



Insights of the Neotropical rice pest *Tibraca limbativentris* (Hemiptera: Pentatomidae) with current distribution and alternative host plants

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ABSTRACT. The ecological story of how a particular insect becomes an agricultural pest is crucial for understanding insect adaptations to cropping systems. *Tibraca limbativentris* Stål is one of the most harmful pests in Neotropical irrigated rice crops. Despite over a century of reports of *T. limbativentris*, there is currently no published evidence confirming its ability to complete its life cycle on native host plants under natural conditions. This work presents a comprehensive review of the published literature on *T. limbativentris*, with a particular focus on its alternative host plant associations in the Neotropics. A total of 198 publications mentioning the species were examined, and thirty host plant species were identified. The most frequently reported plants were *Paspalum urvillei* Steud., *Andropogon bicornis* L., and *Andropogon lateralis* Nees, all grasses that are common elements of the regional rice field landscape. Also, five crop plants were mentioned, yet rice remains the only crop for which the insect is consistently confirmed as a primary pest. For the remaining crops, the evidence is either anecdotal or based on samplings in experimental fields, and given the absence of recent verified reports from commercial fields, caution is advised when mentioning the association of *T. limbativentris* with these crops.

KEYWORDS. Alternative winter hosts. Management strategies. Rice paddies. Rice stem stink bug. Trophic relationships.

Perspectivas sobre la plaga del arroz neotropical *Tibraca limbativentris* (Hemiptera: Pentatomidae), su distribución actual y plantas hospedadoras alternativas

RESUMEN. La historia ecológica de cómo un insecto se convierte en una plaga agrícola es fundamental para comprender sus adaptaciones a los sistemas cultivados. *Tibraca limbativentris* Stål es una de las plagas más dañinas en los cultivos de arroz irrigado neotropicales. A pesar de más de un siglo de reportes sobre *T. limbativentris*, actualmente no existe evidencia publicada que confirme su capacidad para completar su ciclo de vida en plantas hospederas nativas en condiciones naturales. Este trabajo presenta una revisión exhaustiva de la literatura publicada sobre *T. limbativentris*, con especial atención a sus asociaciones con plantas hospederas alternativas en el Neotrópico. Se examinaron un total de 198 publicaciones que mencionan a la especie, identificándose treinta especies de plantas hospederas. Las más frecuentemente reportadas fueron *Paspalum urvillei* Steud., *Andropogon bicornis* L. y *Andropogon lateralis* Nees, gramíneas comunes en el paisaje arroceros regional. También se mencionaron cinco especies cultivadas, siendo el arroz el único cultivo para el que el insecto está consistentemente confirmado como plaga principal. Para los demás cultivos, la evidencia es anecdótica o proviene de muestreos en campos experimentales, y dada la ausencia de reportes recientes verificados en campos comerciales, se recomienda cautela al mencionar la asociación de *T. limbativentris* con estos cultivos.

PALABRAS CLAVE. Arrozales. Chinche del tallo. Estrategias de manejo. Plantas hospederas alternativas invernales. Relaciones tróficas.

INTRODUCTION

The ecological story of how a particular herbivorous/phytophagous insect becomes a crop pest is not only fascinating but also relevant to understanding why these species expand their geographical ranges and how they adapt to survive on new host plants (natural and cultivated) introduced into their natural habitats. It is often overlooked that the classification of an insect as a 'pest' in a crop is purely from a human perspective. On this basis, it is also overlooked that insects are hardy survivors that have adapted over hundreds of years to changes in climate, flora, fauna and, of course, the anthropogenic changes that humans have made to ecosystems (Khaliq et al., 2014; Engel, 2015; McCulloch & Waters, 2023). It then becomes clear that the so-called insect pests (except for the exotic ones) are native organisms that existed in a given region long before humans 'invaded' its spaces and installed their crops, because to establish crops, the first producers had to change the landscape, replacing the native flora with a few species of domesticated, mostly exotic, plant species (Allaby, 2021). As insects are specialists in the art of survival, they have colonized and adapted to cultivated plants due to factors specific to each insect species, i.e. the possible phylogenetic proximity of cultivated plants to their native hosts, the increased nutrient supply provided by these new plants, among others (Morrill, 2004). These opportunistic associations now mean that farmers have to invest more each year to protect their crops from the 'attack' by these 'pests'. However, in the case of native pests, which are insects that have co-evolved with a whole local community, likely, the bitrophic/tritrophic associations and the ecological mechanisms that govern them, can be developed equally outside and inside the crop, in integrated management conditions.

In natural ecosystems, phytophagous insects coexist in a complex relationship with plant communities and natural regulating factors (Sharma et al., 2017). Some hypothesis suggest that factors inherent to insect populations and extrinsic landscape factors (biotic or abiotic) may influence natural regulation (Cyr & Pace, 1993; Leeper & Taylor, 1998). Among the biotic factors, several host-plant-mediated aspects have been shown to determine the abundance of insect herbivores and the attack of their natural enemies, traits related to defense metabolites, plant architecture (such as height) and their phenological stage (Lawton, 1983; Marques et al., 2000; Obermaier et al., 2008; Wang et al., 2024). This is better explained by top-down and bottom-up control theory, which shows that there is a balance between the upward forces that regulate herbivore populations from the resources provided by their host plants, and the downward forces exerted by the consumers of these herbivores (Hairston et al., 1960; Vidal & Murphy, 2018). Top-down control involves the indirect effect of the host plant traits on the herbivore population by mediating the interaction with

its natural enemies, which are largely represented by consumers at the third trophic level of the food chain (predator-prey relationship) and by insect biological controllers present in the ecosystem (parasite or pathogen-host relationship) (Hairston et al., 1960; Denno et al., 2002; Leroux & Loreau, 2015; Vidal & Murphy, 2018). Bottom-up control, on the other hand, is directly related to plant characteristics such as nutritional quality, chemical and mechanical defenses (secondary metabolites and fibers), plant distribution and abundance, among others, and represents the direct effect of the plant on the performance and survival of phytophagous insects that use it as a resource (Leroux & Loreau, 2015; Vidal & Murphy, 2018; Han et al., 2022). These two mechanisms, top-down and bottom-up control, act simultaneously in natural systems to influence phytophagous insect populations.

However, in artificial environments such as crops, these complex factors are disrupted by the use of agrochemicals, which not only eliminate some pests and weeds, but also populations of native insects that play the role of natural enemies such as parasitoids and predators, and other biological controllers such as entomopathogenic fungi, bacteria and viruses (Jonsson et al., 2012; Pandey et al., 2022; Wan et al., 2025). As a result, there are no optimal populations of biological control agents in crops that can exert a successful top-down regulation. On the other hand, the large amounts of nutrients applied to crops to produce high-quality food for humans overload the bottom-up system. Nutrient-rich crops quickly attract phytophagous insects that abandon their low-nutrient native host plants and rapidly feed and reproduce within the crop, as these plants provide better resources for them and their offspring, often favoring the performance of insect pests on cultivated plants (Hwang et al., 2008; Butler et al., 2012; Bala et al., 2018). This creates an imbalance because the system set up in this way cannot balance itself, so there is a large number of bottom-up resources but a small number of top-down resources, and this, coupled with the fact that pests often develop resistance to chemical pesticides over time (Morrill, 2004; McCulloch & Waters, 2023), makes their control increasingly complex. In the end, these phytophagous insects adapt their reproductive cycles to the crop conditions/availability and become economically important pests.

This is the case of the neotropical species *Tibraca limbativentris* Stål (Hemiptera: Pentatomidae) which poses a serious challenge for rice production. This species quickly adapted its feeding/reproduction/performance to the rice crop, with *Oryza sativa* L. (Poales: Poaceae) being an exotic plant introduced to South America during the European conquest (Acevedo et al., 2006). For almost 110 years, *T. limbativentris* has been officially recorded in association with rice cultivation (Bodkin, 1914; Costa Lima, 1935; Bosq, 1940; Fuentes-Rodríguez et al., 2025) and to date no published records have been found indicating its successful natural

reproduction on plants native to the region. It is important to review the published information on *T. limbativentris* and its alternative hosts, as this is a necessary step towards understanding its original tritrophic interactions. In current scenarios, where in many cultivated areas much of the native flora has been cleared, it is interesting to study the plants (native and exotic) that make up the current agricultural landscape, to identify host plants that can be used in pest control strategies, such as agricultural landscape designs that help to enhance natural pest control within integrated management schemes, as well as possible pest trap zones with their alternative host plants. This information can also be useful to understand why pest incidence is higher in some areas than in others, depending on the abundance and composition of alternative host plants present in each situation.

THE RICE STEM STINK BUG *TIBRACA LIMBATIVENTRIS* STÅL

Main insights of this 'pest' species

Tibraca limbativentris is a Neotropical species that was described in 1860 from a female found in Rio de Janeiro, Brazil. In his original description, Stål (1860) refers to the taxonomic aspects of this new species, but does not mention any host plant on which the insect was collected. From this point onward, the lack of this information, which is highly relevant from the perspective of the species' ecology, creates a gap in the understanding of the species' preferred hosts, a gap that is evident in subsequent studies up to the present.

Later, Fernandes and Grazia (1998) conducted a review of the genus *Tibraca*, in which 123 specimens of *T. limbativentris* from several countries were examined, mentioning for various areas that the specimens were found in rice cultivation (among them: Costa Rica, Colombia, Bolivia, Argentina). Its originally known distribution in the Neotropical region extended from southeastern to northwestern and Caribbean areas (Fernandes & Grazia, 1998). However, its range has since expanded and appears to be approaching the southeastern United States, potentially threatening rice cultivation in Florida (Hodges & Morse, 2007; Brambila, 2009; Panizzi, 2015).

At the phenotypic level, it is characterized by a dark brown color on the dorsal part, with a small triangular black pit on each side of the anterior part of the scutellum. The head is longer than wide, the ventral part is typically dotted, with a yellow lateral margin and the legs are castaneous, concolorous with the body. It is the largest species within the genus, with large specimens equal or longer than 13.0 mm (Fernandes & Grazia, 1998), with females generally larger than males.

At the agronomic level, this species is one of the most serious pests in rice paddies of South and Central America

(Cheaney & Jennings, 1978; Trujillo, 1991; Pantoja et al., 1995; Ferreira et al., 1997; Schaefer & Panizzi, 2000; Kruger & Burdyn, 2015). *Tibraca limbativentris* feeds primarily on the stems of rice plants during both vegetative and reproductive stages, and the damage it inflicts is comparable to that caused by stink bugs of the genus *Scotinophara* and *Lagynotomus* on Asian rice crops (McPherson, 2018). Trujillo (1970) pointed out that *T. limbativentris* damages rice plants by causing leaf wilting when feeding on stems, without attacking immature grains. At the histological level, this insect causes significant damage to plants through two main mechanisms: it creates a salivary sheath while feeding on xylem vessels, and it disrupts parenchyma cells through laceration and maceration (Almeida et al., 2020). As it feeds, it injects saliva and extracts internal tissues, causing necrosis at the internodes (symptom known as "dead heart") and the development of sterile panicles that fail to produce seeds due to phloem depletion (symptom known as "white panicles"). This damage results in a substantial reduction in crop yield, with annual losses of up to 65.2 kg per hectare reported in irrigated rice fields due to this insect (Costa & Link, 1992). Additionally, this species commonly resides on the underside of rice plants, often evading pesticide applications by aerial spraying, which highlights the need for alternative control strategies (Trujillo, 1991; Meus et al., 2012).

Rice in the Neotropics and current distribution of *T. limbativentris* in its Asian host

Oryza sativa L. is an Asian plant belonging to Poales clade, introduced to South America during the European conquest (Acevedo et al., 2006). According to the historical records, the Portuguese introduced it to Brazil, while the Spanish established its cultivation in various parts of Central and South America. In North America, rice was introduced from Africa to the region that is now the United States around 1600 (Carney, 2001; Paredes et al., 2021), and the earliest known record of commercial rice production dates back to 1685, when rice was grown in the coastal lowlands and islands of present-day South Carolina (GRISP (Global Rice Science Partnership), 2013). Later, during the latter half of the 18th century, both wheat and rice were cultivated and exported from Brazil. By 1781, Brazil had become the sole supplier of all the rice consumed in Portugal, fully meeting the mother country's demand (Marques, 1978).

Currently, rice is produced in at least 28 of the 35 countries that make up the American continent (Fig. 1), with Brazil, the United States, Peru, Colombia, Uruguay, Ecuador, Argentina and the Dominican Republic being the most important producers in terms of the number of hectares under cultivation (FAO (Food and Agriculture Organization of the United Nations), 2022)). *Tibraca limbativentris* is officially reported as a rice pest in papers and agronomic guides from 18 countries (Fig. 1).



Figure 1. Rice-producing countries and distribution of *Tibraca limbativentris* in rice fields across the American continent. The map shows countries where this insect is considered a native species, as well as countries that have reported it as an exotic pest insect.

In South America, the species is commonly found in rice fields across several countries, including Argentina (Bosq, 1940; Trujillo, 1970; Kruger & Burdyn, 2015), Brazil (Trujillo, 1970; Ferreira et al., 1997), Bolivia (CIAT (Centro de Investigación Agrícola Tropical), 2003), Colombia (Pantoja et al., 2007), Ecuador (Rodríguez Delgado et al., 2018), Paraguay (MADES (Ministerio del Ambiente y Desarrollo

Sostenible), 2006; IPTA (Instituto Paraguayo de Tecnología Agraria), 2019), Perú (Couturier et al., 1996), Uruguay (Bentancourt & Scatoni, 1992; Martínez et al., 2018) and Venezuela (Aponte et al. 1992; INIA (Instituto Nacional de Investigaciones Agrícolas), 2004). Its presence has also been reported, though less frequently, in the rice fields of Guyana (Bodkin, 1914). In Suriname, the only available

reference to *T. limbativentris* is a video documenting the insect in rice fields, its associated damage, and control measures (Adron 2017, Dr. Curt Delice, *pers.comm.*). Chile represents a unique case, as it hosts the world's southernmost rice crops and reports a notably low incidence of pests and diseases (Alvarado & Hernaiz, 1995; Paredes et al., 2021). To date, there are no published records confirming the presence of *T. limbativentris* in Chilean rice fields.

In Central America, *T. limbativentris* is documented as a native pest species in rice fields of Costa Rica (Corrales Castillo et al., 2017), Honduras (Reyes-Discua, 2003; SAG (Secretaría de Agricultura y Ganadería), 2003) and Panamá (Rodríguez et al., 2006; Zachrisson, 2010). It has also been reported as an introduced species associated with rice in Cuba (Grillo Ravelo, 2007), in the Dominican Republic (Serra et al., 2003), in Guadeloupe and Trinidad and Tobago (Perez-Gelabert & Thomas, 2005).

Relationship of the life cycle of *T. limbativentris* with rice crops

No information has been recorded prior to the 20th century regarding the beginning of the trophic and reproductive relationship of *T. limbativentris* with rice cultivation.

The earliest record in Latin America comes from Bodkin (1914), who reported the species in the rice fields of Guyana. In Brazil, the first reference is made by Costa Lima (1935), who mistakenly described *T. limbativentris* as a new species under the genus *Ogmocoris*, unaware that it had already been classified. In his description, Costa Lima linked the insect to rice cultivation, noting that it damaged the panicles in a manner similar to other pentatomids such as *Mormidea*, previously reported in Brazilian rice fields. The identification was later corrected, and Brazilian studies published between the 1950s and 1970s consistently associated *T. limbativentris* with rice cultivation (Silva, 1945; Amaral & Navajas, 1953; Terra, 1960; Buckup, 1961; Silva et al., 1968). In Argentina, Pennington (1920) publishes the first known reference to the presence of the species in the country, and Bosq (1940) provided the first published report of *T. limbativentris* in rice fields, documenting abundant colonies of both nymphs and adults. A broader perspective was later presented by Cheaney & Jennings (1978), who noted the species' widespread presence in rice-growing regions and identified it as a serious pest in Argentina, Brazil, and Bolivia.

One of the pioneers in studying this insect in rice cultivation was agronomist Rafael Trujillo[†], who, beginning in the 1960s, documented beautiful observations of the species in rice fields across Argentina and Brazil. In a report focused on the province of Corrientes (Argentina), Trujillo (1985) described the insect's association with rice, stating: "*Este hemíptero es considerado actualmente como uno de los más peligrosos insectos que se registran en la mayoría de los cultivos de*

arroz. Aunque su presencia es tan antigua como el propio cultivo de arroz en Corrientes, en general nunca se le ha prestado la atención que verdaderamente merece" [this hemipteran is currently considered one of the most dangerous insects found in most rice crops. Although its presence is as old as rice cultivation itself in Corrientes, it has generally never received the attention it truly deserves].

Trujillo completed his master's thesis describing the biology and damage caused by *T. limbativentris* on rice crops in Brazil and Argentina (Trujillo, 1970). Subsequently, he continued his work on rice pests in following years, refining his field observations of *T. limbativentris*. In one of his later publications (Trujillo, 1981), he proposed a figure that represents the insect's life cycle in rice crops. Figure 2 presents a modified and expanded version of Trujillo's original diagram, incorporating in the following description observations from other authors and our own research.

Spring

During this period, changes in photoperiod and rising temperature, trigger the emergence of *T. limbativentris* populations from the imaginal reproductive diapause. Coincidentally, this timeframe (late September to early October in the Southern Cone) also marks the beginning of irrigated rice sowing in the subtropical rice-growing regions of South America, where this stink bug is a major pest of the crop (Fig. 2). Increased rainfall and warmer temperatures during these months cause rice stem bugs to leave their overwintering sites and colonize rice fields around November (Ferreira et al., 1997; Botta et al., 2014). Rice stem bugs initially colonize non-irrigated plots with rice plants between 20 and 30 days after emergence (Trujillo, 1970). They settle at the base of the plant, adopting a head-down feeding posture characteristic of many stem-feeding pentatomids (Panizzi & Machado-Neto, 1992; Panizzi & Lucini, 2019). After irrigation, *T. limbativentris* occupy the tillers near the water surface, often climbing to the upper parts of the plants in the morning for thermoregulation, followed by relocation within the plots. This period marks the onset of mating and oviposition, primarily along field edges, on rice plants located on paddy ridges and in areas with uneven levelling and reduced water irrigation (Fuentes-Rodríguez, 2022).

Summer

During this period, the species reaches its highest abundance in the crop, with both nymphs and adults present (Fig. 2). In Brazil, the peak population abundance of *T. limbativentris* occurs during summer, with more than 600 adult individuals collected between January and March, with no individuals recorded in their overwintering sites throughout this time (Botta et al., 2014). In Argentine commercial rice fields, two sowing periods are practiced: early sowing, which

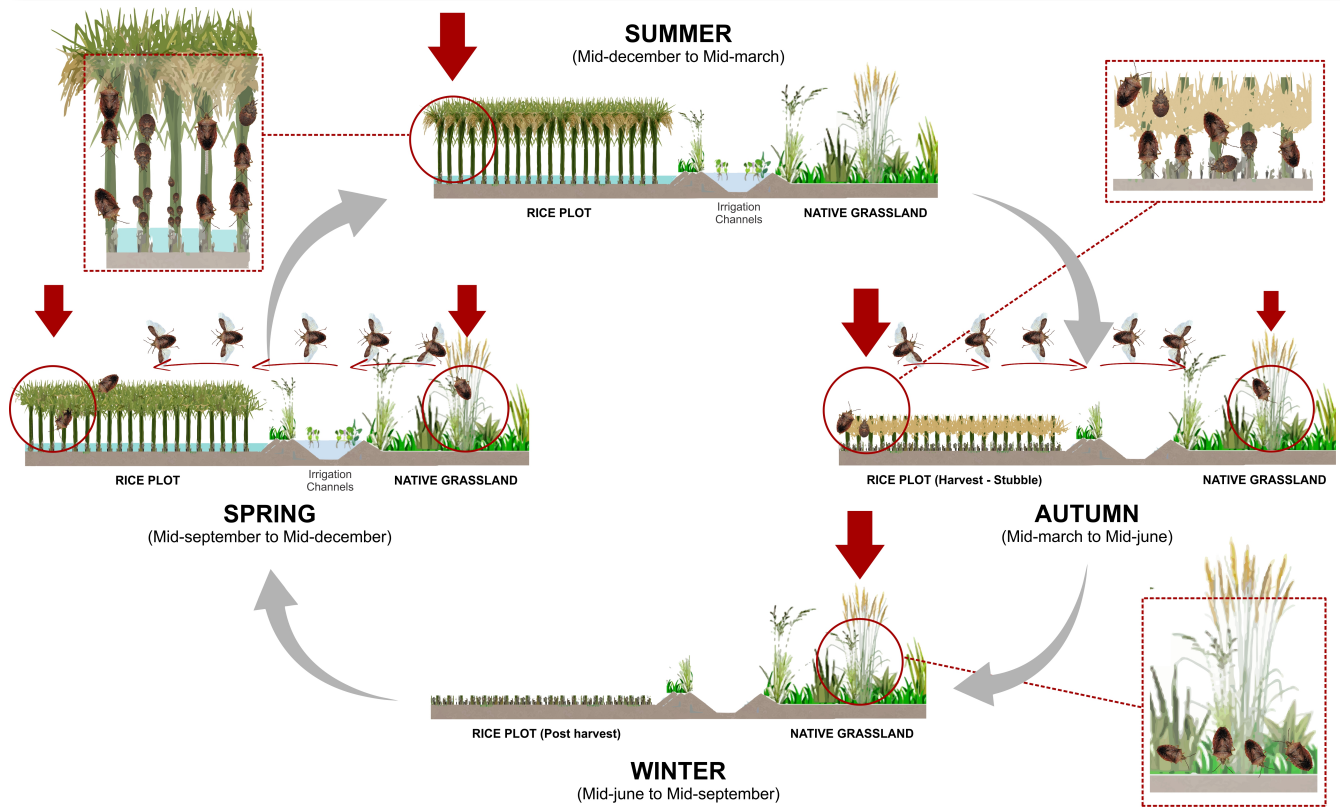


Figure 2. Distribution of *Tibraca limbativentris* in rice paddies during different seasons and stages of the crop cycle. This figure is a modified and updated color version of the black-and-white sketch published by Trujillo (1985), originally printed as “Ciclo a campo de la chinche grande” [Field cycle of the large stink bug].

begins in October and is harvested in late January to early February, and late sowing, which starts in December and is harvested in late March to early April. Differences in stink bug abundance have been observed between these two planting periods, with higher abundance recorded during the reproductive stage of late-sown plots (Fuentes-Rodríguez et al., 2025) with around 240 adult individuals collected between March and April. This pattern arises because pest species reproduce and increase their population in early-sown plots; after harvest, they disperse to late-sown plots where they remain and continue reproducing until early April. Specifically, for *T. limbativentris* in Argentine rice fields, two population peaks have been recorded during the growing season, the first occurring in summer, during the reproductive stage of early-sown plots (Fuentes-Rodríguez, 2022).

Autumn

In Argentina, the onset of autumn (mid-March) coincides with the reproductive stage of late-sown plots, marking the second population peak of *T. limbativentris* during the growing season. Shortly thereafter, the harvest of these late plots takes place, indicating the end of the rice growing season (Fig. 2). In Brazil, Klein et al. (2012) reported that following harvest in late March, *T. limbativentris* population migrate to their overwintering sites. In Argentina, however, post-harvest population of *T. limbativentris* initially take

refuge in the rice stubble (Kruger, 2014; Fuentes-Rodríguez, 2022). As long as the stubble remains fresh, the stink bugs continue feeding, and the last eggs and nymphs of the reproductive season continue to develop into adults. Once the stubble dries out, individuals migrate to overwintering host plants located near rice plots (Fuentes-Rodríguez et al., 2019). With decreasing temperatures and changes in photoperiod, diapause induction begins in the population. Klein et al. (2012) described the diapause of *T. limbativentris* as “imaginal reproductive diapause”, noting that both females and males arrived sexually immature at the overwintering refuges, with a large amount of fat bodies as food reserve. During the diapause period, reproduction does not occur. This trait is particularly interesting, as it appears to be one of the key factors contributing to the species' successful adaptation to rice cultivation. Upon emerging from diapause, the availability of high-quality food provided by the rice crop facilitates the reactivation of reproductive activity and ensures favorable conditions for nymph development and performance.

Winter

During this period, *T. limbativentris* remain in diapause within its overwintering shelters (Fig. 2). Fuentes-Rodríguez et al. (2019) found that individuals at this stage still retained large fat bodies reserves; however, 40 % of the individuals

analyzed had their digestive tract filled with food. This could suggest that the hibernating population “feeds” or “hydrates” on their host plants. Alternatively, it may be the result of digestive lethargy, a common condition caused by metabolic suppression during diapause, in which case the ingested material may not have originated from the overwintering host plant where the insect was collected. Thus, whether *T. limbativentris* actively feeds on its winter host plants remains an open question.

This phase of the *T. limbativentris* life cycle in the rice crop is crucial for integrated pest management, as the overwintering host plants selected by the species allow it to survive low winter temperatures, supporting population persistence within rice fields and enabling recolonization of the crop in the following rice growing season. This suggests that both native vegetation and rice stubble play an important role in maintaining insect populations in rice agroecosystems by providing winter shelters, a potential “bottom-up” effect. However, several studies have also reported a high impact of entomopathogenic fungi infecting *T. limbativentris* individuals in diapause within these overwintering host plants (Klein et al., 2012; Kruger, 2014; Fuentes-Rodríguez et al., 2019, 2020). This makes winter shelters a strategic target for initiating management actions prior to the start of the rice planting.

ALTERNATIVE HOST PLANTS FOR *T. LIMBATIVENTRIS*

Data collection from multiple sources

To gather the necessary information on the host plants of *T. limbativentris*, an exhaustive literature review and revision of entomological museum collections were conducted. First, a bibliographic search was performed using relevant keywords across both scientific databases (Web of Science, Scopus, Google scholar) and non-scientific sources (Google, electronic journals and repositories of universities and entomological societies).

All published papers on *Tibraca limbativentris* were reviewed using the species name as a keyword in scientific databases. This search was complemented by queries in Google in multiple languages (Spanish, Portuguese, and English), using terms such as “+Host plants +*Tibraca limbativentris*”, “+Native plants +*Tibraca limbativentris*”. The goal was to collect agronomic reports, theses, web articles, conference presentations, university repository notes, and other relevant information not published in peer-reviewed journals.

Relevant literature that was not available online, such as books, theses, and conference proceedings, was obtained directly from university libraries and institutional repositories. Specifically, we consulted the library of the Luiz de Queiroz College of Agriculture (University of São Paulo, Brazil), the

historical collection of abstracts from the Brazilian Entomological Society, the joint library of the Faculty of Agricultural and Forestry Sciences at the National University of La Plata (Argentina), and the library of the Faculty of Exact Sciences, Natural Sciences and Surveying at the National University of the Northeast (Argentina).

Specialists from different universities and both institutional and private entomological collections were also consulted to determine whether any records or historical literature mentioned host plants associated with *T. limbativentris* specimens. In Argentina, in-person visits were made to the entomological collections of the La Plata Museum of Natural Sciences (MLP-UNLP), the Bernardino Rivadavia Museum of Natural Sciences (MACN-CONICET), and the entomological collection of the Arthropoda Chair at the Faculty of Exact and Natural Sciences and Surveying, National University of the Northeast (FaCENA-UNNE). Additionally, remote consultations were conducted with the Scientific Entomological Collection of the Miguel Lillo Foundation (Argentina) and the collection of the Fritz Plaumann Entomological Museum (Brazil). For inquiries regarding type material and historical bibliography, direct communication was established with leading Pentatomidae specialists in the Neotropical region, including Dr. Jocelia Grazia (Federal University of Rio Grande do Sul, Brazil) and Dr. Gimena Dellapé (La Plata Museum, National University of La Plata, Argentina).

Alternative host plants were defined as species where overwintering *T. limbativentris* populations were directly quantified under field conditions. Reports were also sought of plants in which the insect's reproduction and performance during the summer had been reported. In field studies reporting *T. limbativentris* abundance on host plants, only those establishing a clear and direct association between the insect and specific plant species were considered. Records based on sample patches containing a mixture of plant species, without a direct link between the insect and any particular host, were excluded (e.g., Kruger et al. 2013), considering only direct references to specific plants.

For reports of the species associated with cultivated plants, each publication was reviewed and the record was classified into one of the following categories: **Fieldwork in Crop** (Published paper or thesis that includes sampling of the species in a crop field during the growing season of the crop), **Agronomy Report** (The species is officially categorized as a pest of the crop in a country's pest guide or technical/agronomic/conference report), **Experimental Report** (Study of *T. limbativentris* on the crop plant in greenhouse or laboratory conditions (e.g., host plant choice, biology), **Mention in Books** (The species is mentioned in a published book, regardless of whether the mention includes sampling or detailed study), **Citation** (An author mentions the association of *T. limbativentris* with the crop and cites other authors' work as the source), **Qualitative** (Casual

observation by an author without formal sampling or experiment, usually anecdotal but published), and **Only Mention** (Mention in a published paper or book without fieldwork, data, or reference to previous studies, no sampling, no citations, no analysis). In addition, agronomic reports were consulted to corroborate the presence of the species in the reported crops. This approach allowed us to determine whether the presence of *T. limbativentris* was incidental, whether it had been reported as a pest, or whether there was insufficient evidence to establish an association.

The reference lists of all documents were reviewed to verify and retrieve the original sources for both alternative and cultivated host plant reports. Original works cited in recent papers were located to confirm the accuracy of the information. Host plants mentioned in secondary sources were excluded if they were not clearly associated with *T. limbativentris* in the original documents (See below section 3.3. Misquotations on host plants for *T. limbativentris*). Additionally, any cases in which an author was cited as reporting host plants for the rice stem stink bug but where the publication lacked a proper bibliographic reference, were also discarded.

Finally, to validate the taxonomy and native range of the host plants, several botanical and biodiversity repositories were consulted, including the Darwinion Institute of Botany (<http://www.darwin.edu.ar/>), the Herbarium of the Public University of Navarra (<https://www.unavarra.es/herbario/index.htm>), the Virtual Herbarium of the Western Mediterranean (<https://herbarivirtual.uib.es/>), the Missouri Botanical Garden (<https://www.missouribotanicalgarden.org/>), Plants of the world Online of the Royal Botanical Garden (<https://powo.science.kew.org/>) and the Global Biodiversity Information Facility (<https://www.gbif.org/>). To verify the status of overwintering host plants within the rice agroecosystem, relevant literature on rice crop weeds was also consulted (Lovato-Echeverría et al., 2018).

Host plants

A total of 198 documents mentioning the species *T. limbativentris* were reviewed. Of these, 44.95 % were scientific papers, 21.21 % were agronomic reports, 13.64 % were conference abstracts, 10.60 % were books or book chapters, and 9.60 % were thesis manuscripts. These documents covered a wide range of topics related to *T. limbativentris*, including biology and distribution, genetic diversity, economic injury levels, reports of natural enemies, pest occurrence in rice crops, insecticide resistance, resistance of rice cultivars, seasonal abundance, population density, the effect of fungal isolates on its control, among others.

Regarding overwintering host plants, 15 documents published between 1937 and 2025 were identified as primary

sources (field sampling) for the plant species reported in the reviewed bibliography (Table I). These studies, conducted in Argentina and Brazil, report a total of 30 host plant species belonging to 7 taxonomic families, with Poaceae being the most represented, accounting for 63.33 % of the reported plants (Table I). The most frequently cited species were the grasses *Paspalum urvillei* Steud (6 publications), *Andropogon bicornis* L. (5 publications), and *Andropogon lateralis* Nees (5 publications). Among these, only the first is considered a weed in rice crops, although all three are main components of the agricultural landscape within rice fields (Table I).

In this review, no published reports were found of native plants in which this insect reproduces and thrives under natural conditions. The first field reference to the relationship between *T. limbativentris* and a host plant were made by Bosq (1937) in Argentina, in the “Lista preliminar de los Hemípteros (Heterópteros), especialmente relacionados con la agricultura nacional” [Preliminary list of Hemiptera (Heteroptera), especially related to national agriculture]. The list includes the author’s own field samplings, as well as bibliographic references to host plants previously reported for the recorded insect species. The author notes that *T. limbativentris* “se encuentra frecuentemente, en gran cantidad entre hojas y hojarascas de la ‘serrucheta’ (*Eryngium agavifolium* Gris.) junto con otros Pentatomidae” [It is frequently found in large numbers among the leaves and leaf litter of the agave-leaved sea holly (*Eryngium agavifolium* Gris.) together with other Pentatomidae]. Unfortunately, neither the season nor the time period of the record is reported, and since the presence of eggs or nymphs on that plant is also not mentioned (as Bosq did report in 1940 for *T. limbativentris* on rice), it was categorized as a winter host plant.

Given the evident preference for plants from the Poales clade (Table I, Poaceae and Cyperaceae, 22 out of the 30 reported plants), it is likely that the pattern of *O. sativa* use by *T. limbativentris* is related to the phylogenetic proximity between this crop and its original host plants (Fuentes-Rodríguez et al., 2019), which has been proposed for other insect species (Morrill, 2004; Gilbert et al., 2015; Nakadai & Murakami, 2015). Other ecological patterns may also influence the selection of alternative plants, such as aspects of plant architecture and habituation to specific characteristics of the main host plant, which may lead to the selection of similar winter hosts (Finch & Collier, 2000; Obermaier et al., 2008). In this regard, it has been suggested that local factors inherent to cultivation, such as the height of the rice variety planted in a particular rice paddy, could influence this insect’s selection of winter shelters (Fuentes-Rodríguez et al., 2020). This is linked to the level of acceptance that *T. limbativentris* exhibits toward rice plants with high nutritional value, which drives adults emerging from rice fields to seek alternative host plants with similar traits. It has been demonstrated that insects rely on visual cues

Table 1. Published reports of alternative winter host plants of *T. limbativentris* (Hemiptera: Pentatomidae) in Neotropical Rice Agroecosystems. This table presents published field records of wild host plants that serve as a winter refuge for the rice stem stink bug.

Family	Alternative Host Plant	Native Range	Habitat	Status in rice crop	Location and Source
Apiaceae	<i>Eryngium agavifolium</i> Griseb.	Argentina (Endemic)	Terrestrial	C	Argentina - Unknown (1)
	<i>Eryngium eburneum</i> Decne.	South America	Terrestrial	B	Argentina - Corrientes Province (2) Brazil - Rio Grande do Sul State (3)
Arecaceae	<i>Eryngium horridum</i> Malme	South America	Terrestrial	B	Argentina - Corrientes Province (4)
	<i>Attalea speciosa</i> Mart. Ex. Spreng	South America	Floodplain	B	Brazil - North Mesoregion, Maranhão State (5)
Asteraceae	<i>Baccharis trimera</i> (Less.) DC.	Americas	Terrestrial	C	Brazil - Rio Grande do Sul State (3)
	<i>Senecio brasiliensis</i> (Spreng.) Less.	South America	Terrestrial - Floodplain	C	Brazil - Rio Grande do Sul State (3)
Cyperaceae	<i>Cyperus</i> sp.	Cosmopolitan	Floodplain	-	Brazil - North Mesoregion, Maranhão State (6)
	<i>Cyperus entrerianus</i> Boeck.	South America	Floodplain	A B	Argentina - Corrientes Province (2)
	<i>Rhynchospora corymbosa</i> (L.) Britton	India, Southern China, Afrotropic, Central and South America	Terrestrial - Floodplain	A B	Argentina - Corrientes Province (2)
Euphorbiaceae	<i>Caperonia castaneifolia</i> (L.) A. St.-Hil.	South America	Terrestrial	A B	Argentina - Corrientes Province (7)
Poaceae	<i>Andropogon bicornis</i> L.	Americas	Floodplain	B	Argentina - Corrientes Province (2) Brazil - Eldorado do Sul & Rio Grande do Sul States (8) (9) (10) (11)
	<i>Andropogon lateralis</i> Nees	Americas	Floodplain	B	Argentina - Corrientes Province (4) (12) Brazil - Rio Grande do Sul State (3) (9) (12)
	<i>Chloris polydactyla</i> Sw.	Central and South America	Terrestrial - Floodplain	B	Argentina - Corrientes Province (4)
	<i>Echinochloa crus-galli</i> (L.) P. Beauv.	Asia	Floodplain	A	Brazil - Rio Grande do Sul State (13)
	<i>Elionurus muticus</i> (Spreng.) Kuntze	Africa, Asia and South America	Terrestrial	B	Argentina - Corrientes Province (2)
	<i>Eragrostis plana</i> Nees	South Africa	Terrestrial/Floodplain	D	Brazil - Rio Grande do Sul State (10)
	<i>Erianthus</i> sp. (<i>Saccharum</i> sp.)	Asia, Europe, and Americas	Floodplain	-	Brazil - Rio Grande do Sul State (3)
	<i>Hymenachne amplexicaulis</i> (Rudge) Nees	Americas	Aquatic	A B	Argentina - Corrientes Province (2) (4)
	<i>Lolium multiflorum</i> Lam.	Europe	Terrestrial	D	Brazil - Rio Grande do Sul State (13) (14)
	<i>Megathyrsus maximus</i> (Jacq.) B.K.Simon & S.W.L.Jacobs	Africa	Terrestrial	D	Brazil - Mato Grosso do Sul State (15)
	<i>Panicum prionitis</i> Nees	South America	Floodplain	A B	Brazil - Rio Grande do Sul State (3)
	<i>Paspalum alnum</i> Chase	South America	Terrestrial - Floodplain	B	Argentina - Corrientes Province (2)
	<i>Paspalum hydrophilum</i> Henr.	South America	Terrestrial - Floodplain	B	Argentina - Corrientes Province (4)
	<i>Paspalum plicatulum</i> Michx.	Americas	Terrestrial - Floodplain	A B	Argentina - Corrientes Province (2) (4)
	<i>Paspalum urvillei</i> Steud.	South America	Terrestrial - Floodplain	A B	Argentina - Corrientes Province (2) (4) (12) Brazil - Rio Grande do Sul State (3) (12) (13)
	<i>Paspalum wrightii</i> Hitchc. & Chase	Central and South America	Terrestrial - Floodplain	A B	Argentina - Corrientes Province (2)
	<i>Schizachyrium condensatum</i> (Kunth) Nees	Mexico, Central and South America	Floodplain	B	Argentina - Corrientes Province (2) Brazil - Rio Grande do Sul State (3)
	<i>Schizachyrium microstachyum</i> (Desv.) Roseng., B.R. Arrill. & Izag.	Mexico, Central and South America	Floodplain	B	Argentina - Corrientes Province (4)
	<i>Tridens brasiliensis</i> (Steud.) Parodi	Americas	Terrestrial	B	Argentina - Corrientes Province (4) (12) Brazil - Rio Grande do Sul State (12)
Solanaceae	<i>Physalis angulata</i> L.	Americas	Terrestrial	A B	Brazil - Rio Grande do Sul State (6)

Notes: Sources= (1) Bosq 1937; (2) Fuentes-Rodríguez et al., 2019; (3) Link et al., 1996; (4) Kruger 2014; (5) Costa et al., 2021; (6) Costa, 2014; (7) Fuentes-Rodríguez et al., 2025; (8) Aner and Becker 1993; (9) Pasini et al., 2018; (10) Botta et al., 2014; (11) Klein et al., 2012; (12) Trujillo 1970; (13) Link and Grazia 1987; (14) Lopes et al., 1974; (15) Arce et al., 2006; Status in rice crop= A. Considered as a weed during the rice growing cycle, B. Component of the agricultural landscape within the rice fields, C. Not reported on rice crops, D. Exotic plant naturalized in South America, reported as weed on Neotropical rice crops

associated with plant characteristics to optimize host plant selection (Finch & Collier, 2000). Therefore, plant height becomes one of the host phenotypical characteristics to consider in studies investigating traits that influence insect host plant selection.

However, the presence of this insect in reproductive imaginal diapause, sheltering on a particular plant during winter, does not necessarily indicate that it can reproduce and complete its life cycle on that host. An example of this can be found in Trujillo (1970), who mentions: “*No que diz respeito a sua alimentação em plantas dicotiledóneas, como caso isolado e curioso, tivemos oportunidade de observar um adulto fêmea alimentar-se de uma erva-má, do gênero Physalys sp., da família Solanácea. Embora se tratasse de uma fêmea copulada em duas oportunidades, morreu, sem haver ovipositado, depois de viver 30 dias alimentando-se da referida solanácea*” [With regard to its diet of dicotyledonous plants, as an isolated and curious case, we had the opportunity to observe an adult female feeding on a weed of the genus *Physalys* sp., of the Solanaceae family. Although it was a female that had copulated twice, she died without laying eggs after living for 30 days feeding on the aforementioned solanaceous plant]. This is related to the fact that not all host plants provide the necessary nutritional quality for an insect to successfully complete its life cycle. Therefore, controlled experiments using arenas with a mix of different host plant species are needed. This is also relevant because some of the plants reported as winter host plants are considered weeds in rice crops (Table I), and previous studies have shown that these plants can influence the population dynamics of stink bug pests in Neotropical agroecosystems (Panizzi & Lucini, 2022).

Regarding the association of *T. limbativentris* with cultivated plants (Table II), references to this insect related to five crops were found in the reviewed documents (Table II). However, the only crop in which the insect has been reported as a pest of economic importance is rice, which has multiple references from fieldwork during the rice growing season, agronomic reports for countries where it has been classified as a crop pest (Table II and Fig. 1), experimental reports of the pest completing its life cycle in rice plants, and mentions in books and citations in documents.

The first published reference of the association between *T. limbativentris* and *O. sativa* was made by Bodkin (1914) in Guyana, a report considered one of the earliest records of the species as a pest in the Americas. This was followed by Costa Lima (1935), who reported the insect as a new rice pest in Rio Grande do Sul, Brazil, and Bosq (1940), who noted that the species was found in abundant colonies of nymphs and adults in rice fields in Corrientes, Argentina. In other countries, records of this species in rice fields are more recent (Table II).

For soybean, wheat, and tomato crops, two studies (1974 and 1987) reported the presence of *Tibraca limbativentris* in

experimental fields cultivated by the Universidade Federal de Santa Maria (Brazil). In the case of wheat, a recent study by Mulero et al. (2024) demonstrated that this plant is unsuitable for the performance of *T. limbativentris*, as the species is unable to complete its life cycle on it (Table II). For tomato, one additional paper was found in which the authors mentioned the presence of the species in this crop, citing the 1974 study (Table II). No records were found of *T. limbativentris* in commercial fields of these crops.

The case of maize cultivation is particularly noteworthy and represents an interesting history to expand upon (Table II). The original mention of *T. limbativentris* on maize plants is a qualitative report (without sampling) and was made by Trujillo (1970), who explain in his thesis: “*Só um caso de fato curioso tivemos a oportunidade de observar. Um percevejo adulto, picando a haste na parte superior de uma inflorescência masculina de milho, ficou embranquecida no dia seguinte*” [We had the opportunity to observe a truly curious case. An adult stink bug, biting the stem at the top of a male corn inflorescence, turned white the next day]. After this, Ferreira et al. (1997) cited Trujillo (1970) in their report and categorized maize as an alternative host. Later, Barros et al. (2021) mentioned the presence of *T. limbativentris* in maize without citing a source, referring to it as an “uncommon occurrence.” More recently, Dueñas-López (2022) mentioned the occasional presence of *T. limbativentris* in maize and cited Barros et al. (2021). This is noteworthy because, in such cases, the species' presence in the crop is often taken for granted, even though the primary source is qualitative and no actual sampling was conducted in the crop to confirm the insect's presence. In addition, a study conducted by de Oliveira et al. (2013) demonstrated that maize plants are unsuitable for the development of *T. limbativentris* (Table II). Based on all this evidence and the lack of fieldwork during the crop growing season to support the insect's association with maize, this plant should be excluded as a host of this insect.

Misquotations on host plants for *T. limbativentris*

For overwintering host plants, Dueñas-López (2022) mentions several host species for *T. limbativentris* and cites Martínez González et al. (2006) as the source. However, *T. limbativentris* is not mentioned in the cited bibliography, nor are the reported plant species: *Urochloa mutica* (Forssk.) T.Q. Nguyen (formerly *Brachiaria mutica*), *Cyperus* sp. (actually reported by Costa, 2014, see Table II), *Digitaria sanguinalis* (L.) Scop., *Murdannia nudiflora* (L.) Brenan and *Rottboellia cochinchinensis* (Lour.) Clayton. Also, in Martínez González et al. (2006), the species *Echinochloa colonum* (L.) Link does appear, as reported by Dueñas-López (2022), but it is listed as a host of the rice pest *Oebalus insularis* Stål (Hemiptera: Pentatomidae), not *T. limbativentris*, and thus is unrelated.

Table II. Published reports linking *T. limbativentris* (Hemiptera: Pentatomidae) with crop plants. This table presents different type of reports of crops in which the rice stem stink bug has been mentioned.

Crop Plant	Pest status	Crop phenology affected	Type of Report	Country (main references per country)
Rice <i>Oryza sativa</i> L. Poaceae Planted in flooded fields (paddies), and dryland	Main pest	Vegetative and reproductive	<i>Fieldwork in Crop During the crop growing season</i> <i>Agronomy Reports</i> <i>Experimental Report</i> <i>Mention in Books</i> <i>Citation</i>	Argentina (Bosq 1940; Trujillo 1970; Quintanilla et al., 1975; Fuentes-Rodríguez et al., 2025). Brazil (Costa Lima 1935; Trujillo 1970; Lopes et al., 1974; Link & Grazia 1987; Santana et al., 2018). Colombia (Pantoja et al., 1995, 2007). Cuba (Grillo Ravelo, 2007). Ecuador (Sánchez Alvarado et al., 2023). Guadeloupe (Perez-Gelabert & Thomas, 2005). Panama (Rodríguez et al., 2006). Peru (Couturier et al., 1996). Trinidad and Tobago (Perez-Gelabert & Thomas 2005). Argentina (Trujillo, 1975, 1991; Kruger & Burdyn, 2015). Brazil (Ferreira & Martins, 1984; Ferreira et al., 1997). Bolivia (CIAT, 2003). Colombia (Pantoja et al., 1997). Costa Rica (Corrales Castillo et al., 2017). Cuba (Meneses, 2008). Dominican Republic (Serra et al., 2003). Ecuador (Rodríguez Delgado et al., 2018). Guyana (Bodkin, 1914). Honduras (Reyes-Discua, 2003; SAG, 2003). Panama (Zachrisson, 2010). Paraguay (MADES, 2006; Instituto Paraguayo de Tecnología Agraria, 2019). Suriname (Adron, 2017). Uruguay (Bentancourt & Scatoni, 1992; Martínez et al., 2018). *United States of America (Brambila, 2009; Panizzi, 2015; Heinrichs & Muniappan, 2017). Venezuela (Aponte et al. 1992; Instituto Nacional de Investigaciones Agrícolas 2004). Argentina (Kruger, 2014; Fuentes-Rodríguez, 2022; Mulero et al., 2024). Brazil (Botton et al., 1996; Silva et al., 2004; de Oliveira et al., 2013). It is concluded that the plant is suitable for the development of <i>T. limbativentris</i> (In each case, a description of the duration of the nymphal stages and the whole life cycle in different rice varieties was obtained) Argentina (Pennington, 1920; Rizzo, 1976; Trujillo, 1981; Grazia & Schwertner., 2008; Coscarón, 2017). Brazil (Garbelotto & Campos, 2014). Latin America (general) (Cheaney & Jennings, 1978; Heinrichs, 1994; Grazia et al., 2015). *United States of America (Schaefer & Panizzi, 2000; Heinrichs & Muniappan, 2017; McPherson, 2018). Venezuela (Martínez García, 1998). Brazil (Fernandes & Grazia, 1998; Barros et al., 2020, 2021) Guadeloupe (Meurgey, 2011; Lupoli, 2023) Brazil (Lopes et al., 1974; Link & Grazia, 1987) United States of America Panizzi 2015 cites Lopes et al. 1974
Soybean <i>Glycine max</i> (L.) Merr. Poaceae Planted in dryland	Unknown	Unknown	<i>Fieldwork in Crop During the crop growing season</i> <i>Citation</i>	Brazil (Lopes et al., 1974; Link & Grazia, 1987) United States of America Panizzi 2015 cites Lopes et al. 1974
Wheat <i>Triticum aestivum</i> L. Poaceae Planted in dryland	Unknown	Unknown	<i>Fieldwork in Crop During the crop growing season</i> <i>Experimental Report</i> <i>Citation</i> <i>Qualitative</i> <i>Citation</i> <i>Only Mention</i> <i>Experimental Report</i>	Brazil (Lopes et al., 1974; Link & Grazia, 1987) Argentina (Mulero et al., 2024) It is concluded that the plant is unsuitable for the development of <i>T. limbativentris</i> (approximately 75 % nymph mortality up to 48 days, longer duration of life cycle and by day 70 the nymphs were unable to reach the adult stage) United States of America Panizzi 2015 cites Lopes et al. 1974 Brazil (Trujillo, 1970) Brazil Ferreira <i>et al.</i> 1997 cites Trujillo 1970 Brazil (Barros et al., 2021) Brazil (de Oliveira et al., 2013) It is concluded that the plant is unsuitable for the development of <i>T. limbativentris</i> (55 % mortality in nymphs II and significantly longer duration of nymphal stages).
Maize** <i>Zea mays</i> L. Poaceae Planted in dryland	Unknown - Uncommon	Unknown	<i>Citation</i> <i>Qualitative</i> <i>Citation</i> <i>Only Mention</i> <i>Experimental Report</i>	 United States of America Panizzi 2015 cites Lopes et al. 1974 Brazil (Trujillo, 1970) Brazil Ferreira <i>et al.</i> 1997 cites Trujillo 1970 Brazil (Barros et al., 2021) Brazil (de Oliveira et al., 2013) It is concluded that the plant is unsuitable for the development of <i>T. limbativentris</i> (55 % mortality in nymphs II and significantly longer duration of nymphal stages).

Crop Plant	Pest status	Crop phenology affected	Type of Report	Country (main references per country)
Tomato <i>Solanum lycopersicum</i> L. Solanaceae	Unknown	Unknown	<i>Fieldwork in Crop</i> <i>During the crop</i> <i>growing season</i> <i>Citation</i>	Brazil (Lopes et al., 1974; Link & Grazia, 1987) Brazil Alves et al. 2016 cites Lopes et al. 1974 United States of America Panizzi 2015 cites Lopes et al. 1974
Planted in dryland				

Notes: * = Reports from the United States have highlighted the potential of *T. limbativentris* as an invasive species in rice crops within the country. However, to date, the species has not been detected in the United States. ** = This report is mentioned because it is included among the plants reported for the species; however, its origin is based on a qualitative observation. Given the lack of fieldwork evidence during the crop growing season to confirm the presence of *T. limbativentris* in this crop, this plant should be excluded as a host associated with *T. limbativentris* (see explanation in the paper, section 3.2 Host Plants).

Considering that the Dueñas-López report is a Compendium of the Centre for Agriculture and Biosciences International (CABI) and is presented in a web page format, it is recommended that the cited bibliography be reviewed and corrected, given the importance of CABI as a reliable and authoritative bibliographic source.

Regarding cultivated plants, due to the lack of field reports, maize should be excluded from the list of crops associated with *T. limbativentris*. Similarly, for all crops other than rice, no current evidence was found confirming the presence of *T. limbativentris* in commercial fields. Therefore, caution is recommended when mentioning the association of *T. limbativentris* with these crops.

CONCLUDING REMARKS AND FUTURE PROSPECTS

As has become evident throughout this review, many questions regarding the host plants of *T. limbativentris* remain unanswered to date. These are key questions for understanding its ecology both within and outside rice cultivation, as well as for the development of effective integrated management tools. The main unknown (and perhaps the most difficult to resolve) is which were the original host plants of this economically important stink bug, on which it fed and reproduced prior to the expansion of rice cultivation. From this central question stem others that are somewhat 'less complex': on which native plants does it currently complete its life cycle in the absence of rice, in natural conditions? On which other economically important plants in the Neotropical region could this insect successfully develop? And, from a more applied perspective, what is the best way to use rice and overwintering host plants to enhance the biological control of this native pest species?

In this context, and in order to make progress toward answering some of these questions, it is essential to conduct laboratory research under controlled conditions to assess, on the one hand, whether certain native plants of the region or crops alternative to rice are suitable for this insect to complete its life cycle with good performance. On the other hand, it is necessary to identify which of these plants contribute to

enhancing native biological control agents that affect *T. limbativentris* in local rice-growing regions, taking into account the tritrophic interactions involved. This is particularly relevant under current climate change scenarios, which make the continued expansion of insect distribution ranges highly likely. Ideally, such expansion will include not only pests but also their natural enemies; therefore, advancing in the resolution of these unknowns will represent a significant contribution to efforts aimed at implementing integrated pest management and reducing pesticide use in agricultural systems.

COMPETING INTERESTS

The authors have declared that no competing interests exist.

AUTHORS CONTRIBUTIONS

DF conceived and designed the research, collected and processed data. D.F., M.M. N.P. and A.T. jointly analyzed and interpreted data. D.F. drafted the manuscript. All authors discussed the results, made critical revisions, approved the manuscript's final version, and agreed to be responsible for its content.

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