou University, Guiyang 550001, China
[3] Institute of Plant and Environment Protection, Beijing Academy of Agricultural and Forestry Sciences, Beijing 100097, China
[4] Institute of Plant Protection and Microbiology, Zhejiang Academy of Agricultural Sciences, Hangzhou 310021, China
* Corresponding authors: lsz0415@163.com, wangsu@ipepbaafs.cn

With 1 table

Abstract: A dead-end trap plant is a plant species that is highly attractive for oviposition and other activities of target pests, but on which they cannot complete their development, reproduction or survival. Due to its unique insecticidal mechanism and environment-friendly characteristics, it has received increasing attention in recent years. There are many species that can be used as trap plant, but few of them can be used as dead-end trap plants. These plants are commonly utilized for lepidopteran pest management in graminaceous crops, cruciferous vegetables and other cropping systems. At present, vetiver grass, *Chrysopogon zizanioides*, is widely used in the integrated pest management (IPM) of rice borers in southern China as an alternative to chemical pesticides. This article lists plant species that can be used as dead-end trap plants, together with the target pests and relevant cropping systems. In addition, the trapping principle and insecticidal mechanism of dead-end traps is reviewed, and the application of vetiver grass as a dead-end trap in rice borer IPM introduced. The future research directions of dead-end trap plants towards the protection of crops are also discussed.

Keywords: *Chrysopogon zizanioides*; trap plant; lepidopteran pest; integrated pest management

1 Introduction

Trap plants and dead-end trap plants are two similar but also different concepts. A trap plant refers to a plant that is more attractive to pest oviposition than the main crop. A trap crop is planted to attract, retain or kill insects in order to reduce damage to the main crop (Hokkanen 1991; Parolin et al. 2012; Han et al. 2022). Dead-end trap plants are plants on which the offspring of the pest insect cannot survive, thus effectively preventing the damage of its offspring on the main crops (Shelton & Nault 2004; Gyawali et al. 2021). By trapping pests while simultaneously interrupting their life cycle, dead-end trap plants provide a sustainable and environmentally friendly approach to conventional insect pest control. This approach reduces the reliance on chemical pesticides and minimizes the negative impact on beneficial organisms, making it an increasingly desirable option in pest management (Cheruiyot et al. 2018). Both trap plants and dead-end trap plants play an important role in pest management, the latter provides a more comprehensive solution by not only attracting pests away from main crops but also preventing the survival and reproduction of their offspring.

Vetiver grass, *Chrysopogon zizanioides* (L.) Roberty, also called khus, is a typical dead-end trap plant. It is a perennial grass of the family Poaceae, native to India and widely cultivated in tropical and subtropical regions for soil and water conservation, soil improvement and environmental rehabilitation (Aziz & Islam 2023; Otunola et al. 2023; Gao et al. 2023). In addition, it has important agricultural biological activities against insects (Zhu et al. 2001; Bajwa et al. 2017), bacteria (Champagnat et al. 2007; Sridhar et al. 2003) and weeds (Mao et al. 2004). Currently, vetiver grass is extensively employed in southern China as a substitute for chemical pesticides in the integrated management of rice borers. Most rice (*Oryza sativa* L.) planting areas are also suitable for vetiver grass planting. Therefore, it is feasible to promote the use of vetiver in rice planting areas for rice borer control.

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E. Schweizerbart'sche Verlagsbuchhandlung, 70176 Stuttgart, Germany, www.schweizerbart.de

This article reviews the trapping principle, insecticidal mechanisms of dead-end trap plants and their application in the management of rice borers, and prospect the future research directions in order to improve the use of dead-end trap cropping as a pest management tool.

2 Dead-end trap plants for attracting and killing pest insects

While there are many species of trap plants and their application in agricultural production is wide, only a few species can be used as dead-end trap plants (Table 1). Dead-end trap plants are largely used against lepidopteran pests. This may be due to two factors: (1) lepidopteran pests are very sensitive to plant chemical signals and can be induced to aggregate through the kairomones emitted by plants (Chiu et al. 2018); and (2) the behavior of lepidopteran pests, such as their mating behaviour and oviposition preferences, make them suitable targets for attracting and killing approaches (Wilson 2010). Based on their characteristics, dead-end plants can be classified into four main categories: crop wild relatives (CWR), herbaceous plants, artificially modified plants, and other plants. The CWR have significant potential for natural development into dead-end trap plants, due to their genetic similarity with their cultivated counterparts. For example, tropical soda apple (*Solanum viarum* Dunal) (Solanaceae) as a CWR of tomato, has potential as a dead-end trap plant for tomato fruitworm (*Helicoverpa armigera* Hübner) (Lepidoptera: Noctuidae) (Gyawali et al. 2021). Wild crucifer (*Barbarea vulgaris* (R. Br.)) (Brassicaceae) can be developed into a dead-end trap plant for diamondback moth (*Plutella xylostella* (L.)) (Lepidoptera: Plutellidae) (DBM) in cruciferous vegetables (*Brassica* spp.) (Brassicaceae) (Lu

Table 1. Some examples of plant species that can be used as dead-end trap plants and their associated cropping system and pest.

Dead-end trap plant	Target main crop	Target pest	Reference
Tropical soda apple (*Solanum viarum* Dunal)	Tomato (*Solanum lycopersicum* L.)	*Helicoverpa armigera* (Hübner)	Gyawali et al. 2021
Radish (*Raphanus sativus* Pers.)	Cruciferous vegetables	*Meligethes aeneus* (Fab.)	Veromann et al. 2014
Wild sugarcane (*Erianthus arundinaceus* (Retzius) Jeswiet)	Sugarcane (*Saccharum officinarum* L.)	*Chilo glyciphagus* (Bojer) *Chilo sacchariphagus* (B.)	Jacob et al. 2021; Nibouche et al. 2012
Wild crucifer (*Barbarea vulgaris* (R. Br.))	Cruciferous vegetables (Brassicaceae)	*Plutella xylostella* L.	Lu et al. 2004; Badenes-Perez et al. 2010, 2014
Brachiaria grass (*Brachiaria brizantha* (Hochst. ex A. Rich.) Stapf)	Sorghum (*Sorghum bicolor* L. Moench), maize (*Zea mays* L.)	*Chilo partellus* (Swinhoe)	Cheruiyot et al. 2018
Vetiver grass (*Chrysopogon zizanioides* (Linnaeus) Roberty)	Rice (*Oryza sativa* L.)	*Chilo suppressalis* Walker, *C. partellus, Sesamia inferens* Walker, *Busseola fusca* (Fuller)	van den Berg 2006a; Chen et al. 2007; Zheng et al. 2009; Lu et al. 2018b, 2019
Sudan grass (*Sorghum sudanense*)	Rice (*O. sativa*)	*C. suppressalis*	Zheng et al. 2009
Napier grass (*Pennisetum purpureum* Schum)	Maize (*Z. mays*)	*C. partellus, B. fusca*	Hari & Jindal 2009; van den Berg et al. 2006b, 2006c
Faba bean (*Vicia faba* L.) (treated with the extract of Chinese kale)	Cruciferous vegetables (Brassicaceae)	*P. xylostella*	Zhu et al. 2021
Sunn hemp (*Crotalaria juncea* L.)	Cowpea *Vigna unguiculata*	*Maruca testulalis* Geyer	Jackai & Singh 1983
Tidalmarsh flatsedge (*Cyperus serotinus* Rottb)	Rice (*O. sativa*)	*S. inferens*	Liu et al. 2011
Benzylglucosino-late-producing tobacco (*N. tabacum* L. cv. Xanthi)	Cruciferous vegetables (Brassicaceae)	*P. xylostella*	Møldrup et al. 2012
Bt-maize (*Zea mays* L.)	Sugarcane (*S. officinarum*)	*Eldana saccharina* Walker	Keeping et al. 2007
Bt rice (*Oryza sativa* L.)	Rice (*O. sativa*)	*C. suppressalis*	Jiao et al. 2018
Indian mustard (*B. juncea* L.)	Cruciferous vegetables	*P. xylostella*	Cao et al. 2008
Firethorn (*Pyracantha coccinea* Roemer)	Strawberry (*Fragaria ananassa* Duch.)	*Drosophila suzukii* Matsumura	Ulmer et al. 2020

et al. 2004; Badenes-Perez et al. 2010, 2014). Wild sugarcane (*Erianthus arundinaceus* (Retzius) Jeswiet) (Poaceae) can also be used as a dead-end trap plant to control *Chilo sacchariphagus* Bojer (Lepidoptera: Crambidae), an important insect pest of sugarcane (Nibouche et al. 2012; Jacob et al. 2021).

Some herbaceous plants, especially grasses, have attracting and killing effects on lepidopteran pests of gramineous crops, and have been identified as dead-end trap plants. Since the discovery that vetiver grass can effectively attract *Chilo partellus* Swinhoe (Lepidoptera: Crambidae) away from maize (van den Berg 2006a), it has attracted considerable attention. Subsequently, its homologous species *Chilo suppressalis* Walker (Lepidoptera: Crambidae) was also confirmed to have a strong oviposition preference for vetiver grass (Zheng et al. 2009). More evidence that vetiver grass can function as a dead-end trap plant for most rice stem borers was provided by several authors (Chen 2007a; Zheng et al. 2009; Xia & Sun 2012). Other dead-end trap plants identified for use in rice cropping ecosystems, include sudan grass (*Sorghum sudanense* (Piper) Stapf) (Poaceae) (Zheng et al. 2009) and tidalmarsh flatsedge (*Cyperus serotinus* Rottb) (Cyperaceae) (Liu et al. 2011). Furthermore, it was found that brachiaria grass (*Brachiaria brizantha* (Poaceae) (Hochst. ex A. Rich.) Stapf) and napier grass (*Pennisetum purpureum* Schum) (Poaceae) can function as dead-end trap plants for *C. partellus* in sorghum (*Sorghum bicolor* L. Moench) (Poaceae) and maize (*Zea mays* L.) (Poaceae) (Hari & Jindal 2009; van den Berg 2006b, c; Cheruiyot et al. 2018).

The use of genetically modified plants that express insecticidal proteins has also been reported to act as a trap crop for *C. suppressalis* (Jiao et al. 2018). For instance, one of the effective means used to control pests, such as *C. suppressalis* in rice or *Eldana saccharina* Walker (Lepidoptera: Pyralidae) in sugarcane, is planting the crops that express *Bacillus thuringiensis* (Bt) genes (Jiao et al. 2018; Keeping et al. 2007). For controlling DBM on cruciferous vegetables, dead-end trap plants are commonly employed. These trap plants include benzylglucosinolate-producing tobacco (*Nicotiana tabacum* L. cv. Xanthi) and vegetable Indian mustard (*Brassica juncea* L.) (Cao et al. 2008; Møldrup et al. 2012). Benzylglucosinolate-producing tobacco plants were more attractive for oviposition by female DBM moths than wild-type tobacco plants (Møldrup et al. 2012).

Several other plant species have been reported to be used as dead-end plants. Sunn hemp (*Crotalaria juncea* L.) can be used as dead-end trap plant to control *Maruca testulalis* (Geyer) (Lepidoptera: Pyralidae) on cowpea (*Vigna unguiculata* (L.) Walp.) (Jackai & Singh 1983). Planting firethorn (*Pyracantha coccinea* Roemer) near strawberry (*Fragaria ananassa* Duch.) provides an effective and low-maintenance solution to minimize damage caused by *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae) (Ulmer et al. 2020). The highly attractive fruits of *P. coccinea* act as a trap, luring *D. suzukii* while preventing the survival of its offspring (Ulmer et al. 2020). Faba bean (*Vicia faba* L.) plants sprayed with the aqueous extract of Chinese kale can be used as dead-end trap plant to control DBM on cruciferous vegetables (Zhu et al. 2021).

3 Trapping principle and insecticidal mechanism

3.1 Trapping principle

Plants are masters of volatile production and release (Farmer et al. 2001; Liechti & Farmer 2002; Adebesin et al. 2017). Insects interact with plants by recognizing these volatiles. Insect-plant interactions primarily rely on chemical communication systems among plants, herbivores and their natural enemies (Chiu & Bohlmann 2022; Tumlinson 2023). The principle of using dead-end trap plants to lure pests is based on the release of kairomones or other chemical cues by plants that attract target pests for oviposition and other activities. Plant volatiles (PVs) are lipophilic molecules with high vapor pressure that serve various ecological roles (Pichersky et al. 2006). PVs may play an important role in host location, mate-finding, oviposition and aggregation of insects (Arx et al. 2012; Xu & Turlings 2018; Pérez-Hedo et al. 2021; Cascone et al. 2022; Cruz-Miralles et al. 2022; Nieri et al. 2022; Levi-Zada 2023). Specifically, dead-end trap plants simulate the mate location of target pests by releasing chemical cues similar to those of insect pheromones or other chemicals, which diffuse through the surrounding atmosphere (Schuman et al. 2023) and are eventually detected by insects, thereby attracting and aggregating the target pest (Schmidt-Büsser et al. 2009; Arx et al. 2012; Kromann et al. 2015), and triggering a range of behavioral and physiological responses. Insects also produce a large repertoire of chemically diverse secondary metabolites, including pheromones, hormones or other chemical substances (Morgan 2010), which are used for defense against attackers and also within species as sex pheromones, aggregation signals (Chiu et al. 2018) and alarm signals (Beran et al. 2019). In response to visual, tactile and olfactory cues, insects often demonstrate preferences for particular plant species, cultivars or crop stages (Shelton & Nault 2004). Olfactory cues play a crucial role in the entire attraction process.

Numerous volatile compounds have been identified from plants such as cruciferous vegetables and vetiver grass, some of which exhibit attractive properties towards centain insects. Specifically, 190 volatiles were identified from cauliflower, turnip, broccoli, watercress, radish and cabbage leaves. Aldehydes and ketones appeared as the most discriminatory among leaves, accounting for the distinct aroma (Baky et al. 2022). Pathway analysis showed that three secondary metabolism pathways, including the fatty acid pathway, methylerythritol phosphate (MEP) pathway and glucosinolate (GLS) pathway, in a set of 12 common

Brassica vegetables, behave distinctively in these vegetables. These pathways are responsible for the biosynthesis and release of green leaf volatiles (GLVs), terpenes, and isothiocyanates (ITCs), respectively (Ameye et al. 2018; Liu et al. 2018). The aqueous extract of Chinese kale applied to faba bean plants significantly increased the number of DBM eggs compared to Chinese kale. This suggests that the extract attracts DBM females and influences their egg-laying behavior (Zhu et al. 2021).

3.2 Insecticidal mechanism

After insects deposit their eggs on dead-end trap plants, the hatching larvae start feeding and ingesting these plant tissues. This can affect their physiology and behavior, such as reducing their reproductive capacity, interfering with their neurological function, affect their digestive system, suppressing their feeding, and decreasing their feeding volume, leading to insect death or population decline (Schellenberger et al. 2016). Previous studies have demonstrated that feeding on dead-end trap plants, such as napier grass can result in mortality rates of up to 96% of *C. partellus* larvae. Larval development is significantly delayed, and their weight is noticeably reduced, indicating severe developmental inhibition (Khan et al. 2006; Gao et al. 2015; Lu et al. 2017b, c). Therefore, it is reasonable to speculate that dead-end trap plants contain toxic substances to the larvae of these insect species.

Evidence suggests that the consumption of plant secondary metabolites may influence the growth and development of herbivorous insects and it could also result in their death (Ansante et al. 2015; Giongo et al. 2016; Badgujar et al. 2017; Ma et al. 2019; Divekar et al. 2022; Gross et al. 2022; Elshafie et al. 2023). The mechanisms of plant defense against herbivorous insects largely involve the following: (1) repellent or antifeedant effects (Bett et al. 2016; Lea et al. 2021); (2) interfere with the enzyme activity (Wang et al. 2019; Mashhoor et al. 2021); (3) inhibition growth and development (Rahman-Soad et al. 2021; Ma et al. 2021; Chabaane et al. 2022; Tougeron & Hance 2022); (4) lethal effects (Mordue & Blackwell 1993; de Leao et al. 2020; Paspati et al. 2021).

Transgenic plants that express Cry proteins were developed as dead-end trap plants offer a promising alternative to traditional insecticides for controlling lepidopteran pests. Bt insecticidal proteins primarily function by targeting specific pests and disrupting their digestive systems. These proteins, such as Cry1Ba2, Cry1Ca4 and Cry1Ab, have been found to be effective against various pests, including DBM, *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae) and *Manduca sexta* (L.) (Lepidoptera: Sphingidae). They bind to specific receptors on the insect's midgut epithelial cells, leading to pore formation and cell lysis, ultimately causing insect mortality (Shelton et al. 2009; Dhania et al. 2019; Wang et al. 2018; Chen et al. 2007b; García--Ruiz et al. 2022; Lu et al. 2022).

4 Case study: Application of vetiver grass in IPM of rice stem borers

Rice is one of the most important food crops in the world. Asia is an important producer of rice, planting more than 90% of the world's rice (Chen et al. 2022). Almost all paddy fields throughout Asia have been invaded by rice stem borers, such as *C. suppressalis, C. partellus, S. inferens* and *Scirpophaga incertulas* (Walker) (Lepidoptera: Pyralidae) causing economic losses (Qu et al. 2003; Lu et al. 2019; Sakib et al. 2022; Babendreier et al. 2022). In addition, Africa also grows rice. In African rice areas, *Maliarpha seperatella* Ragonot (Lepidoptera: Pyralidae), *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae), *C. partellus* and *Diopsis thoracica* Westwood (Diptera: Diopsidae) are the main rice stem borers (January et al. 2020). Over the past several decades, the management of these rice stem borers has predominately relied on the use of synthetic chemical insecticides (Peng et al. 2021). The problems of environmental safety, food safety and pest resistance caused by chemical control have forced humans to find new alternative control strategies. The use of trap plants as a traditional tool of rice pest management has increased considerably in the recent years, especially for lepidoptera pests (Shelton & Badenes-Perez 2006; Zheng et al. 2009; Liang et al. 2015; Lu et al. 2018b, 2019). Vetiver grass does not only attract female moths of rice stem borers to lay eggs on it, but it also has a lethal effect on the hatched larvae. It has been identified as a dead-end trap plant for the alternative control of rice stem borers, such as *C. suppressalis* and *S. inferens* in rice systems (Lu et al. 2018b). Therefore, vetiver grass has broader development and application prospects. This technology was initially extended in Zhejiang Province, China. At present, it has been become one of the most important agricultural technologies recommended by the Ministry of Agriculture and Rural Affairs for use in the management of rice pests in China, and it has been widely adopted in rice-growing areas in southern China. Based on the effectiveness and environmental friendliness of this technology, it can significantly reduce (> 30%) the use of chemical pesticides, reduce management costs, improve crop quality, subsequently increase income, thereby benefiting millions of farmers (Lü et al. 2019).

4.1 Trapping and killing mechanism

More than 300 compounds have been identified from vetiver (Liang et al. 2015). The volatile oil of vetiver contains a range of terpenoids that are strong attractants and oviposition stimulants for lepidopteran stemborer moths on vetiver (Li et al. 2018). Electrophysiological assays showed that the compounds released from vetiver grass elicited significant the electroantennography (EAG) responses in female adults of *C. suppressalis*, and these compounds were identified as caryophyllene, β-ocimene, linalool and α-pinene. Further bioassays showed that individual compounds, their combinations, as well as differences in compound ratios play important roles in the process of inducing female moths to lay eggs (Lu et al. 2017a). The compounds which elicited strong EAG responses in antennae of female moths were subsequently selected for further development of an attractant volatile formula. Among the numerous (450) formulations, 17 showed the greatest trapping effect for *C. suppressalis* (> 15 per trap) (Lu et al. 2019). In another study, 16 compounds from vetiver volatiles produced EAG responses in *C. suppressalis*, but the EAG response to vetiver extract was significantly higher than that of individual compounds, which means that multiple compounds are involved in the regulation of the olfactory behavior of *C. suppressalis*. Wind tunnel assays further showed that six compounds (cholesterol, citral, n-pentadecanoic acid, myristic acid, glycerol 1-palmitate and diisooctyl phthalate) had clear attractive activity, while four of these: cholesterol : citral : myristic acid (33 : 24 : 11), diisooctyl phthalate:citral : glycerol 1-palmitate (130 : 48 : 1), cholesterol : citral : myristic acid : glycerol 1-palmitate (66 : 48 : 22 : 1), and citral : glycerol 1-palmitate (48 : 1) were identified as the attractive compounds in vetiver extracts (Wang et al. 2016).

Components isolated from a petroleum ether extract of vetiver grass had significant lethal effect on third-instar larvae of *C. suppressalis*, and the mortality rate was 85.0% after feeding at a concentration of 0.05 g/mL for 3 days (Lü et al. 2019). Further, by comparing the nutrients and secondary metabolites of rice and vetiver grass, it was found that the contents of total protein, total sugar, amino acids and cellulose in vetiver grass were significantly lower than those in rice, especially the methionine (MET) content in rice was 7-fold higher than that in vetiver grass. In contrast, the tannin content in vetiver was 30% higher than that in rice (Lu et al. 2017b). This low nutrient content and high concentrations of defensive compounds in dead-end trap plants such as vetiver may provide an explanation for the death of some lepidopteran pest larvae on such crops (Schellenberger et al. 2016). Toxic and harmful compounds enter insect tissues through the midgut, affecting protective enzyme and detoxification metabolic enzyme activities. Specifically, the activity of superoxide dismutase (SOD) in third-instar larvae of *C. suppressalis* feeding on extracts of vetiver grass was higher than the control (artificial diet), while activity of catalase (CAT) and peroxidase (POD) was lower than the control (Gao et al. 2015). The imbalance of protective enzyme activity in the insect body may lead to obstacles in the scavenging of free radicals, resulting in toxic action. Induction of changes in insect digestive enzyme activity may be another manifestation on the toxic effects of vetiver grass. The activities of digestive enzymes, including protease, amylase, alginase and sucrase, were significantly decreased in some specific stages of larvae of *C. suppressalis* and *S. inferens* feeding on vetiver grass (Lu et al. 2017b, c). Insect metabolic detoxification and phytochemical defense are the most important relationships in the evolutionary "arms race" between herbivorous insects and host plants. The detoxification metabolic mechanism has always been considered as a common mechanism for herbivorous insects to adapt to their hosts. Cytochrome P450 monooxygenases (P450s), glutathione S-transferases (GSTs), and carboxylesterases are three major multigene enzyme families that primarily participate in xenobiotic metabolism, including the detoxification of insecticides and plant-derived allelochemicals (Ranson et al. 2002; Bao et al. 2012; Lu et al. 2018a). It was found that the activities of cytochrome P450 and carboxylesterase in *C. suppressalis* larvae that fed on vetiver grass leaf tissue were significantly lower than those that fed on rice (Lu et al. 2017b). Furthermore, transcriptional dynamics suggested that digestion-related genes, immune-related genes and detoxification-related genes may be involved in the toxicity responses after exposure to vetiver grass. Because most of these genes were significantly down-regulated in the midgut of *C. suppressalis* larvae at 6, 8, and 10 days after feeding on vetiver grass compared to rice (Lu et al. 2018a). Further study found that two cytochrome P450 monooxygenase (P450) genes, CsCYP6SN3 and CsCYP306A1, were involved in the toxic responses after exposure to vetiver grass. Vetiver grass significantly inhibited the expression levels of CsCYP6SN3 and CsCYP306A1 in third-instar larvae after feeding. RNAi showed that the silencing of *CsCYP6SN3* and *CsCYP306A1* significantly reduced pupation rate and pupal weight. After silencing of *CsCYP6SN3* and *CsCYP306A1,* the mortality caused by feeding vetiver was also higher than that of feeding on rice (Lu et al. 2022).

4.2 Application principles and control efficiency

The efficacy of Vetiver as a trap crop under field conditions is closely related to how the it is deployed and managed inside the rice ecosystem. The following recommendations on the establishment of Vetiver trap plantings were developed based on the adoption of these technologies in paddy fields in southern China: (1) ensure that the width of the paddy field ridge is greater than 80 cm, so that vetiver grass has sufficient growth space (Xia & Sun 2012); (2) the Vetiver planting area should account for 6–10% of the total area of the paddy field, which is based on the effective trapping distance of vetiver grass. Previous studies showed that the incidence of rice plants with withered heart symptoms within 10 m from vetiver grass strips was lower (< 1.66%), and the incidence of plants with such symptoms increased to more than 4% at distances of further than 30 m (> 4.03%) (Chen et al. 2007a; Xia & Sun 2012). Moreover, vetiver grass can significantly reduce the population density of overwintering *C. suppressalis*. A reduction rate of 83.8% within 25 m from the vetiver grass strip was reported (Zheng et al. 2017a; Lu et al. 2019); (3) timely access to large numbers of eggs for unified killing to reduce the damage to rice (Chen et al. 2007a, 2016; Liang et al. 2015); (4) vetiver grass should be planted in spring and earlier than rice to obtain the maximum biomass and trapping effect. The trapping effect of biennial vetiver grass was greater than that of annual vetiver grass (Zheng et al. 2017b; Lu et al. 2019); (5) after transplanting, vetiver grass and rice were equally fertilizer managed at the same time to ensure that the trapping effect continued (Chen et al. 2007a). In order to improve the trapping effect, vetiver should usually be cut twice, once after early rice harvest and again after late rice harvest, leaving 10–20 cm stubble (Lu et al. 2019).

Overall, planting of vetiver grass can result in 30–70% reduction of *C. suppressalis* in rice systems (Lu et al. 2019). Vetiver grass is therefore one of the most important alternative control measures for green management of *C. suppressalis* in rice. In growing seasons or specific fields where *C. suppressalis* infestation levels are low, the presence of vetiver can lead to such low damage levels in rice fields, that insecticide applications may not be needed.

4.3 Proliferation effect on natural enemy insects

Vetiver grass attracts rice stem borers to lay eggs on it, and then these eggs attract the parasitism of various egg parasitoid species. Surveys of parasitoids associated with vetiver showed that the number of egg parasitoids of rice stem borers in the vetiver grass-planted fields were significantly higher than those in fields without vetiver grass (Zheng et al. 2017a). Among them, the main parasitoids are the species in the genus *Telenomus* (*T. sesamtae* and *T. chilocolus*) and the genus *Trichogramma* (*T. japonicun* and *T. chilonis*). In addition, the survey also found some larval parasitoids of rice borers, including *Aceratoneuromyia indica* (Silvestri), *Apanteles baoris* (Wilkinson) and *Apanteles flavipes* (Cameron). The number of *Telenomus, Trichogramma* and other parasitic wasps in vetiver grass-planted rice fields was 2.8, 1.7 and 0.8 times higher than in the control rice fields without vetiver grass (Zheng et al. 2017a).

5 Perspective

Dead-end trap plants have promising prospects and potential applications in pest management strategies, as an important part of IPM programs. These plants can serve as an alternative approach for reducing the use of synthetic pesticides and promoting sustainable agriculture. Additionally, they can also contribute to the conservation of natural enemies by creating a suitable habitat for them, thereby enhancing the biological control of pests.

Looking into the future of dead-end trap plant systems, there are several design directions to consider. Firstly, expanding the range of target pests by diversifying dead-end trap plants can achieve more comprehensive pest control. Secondly, considering the characteristics and requirements of crops when designing dead-end trap plants can minimize the negative impact on the health and productivity of the crop, while optimizing crop resilience against pests. Thirdly, enhancing the efficacy of dead-end trap plants through gene editing and genetic improvement can improve their ability to attract and eliminate pests. Lastly, integrating multiple pest control methods, such as chemical pesticides and biological control, and strengthening monitoring and early warning systems using modern technology, can enhance the overall effectiveness of the system. While these design directions hold promise, it is important to note that there are still many challenges and difficulties to be addressed in the trapping and killing process. Dead-end trap plants cannot only attract certain species of moths to lay eggs on them, but also kill larvae. This suicidal behavioral decision-making is contrary to the theories of species evolution and preference-performance (also known as optimal host selection or mother-knows-best) (Thompson 1988; Moravie et al. 2006; Wist & Evenden 2016; Altesor & González 2018). Therefore, there are still many unresolved issues to be uncovered in the interaction between the borer and the dead-end trap plants, mainly including:

(1) Dead-end trap plants can specifically attract some stem borers, such as *C. partellus, C. suppressalis* and *S. inferens*. So, how to realize chemical communication between them is a basic issue to be answered in the field of chemical ecology. Chemical communication is essentially a process of transmitting chemical signals and receiving chemical signals. In this process, plant volatiles are the signal sources, and insect olfactory receptors act as receivers (Mahadevan et al. 2022). Which volatile organic compounds (VOCs) (ligands) released by dead-end trap plants are specifically recognized by these borers, and what are the insect receptors that recognize these VOCs? Are the VOCs released by trap plants chemical communication signals in order to achieve a purpose of their own? This in turn is in the interest of certain borers that they eavesdropped on. Eavesdropping events have been confirmed to be widespread between the same species (Baldwin et al. 2006) or between different species (Fatouros et al. 2005; Gurr et al. 2016; Shen et al. 2020; Righetti et al. 2021; Xuan et al. 2023).

(2) Plant metabolites show significant changes across the entire plant life (Li et al. 2020; Wang et al. 2022; Yang et al. 2022). Previous evidence has showed that there are significant differences in the attractive effect of dead-end trap plants (vetiver grass) on *C. suppressalis* in different periods (planting time) (Chen et al. 2007a; Lu et al. 2019).

(3) In Lepidoptera, the larvae, especially during the early stages, are often have limited mobility, and hence the mother's choice of a host plant determines the conditions the offspring experience, consequently impacting their development and survival (Rausher 1979; Jaumann & Snell-Rood 2017). Accordingly, the preference-performance hypothesis predicts that females should prefer to lay eggs on host plant species that increase their offspring's performance and fitness. That means females will choose to oviposit on plants that maximize offspring development (Altesor & González 2018). Vetiver grass has been identified as a dead-end trap plant of some stem borers (van den Berg 2006b, c; Chen

et al. 2007a; Hari & Jindal 2009; Lu et al. 2022). Dead-end trap plants contain substances (plant defense substances) that have a toxic effect on target pests (Lu et al. 2017b; Li et al. 2018). The preference of these stem borers to lay eggs on vetiver grass is contradictory to the above views. Phytophagous insects usually locate their hosts through odor cues (host plant volatiles) in long-distance, while the selection of oviposition sites requires the participation of the taste system to evaluate the vegetative traits of the host (Jacobsen & Raguso 2021). In addition to the selection of oviposition sites by female adults, it is still unknown whether the offspring larvae can perceive the harmful substances in the dead-end trap plants and subsequently drive host escape behavior during feeding. In these processes, the participation of insect taste system is required (Robertson et al. 2019; Aryal & Lee 2022). Therefore, the taste system of these stem borers is not involved in the selection of oviposition sites and assessment of harmful substances, which seems to be contrary to common sense. If it is involved, it is not known which gustatory receptors play a role, and what are the ligands (plant metabolites) of gustatory receptors.

(4) The lethal mechanism of dead-end trap plants to stem borers involves changes of various detoxification metabolic enzyme activities (Gao et al. 2015; Lu et al. 2017a, b). At present, only the function of two P450 genes has been identified (Lu et al. 2022), and the other relative genes and their mechanism of action at the molecular level need to be further studied in depth.

(5) Endosymbionts play an important role in insect growth and development, reproduction and detoxification metabolism (Cheng et al. 2017). A most recent study has showed that plants can use secondary metabolites to indirectly defend phytophagous insects by inhibiting beneficial symbiotic bacteria in the host. Results revealed that sakuranetin are dramatically accumulated in leaf sheaths and phloem exudates through an intact jasmonate (JA) signaling when rice is attacked by the brown planthopper (BPH) (*Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae). In turn, rice manipulate sakuranetin in defense against BPH by inhibiting its beneficial endosymbionts (Liu et al. 2023). The analysis of midgut transcriptomics of *C. suppressalis* feeding on vetiver grass has been reported, and some hypothetical genes related to detoxification metabolism have been obtained (Lu et al. 2018a). Whether the intestinal flora of *C. suppressalis* feeding on vetiver grass has changed and how is the interaction among plant-insect-endosymbionts, are worthy of further study.

(6) There is a limited variety of dead-end trap plants currently available. Moreover, the research on dead-end trap plants, including vetiver grass, has primarily focused on the trapping and killing effect of specific pests, mainly Lepidoptera. At present, almost no dead-end trap plant system developed for other insect pests. Furthermore, the application of trap plants has been mainly focused to the graminaceous crop and cruciferae crop systems, very few are for other crop systems, such as tomatoes and legumes (Table 1). Consequently, there is a necessity to conduct field investigations to assess the effectiveness of dead-end trap plants in trapping and killing pests that are infesting others crops. It is essential to expand our understanding and practical implementation of trap plants in pest control across various agricultural systems.

Although the mechanism of dead-end trap plants luring some lepidopteran pests such as *C. suppressalis* is not clear, there is good evidence that dead-end trap plants can strongly attract some kinds of moths to lay eggs on it and kill the larvae after hatching. More importantly, long-term field data have showed that dead-end trap plants have a good control efficiency on rice borers (Lu et al. 2019). In recent years, China has vigorously implemented chemical pesticide reduction actions to continuously increase the numbers of farmers making use environmentally friendly pest control methods. Moreover, the infestation of rice stem borers such as *C. suppressalis* is increasing. On the one hand, rice stem borers such as *C. suppressalis* have a high level of resistance to bisamide insecticides, and on the other hand, mechanical harvesting provides high rice stubbles for a good survival and overwintering environment for *C. suppressalis* and other stem borers. Globally, reliance on pesticides has been increasing (Epstein 2014), exacerbating the impact of insecticide resistance (Gould et al. 2018). In this context, dead-end trap plants have broad development and application prospects as an effective management alternative to chemical synthetic pesticides. According to the action principle of dead-end trap plants, it is not only safe for crops and environment, but also sustainable. It is worth mentioning that vetiver grass blooms without fruiting and reproduces asexually by tillering, so it will not become a weed (Xia & Sun 2012; Lu et al. 2018b). In addition, as a trap plant, it could contribute to increase the biodiversity and provide shelter and alternative food for natural enemies (Sarkar et al. 2018; Shrestha et al. 2019), thereby increasing biological control ecosystem services (Hokkanen 1991). In conclusion, the successful application of dead-end trap plants in the sustainable control of rice borers in China will be a useful reference for the control of pests in other rice growing areas. Dead-end trap plant systems as an environmentally friendly and sustainable IPM technology, has broad prospects for development and application, which could potentially aid in enhancing crop production, promoting sustainable agricultural practices, and ensuring food security.

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