

Host plant interactions of the corn planthopper, *Peregrinus maidis* Ashm. (Homoptera: Delphacidae) in maize and sorghum agroecosystems

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Abstract The corn planthopper, *Peregrinus maidis* (Ashmead) (Homoptera: Delphacidae) causes serious economic losses in corn and sorghum. The insect occurs mostly at humid low elevations in the tropics and coastal areas of subtropical and temperate regions of all continents, the Caribbean Islands, and islands in the Atlantic, Indian, and Pacific Oceans. This review provides a detailed compilation on the chronological progress made in basic and strategic aspects of research on the interactions between *P. maidis* and various host plants. The nature of damage by *P. maidis* and its economic impact, ecobiology in relation to host diversity, abiotic, and seasonal interactions; and life tables and alary polymorphism are discussed. Host plant resistance studies indicate that very few sources of resistance to *P. maidis* have been identified in maize, sorghum, or pearl millet, warranting a need to standardize rapid and reliable screening methods. The behavioral responses vis-à-vis mechanisms of resistance show the predominance of antixenosis for colonization and/or oviposition with variable degrees of antibiosis affecting life cycle parameters of *P. maidis* on maize and sorghum. The role of

morphological traits, physiological mechanisms, and biochemical factors governing resistance are described. Population dynamics based on density-dependent and density-independent interactions are also discussed. In addition, aspects of *P. maidis* on chemical control, biological control, and trophobiosis interactions are listed. Future thrusts on research approaches are also discussed. Genetic engineering techniques involving lectin genes in the development of transgenic plants, and the molecular mapping of genes conferring resistance to both *P. maidis* and its transmitted virus diseases may stimulate further research and lead to better understanding of *P. maidis*—host plant interactions.

Keywords Corn planthopper · *Peregrinus maidis* · Ecobiology · Abiotic factors · Life-tables · Host diversity · Host plant resistance · Mechanisms of resistance · Population dynamics · Alary polymorphism · Maize · Sorghum · Natural enemies · Management

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Introduction

The corn planthopper, *Peregrinus maidis* (Ashmead) (Homoptera: Delphacidae) was first recorded on corn in Hawaii by Perkins in 1892 (Zimmerman 1948), and is believed to have been established as early as in 1880 (Fullaway and Krauss 1945). It was included in the genus *Delphax* (Fabricius 1798), and described as *Delphax maidis* by Ashmead (1890), Quaintance (1898), and Muir (1917) and *Delphax psylloides* by Lethierry (1897). Subsequently, it was transferred to the genus *Dicranotropis* as *Dicranotropis maidis* (van Duzee 1897), and *Liburnia* as *Liburnia psylloides* Lethierry (Melichar 1903; Kirkaldy

1904). Distant (1906) described the Ceylonese specimens as *Pundaluoya simplicia*. Kirkaldy (1907) erected the genus *Peregrinus*, and redescribed it as *Peregrinus maidis* Ashmead. Metcalf (1943) published an extensive bibliography and synonymy of the species. The common name of ‘corn planthopper’ was approved by the Entomological Society of America (Blickenstaff 1965).

Geographical distribution

Peregrinus maidis is widely distributed and more prevalent in tropical regions of both hemispheres in Africa, the Americas, Asia, Australia, the Caribbean Islands, and islands in the Atlantic, Indian and Pacific oceans (Metcalf 1943; CIE 1973; Tsai et al. 1986) (Table 1). It thrives mostly in low humid elevations, but with a sharp decline at >800 m elevations in the tropics and coastal areas of subtropical and temperate regions of the world (Napompeeth 1973).

Nature of damage

Peregrinus maidis pierces the vascular tissues in the vessels of corn and sorghum by sucking sap from the leaves, leaf sheaths, and stem during exploratory feeding. Direct damage consists of sap removal from the leaves by adults and nymphs massed inside the leaf whorl, and on the inner side of the leaf sheath, causing reduced plant vigor, stunting, yellowing of leaves, and predisposition of the plant to moisture stress. Severe infestations result in withering of leaves downwards from the top of the plant, inhibition of panicle formation or emergence, and sometimes death of plant (Chelliah and Basheer 1965), through girdling of stems (Singh and Rana 1991; Chandra Shekar 1991; Chandra Shekar et al. 1993a; Singh 1997). However, infestation during later stages of sorghum results in poorly developed panicles (Rawat and Saxena 1967). This is mainly due to disruption of photosynthetic flow to the root system leading to leaf senescence. Severe oviposition in the midribs of leaves causes leaves to desiccate (Chelliah and Basheer 1965), and the tissue surrounding the eggs sometimes becomes septic and turns reddish (Napompeeth 1973). Indirect damage due to oviposition and feeding punctures, and copious excretion of honeydew by *P. maidis* predisposes corn or sorghum plants to sooty mold development (Chelliah and Basheer 1965; Borikar and Deshpande 1978), which is considered as an important contributing factor to poor quality silage, especially during the wet season (Nishida 1978). Several factors influence the plant response to feeding by *P. maidis*, such as density and nutritional status of the plant. In particular, growth stage, and water balance are critical, because small or

drought stressed plants have less ability to tolerate or recover from feeding damage. *P. maidis* feeding not only has a strong impact on the mobility of mineral nutrients, amino compounds, and carbohydrates in the phloem, but it also alters the carbohydrate-partitioning patterns, suggesting that infestation might alter sink–source relationships within the infested plant. In addition, *P. maidis* transmits a number of virus diseases in cereal crops. In India, the leaf sugary exudation (‘chikta’) due to oviposition and feeding punctures as well as excretion of honeydew by *P. maidis* is a serious menace in sorghum, and more so in soils of low fertility and in banded areas (Managoli 1973; Borade et al. 1993).

Peregrinus maidis vectors several important virus diseases in corn/maize and sorghum such as maize mosaic, maize stripe, maize streak, maize line, freckled yellow, and male sterile stunt. In addition, *P. maidis* possess staphylococcus, paramyxovirus-like, rickettsia-like, and other structures (Ammar et al. 1987) also known to cause chlorosis in sorghum (Capoor et al. 1968; Peterschmitt et al. 1991).

Crop losses

The economic impact of *P. maidis* throughout the maize and sorghum agroecosystems can be categorized as: (i) destruction of young seedlings, (ii) stunted growth, (iii) predisposition of the crop to severe moisture stress, (iv) plant mortality due to transmission of virus disease(s), and (v) reduction in crop yields. Thus, it has been difficult to accurately associate specific levels of damage with reduction in crop yields. In India, it has been estimated to cause a loss of 10–15% due to leaf sugar exudation (Chavan et al. 1959; Naik 1965; Borikar and Deshpande 1978; Mote et al. 1985; Mote and Shahane 1993), 10–18% loss of plant stand (Managoli 1973) and 30% of grain sorghum yield (Mote et al. 1985). Similarly, losses caused by viruses transmitted by *P. maidis* in corn/maize range from 9 to 90% with crop damage estimates of 22–64% in Indonesia (Baru 2000); 20–70% in Mexico (Rocha-Pena et al. 1984), and Australia by maize mosaic virus (Autrey 1983), and in Burundi by maize stripe virus (Anonymous 1999). An economic injury level of 3.7 nymphs plant⁻¹ has been determined in sorghum (Rajasekhar 1996a), and an economic threshold level of 30–40% infestation was reported in corn (Nishida 1978).

Ecobiology

The ecobiology of *P. maidis* varies geographically (Table 2). Adults mate for 40–60 min after eclosion (Rioja et al. 2006). The preoviposition period ranges from 1 to 3 days on sorghum (Chelliah and Basheer 1965;

Table 1 Geographical distribution of the corn planthopper, *Peregrinus maidis* Ashmead reported from different countries

Continent	Country/State/Territory	Reference
Africa	Angola (Quirimbo—Mozambique)	Metcalf (1943)
	Annobon Islands	Metcalf (1943)
	Ethiopia (Harar Province)	Hill (1975)
	Grand Canary	Briton-Jones (1933)
	Ghana (Accra)	Muir (1929); Metcalf (1943)
	Kenya	Metcalf (1943); Kulkarni (1973)
	Mozambique (Inhambane)	Metcalf (1943); Kulkarni (1973)
	Nigeria	Distant (1914); Lamborn (1914); Fletcher (1917)
	Republic of South Africa (Natal, Tranekei, Umtata)	Muir (1929); Metcalf (1943)
	Sierra Leone (Njala)	Muir (1929)
	Sudan	Schmutterer (1969)
	Tanzania/Tanganyika (Gentry, Zanzibar)	Metcalf (1943)
	Uganda	Metcalf (1943)
	Zambia	Fennah (1959)
Asia	India (Andhra Pradesh, Bihar, Karnataka, Madhya Pradesh, Maharashtra, Tamil Nadu)	Fletcher (1917); Rawat and Saxena (1967); Bagal and Trehan (1945); Lefroy (1915); Cherian (1937); Cherian and Kylasam (1937, 1939); Ayyar (1940); Chelliah and Basheer (1965)
	Indonesia (Amboina, Java, Kalimantan, and Mentawai Islands)	Dammerman (1919, 1929); Metcalf (1943)
	Japan (Bonin Islands, Okinawa, Ryukyus Islands, and Sanwa)	Muir (1917); Metcalf (1943); Fullaway and Krauss (1945); Fennah (1957); Ishihara (1965)
	Malaysia (East-Sabad)	Muir (1917); Metcalf (1943); Fullaway and Krauss (1945);
	People's Republic of China	Tsai et al. (1986)
	Sri Lanka	Melichar (1903); Distant (1906); Metcalf (1943)
	Taiwan (Formosa Island)	Metcalf (1943); Teson and Remes Lenicov (1989)
	Thailand	Areekul et al. (1965)
	Philippines	Fullaway (1919); Otones and Karganilla (1940); Fullaway and Krauss (1945); Capco (1959); Exconde (1977)
	Atlantic Ocean	Bermuda Islands
Canary Islands		Metcalf (1943)
Cape Verde Islands (San Nicolau)		Metcalf (1943)
Australia	Brisbane	Fennah (1965); Fletcher and Lariviere (2003)
	Gaythorn	Metcalf (1943)
	Grenada	Metcalf (1943)
	New South Wales	Metcalf (1943); Fennah (1965); Fletcher and Lariviere (2003)
	Queensland	Fennah (1965); Metcalf (1943); Perkins (1906); Carver et al. (1991)
	St. Lucia	Metcalf (1943)
	Sunnybank	Metcalf (1943)
	Wallis Islands	Metcalf (1943)
Caribbean Islands	Barbados	Metcalf (1943)
	Haiti	Dozier (1932); Metcalf (1943)
	Martinique	Metcalf (1943); Schmutterer (1990)
	Tobago	Metcalf (1943); Schmutterer (1990)
	Virgin Islands	Metcalf (1943); Fennah (1959); Eden-Green Waters (1981)
	Bahamna Islands	Metcalf (1943)
	Cuba	Crawford (1914); Loftin and Christenson (1933); Metcalf (1943)
	Guadeloupe	Metcalf (1943)
	Dominician Republic	Metcalf (1943)
Haiti (Hispaniola)	Dozier (1932); Metcalf (1943)	

Table 1 continued

Continent	Country/State/Territory	Reference
	Puerto Rico	App (1942); Dozier (1932); Wolcott (1936, 1955); Metcalf (1943); Caldwell and Martorell (1950)
	Grenada	Metcalf (1943)
	Jamaica	Metcalf (1943); Fennah (1959); Eden-Green and Waters (1981)
	Trinidad	Metcalf (1943); Waterhouse (1913)
	St Kitts	Metcalf (1943)
Central America	Costa Rica	Metcalf (1943)
	Guatemala (Tiquisate)	Painter (1955)
	Mexico (Baja California, Chiapas, Guerrero, Veracruz)	Crawford (1914); Loftin and Christenson (1933); Metcalf (1943)
	Nicaragua	Crawford (1914); Metcalf (1943)
Europe	Scotland (Ayr)	Metcalf (1943)
Indian Ocean	Madagascar	Williams (1957)
	Mariana Islands	Metcalf (1943); Fennah (1965)
	Mauritius (Rodrigues Island)	Metcalf (1943); Williams (1957)
	New Caledonia	Metcalf (1943)
	Reunion Island	Dadant and Etienne (1973)
	Seychelles (Mahe, Praslin)	Distant (1914); Fletcher (1917); Metcalf (1943)
North America	USA (Alabama, California, Florida, Hawaii, Illinois, Louisiana, New Jersey, North Carolina, South Carolina, Ohio, Tennessee, Texas, Virginia, Washington DC)	Crawford (1914); Metcalf (1943); Zeyen and Morrison (1975); Ashmead (1890); Quaintance (1898); Watson et al. (1939); Van Dine (1904); Kirkaldy (1904, 1907, 1910); Fullaway (1912, 1918); Fletcher (1917); Giffard (1922); Fullaway and Krauss (1945); Zimmerman (1948); Verma (1954, 1955a); Beardsley (1959); Barber and Pepper (1942); Brimley (1938); Thomas (1913); Brooks and Anderson (1947)
Pacific Ocean	Caroline Islands (Micronesia)	Fennah (1965)
	Fiji Islands	Swaine (19); Metcalf (1943)
	Island of Lanai	Illingworth (1928)
	Guam Island	Metcalf (1943); Swezey (1936, 1942)
	New Zealand	Fennah (1965); Fletcher and Lariviere (2003)
	New Hebrides Island	Metcalf (1943)
	Palau Islands (Angaur, Koror, Ngarmalk, and Peleliu)	Fennah (1965)
	Samoa Islands	Metcalf (1943)
	Solomon Islands	Metcalf (1943)
	Tonga (Friendly) Islands	Metcalf (1943)
	Tahiti, Taumoto (Low Archipelago)	Metcalf (1943); Dammerman (1919, 1929)
South America	Argentina (Bahia Blanca, Buenos Aires, Chaco, Corrientes, Entre Rios, Formosa, Para, Salta, and Tucuman)	Crawford (1914); Metcalf (1943); Teson and de Remes Lenicov (1989); Remes Lenicov and Virla (1992, 1999); Remes Lenicov and Mariani (2001); Remes Lenicov et al. (2006)
	Brazil (Bahia, Campinas, Guanabar, Rio de Janeiro, Salta, and St. Paulo)	Crawford (1914)
	Chile	Aguilera (1972); Borrer et al. (1976); Cisneros (1995)
	Colombia	Varon de Agudello and Martinez Lopez (1980)
	Guanabara	Metcalf (1943)
	Guiana Island	Metcalf (1943)
	Surinam	Metcalf (1943)
	Venezuela (Maracay-Araqua, Cotaxtla, and La Granja)	Giffard (1922); Fullaway and Krauss (1945); Zimmerman (1948); Malaguti and Naranjo (1963); Marin Acosta (1964); Malaguti (1963); Herold (1963); Trujillo et al. (1974)
	Peru	Alata (1973)

Table 2 Biological parameters of the corn planthopper, *Peregrinus maidis* Ashmead, on different host plants reported from different countries

Biological parameter	Host	Mean	Range	Country from which reported	Reference
Preoviposition period (d)	Maize		3–6	USA (Florida)	Tsai and Wilson (1986)
	Maize		4–10	USA (Hawaii)	Napompeth (1973)
	Maize		15–19	Argentina	Fernandez-Badillo (1984); Fernandez-Badillo and Clavijo (1990a)
Oviposition period (d)	Sorghum	8.5		Taiwan	Chen (1991)
		2	1–3	India (Tamil Nadu)	Chelliah and Basheer (1965)
			2–3	India (Andhra Pradesh)	Rajasekhar (1989, 1997)
	Maize	27	5–45	Hawaii	Napompeth (1973)
	Maize	27	11–48	USA (Florida)	Tsai and Wilson (1986)
	Maize		19–30	Argentina	Fernandez-Badillo and Clavijo (1990a)
Eggs female ⁻¹ day ⁻¹ (no)	Sorghum		6–7	India (Andhra Pradesh)	Rajasekhar (1989)
	Maize		3–4	Argentina	Fernandez-Badillo (1984); Fernandez-Badillo and Clavijo (1990a)
	Maize	19.6	15.6–25.1	USA (Florida)	Tsai and Wilson (1986)
	Maize	50		USA	Fullaway (1918); Zimmerman (1948)
	Sorghum		3–20	India (Tamil Nadu)	Chelliah and Basheer (1965)
Eggs female ⁻¹ generation ⁻¹ (no)	Maize	76		Philippines	Catindig (1993); Catindig et al. (1996)
	Maize	200			Fullaway (1918); Zimmerman (1948)
Brachypters	Maize		90–125	Argentina	Fernandez-Badillo (1984); Fernandez-Badillo and Clavijo (1990a)
	Maize	605	297–938	USA (Florida)	Tsai and Wilson (1986)
	Sorghum ^a		29–46	India (Andhra Pradesh)	Rajasekhar (1989)
	Sorghum ^b		34–45	India (Andhra Pradesh)	Rajasekhar (1989)
	Sorghum		18–94	India (Andhra Pradesh)	Rajasekhar (1989)
Macropters	Sorghum		5–64	India (Andhra Pradesh)	Rajasekhar (1989)
	Maize	5.2		Philippines	Catindig (1993); Catindig et al. (1995, 1996)
Egg incubation (d)	Maize	8	5–8	Argentina	Fernandez-Badillo (1984); Fernandez-Badillo and Clavijo (1990a)
	Maize	8.4		USA (Hawaii)	Napompeth (1973)
	Maize	8.5		Taiwan	Chen (1991)
	Maize ^c		9–20	USA	Fullaway (1918); Zimmerman (1948)
	Maize ^d	8.2		USA (Florida)	Tsai and Wilson (1986)
	Maize ^b	8		USA (Florida)	Tsai and Wilson (1986)
	Sorghum		4–5	India (Tamil Nadu)	Chelliah and Basheer (1965)
	Sorghum	8.2	7–10	India (Andhra Pradesh)	Rajasekhar (1989)
	Sugarcane		9–12	Venezuela	Guagliumi (1962)

Table 2 continued

Biological parameter	Host	Mean	Range	Country from which reported	Reference
Nymphal period (d)					
Instar-1					
	Barnyard grass	5.2		USA (Florida)	Tsai and Wilson (1986)
	Gamagrass	4.6		USA (Florida)	Tsai and Wilson (1986)
	Goosegrass	4.4		USA (Florida)	Tsai and Wilson (1986)
	Itchgrass	3		USA (Florida)	Tsai and Wilson (1986)
	Maize	3		Argentina	Fernandez-Badillo (1984); Fernandez-Badillo and Clavijo (1990a)
	Maize	3.8		USA (Florida)	Tsai and Wilson (1986)
	Maize	10.1		Chile	Rioja et al. (2006)
	Maize		2–4	Hawaii	Verma (1954, 1955a)
	Maize		3–4	USA	Fullaway (1918); Zimmerman (1948)
	Maize	4	2–7	Hawaii	Napompeth (1973)
	Sorghum	3.4		India (Tamil Nadu)	Chelliah and Basheer (1965)
	Sorghum	3.9		USA (Florida)	Tsai and Wilson (1986)
	Barnyard grass	5.1		USA (Florida)	Tsai and Wilson (1986)
	Gamagrass	8.6		USA (Florida)	Tsai and Wilson (1986)
	Goosegrass	5.3		USA (Florida)	Tsai and Wilson (1986)
	Itchgrass	3.1		USA (Florida)	Tsai and Wilson (1986)
	Maize	2		Argentina	Fernandez-Badillo (1984); Fernandez-Badillo and Clavijo (1990a)
	Maize	3		USA (Florida)	Tsai and Wilson (1986)
	Maize	8.9		Chile	Rioja et al. (2006)
	Maize		2–3	USA (Hawaii)	Verma (1954, 1955a)
	Maize		2–4	USA	Fullaway (1918); Zimmerman (1948)
	Maize	4	2–7	USA (Hawaii)	Napompeth (1973)
	Sorghum	3		India (Tamil Nadu)	Chelliah and Basheer (1965)
	Sorghum	3.5		USA (Florida)	Tsai and Wilson (1986)

Table 2 continued

Biological parameter	Host	Mean	Range	Country from which reported	Reference
Instar-3	Barnyard grass	5.7		USA (Florida)	Tsai and Wilson (1986)
	Gamagrass	12.3		USA (Florida)	Tsai and Wilson (1986)
	Goosegrass	4.8		USA (Florida)	Tsai and Wilson (1986)
	Itchgrass	4		USA (Florida)	Tsai and Wilson (1986)
	Maize	2		Argentina	Fernandez-Badillo (1984); Fernandez-Badillo and Clavijo (1990a)
	Maize	3.1		USA (Florida)	Tsai and Wilson (1986)
	Maize	9.9		Chile	Rioja et al. (2006)
	Maize		3–5	Hawaii	Verma (1954, 1955a)
	Maize		3–4	USA	Fullaway (1918); Zimmerman (1948)
	Maize	3.8	2–6	USA (Hawaii)	Napompeth (1973)
	Sorghum	2.9		India (Tamil Nadu)	Chelliah and Basheer (1965)
	Sorghum	4.1		USA (Florida)	Tsai and Wilson (1986)
	Barnyard grass	5.1		USA (Florida)	Tsai and Wilson (1986)
	Gamagrass	16.2		USA (Florida)	Tsai and Wilson (1986)
	Goosegrass	5.3		USA (Florida)	Tsai and Wilson (1986)
	Instar-4	Itchgrass	4.3		USA (Florida)
Maize		3		USA (Florida)	Tsai and Wilson (1986);
Maize		3		Argentina	Fernandez-Badillo (1984); Fernandez-Badillo and Clavijo (1990a)
Maize		3.1		USA (Florida)	Tsai and Wilson (1986)
Maize		10.4		Chile	Rioja et al. (2006)
Maize			2–4	Hawaii	Verma (1954, 1955a)
Maize			3–4	USA	Fullaway (1918); Zimmerman (1948)
Maize		4	3–6	USA (Hawaii)	Napompeth (1973)
Sorghum		2.8		USA (Florida)	Tsai and Wilson (1986)
Sorghum		3.2		India (Tamil Nadu)	Chelliah and Basheer (1965)

Table 2 continued

Biological parameter	Host	Mean	Range	Country from which reported	Reference
Instar-5	Barnyard grass	6.2		USA (Florida)	Tsai and Wilson (1986)
	Gamagrass	18.6		USA (Florida)	Tsai and Wilson (1986)
	Goosegrass	5.3		USA (Florida)	Tsai and Wilson (1986)
	Itchgrass	3.5		USA (Florida)	Tsai and Wilson (1986)
	Maize	4.2		USA (Florida)	Tsai and Wilson (1986)
	Maize	5		Argentina	Fernandez-Badillo (1984); Fernandez-Badillo and Clavijo (1990a)
	Maize	11		Chile	Rioja et al. (2006)
	Maize		3–6	USA (Hawaii)	Verma (1954, 1955a)
	Maize		4–5	USA	Fullaway (1918); Zimmerman (1948)
	Maize	4.7	3–7	USA (Hawaii)	Napompeth (1973)
	Sorghum	3.7		India (Tamil Nadu)	Chelliah and Basheer (1965)
	Sorghum	4.9		USA (Florida)	Tsai and Wilson (1986)
	Barnyard grass	27.3		USA (Florida)	Tsai and Wilson (1986)
	Gamagrass	60.3		USA (Florida)	Tsai and Wilson (1986)
	Goosegrass	25.1		USA (Florida)	Tsai and Wilson (1986)
	Itchgrass	17.9		USA (Florida)	Tsai and Wilson (1986)
	Total nymphal period (d)	Maize	14		Puerto Rico
Maize		15		Argentina	Fernandez-Badillo (1984); Fernandez-Badillo and Clavijo (1990a)
Maize		17.1		Taiwan	Chen (1991)
Maize		17.2		USA (Florida)	Tsai and Wilson (1986)
Maize		17.2		Philippines	Catindig (1993); Catindig et al. (2006)
Maize		50.4		Chile	Rioja et al. (2006)
Maize			17–25	USA (Hawaii)	Verma (1954, 1955a)
Maize				USA	Fullaway (1918); Zimmerman (1948)
Maize			15–25	Venezuela	Guagliumi (1962)
Maize		21	17–25	USA (Hawaii)	Napompeth (1973)
Sorghum		19.2		USA (Florida)	Tsai and Wilson (1986)
Sorghum		24.5	18–31	India (Tamil Nadu)	Chelliah and Basheer (1965)
Sorghum			22–26	India (Andhra Pradesh)	Rajasekhar (1997)
Sugarcane			15–25	Venezuela	Guagliumi (1962)

Table 2 continued

Biological parameter	Host	Mean	Range	Country from which reported	Reference
Nymphal mortality (%)	Instar-1	Barnyard grass	13.6	USA (Florida)	Tsai and Wilson (1986)
		Gamagrass	8.6	USA (Florida)	Tsai and Wilson (1986)
		Goosegrass	17.1	USA (Florida)	Tsai and Wilson (1986)
	Instar-2	Itchgrass	29.5	USA (Florida)	Tsai and Wilson (1986)
		Maize	5.3	USA (Florida)	Tsai and Wilson (1986)
		Sorghum	10	USA (Florida)	Tsai and Wilson (1986)
		Barnyard grass	55.6	USA (Florida)	Tsai and Wilson (1986)
		Gamagrass	21.9	USA (Florida)	Tsai and Wilson (1986)
		Goosegrass	17.2	USA (Florida)	Tsai and Wilson (1986)
		Itchgrass	15	USA (Florida)	Tsai and Wilson (1986)
		Maize	34.4	USA (Florida)	Tsai and Wilson (1986)
		Sorghum	0	USA (Florida)	Tsai and Wilson (1986)
		Barnyard grass	31	USA (Florida)	Tsai and Wilson (1986)
		Gamagrass	14	USA (Florida)	Tsai and Wilson (1986)
		Goosegrass	34.2	USA (Florida)	Tsai and Wilson (1986)
Instar-3	Itchgrass	26.5	USA (Florida)	Tsai and Wilson (1986)	
	Maize	25.4	USA (Florida)	Tsai and Wilson (1986)	
	Sorghum	14.4	USA (Florida)	Tsai and Wilson (1986)	
	Barnyard grass	16.7	USA (Florida)	Tsai and Wilson (1986)	
	Gamagrass	18.6	USA (Florida)	Tsai and Wilson (1986)	
	Goosegrass	28.9	USA (Florida)	Tsai and Wilson (1986)	
	Itchgrass	20	USA (Florida)	Tsai and Wilson (1986)	
	Maize	13.6	USA (Florida)	Tsai and Wilson (1986)	
	Sorghum	0	USA (Florida)	Tsai and Wilson (1986)	
	Barnyard grass	12	USA (Florida)	Tsai and Wilson (1986)	
	Gamagrass	68.6	USA (Florida)	Tsai and Wilson (1986)	
	Goosegrass	39.6	USA (Florida)	Tsai and Wilson (1986)	
	Itchgrass	41.7	USA (Florida)	Tsai and Wilson (1986)	
	Maize	44.7	USA (Florida)	Tsai and Wilson (1986)	
	Adult longevity (d)	Sorghum	20	USA (Florida)	Tsai and Wilson (1986)
Maize		10–11	USA (Florida)	Tsai and Wilson (1986)	
Maize		11.7	Philippines	Catindig (1993); Catindig et al. (1995, 1996)	
Maize		31.9	Taiwan	Chen (1991)	
Maize		62.1	USA (Florida)	Napompeth (1973)	
Maize			Chile	Rioja et al. (2006)	

Table 2 continued

Biological parameter	Host	Mean	Range	Country from which reported	Reference
Macropters (♀)					
Generation-1	Sorghum	43		India (Andhra Pradesh)	Rajasekhar (1989, 1997)
Generation-2	Sorghum		14–53	India (Madhya Pradesh)	Rawat and Saxena (1967)
Macropters (♂)	Sorghum	37		India (Andhra Pradesh)	Rajasekhar (1989, 1997)
Generation-1	Sorghum	16		India (Andhra Pradesh)	Rajasekhar (1989, 1997)
Generation-2	Sorghum	12	19–71	India (Madhya Pradesh)	Rawat and Saxena (1967)
Brachypters (♀)	Sorghum	42		India (Andhra Pradesh)	Rajasekhar (1989, 1997)
Brachypters (♂)	Sorghum	14	22–61	India (Madhya Pradesh)	Rawat and Saxena (1967)
	Sorghum		17–41	India (Andhra Pradesh)	Rajasekhar (1989, 1997)
	Sorghum			India (Madhya Pradesh)	Rawat and Saxena (1967)

a, Month: September

b, Month: November–January

c, Season: Summer

d, Month: September–November

Rajasekhar 1989, 1997); and 3 to 19 days on maize (Napompeth 1973; Tsai and Wilson 1986; Fernandez-Badillo 1984; Fernandez-Badillo and Clavijo 1990a; Chen 1991). Each female lays 500–600 eggs in her life time, and prefers laying eggs in a row on the upper surface of the midrib of basal mature corn/sorghum leaves. At each instance, 1–4 eggs are laid by the female and covered from outside with a secretion of white waxy substance (Otanés and Karganilla 1940). The oviposition period ranges from 5 to 45 days on maize (Fernandez-Badillo 1984; Napompeth 1973; Tsai and Wilson 1986; Fernandez-Badillo and Clavijo 1990a); and 6–7 days on sorghum (Rajasekhar 1989). The number of eggs $\text{♀}^{-1} \text{day}^{-1}$ ranges from 3 to 4 (Fernandez-Badillo 1984; Fernandez-Badillo and Clavijo 1990a), 15.6–25.1 (Tsai and Wilson 1986), with 50 on maize (Fullaway 1918; Zimmerman 1948); and 20 on sorghum (Chelliah and Basheer 1965). In general, the total number of eggs ♀^{-1} averages 76 (Catindig 1993; Catindig et al. 1996), and ranges from 90 to 125 (Fernandez-Badillo 1984; Fernandez-Badillo and Clavijo 1990a), 200 (Fullaway 1918; Zimmerman 1948), and 297–938 (*av.* 605) on maize (Tsai and Wilson 1986). Seasonal variations of 29–46 and 34–45 during September and November–January, respectively occur on sorghum (Rajasekhar 1989). The total fecundity of brachypterous and macropterous forms ranges from 18 to 94 and 5 to 64, respectively on sorghum (Rawat and Saxena 1967). Egg incubation time ranges from 4 to 10 days on sorghum (Chelliah and Basheer 1965; Rajasekhar 1989, 1997) and 5–12 days on maize (Napompeth 1973; Marin Acosta and Sarmiento 1981; Fernandez-Badillo 1984; Fernandez-Badillo and Clavijo 1990a; Catindig 1993; Catindig et al. 1995, 1996), and 9–12 days on sugarcane (Guagliumi 1962), but extended upto several weeks in cooler temperatures on maize (Fullaway 1918; Zimmerman 1948).

On hatching, nymphs crawl inside the whorls of corn and sorghum plants for congregation (Otanés and Karganilla 1940; Verma 1954, 1955; Chelliah and Basheer 1965; Rawat and Saxena 1967; Napompeth 1973), and pass through five instars. The duration of each nymphal instar has been given as 2–11 days by various authors (Table 2) (Fullaway 1918; Zimmerman 1948; Verma 1954, 1955a; Napompeth 1973; Fernandez-Badillo 1984; Fernandez-Badillo and Clavijo 1990a; Rioja et al. 2006; Chelliah and Basheer 1965; Tsai and Wilson 1986). The total nymphal period averages 22–26 days on sorghum (Chelliah and Basheer 1965; Rajasekhar 1989, 1997); 14–50 days on maize (Wolcott 1955; Napompeth 1973; Fernandez-Badillo 1984; Fernandez-Badillo and Clavijo 1990a; Chen 1991; Catindig 1993, 1996; Catindig et al. 1995, 1996); and 15–25 days on sugarcane (Guagliumi 1962). The mean life expectancy of adults is only 10–11 days on maize in the Philippines but upto 30 even over 60 days in Florida and

Chile, respectively (Napompeth 1973; Chen 1991; Catindig 1993; Catindig et al. 1996; Rioja et al. 2006). The adult longevity on sorghum ranges between 14–53 and 19–71 days for male and female macropters (Rawat and Saxena 1967, Rajasekhar 1989, 1997), and an average of 14–42 days and 12–61 days for male and female brachypters, respectively, in the first and second generations (Rawat and Saxena 1967, Rajasekhar 1989, 1997), and a sex ratio of 1♂:1.27♀ (Raja Sekhar 1997). The total life cycle from egg-to-adult was 22.4 days (Catindig 1993; Catindig et al. 1996), and exclusive of incubation period ranged between 22 and 84 days (*av.* 53 days) on corn (Napompeth 1973); and 34 days on sorghum (Rajasekhar 1989, 1997) (Table 2).

In general, brachypterous females are more abundant and reproductively more efficient based on faster developing offspring, shorter preoviposition period, higher number of eggs female⁻¹, longer ovipositional period, and greater longevity (Fernandez-Badillo 1984; Fernandez-Badillo and Clavijo 1990a). Usually, first and second instar nymphs prefer moist shady places for aggregation in corn leaf axils or sorghum leaf sheaths. Late instar nymphs are more active than early instars, and their activity is more or less equivalent to the brachypterous form. Although plants at tasseling in maize and preboot stage in sorghum are less susceptible to the *P. maidis*, infestation may result in twisting of the top-most leaves and prevent emergence and/or development of the panicle (Singh and Rana 1992; Chandra Shekar et al. 1993; Singh 1997).

Host plant diversity

Peregrinus maidis exhibits oligophagy, which may be due to host range expansion and/or selective pressures associated with a common habitat. Among cultivated crops, corn/maize and sorghum are principal hosts; while the latter species is considered as the ancestral host (Nault 1983). In addition, a wide range of commonly found grasses and grassy weeds from the families of Gramineae, Cyperaceae, Cannaceae, Commelinidae, and Sterculiaceae serve as spring, summer or overwintering principal, accidental, or alternate hosts for oviposition and feeding by *P. maidis* (Table 3). Many wild warm-season grasses that serve as summer hosts may be colonized by macropters for feeding that complete development on spring hosts. Under natural conditions, *P. maidis* is generally observed on itchgrass (*Rottboellia exaltata* Lf.), where its active multiplication confirms a significant role as a host and also as a vector of maize mosaic and maize stripe viruses (Greber 1981). However, diverse host species have also been recorded as insusceptible hosts to *P. maidis*. In general, *P. maidis* maintains small populations on grassy weeds in temperate countries during spring before the cereal crops are planted.

Paragrass (*Panicum purpurescens* Raddi Henr.) is second to sorghum, but better than panola grass (*Digitaria decumbens* Stent.) for its population buildup. *Peregrinus maidis* is unable to complete its life cycle on Napier grass (*Pennisetum purpureum* Schumach), California grass (*Brachiaria mutica* Stapf.), job's-tears (*Coix lachrymal-jobi* L.), and sugarcane (*Saccharum officinarum* L.), while sour grass [*Trichachne insularis* (L.) Nees.], vaseygrass (*Paspalum urvillei* Steud.), and nutgrass [*Cyperus rotundus* (L.)] (Namba and Higa 1971) support some populations. Chelliah and Basheer (1965) reported that *P. maidis* utilized pearl millet [*Pennisetum typhoides* (Stapf. and Hubbard)], Johnsongrass [*Sorghum halepense* (L.)], Foxtail millet [*Setaria italica* (Beauv.)], Jungle ricegrass [*Echinochloa colona* var. *frumentacea* (L.)], and Kodo millet [*Paspalum scrobiculatum* (L.)] for feeding. During the period of suitable host plant shortage, *P. maidis* oviposits indiscriminately on *C. lachrymal-jobi*, *S. halepense*, and sugarcane (Napompeth 1973).

The influence of diverse hosts on oviposition preference and life history table studies revealed that although *P. maidis* feeds and reproduces on gamagrass (*Tripsacum dactyloides* L.) this species is not as suitable a host as sweet corn, sorghum or itchgrass (Tsai 1986). There is a significant response as a reproductive sink for oviposition and survival of eggs on maize and itchgrass as compared to wild Proso millet (*Panicum maximum* Jacq.) and Asian sprangletop [*Leptochloa chinensis* (L.) Nees.], while Mexican Primrose willow [*Ludwigia octovalvis* (Jacq.) Raven] was a poor host for oviposition (Catindig 1993; Catindig et al. 1996). Nymphs do not develop, but adults survive for various lengths of time on rye (*Secale cereale* L.), oats (*Avena sativa* L.), rice (*Oryza sativa* L.), and sugarcane. In contrast, nymphal development is significantly shorter on maize, itchgrass, Proso millet, and *L. chinensis* (Catindig 1993; Catindig et al. 1995); and corn, itchgrass, and sorghum as compared to goosegrass [*Eleusine indica* (L.) Gaertn.], barnyard grass (*Echinochloa crusgalli* L.), and gamagrass (Tsai 1996). These alternate hosts are considered as reservoirs for *P. maidis*, and responsible for the outbreaks. In addition to corn and sorghum, many wild warm-season grasses also serve as summer hosts, and may be colonized by macropters that complete development on spring hosts. First stage nymphs have greater survival rates compared with other nymphal instars. The cumulative survival rate of neonate-to-adult was high on maize, itchgrass, *P. maximum*, and *L. chinensis* (Catindig 1993; Catindig et al. 1995), including sorghum (Tsai 1996). Adult longevity is higher on gamagrass, corn, and itchgrass than on sorghum, goosegrass, and barnyard grass (Tsai 1996); but the total number of eggs produced is considerably greater on sorghum, goosegrass, barnyard grass, and gamagrass. The number of *P. maidis*

eggs $\text{♀}^{-1} \text{ day}^{-1}$ and number of eggs $\text{♀}^{-1} \text{ generation}^{-1}$ are approximately four times greater on corn compared to itchgrass and gamagrass (Tsai 1996); and 4- and 6-times greater on maize and itchgrass over Proso millet, and *L. chinensis*, respectively (Catindig 1993; Catindig et al. 1995). The combined effects of increased *P. maidis* colonization and improved performance on nitrogen-rich plants often results in rapid population growth and larger population size (Wang et al. 2006).

Abiotic interactions

Differential mating combinations of macropterous and brachypterous *P. maidis* adults show a gradual decline in the preoviposition period and in egg mortality in relation to increases in temperature from 15 to 25°C (Fernandez-Badillo 1984; Fernandez-Badillo and Clavijo 1990a). At 25°C, the preoviposition ranges from 15 to 19 days, total eggs ♀^{-1} are 90–125 with a daily rate of 3–4 eggs ♀^{-1} , and the oviposition period ranges from 19 to 30 days, and an egg incubation period of 8 days.

At optimal temperatures of 21.1 and 26.7°C, the nymphal duration is longer but adult longevity is shorter. The nymphal duration of macropterous and brachypterous adults proportionately increases at 15 and 20°C, is reduced at 25°C, while the fifth instar is eliminated at 10°C (Table 4) (Fernandez-Badillo and Clavijo 1990a). The duration from egg hatching to adult is extended to 73.5 days at 10°C, which is four-fold increase compared to 26.7°C (18.4 days). A supernumerary sixth instar nymph appears only at 15.6°C, with a total development period of 65.2 days. Interestingly, at 10 and 32.2°C, fourth instar nymphs molt directly to adults in 33.5 days, which is almost twice as long as the time required at the optimal temperature. Developmental times of each instar nymph range from 10–24 days for instar-1 to instar-4 at 10°C; 7.7–13.5 days for instar-1 to instar-6 at 15.6°C; 4.6–6 days for instar-1 to instar-5 at 21.1°C; 7.7–13.5 days at 26.7°C; and 10.9–16.8 days for instar-1 to instar-4 at 32.2°C (Table 5). The duration of nymphal stages is longer, but adult longevity is shorter at >26.6°C (Tsai and Wilson 1986). The development of nymphs is faster during September–November with a survival rate of 75% (Rajasekhar 1989, 1996b). There is a gradual decline in mortality as nymphs mature from the first to fifth instars in relation to temperatures between 15 and 25°C. Egg-to-adult duration takes 25, 46, and 62 days at 25, 15, and 20°C, respectively (Fernandez-Badillo 1984; Fernandez-Badillo and Clavijo 1990b). At hot (30°C) compared to cool (10°C) temperatures, eggs and nymphs develop more rapidly, but the rates of survival are reduced. *Peregrinus maidis* individuals develop fastest between 25 and 28°C, and temperature variations in either direction cause delayed development.

There is a gradual increase in longevity of macropterous and brachypterous adults during 15–25°C (Fernandez-Badillo 1984; Fernandez-Badillo and Clavijo 1990a). In contrast, Tsai and Wilson (1986) observed that the longevity of adult males and females was low at 10°C and high at 15.6°C with a gradual decline at 21.1, 26.7, and 32.2°C. Normal development occurred at 13.1–22.8°C and 28.5–31.2°C in India (Rajasekhar 1989, 1997); 18–25°C in Argentina (Marin Acosta 1964); 21.1–26.7°C in the USA (Tsai and Wilson 1986); and 25°C in Brazil (Fernandez-Badillo 1984; Fernandez-Badillo and Clavijo 1990a). Each generation is completed in 25–30 days at 25°C. In general, the pre- and post-reproductive survival, and longevity were all shortened as the temperatures increased (Tsai and Wilson 1986; Fernandez-Badillo 1984; Fernandez-Badillo and Clavijo 1990a). The shorter life expectancy is associated with higher mean daily temperatures, and reduced duration of instar-3 and instar-4 nymphs (Tsai and Wilson 1986).

The development of *P. maidis* was unfavorable at 23.5–25.6°C, 20–180 mm rainfall, and 58–75% relative humidity, with a threshold being 18.3°C (Marin Acosta 1964). Total development time from egg hatch-to-adult emergence was 73.5, 65.2, 27.2, 18.4, and 33.5 days correspondingly at 10, 15.6, 21.1, 26.78, and 32.5°C. Longevity of adults was highest at 15.6°C and lowest at 10°C, but normal development occurs between 21.1 and 26.7°C (Tsai and Wilson 1986). In general, the temperature ranges of 13.1–22.8°C and 28.5–31.2°C was considered as optimal for the incidence of *P. maidis* (Rajasekhar 1989, 1997). Oviposition activity was higher during the morning and evening hours. On overcast and cool days, the females were seen depositing eggs until later in the day. Light intensity and temperature were suspected as the governing factors for egg-laying (Napompeth 1973). Increase in night temperatures and low humidity during October–December, had a greater impact on the population dynamics reaching from 200 to 700 plant⁻¹ (Mote 1983). In addition, the population buildup was influenced by damp, cloudy, and drizzling weather (Chelliah and Basheer 1965; Rawat and Saxena 1967), and associated with RH, but neither with temperatures (Prabhakar et al. 1986) nor hot dry conditions (Rawat and Saxena 1967). In contrast, low density of immigrant macropters, unexpected rainfall, and low temperatures in late stages of sorghum during the postrainy season seem to play a greater role in reducing the population density and damage.

Seasonal interactions

In India, the seasonal fluctuations of *P. maidis* on sorghum was found during July–December with a peak in September (Agarwal et al. 1978); July–March with a peak during

Table 3 Susceptible host plant range and status of the corn planthopper, *Peregrinus maidis* Ashm. reported from different countries

Scientific name	Family	Common name	Host status	Country (State) from which reported	Reference
<i>Agropyron repens</i> (L.) Beauv.	Poaceae/Gramineae	Couch grass, dog-grass, quich-grass, ray-grass scotch quelch, twitch grass		Chile	Rioja et al. (2006)
<i>Avena fatua</i> L. [Syn: <i>Avena patens</i> Saint-Lager]	Poaceae/Gramineae	Wild oat		Chile	Rioja et al. (2006)
<i>Avena sativa</i> L. Havre. [Syn: <i>Avena byzantina</i> , <i>Avena byzantina</i> var. <i>anopla</i> , <i>Avena byzantina</i> var. <i>byzantina</i>]	Poaceae/Gramineae	Wild oat		Surinam	Van Hoof (1960)
<i>Axonopus compressus</i> (Sw.) P. Beauv.	Poaceae/Gramineae	Broadleaf carpet grass		Hawaii	Namba and Higa (1971)
<i>Brachiaria mutica</i> (Forsskal) Stapf.	Poaceae/Gramineae	California grass, carpet grass, flat joint grass, giant couch, mat grass, Mauritius grass, para grass, savannah grass, tropical carpet grass, watergrass		Venezuela	Malaguti (1963)
<i>Bromus unioloides</i> (Willd.) Kunth.	Poaceae/Gramineae	Prairiegrass, rescuegrass	A	Australia (Queensland)	Kirkaldy (1910); Pemberton and Williams (1938)
<i>Canna indica</i> L. var. <i>orientalis</i> (Rosc.) [Syn: <i>Canna edulis</i> Kerr.-Gawl., <i>Canna indica</i> L., <i>Canna patens</i> Rosc.]	Cannaceae	Bandera, canna, chancle, coyol, Indian shot, lily, platanielo, saka siri		India (Maharashtra)	Capoor et al. (1968)
<i>Chenopodium album</i> L.	Chenopodiaceae	Anserine blanche,		Chile	Rioja et al. (2006)

Table 3 continued

Scientific name	Family	Common name	Host status	Country (State) from which reported	Reference
[Syn: <i>Blitum capitulatum</i> L.]		fat-hen, lamb-quarters, strawberry blite			
<i>Coix lachryma-jobi</i> L.	Poaceae/Gramineae	Adlay millet,	O	USA (Hawaii)	Fullaway (1918); Fullaway and Krauss (1945); Namba and Higa (1971)
		adlay, job's tears			
<i>Cola acuminata</i> Schott. & Endl.	Sterculiaceae	Cola nut, kola		Nigeria	Distant (1914); Lamborn (1914)
[Syn: <i>Sterculia acuminata</i> Beauv.]					
<i>Cynodon dactylon</i> (L.) Pers.	Poaceae/Gramineae	African couch,	A	Australia (Queensland), Chile, India (Maharashtra)	Kirkaldy (1910); Pemberton and Williams (1938) Rioja et al. (2006) Capoor et al. (1968)
[Syn: <i>Cynodon dactylon</i> var. <i>densus</i>]		Bermudagrass, Baramagrass, common stargrass, devil grass, dhoub, dhubgrass, kiri-hiri, kweekgrass, stargrass			
<i>Cyperus rotundus</i> L.	Cyperaceae	Nutgrass purple nutsedge		Hawaii	Verma (1954, 1955a); Namba and Higa (1971)
<i>Dichanthium amulatum</i> (Forsskal) Stapf.	Poaceae/Gramineae	Blue stem, Delhi grass (India), Kleberg blue-stem, marvel grass		India (Maharashtra)	Capoor et al. (1968)
<i>Digitaria decumbens</i> Stent.	Poaceae/Gramineae	Pangola grass, Panola grass, pasto pangola, slenderstem, transvala digitgrass		South Africa (Burundi), USA (Hawaii)	Anonymous (1999) Namba and Higa (1971)
[Syn: <i>Digitaria eriantha</i> Stent.]					
<i>Dinebra retroflexa</i> (Vahl) Panz.	Poaceae/Gramineae	Cat's tail vlegrass, viper grass		India (Maharashtra)	Capoor et al. (1968)
[Syn: <i>Cynosurus retroflexus</i>]					
<i>Echinochloa colonum</i> var. <i>frumentacea</i> Linn.	Poaceae/Gramineae	Jungle ricegrass,	A	India (Tamil Nadu)	Chelliah and Basheer (1965)

Table 3 continued

Scientific name	Family	Common name	Host status	Country (State) from which reported	Reference
[Syn: <i>Echinochloa colona</i> (L.) Link., <i>Panicum colonum</i> (L.) Link.]	Poaceae/Gramineae	jungle-rice, shama millet	O	India (Tamil Nadu)	Cherian and Kylasam (1937)
<i>Eleusine coracana</i> Gaertn. [Syn: <i>Cynosurus coracanus</i> (L.), <i>Eleusine filiformis</i> (L.), <i>Eleusine mucronata</i> Llanos., <i>Leptochloa mucronata</i> (Michx.) Kunth., <i>Triticum cylindricum</i> (Host) Ces.]	Poaceae/Gramineae	African millet, finger millet, kurakkan, ragi			
<i>Eleusine indica</i> (L.) Gaertner [Syn: <i>Cynosurus indicus</i> (L.), <i>Eleusine indica</i> (L.) Gaert., <i>Eleusine japonica</i> Steud.]	Poaceae/Gramineae	Goosegrass, Indian goosegrass, wiregrass, yardgrass		South Africa (Burundi)	Anonymous (1999)
<i>Eragrostis</i> spp.	Poaceae/Gramineae	China lovegrass		Chile, South Africa (Burundi), Australia, Egypt,	Rioja et al. (2006) Anonymous (1999) Grylls (1979) Ammar (1987)
<i>Euchlaena mexicana</i> Schrad. [Syn: <i>Zea mays</i> sp. <i>mexicana</i> (Schrad.), <i>Zea mexicana</i> (Schrad.) Kuntze]	Poaceae/Gramineae	Teosinte	A	Hawaii, India (Maharashtra), Nigeria, ReUnion Chile Trinidad	Swezey (1942) Capoor et al. (1968) Akingbohunge (1983) Dadant and Etienne (1973) Rioja et al. (2006) Briton-Jones (1933)
<i>Euphorbia</i> sp. <i>Hordeum vulgare</i> L. [Syn: <i>Hordeum lagunculiforme</i> Bachtsee ex Nikif.]	Euphorbiaceae Poaceae/Gramineae	Spurge Barley			
<i>Leptochloa chinensis</i> (L.) Nees. [Syn: <i>Poa chinensis</i> L.]	Poaceae/Gramineae	Asian sprangletop, Chinese sprangletop, red sprangletop		Philippines	Catindig (1993); Catindig et al. (1995, 1996)
<i>Lolium perenne</i> L. <i>Ludwigia octovalvis</i> (Jacq.) P.H. Raven	Poaceae/Gramineae Onagraceae	Perennial ryegrass Mexican Primrose willow		Chile Philippines	Rioja et al. (2006) Catindig (1993); Catindig et al. (1995, 1996)
<i>Medicago</i> sp. <i>Melilotus indicus</i> (L.) All.	Fabaceae Fabaceae- Leguminosae	Alfalfa Alligator weed,		Chile Chile	Rioja et al. (2006) Rioja et al. (2006)

Table 3 continued

Scientific name	Family	Common name	Host status	Country (State) from which reported	Reference
[Syn: <i>Melilotus indica</i> (L.)]		annual yellow sweet clover, common yellow melilot, field melilot, Indian sweet clover, medicinal sweet clover, sour clover, yellow sweet clover			
<i>Oryza sativa</i> L.	Poaceae/Gramineae	Rice grass, blackseeded proso millet, broomcorn millet, broomcorn panic, panic grass	A	Philippines South Africa (Burundi)	Capco (1959); Catindig (1993); Catindig et al. (1996) Anonymous (1999)
<i>Panicum</i> spp.	Poaceae/Gramineae	Guineagrass		Philippines	Catindig (1993); Catindig et al. (1995, 1996)
<i>Panicum maximum</i> Jacq. [Syn: <i>Urochloa maxima</i> Jacq. (R.D. Webster) <i>Megathyrsus maximus</i> Jacq.]	Poaceae/Gramineae	Broomcorn millet, wild Proso millet		Puerto Rico	Caldwell and Martorell (1950)
<i>Panicum miliaceum</i> L.	Poaceae/Gramineae	Buffalo grass, California grass, carib grass, hanegrass, para grass, scotchgrass, water grass		USA (Hawaii)	Namba and Higa (1971)
<i>Panicum purpurens</i> (Raddi) Henr. [Syn: <i>Brachiaria purpurens</i> (Raddi) Henr.]	Commelinidae	Ditch millet, Indian crown grass, kodo millet, ricegrass, scrobic millet, varagu	O	India (Tamil Nadu)	Chelliah and Basheer (1965)
<i>Paspalum scrobiculatum</i> Linn. [Syn: <i>Paspalum commersonii</i> , <i>Paspalum scrobiculatum commersonii</i>]	Poaceae/Gramineae	Vasey grass		USA (Hawaii)	Namba and Higa (1971)
<i>Paspalum urvillei</i> Steud. [Syn: <i>Paspalum larranagai</i> Arech.]	Poaceae/Gramineae	Elephant grass,		Florida,	Watson et al. (1939)

Table 3 continued

Scientific name	Family	Common name	Host status	Country (State) from which reported	Reference
[Syn: <i>Pennisetum berthanii</i> , <i>Pennisetum merkerii</i>]		Napier grass, Uganda grass		USA (Hawaii)	Namba and Higa (1971)
<i>Pennisetum typhoides</i> (Burm. F.) Stapf. & C.E. Hubb.	Poaceae/Gramineae	Bajra,		India (Tamil Nadu),	Rao (1923a); Cherian and Kylasam (1937); Chelliah and Basheer (1965)
[Syn: <i>Chaetochloa lutescens</i> , <i>Chaetochloa glauca</i> , <i>Panicum glaucum</i> , <i>Pennisetum glaucum</i>]		bulrush millet, spiked millet, pearl millet		India (Karnataka), India (Madhya Pradesh)	Thontadarya and Channa-Basavanna (1968) Rawat and Saxena (1967)
<i>Pitiraea cuneata ovata</i> (Cav.) Caro	Verbenaceae			Chile	Rioja et al. (2006)
<i>Rottboellia exaltata</i> Lf.	Poaceae/Gramineae	Buffalo grass, corn grass,		Cuba, French West Indies,	Stahl (1927) Migliori and Lastra (1980)
[Syn: <i>Manisuris exaltata</i> (L.) Kuntze., <i>Rottboellia cochinchinensis</i> (Lour.), <i>Siegosia cochinchinensis</i> (Lour.) Clayton]		itchgrass, raoutgrass, wild grass		Guadeloupe, India (Tamil Nadu), India (Maharashtra), Philippines, Venezuela	Migliori and Lastra (1980) Chelliah and Basheer (1965) Capoor et al. (1968) Catindig (1993); Catindig et al. (1995, 1996) Malaguti (1963)
<i>Saccharum officinarum</i> L.	Poaceae/Gramineae	Sugarcane	O	Cuba, USA (Hawaii),	Plana and Pendas (1991) Van Dine (1904); Kirkaldy (1910); Fullaway (1918); Zimmerman (1948); Box (1953); Namba and Higa (1971) Williams (1957)
<i>Secale cereale</i> L. Svenska	Poaceae/Gramineae	Hostrag, rye, varrag		Mauritius India (Maharashtra), Venezuela	Capoor et al. (1968) Herold (1963)
<i>Senecio vulgaris</i> L.	Asteraceae			Chile	Rioja et al. (2006)
<i>Setaria italica</i> Beauv. [Syn: <i>Chaetochloa italica</i> (L.) Scribn., <i>Panicum flavum</i> Nees., <i>Panicum italicum</i> L.]	Poaceae/Gramineae	Foxtail millet, German millet, golden-Wonder millet, hay millet, Italian millet	O	India (Tamil Nadu)	Chelliah and Basheer (1965)
<i>Setaria verticillata</i> L. Beauv. [Syn: <i>Panicum verticillatum</i> L.]	Poaceae/Gramineae	Bristly foxtail, rough panic grass, rough bristle grass		Chile	Rioja et al. (2006)

Table 3 continued

Scientific name	Family	Common name	Host status	Country (State) from which reported	Reference
<i>Setaria vulpiseta</i> (Lam.) Roem. & Schult	Poaceae/Gramineae	Giant bristlegrass,		Costa Rica,	Autrey (1983)
		green foxtail grass,		Fiji	Lastra (1977); Tsai and Falk (1993)
		plains bristlegrass			
<i>Solanum nigrum</i> L.	Solanaceae	Black nightshade, deadly nightshade, garden nightshade		Chile	Rioja et al. (2006)
<i>Sonchus</i> sp.	Asteraceae	Sowthistle		Chile	Rioja et al. (2006)
<i>Sonchus oleraceus</i> L.	Asteraceae	Groundsel,		Chile	Rioja et al. (2006)
[Syn: <i>Senecio vulgaris</i> L.]		spynsow thistle			
<i>Sorghum bicolor</i> (L.) Moench.	Poaceae/Gramineae	Jowar,	O	Chile	Rioja et al. (2006)
[Syn: <i>Sorghum vulgare</i> L.]		sorghum		Cuba,	Lofin and Christenson (1933)
				USA (Hawaii),	Zimmerman (1948); Namba and Higa (1971)
			P	India (Karnataka),	Ayyar (1940)
				India (Madhya Pradesh),	Bagal and Trehan (1945); Vasudeva (1960)
				India (Maharashtra),	Capoor et al. (1968)
				India (Tamil Nadu)	Lefroy (1915); Rao (1923a, b); Cherian and Kylasam (1937); Cherian (1937); Caldwell and Martorell (1950)
<i>Sorghum halepense</i> (L.) Pers.	Poaceae/Gramineae	Johnsongrass	O	Puerto Rico,	Ferreira et al. (1989)
[Syn: <i>Andropogon halepense</i> (L.) Brot.]				Venezuela (Aragua)	Rioja et al. (2006)
				Chile,	Namba and Higa (1971); Chelliah and Basheer (1965)
<i>Sorghum sudanense</i> (Piper) Stapf.	Poaceae/Gramineae	Sudangrass	O	Hawaii & India (Tamil Nadu)	Greber (1981)
<i>Sturtevant</i> sp.				Australia	Rioja et al. (2006)
<i>Theobroma cacao</i> L.	Sterculiaceae	Cacao	A	Chile	Distant (1914); Lamborn (1914)
<i>Trichachma insularis</i> (L.) Nees	Poaceae/Gramineae	Sour grass		Nigeria	Namba and Higa (1971)
<i>Triticum aestivum</i> L.	Poaceae/Gramineae	Bread wheat, common wheat, wheat		USA (Hawaii)	Capoor et al. (1968)
				India (Maharashtra)	

Table 3 continued

Scientific name	Family	Common name	Host status	Country (State) from which reported	Reference
<i>Zea mays</i> L.	Poaceae/Gramineae	Corn, maize	P	Argentina,	Teson and de Remes Lenicov (1989)
				Australia (Queensland),	Perkins (1906); Kirkaldy (1910); Pemberton and Williams (1938)
				Chile	Rioja et al. (2006)
				Egypt,	Metcalf (1943)
				Guam,	Swezey (1936, 1942)
				Guatemala,	Painter (1955)
				India (Tamil Nadu),	Lefroy (1915); Rao (1923a, b); Ayyar (1940)
				India (Madhya Pradesh),	Rawat and Saxena (1967)
				India (Maharashtra)	Capoor et al. (1968)
				Mauritius,	Anonymous (1979)
				Mexico,	Malaguti (1963)
				Peru,	Metcalf (1943)
				Philippines,	Muir (1917); Olanes and Karganilla (1940); Exconde (1977); Catindig et al. (1996)
				Puerto Rico,	Dozier (1932); Cook (1936); Wolcott (1936); App (1942)
				South Africa,	Anonymous (1979)
Spain,	Briton-Jones (1933)				
Taiwan,	Chen (1991)				
Thailand,	Areekul et al. (1965)				
USA (Florida),	Ashmead (1890); Watson et al. (1939)				
USA (Hawaii),	Fullaway (1918); Zimmerman (1948)				
USA (New Jersey),	Barber and Pepper (1942)				
Venezuela	Malaguti and Naranajo (1963); Marin Acosta (1964)				

Accidental host (A) = corn planthopper feed or lay eggs, but unable to reproduce and develop

Occasional host (O) = corn planthopper fed and lay eggs occasionally, but do not multiply

Principal host (P) = corn planthopper reproduce, develop, and multiply normally

August–October in Madhya Pradesh (Rawat and Saxena 1967); September–January with a population decline in February in Tamil Nadu (Chelliah and Basheer 1965); and June–October with a peak in August and decline in October in Andhra Pradesh (Rajasekhar 1989). The prevalence of hot weather during March–June was unfavorable for *P. maidis* either due to absence of cultivated crops or by rendering inadequate nutrient supply in the alternate hosts/weeds.

Life table studies

Life table studies of *P. maidis* on maize showed the following values: net reproductive rate of increase $R_0 = 31.96$, innate capacity for increase $r_m = 0.07$, finite rate of increase $\lambda = 17$, generation time $T = 49.39$, instantaneous birth rate $b = 0.2$ and death rate $d = 0.13$ (Napometh 1973). For sorghum, the values are $R_0 = 17.99$, $r_m = 0.08$, $\lambda = 1.09$ (Rajasekhar 1989, 1997). But the age-specific mortality rates varied among the cohorts in response to different ambient conditions (Tsai and Wilson 1986). Nymphal survival percentage, R_0 , and T on sorghum was 75, 18, and 34.1, respectively (Rajasekhar 1989, 1997). Based on R_0 , it was estimated that *P. maidis* multiplies 1.07 times in every 3 days, doubled in 9.89 days, and 32 times in each generation. The stable age distribution of eggs, nymphs, and adults was 51.04, 38.42, and 10.54 on maize (Napompeth 1973); and 64.98, 30.82, and 4.18 on sorghum, respectively (Rajasekhar 1989, 1997). Wang et al. (2006) reported a significant relationship between leaf nitrogen levels and intrinsic rate of population increase.

Alary polymorphism

A common colonization syndrome in *P. maidis* illustrates its adaptive nature of polymorphic life-history, a feature

Table 4 Effect of temperature on instar duration of nymphs and adult longevity of the corn planthopper, *P. maidis* on corn in Florida (USA) (Tsai and Wilson 1986)

Biological parameter	Temperature (°C)				
	10	15.6	21.1	26.7	32.2
Nymphal period (d)					
Instar-1	10	7.7	5.2	4.3	1.9
Instar-2	20.2	11.1	4.6	3.1	4.2
Instar-3	24.3	10.5	5.4	3.3	10.6
Instar-4	19	13.5	6	3.3	16.8
Instar-5		12.7	6	4.4	
Instar-6		9.7			
Adult longevity (d)					
♂	8	107.6	26.3	35.1	18.5
♀	1	96.6	28.5	32.1	10

Table 5 Temperature interactions with the biological parameters of the adult dimorphic forms of the corn planthopper, *P. maidis* on maize in Argentina (Fernandez-Badillo 1984; Fernandez-Badillo and Clavijo 1990a)

Biological parameter	Temperature (°C)		
	15	20	25
Preoviposition (d)			
M (♀) : B (♂)	23.8	19	16.2
B (♀) : B (♂)	23.5	19	16.5
B (♀) : M (♂)	26.5	21.7	19.8
B (♀) : M (♂)	28	22.3	19.7
Preoviposition period (d)			
B	10.4	22	29.1
M	7.6	16.4	19.3
Eggs ♀⁻¹ (no.)			
B	19.8	78.3	90.1
M	18.9	86.4	125.4
Egg incubation period (d)			
B	22.3	14.3	8.8
M	22.1	14.7	8.2
Egg mortality (%)			
B	73.3	16.4	12.9
M	71.3	22.1	21.7
Oviposition period (d)			
B	10.4	22	29.5
M	7.6	16.4	19.3
Nymphal period (d)			
Instar-1			
B	6.4	4.3	3.9
M	6.3	4.6	3.7
Instar-2			
B	7.3	5.8	2.6
M	7.5	5.9	2.8
Instar-3			
B	7.6	6.6	2.6
M	8.2	6.4	2.5
Instar-4			
B	7.8	7.3	2.9
M	8.7	6.7	3.2
Instar-5			
B	9.3	8	4.7
M	9.7	8.2	4.7
Total duration (d)			
B	43.9	40.2	38.7
M	39.2	37.9	36.2
Nymphal mortality (%)			
Instar-1			
B	60	35.5	28.8
M	54.1	39.6	31.1
Instar-2			
B	21.4	12.7	22.1

Table 5 continued

Biological parameter	Temperature (°C)		
	15	20	25
M	23.5	15.4	17.4
Instar-3			
B	9.1	8.7	11.2
M	15.4	9.4	7.2
Instar-4			
B	10	9.5	6.2
M	27.3	8.6	6.4
Instar-5			
B	3.3	7	2.8
M	2.5	4.7	3
Adult longevity (d)			
B	2.4	3.8	3.9
M	2.3	3.8	4.1

B: brachypterous

M: macropterous

that affords great flexibility and allows exploitation of changing host habitats. Dispersal mechanism allows *P. maidis* to exploit temporary crop habitats, track changes in host plant quality, escape crowded or otherwise fitness reducing conditions, and locate mates. As a common phenomenon of polymorphism among the delphacids, three winged adult forms are recognized in *P. maidis* viz., macropters (winged), koelopters (intermediate), and brachypters (wingless) (Fullaway 1918; Rao 1923b; Zimmerman 1948; Verma 1954, 1955a; Williams 1957; Metcalfe 1969; Napompeth 1973). The development switch of nymphs to different morphological types is triggered not only by interaction of environmental cues such as host plant condition, temperature, and photoperiod (Napompeth 1973) but also by population density (Fisk 1981; Fernandez-Badillo 1984, 1988; Fernandez-Badillo and Clavijo 1990a). Higher population density of nymphs promotes the appearance of macropters. Similarly, favorable and stable environmental conditions favor brachyptery; and adverse conditions determine the appearance of macropterous adults. Although higher temperatures appear not to play a direct role in wing polymorphism, they favor the appearance of a higher proportion of adult macropters. However, this phenomenon seems to respond to a strategy in the distribution and reproductive strategies of *P. maidis*, in which the brachypters mostly remain on the same plant, and assure lineage contribution maximally to future generations, while the macropters serve to distribute, locate, and colonize newer habitats (Fernandez-Badillo 1984; Fernandez-Badillo and Clavijo 1990a).

During the long rainy season, several overlapping breeding populations of both brachypters and macropters

are maintained on differently maturing cultivars of maize and sorghum. Throughout the range of distribution, a minimum of two generations of *P. maidis* develop on a single maize or sorghum crop. The number of generations indicate 'cryptovoltinism' (no diapause or an obscure diapause with an unknown number of generations), which is associated and governed by the behavioral pattern of macropters, and in turn influenced by the crop, cultural practices, and surrounding vegetation in the cropping area. The degree of overlapping generations depends on the duration of the initial wave of gravid female macropters immigrating into the new crop (Napompeth 1973). Geographically, the number of generations obtained each year is highly variable, and largely dependent on the length of the growing season (a latitudinal phenomenon). Higher altitudes, and patterns of nitrogen availability in the host plants restricts the number of generations annually.

The immigration of macropterous adults onto the whorls of young corn/maize and sorghum planted at the beginning of the rainy season suggests that they might have over-seasoned in nearby protected habitats (Takara 1981; Takara and Nishida 1983). Macropters colonize in very low densities, but their offspring are mostly brachypters ensuring rapid population growth. In general, the level of dispersal by macropters is influenced by host plant canopy, habitat persistence, planting succession, and resource isolation. The trade-offs between dispersal and reproduction of macropters appears to constrain the extent to which selection might maximize both traits. The reproductive delay and decreased fecundity of macropterous adults supports the notion that flight capability is costly, and that phenotypic trade-offs between dispersal and reproduction exist (Denno et al. 1989). Monsoon rains stimulate the flight activity and host searching ability of macropters, which are gregarious and tend to aggregate during the day inside the whorl and/or leaf sheath, where the moisture is high and where they are protected from sunlight (Otanés and Karganilla 1940; Verma 1954, 1955a; Chelliah and Basheer 1965; Rawat and Saxena 1967; Napompeth 1973). In contrast, low rainfall and fewer numbers of rainy days have a deleterious effect on their incidence (Rajasekhar 1989, 1996b). Whether selection of one trait (dispersal) will influence the other (reproduction) depends on the genetic correlation between the macropters. Dispersal may also be an adaptation for spreading the risk of reproductive failure.

The male and female macropters, and female brachypters are common, while koelopterous forms occur in low numbers in the field. The macropterous form is more active and twice as abundant as the brachypterous form (Fullaway 1918). In general, more females than males were found at early growth stages of corn and sorghum, and the females lived longer than males. Both the dimorphic forms of

macropters and brachypters were also noticed on compact panicles and exposed roots of sorghum (Chelliah and Basheer 1965). Although repeated matings were observed in the early morning, single mating was apparently sufficient for the entire life of the female (Chelliah and Basheer 1965).

Usually, two population peaks of macropters were observed on sorghum and maize coinciding with the immigration/colonization and emigration of large proportion of females at the beginning (30–40 days) and end of the crop season (80–110 days), respectively; and brachypters became dominant in 40–80 day old crop (Marin Acosta 1964; Napompeth 1973; Nishida et al. 1976; Nishida 1978; Clavijo and Notz 1978; Fernandez-Badillo 1984; Fernandez-Badillo and Clavijo 1989). Population of nymphs appear from the 4th week, reach peak levels between 8- and 12th week, and decrease at the crop season end on maize (Fernandez-Badillo 1984; Fernandez-Badillo and Clavijo 1989) and sorghum (Chelliah and Basheer 1965; Chandra Shekar 1991; Chandra Shekar et al. 1993a; Singh 1997).

Host plant resistance

Sources of resistance

A wide range of genotypes have been evaluated, but very few sources of resistance have been reported in corn/maize and sorghum, and are linked to virus diseases transmitted by *P. maidis*. The genotypes of DH 7, Giant White, Hybrid 4050, Jawahar, Sona, and Vikram in maize (Chatterjee and Nimbalkar 1977); and Kafir Suma and Dwarf Hegari (Khan and Rao 1956); and I 753, H 109, GIB, 3677B, and BP 53 (IS 1055) in sorghum are free from infestation (Agarwal et al. 1978). IS 19349 (Chandra Shekar 1991; Chandra Shekar et al. 1993a, b), and IS 18657, IS 18677, and PJ 8K(R) were stable in resistance across different stages of crop growth in sorghum (Singh and Rana 1992; Chandra Shekar 1991; Chandra Shekar et al. 1992, 1993a, b). In contrast, the sorghum genotypes M 35-1, Bilinchigan, BS 12-2-11, Farm Aispuri, Fulgar White, Fulgar Yellow, GAR 2, Gundinni, Hegari 1, Improved Ramkel, Improved Saroner, Khadi BK 1-1, M 47-3, Nandyal, ND 15, NJ 16K, NJ 156, PJ 16K, PJ 24K, PJR 4, PS 13, Sampgaon, Shanali 4-2, Shanali 4-5, and Striga-1 are highly susceptible to *P. maidis* (Capoor et al. 1968).

Behavioral responses vis-à-vis mechanisms of resistance

Oviposition is greater during the vegetative crop stage and greatly declines after flowering in maize and sorghum.

Behavioral responses of adults and nymphs indicate that antixenosis for colonization, oviposition, and/or feeding is one of the predominant mechanisms of resistance in sorghum (Chandra Shekar 1991; Chandra Shekar et al. 1992, 1993a). However, plant damage is not directly related to the population established. Spectral responses of visual orientation indicated that shorter wavelengths at <550 nm (green-yellow, green, blue, violet, and ultra violet) attract both adult and nymph *P. maidis*, but there are no responses at longer wavelengths (yellow, orange, red, and infra-red) (Pospisil 1971). Based on the position of its salivary sheaths, Buduca et al. (1996) observed two temporal distinctions of electronic penetograph signal classes produced by *P. maidis* in maize as: (i) exploration activity of tissues and probing in parenchyma to quickly locate the deeper vascular bundles, and (ii) ingestion of xylem or/and phloem. Plant moisture stress is considered as a main stimulus for olfactory orientation of CPH (Pospisil 1972). In sorghum, the orientation and settling behavior of nymphs and brachypterous adults is influenced by olfactory and visual responses, but feeding is not sustained, suggesting that a lack of gustatory stimuli plays a significant role in determining the degree of antixenosis for feeding (Chandra Shekar 1991; Chandra Shekar et al. 1992, 1993a).

Accumulations of *P. maidis* nymphs and adults on leaves near the top of plants indicate a greater preferential response to feeding on tender shoots over those in middle or basal portions of plants. Low preferential response to colonization was observed on sorghum cultivars such as SPV 736 and MSH 65 (Rajasekhar et al. 1995); and pearl millet [*Pennisetum typhoides* (Burn. F.) Stapf. & C.E. Hubb.] cultivars of MH 66, MH 90, MH 94, MH 110, MH 80, MH 97, MP 51, and IHC-B-77 (Prem Kishore 1995). *Peregrinus maidis* normally oviposit on the upper surface of the leaf midrib of corn and sorghum, but on the commercial sorghum hybrid, CSH 1 oviposition occurs on both upper and lower surfaces of the midrib. On corn seedlings, eggs are laid indiscriminately on any available fleshy tissue including roots, and also on the outer surface of the leaf sheath. During grain development and maturation of the corn plant, any fleshy tissue except the hard stem is utilized for oviposition including the husk around the ear, and eggs are rarely laid on the midribs of the leaves between the upper ear and tassel (Napompeth 1973). Resistant genotypes of sorghum receive 5–10 times fewer eggs, and those deposited are arranged in a disorderly manner, compared to the susceptible hybrid, CSH 1, even in no-choice conditions (Chandra Shekar 1991; Chandra Shekar et al. 1993a). On corn and sorghum plants, there is also a marked preference for oviposition on mature leaves of older plants compared to very few eggs on young leaves (Napompeth 1973) even in no choice conditions (Fisk 1978a; Singh and Rana 1991). Poor growth of *P. maidis* on smaller sorghum

plants is associated with less time spent in feeding and corresponding increase in probing activity (Fisk 1978a, b). Antixenosis for oviposition at different stages of crop growth exerts a profound influence not only on oviposition, but on the behavior of nymphs, macropters, and brachypters in maize (Napompeth 1973), and sorghum (Chandra Shekar 1991; Chandra Shekar et al. 1993a). Antibiosis is expressed as increased *P. maidis* mortality, prolonged nymphal development, and reduced fecundity in sorghum (Chandra Shekar 1991; Chandra Shekar et al. 1993b). Fewer offspring of *P. maidis* were noted to be produced on the younger plants (Fisk 1978a, b), and some sorghum germplasm accessions are relatively less susceptible to leaf sugary exudates (Mote and Shahane 1993).

Morphological traits, physiological mechanisms, and biochemical factors associated with resistance

The invasion of macropterous adults of *P. maidis* on sorghum plants at >20 cm height has been attributed to physical factors rather than chemical cues, as compact and tightly wrapped whorl leaves around the stem of some sorghum genotypes impart resistance (Agarwal et al. 1978). High levels of nitrogen, sugar and total chlorophyll contents have been shown to be strongly associated with susceptibility to *P. maidis* in sorghum, and conversely genotypes with high phosphorus, potash, and polyphenol content are less preferred by *P. maidis* (Mote and Shahane 1994). Fisk (1980) observed that mixtures of phenolic acids and esters or their proportions interfere with settling behavior and reduce feeding by *P. maidis* in a complex manner not only in plants but also on assayed diets with sorghum. However, higher concentration of phenolic acids was also correlated with reduced ability of *P. maidis* to locate the phloem tissues. These results indicate that both phenolic acids and esters play a dual role in promoting probing activity but also deterring feeding. Generally, *P. maidis* feeds on the xylem and phloem sap of resistant and susceptible sorghum genotypes, respectively. Xylem fluid is poor in amino acids but contains monosaccharides, organic acids, potassium ions, and other minerals, but phloem is rich in sucrose and relatively poor in amino acids and minerals. During the process of feeding, the salivary stylets of *P. maidis* block the phloem, resulting in an accumulation of nitrogen, eventually turning into ammonia and causing chlorosis; and also changing the carbohydrate partitioning patterns affecting the source–sink relationships in the plant. Plant moisture stress causes a conversion of starch to sugars and the accumulation of high concentrations of proline, which acts as a phagostimulant, and increases the nitrogen titers. Heavy feeding generally induces proteolysis and a dramatic increase in amino acids, which results in promoting higher fecundity.

Population dynamics

The success of *P. maidis* as a key pest on corn and sorghum largely stems from its adaptability to continual changes of the environment in both quality and quantity. Continuous cropping, reduced genetic variability in short duration and high yielding cultivars of maize and sorghum, and the application of high levels of nitrogenous fertilizers have compounded the problem. In India, the growing severity of outbreaks of *P. maidis* in the sorghum agroecosystem have been reported from different states such as Maharashtra (AICSIP 1982, 1987); Karnataka (AICSIP 1989, 1990), Tamil Nadu (AICSIP 1987, 1989, 1990), Andhra Pradesh (AICSIP 1988, 1989, 1990, 1991), and Madhya Pradesh (AICSIP 1980, 1985). During the last decade, *P. maidis* has established as a key pest in the sorghum agroecosystem.

The quantitative analysis of the reaction of a maize/sorghum agroecosystem to infestation by *P. maidis* can be based on the initial wave of immigrant macropterous populations. Continuous cultivation of corn and sorghum stabilizes the spread of infestation of *P. maidis* from one crop or field to another within a localized area. When the crop is harvested, residual populations leave the field to settle on alternate weedy hosts. The macropterous adults are capable of moving short distances from their wild host plants, and may take advantage of long range dispersal by wind and weather frontal systems in search of suitable habitats. By the time volunteer crop plants become available, the population decreases considerably, but is still large enough to colonize and settle on them. However, when volunteer crop plants are unavailable or destroyed, macropterous adults survive on alternate hosts either in the field or in surrounding areas as refugia. The population dynamics of *P. maidis* have fundamentally different characteristics depending on the strength and form of density-dependent and density-independent interactions. However, it is generally agreed that some degree of negative density dependence is required for population persistence. But density-independent interactions exert their effects and play an important role in determining the components of fitness for *P. maidis*.

Density-dependent interactions

The effects of abiotic factors indirectly involve in density-dependent interactions on the components of fitness of *P. maidis* partly by innate capacity to increase, changes in the quality and quantity of food associated with aging, and the condition of the corn/sorghum plants. The negative effects of density on fitness are intensified by poor host quality (aging, senescing, or wilting) in the production of macropters, from where they disperse to new habitats. However, the levels of dispersal are further influenced by a

variety of interactions including the host canopy, habitat persistence, planting succession, and resource isolation (Napompeth 1973). At high population densities, intra-specific competition can be intense and adversely affect many components of fitness. However, under crowded conditions, the rates of survival are reduced, individuals develop more slowly, and fecundity is lower because of competition for oviposition sites. Thus, density-dependent interactions result in decreased reproductive rate (R_0) and population growth. Reductions in fitness may not only be associated with crowded conditions, but may also occur at very low densities. When individuals are very rare and scattered, the searching ability for mates may be limiting. Above all, factors such as host plant nutrition, natural enemies, dispersal competition, and physical stresses also influence the population growth and determine the spatial and temporal variation. Diverse vegetation texture has a great influence on the functional and numerical responses of natural enemies by affecting the population abundance.

Density-independent interactions

Density-independent interactions include cultural practices, and micro-environmental and climatic factors, which concurrently operate, but their effects are obscured by endogenous factors. Soil moisture and relative humidity changes in the agroecosystem may exert immense effects on the nutritional quality and quantity of crop/weed hosts. The populations of *P. maidis* fluctuate dramatically within and among seasons in the same patch as well as spatially among the patches. Population growth can be exponential during different growing seasons, and particularly rapid in local patches where aggregations of brachypterous adults occur.

Effect of chemicals and botanicals

Effective control of *P. maidis* with increased yields was achieved with demeton-S-methyl, monocrotophos (Gandhale et al. 1986), carbaryl (sevin) and phosphamidon (Malaguti and Naranjo 1963). The best knockdown effect was realized with endosulfan and malathion (Tsai et al. 1990). However, the persistence of oxydemeton-methyl was shorter (3 days) (Tsai et al. 1990), and sevin, malathion, parathion, BHC, endrin, chlordane, isodrin, DDT, aldrin (Sarup et al. 1960), phosphamidon, endrin (Rathore et al. 1970), and carbaryl persisted for longer times (10–15 days) (Tsai et al. 1990). In addition, botanicals such as seed extracts of taramira oil (*Eruca sativa*), and leaf and shoot oil extracts of artemisia oil (*Artemisia kurramensis*) alone or in combination with DDT have increased toxicity (Khan 1984). Similarly, the seed extracts of custard apple

(*Annona squamosa*) (Yasin and Syamsuddin 1999), and cucurbitacins (Tallamy et al. 1997), when sprayed, showed antixenosis for oviposition and/or feeding by *P. maidis*.

Natural enemy interactions

Numerous natural enemies of *P. maidis* have been recorded, but their role in controlling its population growth is not fully understood, because mortality factors associated with natural enemies are predominantly stage specific. Moreover, parasitoid and predator species diversity may vary within and among cultivars, and depend on a variety of factors such as microclimate, timing, rate of immigration/emigration, and geographic location. Excellent sources of basic information on the natural enemies of *P. maidis* are available (Fullaway 1918; Timberlake 1924; Swezey 1929, 1936; Dozier 1932, 1936; Pemberton 1944; Thompson 1944; Thompson and Simmonds 1944; Zimmerman 1948; Napompeth 1973; Singh et al. 1993). The population density of *P. maidis* is regulated in part by increases in the quality and quantity of food associated with age and nutritional condition of corn or sorghum plants (Napompeth 1973).

The eggs of *P. maidis* are attacked by a wide spectrum of parasitoids (Table 6) and predators (Table 7). Egg parasitism by *Paranagrus optabilis* Perkins, was observed on Johnsongrass during the fallow period in Hawaii (Verma 1954, 1955a, b, 1956; Napompeth 1973), and by *P. flaveolus* Waterhouse, in Argentina (Marin Acosta 1964), but their effectiveness was negligible. Common parasitoids of nymphs are Dryinidae (Hymenoptera), and endoparasitoids oviposit in and emerge from nymphs and/or adults. Nymph and adult parasitism is relatively low. Parasitism by *Pseudogonatopus hospes* Perkins, *Ootetranchus beatus* Perkins, and *P. optabilis* on corn in Hawaii was found to be limited (Napompeth 1973), and an ectoparasitic red mite (*Bochartia* sp.) also proved ineffective on sorghum in India (Rawat and Saxena 1967) (Table 6).

There are several important egg predators from the families of Miridae, Nabidae, and Veliidae in Hemiptera (Table 7). Among them, the tettigoniids [*Conocephalus saltator* (Saussure) and *Xiphidiopsis lita* Hebard] are fairly common during early stages, the mirids, *Cyrtorhinus lividipennis* Reuter and *Tytthus mundulus* (Breddin) occur at later stages, and *Chelisoche morio* (F.) is found throughout the crop cycle of corn (Swezey 1936; Usinger 1939) but its predation has not been observed (Verma 1955a; Napompeth 1973). Among them, *C. lividipennis* is considered as an important density-dependent factor on corn on adults and nymphs of *P. maidis*. Whereas, *Orius persequens* (White), *Nabis blackburnii* (White), *Zelus renardii* Kolenati, *Chrysoperla basalis* Walker, and *Geocoris*

Table 6 Parasites and stage of parasitism of the corn planthopper, *Peregrinus maidis* Ashm. reported from different countries

Parasite	Order	Family	Stage of parasitism	Country from which reported	Reference
<i>Bochartia</i> sp.	Acarina	Tetranychidae	Adults & nymphs	Haiti,	Olmi (1984)
<i>Haplogonatopus vitiensis</i> Perkins	Hymenoptera	Dryinidae	Adults & nymphs	India (Madhya Pradesh) Trinidad, USA (Hawaii)	Rawat and Saxena (1967) Olmi (1984) Olmi (1984)
<i>Ootetrastichus pallidipes</i> Perkins	Hymenoptera	Dryinidae	Adults & nymphs	Fiji, USA (Hawaii)	Perkins (1905); Swezey (1936) Pemberton (1944); Zimmerman (1948)
<i>Paranagrus</i> sp.	Hymenoptera	Mymaridae	Eggs	Chile	Rioja et al. (2006)
<i>Paranagrus flaveolus</i> Waterhouse [Syn: <i>Anagrus flaveolus</i> Waterhouse]	Hymenoptera	Mymaridae	Eggs	Argentina, Brazil, Cuba, Haiti, Mauritius, Puerto Rico, Trinidad, USA (Hawaii), Venezuela	Marin Acosta (1964); De Santis et al. (1992) Leao Veiga (1977) Box (1953) Waterhouse (1913); Dozier (1932, 1936); Wilson (1980) Williams (1957) Waterhouse (1913); Dozier (1932, 1936) Wilson (1980) Wilson (1980) Box (1953); Marin Acosta (1964)
<i>Paranagrus frequens</i> Perkins [Syn: <i>Anagrus frequens</i>]	Hymenoptera	Mymaridae	Eggs	Australia, Haiti, Trinidad, USA (Hawaii)	Fullaway (1918); Timberlake (1924); Dozier (1932, 1936); Swezey (1936) Dozier (1932); Wilson (1980) Dozier (1932); Wilson (1980) Fullaway (1918); Timberlake (1924); Dozier (1932, 1936); Swezey (1936); Zimmerman (1948)
<i>Paranagrus optabilis</i> Perkins [Syn: <i>Paranagrus osborni</i> Fullaway, <i>Anagrus panicicolae</i> Sahid]	Hymenoptera	Mymaridae	Eggs	Australia, Guam, Java, Philippines, Samoa, USA (Hawaii)	Perkins (1906); Swezey (1936) Swezey (1936) Girault (1914) Fullaway (1918, 1919) Swezey (1936); Zimmerman (1948) Fullaway (1918); Swezey (1936); Zimmerman (1948); Napompeth (1973)
<i>Pseudogonatopus hospes</i> Perkins	Hymenoptera	Dryinidae	Adults & nymphs	China, USA (Hawaii)	Perkins (1905); Williams (1931); Swezey (1936) Perkins (1905); Williams (1931); Swezey (1936); Napompeth (1973)
Unidentified	Diptera	Chalcidoidae	Eggs & nymph instar-1	India (MP)	Rawat and Saxena (1967)

tricolor Fabr. (Lygaeidae) (Rawat and Modi 1969) are frequently observed, but their role in regulating populations is apparently of little importance. Basic information on the geographic distribution, life-history, rearing, and host relationships is available for *C. lividipennis* (Usinger 1939; Davis 1960; Nakao 1960; Bae and Pathak 1966, 1968; Napompeth 1973; Reyes and Gabriel 1975; Liquido and Nishida 1983, 1985a, b, c; Chua and Mikil 1989; Bae and

Yin 1994; Song et al. 1995; Bae and Park 1997; Bae et al. 2002), and *T. mundulus* (Verma 1954, 1955a, b, 1956). Other natural enemies present in the corn agroecosystem include *Cheilomenes sexmaculata* (Fabricius), *Termatophyllum* sp., and *Mallada boninensis* (Okamoto) (Singh et al. 1993); *Coccinella septempunctata* var. *brucki* and *Coelophora inequalis* Fabricius (Marin Acosta 1964) *C. septempunctata* and *Menochilus sexmaculatus* (F.) are

Table 7 Predators and stage of predatorism of the corn planthopper, *Peregrinus maidis* Ashm. reported from different countries

Predators	Order	Family	Stage of predation	Country from which reported	Reference
<i>Allograpta exotica</i> (Wiedemann)	Diptera	Syrphidae	Nymphs	USA (Hawaii)	Napompeth (1973)
<i>Allograpta javana</i> (Wiedemann)	Diptera	Syrphidae	Nymphs	India	Ghorpade (1983)
<i>Argiope avara</i> Thorell	Araeneida	Mimetidae	Adults & nymphs	Chile, USA (Hawaii)	Rioja et al. (2006) Napompeth (1973)
<i>Brumoides saturalis</i> F.	Coleoptera	Coccinellidae	Adults & nymphs	India (Andhra Pradesh)	Fisk (1980)
<i>Camponotus compressus</i> F.	Hymenoptera	Formicidae	Adults & nymphs	India (Andhra Pradesh)	Fisk (1980)
<i>Camponotus acvapimensis</i> (Mayr)	Hymenoptera	Formicidae	Adults & nymphs	Brazil	Dejean et al. (2000)
<i>Cheliosoches morio</i> (F.)	Dermaptera	Chelisochidae	Adults & nymphs	USA (Hawaii)	Swezey (1936); Napompeth (1973)
<i>Chrysoperla</i> sp.	Neuroptera	Chrysopidae	Adults & nymphs	Chile	Rioja et al. (2006)
<i>Chrysoperla basalis</i> Walker	Neuroptera	Chrysopidae	Adults & nymphs	USA (Hawaii)	Swezey (1936); Zimmerman (1948); Napompeth (1973)
<i>Chrysoperla 7-punctata</i> var. brucki	Neuroptera	Chrysopidae	Adults & nymphs	USA (Hawaii)	Napompeth (1973)
	Neuroptera	Hemerobiidae	Adults & nymphs	Chile	Rioja et al. (2006)
<i>Coccinella 7-punctata</i> var. brucki.	Coleoptera	Coccinellidae	Adults & nymphs	Venezuela	Marin Acosta (1964)
<i>Coccinella septempunctata</i> L.	Coleoptera	Coccinellidae	Adults & nymphs	India (Madhya Pradesh)	Bagal and Trehan (1945); Rawat and Saxena (1967)
<i>Coelophora inaequalis</i> Fabricius	Orthoptera	Tettigonidae	Adults & nymphs	USA (Hawaii)	Fullaway (1918); Swezey (1936); Zimmerman (1948)
<i>Conocephalus saltator</i> (Saussure)	Hemiptera	Miridae	Eggs	USA (Hawaii)	Swezey (1936); Napompeth (1973)
<i>Cyrtorhinus mundulus</i> (Breddin) [Syn: <i>Cimex triguttatus</i> Linnaeus]	Hemiptera	Miridae	Eggs	USA (Hawaii)	Verma (1955a)
<i>Crematogaster</i> sp.	Hymenoptera	Formicidae	Adults & nymphs	Brazil	Dejean et al. (2000)
<i>Doru lineare</i> (Eschscholtz)	Hymenoptera	Formicidae	Adults & nymphs	Venezuela	Marin Acosta (1964)
<i>Geocoris tricolor</i> Fabr.	Hemiptera	Lygaeidae	Adults & nymphs	India (Madhya Pradesh)	Rawat and Modi (1969)
<i>Hasarius adansonii</i> (Aud.)	Araeneida	Salticidae	Adults & nymphs	USA (Hawaii)	Napompeth (1973)
<i>Illeis indica</i> Timberlake	Coleoptera	Coccinellidae	Adults & nymphs	India (Andhra Pradesh)	Fisk (1980)
<i>Leis dimidiata</i> Fabricius	Coleoptera	Coccinellidae	Adults & nymphs	USA (Florida)	Watson et al. (1939)
<i>Mallada boninensis</i> (Okamoto)	Neuroptera	Chrysopidae	Adults & nymphs	India (Karnataka)	Singh et al. (1993)
<i>Menochilus sexmaculatus</i> (F.) [Syn: <i>Cheilomenes sexmaculatus</i>]	Coleoptera	Coccinellidae	Adults & nymphs	India (Madhya Pradesh), India (Andhra Pradesh), India (Karnataka)	Bagal and Trehan (1945); Rawat and Saxena (1967) Fisk (1980) Singh et al. (1993)
<i>Mesogramma subannulatum</i> Loew	Diptera	Syrphidae	Adults & nymphs	Cuba	Loftin and Christenson (1933)

Table 7 continued

Predators	Order	Family	Stage of predation	Country from which reported	Reference
<i>Myrmecaria opaciventris</i> (Emery)	Hymenoptera	Formicidae	Adults & nymphs	Brazil	Dejean et al. (2000)
<i>Nabis</i> sp.	Hemiptera	Nabidae	Adults & nymphs	Chile	Rioja et al. (2006)
<i>Pagiopalus atomarius</i> Simon	Araeneida	Salticidae	Adults & nymphs	USA (Hawaii)	Napompeth (1973)
<i>Pheidole megacephala</i> (F.)	Hymenoptera	Formicidae	Adults & nymphs	USA (Hawaii)	Fullaway (1915); Zimmerman (1948)
<i>Plexippus paykulli</i> (Aud.)	Araeneida	Salticidae	Adults & nymphs	USA (Hawaii)	Napompeth (1973)
Red mite	Acarina	Tetranychidae	Adults & nymphs	Venezuela	Marin Acosta (1964)
<i>Rhyncoris fuscipes</i> F.	Hemiptera	Reduviidae	Adults & nymphs	India (Tamil Nadu)	Cherian and Kylasam (1939)
<i>Termtophyllum</i> sp.	Hemiptera	Termtophyllidae	Adults & nymphs	India (Karnataka)	Singh et al. (1993)
<i>Tetragnatha mandibulata</i> Walck.	Orthoptera	Tetragnathidae	Adults & nymphs	USA (Hawaii)	Napompeth (1973)
<i>Tytthus lividipennis</i> Reuter [Syn: <i>Cyrtorhinus lividipennis</i> Reuter]	Hemiptera	Miridae	Eggs	Guam, USA (Hawaii)	Pemberton (1937) Pemberton (1937); Fullaway and Krauss (1945); Verma et al. (1955a); Nakao (1960); Davis (1960); Napompeth (1973); Liquido and Nishida (1985a, b)
<i>Tytthus mundulus</i> (Breddin)	Hemiptera	Miridae	Eggs	Australia, Fiji, USA (Hawaii)	Swezey (1936) Swezey (1936) Williams (1931); Swezey (1936); Usinger (1939); Zimmerman (1948); Verma (1954, 1955a); Napompeth (1973)
<i>Xiphidiopsis lita</i> Hebard [Syn: <i>Chrysotus pallidipalpus</i> van Duzee]	Orthoptera	Tettigonidae	Adults & nymphs	USA (Hawaii)	Swezey (1936); Napompeth (1973)
<i>Zelus renardii</i> Kolenati	Hemiptera	Reduviidae	Adults & nymphs	USA (Hawaii)	Fullaway (1918); Swezey (1936); Zimmerman (1948); Napompeth (1973)

often abundant (Rawat and Saxena 1967) and found feeding on the young nymphs of *P. maidis* (Napompeth 1973). The chrysopid *C. basalis* and syrphid larvae *Allograpta exotica* (Wiedemann) are frequent predators on the nymphs of *P. maidis* at later stages of corn (Beardsley 1971; Napompeth 1973), but their role as regulating agents is negligible.

In addition, there is a rich community of spiders (Lycosidae, Linyphiidae, and Tetragnathidae) predated upon the nymphs and adults. Among them, *Plexippus paykulli* (Aud.), *Hasarius adansoni* (Aud.), *Pagiopalus atomarius* Simon, *Argiope avara* Thorell, and *Tetragnatha mandibulata* (Walck.) prey on the nymphs and adults inside the whorls at early stages of corn (Napompeth 1973).

Trophobiosis interactions

Trophobiosis interactions occur convergently between ants and *P. maidis* (Dejean et al. 1996, 1997, 2000; Delabie 2001). In addition to the big-head ant, *Pheidole megacephala* (F.) (Zimmerman 1948; Napompeth 1973), other species that were most abundant in corn fields feeding on honeydew excreted by *P. maidis* include the fire ant, *Solenopsis geminate* (F.), European red mite, *Paratetranychus longicornis* (Latrielle) (Verma 1954, 1955a; Napompeth 1973) and Japanese ant, *Cardiocondyla nuda* (Mayr) (Napompeth 1973). Marin Acosta (1964) observed seven species of ants that were associated with the infestation of *P. maidis*, but the earwig, *Doru lineare*

(Eschscholtz), was considered predatory on nymphs. In sorghum, the rate of initial infestation by *P. maidis* was increased with the reproductive activity of ants such as the black common ant, *Camponotus compressus* (Fabricius 1787) (Khan and Rao 1956; Chelliah and Basheer 1965), Singapore ants, *Monomorium destructor* (Jerdon), and *M. criniceps* (Mayr 1879), and the European red mite (Chelliah and Basheer 1965). In maize, the population of *P. maidis* was significantly higher when attended by *Camponotus acvapimensis* (Mayr.) than by *Crematogaster* sp. or *Pheidole megacephala* (F.) and was also higher when attended by both of the latter than by *Myrmecaria opaciventris* (Emery) (Dejean et al. 2000).

Future research

Although much work has been done on the ecobiology of *P. maidis*, many basic and strategic aspects need investigation. In view of the primary consideration of feeding injury and oviposition punctures, increased emphasis should be given to antixenosis mechanism governing the colonization and oviposition during the vegetative stage of maize and sorghum.

Identification of genotypes with antibiosis resistance, and the role of oviposition deterrents due to toxins or antifeedants that deter feeding leading to mortality by starvation and desiccation during nymphal stadia need to be initiated. The breeding cycle and seasonal shifts are little studied, and comprehensive studies are needed on the factors involved in the rapid population buildup of *P. maidis*. This information will be useful to develop and standardize faster and reliable techniques for resistance screening, and to formulate appropriate sustainable management strategies. Research efforts must also expand to assess the effects of genetic diversity and identify potential sources of resistance to *P. maidis* in corn (maize) and sorghum.

Some wild hosts were believed to be a reproductive sink for outbreaks, their relative contribution to fitness as opposed to corn and sorghum is little understood. It is clear that *P. maidis* utilize alternate hosts between growing seasons, and the extension of host diversity range play a significant role on the ecobiology of *P. maidis*. There is a need to gain a better understanding about the differential reaction of certain hosts used as susceptible and insusceptible hosts by *P. maidis* reported from different countries such as wild oats (*A. sativa*), nutgrass (*C. rotundus*), finger millet (*E. coracana*), goosegrass (*E. indica*), barley (*H. vulgare*), broomcorn millet (*P. miliaceum*), ditch millet (*P. scrobiculatum*), Napier grass (*P. purpureum*), sugarcane (*S. officinarum*), foxtail millet (*S. italica*), and Johnsongrass (*S. halepense*). The chemicals that could

interrupt access to the vascular bundle or ingestion events need thorough investigation. Why are some plants insusceptible hosts? Does the presence and location of chemicals interrupt access to the vascular bundles or infestation events, including the induction of a quick defense response to feeding by *P. maidis*? Currently no information is available in the literature whether *P. maidis* can overwinter or enter diapause at any stage of its development. In the absence of crop rotation, adoption of fallow period associated with narrow host can range to some extent reduce its population buildup. There is a need to examine the consequences of macronutrients on the life-history parameters as well as the role of dispersal mechanisms due to imposition of constraints on the ingestion capacity by migratory macropters, which are sensitive to nutrient limitation. These studies will greatly aid in the prediction of population dynamics of *P. maidis*. The cues stimulating colonization and host plant utilization can greatly influence the understanding of the mechanisms generating biological diversity, and a better understanding of these events may lead to improved management strategies. Comprehensive information is needed on the degree of tolerance due to nutrient drain imposed by feeding, and the role of morphophysiological traits and biochemical mechanisms associated with resistance to *P. maidis* in a diverse array of genotypes. The measurement of photosynthate levels and carbohydrate partitioning in relation to source–sink ratio has not been studied to determine the feeding changes such as reduction in photosynthesis or alteration in the translocation of photosynthates, including the metabolic changes at various growth stages in crop plants induced by *P. maidis* feeding. No attention has so far been given to the feeding effects on the carbon exchange rates, changes in nonstructural carbohydrates, alterations in cell membrane stability, and diminished ability of the plant to adjust osmotically. In addition, plants also experience different types of stress, including alterations in chlorophyll content and photosynthesis activity in response to *P. maidis* feeding, resulting in synthesis of several stress-related proteins whose role in defense response is unknown. Since oxidative enzymes are involved in many stress responses in plants, it may be speculated that these enzymes may play a direct role in the plant's response by strengthening the cell walls through lignification.

The role of density-dependent and density-independent interactions as well as their relative contribution to the population buildup of *P. maidis* still remains to be resolved, because the relevant variables are usually not measured. Although a wide spectrum of natural enemies have been recorded, some of these associations may be incidental and their precise role in controlling *P. maidis* is not fully understood. Their abundance and effectiveness in relation to the geographic locations and seasons have not

been extensively assessed. Moreover, the biology of most of the natural enemies is unknown and their role in regulating the population of *P. maidis*, individually or as a group has not been quantified. The performance of *C. lividipennis* under natural conditions was not as effective as expected, and the role of *T. mundulus* was less important. However, systematic studies are required on the combined interaction of these natural enemies in corn and sorghum agroecosystems. The positive association of ants that feed on sugary excretions and indirectly protecting the *P. maidis* populations from the predators is not clearly known. Predation by spiders has always been underestimated due primarily to the difficulties in making reliable evaluation of their effectiveness and their role in the regulation of population density of *P. maidis* needs further investigation.

There is also a need to explore the impact of cultural practices such as plowing and burning of crop stubble and residues immediately after harvest to destroy the unhatched eggs, nymphs, and adults of *P. maidis*. Exploration of cropping sequence or systems, which discourage the colonization including the breaks in continuous survival, and suppression of outbreaks of *P. maidis* and promote enhanced natural enemy activity needs to be addressed. Further, the role of insusceptible hosts that are less attractive to *P. maidis* in cropping systems for reduction in population buildup and virus spread, and the use of highly attractive, virus resistant hosts as trap crops, including the elimination of preferred hibernacula need to be studied.

With the advent of novel biotechnological tools as well as plant lectins, preferably snowdrop lectins, which are potentially effective not only for homopteran but also lepidopterous pests, future research efforts may have exciting potential in the development of transgenic maize and sorghums, and molecular mapping of genes conferring resistance to *P. maidis* and its transmitted virus diseases. Sustainable management strategies can be devised with the understanding of the tritrophic interactions between the *P. maidis*, their cultivated and wild hosts, and natural enemy diversity.

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