CHAPTER II

LITERATURE REVIEW

2.1. BIOECOLOGY OF THE SWEET POTATO WEEVIL, *Cylas formicarius* (F.) COLEOPTERA: CURCULIONIDAE)

2.1.1. Taxonomic status and distribution

Latreille in 1802 was the first entomologist to use the genus *Cylas* (Neave 1939) for describing weevils of the Cyladinae that have the following characteristics: (a) slender, elongate body with a cylindrical beak, (b) posterior femora not as a rule exceeding the tip of the elytra, and (3) the elytra not inflated (Pierce 1940, Subramanian 1957).

The genus *Cylas* contains 27 species (Schalk & Jones 1985, Austin *et al*. 1991). Of these, *C. formicarius* (Fabricius), *C. turcipennis* Boheman, *C. brunneus* (Fabricius), *C. femoralis* Faust, and *C. puncticollis* Boheman, are associated exclusively with sweet potato (Pierce 1918, 1940, Austin *et al*. 1991).

A recent taxonomic and distributional study, however, indicated that there may be as many as nine species of *Cylas* that are potential pests of sweet potato. These nine species are classified into three monophyletic species groups: *C. formicarius*, *C. brunneus*, *C. puncticollis* (Wolfe 1988, 1991). Of the above three main species groups, *Cylas formicarius* and *C. puncticolis* are the most widely distributed. *C. formicarius* occurs in Africa, the Americas and Asia, whereas *C. puncticollis* occurs only in certain African countries (Commonwealth Institute of Entomology 1970, Singh 1977). *Cylas brunneus* may have a similar status and distribution in West Africa as *C. puncticollis* (Hahn *et al*. 1989).

Cylas formicarius was first described by Fabricius (1798) as *Brentus formicarius*. This was based on specimens from India that had a piceous-brown body, with a reddish thorax (Pierce 1918). His description of this species is as follows:

> "Habitat Tranquebariae.
> Parvus in hoc genere. Rostrum cylindricum, atrum antennis
> rufis, moniliformibus: articulo ultimo longiori,
> cylindrico, clavato. Thorax rufus, antice globosus.
> Elytra laevia, atra, nitida. Pedes rufi, femoribus
> clavatis, at inermibus: annulo nigro" (Pierce 1918)

This species seemed not to be the same as the common sweet potato weevil found in the USA that has shiny blue-black elytra, red thorax and appendages, and a black head and beak. For that reason, Summers (1875) named the American species *C. elegantulus* to distinguish it from the Asian species (Pierce 1918).

The name was not, however, applied, partly out of respect to Fabricius (Pierce 1918). But, based on the color of the elytra (greenish for the Asian species and bluish for the American species, Pierce 1918), and karyological differences in the sex determining system (Hung 1985), two sub-species of *Cylas formicarius* have now been recognized: *Cylas formicarius formicarius* (F.), which is widespread throughout the Asian tropics, and *Cylas formicarius elegantulus* (Summers), which occurs in tropical and sub-tropical regions of the Americas (Sutherland 1986[a], Talekar 1988). In subsequent chapters, unless otherwise indicated, the use of *C. formicarius* refers to *C. formicarius formicarius*, the Asian sub-species.

2.1.2. Host range

The prefered host for *C. formicarius* is the sweet potato, *Ipomoea batatas* (Cockerham 1943, Sherman & Tamashiro 1954, Hill 1983, Talekar 1989, Austin *et al*. 1991), although this insect also attacks other *Ipomoea* and related species (Table 2).

Table 2. Alternative hosts of *Cylas formicarius* (F.) (Coleoptera: Curculionidae)

Alternative host	Common name	Country
Calonyction aculeata	Moon-flower	India
Calystegia soldanella	Bindweed	Taiwan
Ipomoea batatas	Sweet potato	Worldwide
I. ararica		India
I. barleirioides		India
I. congesta	Blue morning glory	Papua New Guinea
I. dissecta	Alamo-vine	U.S.A.
I. hederacea	English Ivy	U.S.A.
I. heptaphylla	Bush morning glory	U.S.A.
I. lacunosa	Diminute morning glory	U.S.A.
I. lateralis		India.
I. learii	Blue dawn-flower	India.
I. littoralis		U.S.A.
I. macrorhiza		U.S.A.
I. muricata		U.S.A.
I. palmata		India
I. pandurata	Man-of-the-earth	U.S.A
I. pres-caprae	Beach morning-glory	India
I. purpuria	Common morning-glory	India
I. quamoclit	Cypress vine	U.S.A
I. sagittata		U.S.A.
I. sepiaria		India
I. setosa	Brazilian morning-glory	U.S.A.
I. trichocarpa		U.S.A/India
I. trilobia		Philipp./India
I. tripida		India
Ipomoea sp.		U.S.A/Taiwan
Jaquemontia tamnifolia		India
Thunbergia sp.	Clock vine	India

Source: Sutherland 1986[a].

2.1.3. Life cycle

Research on the life cycle of SPW has been reviewed by Sutherland (1986^a; Table 3). Apparently it varies from one location to another, probably mainly in relation to changes in temperature (Mullen 1981, Sutherland 1986^a). At low temperatures, fecundity is higher and the life cycle is longer (Table 4; Mullen 1981). Thus, these properties vary with the season (Gonzales 1925, Rajamma 1983).

The optimum temperature for development is 27^0C to 30^0C, when the life cycle is completed in ca. 33 d. At 27^0C and 60 % RH the adult weevil lives for 94 d (Mullen 1981).

a. Egg

The adult female lays cream colored eggs (0.75 x 0.40 mm), singly in a cavity in vines or tubers (Reinhard 1923, Sutherland 1986^a). After laying each egg, she seals the cavity with a grey fecal plug. This conserves moisture, protects the eggs from predacious mites, and "hides" the location of the oviposition site (Sherman & Tamashiro 1954).

Recorded oviposition rates differ from one geographic area to another in relation to the temperature of the region. For example, in India, Rajamma (1983) found that females lay 1 to 9 eggs per day, with an average of 3 to 5 eggs. In the USA, however, Reinhard (1923) reported an oviposition rate of up to 2 eggs per day.

Table 3. Life cycle of the sweet potato weevil, Cylas formicarius (F.) Coleoptera: Curculionidae), on sweet potato

Stage	Reinhard (1923) USA[1]	Sherman & Tamashiro (1954) Hawaii[1]	Kemner (1924) Indonesia[2]	Gonzales (1925) Philippines[2]	Trehan & Bagal (1957) India[2]	Subramanian (1959) India[2]	Jayaranaiah (1975) India[2]	Rajamma (1983) India[2]
Temperature (°C)	28	27	-	-	-	-	-	-
Egg (d)	5-11	8	5-9	6-9	6	6	9	6
Larva (d)	20	15	25-26	-	17	24	28	16
No. of instars	-	3	-	-	-	5	5	-
Pre-pupa (d)	1-3	4	-	-	-	1-2	-	-
Pupa (d)	15	8	6-7	4-6	7	10	7	4
Pre-oviposition (d)	6-9	-	7-9	-	-	7	-	8
Oviposition (d)	104	-	-	63-120	-	80	90	83
No. of eggs	56	-	-	256	-	148	166	-
Longev. female (d)	-	-	-	-	83	94	-	-
Longev. male (d)	-	-	-	-	83	110	-	-
Egg to egg (d)	53	32	43-51	26-52	31	47	46	30-36

Source: Sutherland 1986[a]. [1] Cylas formicarius elegantulus (Summers)
[2] Cylas formicarius formicarius (F.)
- = data unavailable

Table 4. Effect of temperature on development of *Cylas formicarius elegantulus* (Summers) (Coleoptera: Curculionidae) on sweet potato (cv.'Jewel')

Stage	Average duration (d) of development stages of the SPW at different temperatures			
	20°C	25°C	27°C	28°C
Egg	7.9	5.7	4.8	4.0
Larva	58.2	23.7	16.3	16.2
Pupa	10.7	5.0	5.5	8.6
Pre-oviposition	7.7	6.5	6.3	4.5
Egg to egg	84.5	40.9	32.9	33.3

Source: Mullen 1981.

The egg stage lasts 4 to 8 d (Sutherland 1986[a]). Over the 60 to 120-day oviposition period, the total number of eggs laid ranges from 50 to over 250.

b. Larva

The newly hatched larva has a delicate appearance and is initially white in color (Reinhard 1923, Gonzales 1925, Cockerhan et al. 1954, Trehan & Bagal 1957). As it matures its body darkens (Reinhard 1923, Cockerhan et al. 1954) and becomes slightly curved (Trehan & Bagal 1957, Sutherland 1986[a]).

Its body size increases through the four larval instars from < 1 mm at hatching to up to 8.5 mm during the final instar (Reinhard 1923, Cockerhan et al. 1954, Trehan & Bagal 1957).

c. Pupa

The final larval stage excavates a pupal cavity , measuring two or three times the size of its body, inside the tuber (Reinhard 1923, Cockerhan _et al_. 1954, Sherman & Tamashiro 1954, Sutherland 1986^{a}). It then stops feeding and becomes quiescent for one or more days before pupating (Cockerhan _et al_. 1954).

The first external indication of pupation is the splitting of the head capsule of the prepupa between the rudimentary antennae and the skin of the dorsal thoracic region (Reinhard 1923, Cockerhan _et al_. 1954).

The pupa usually remains motionless, but if disturbed it makes a circular twisting movement of the abdomen, and sometimes turns over (Reinhard 1923, Cockerhan _et al_. 1954).

At first the pupa is white (Reinhard 1923, Trehan & Bagal 1957), and later it becomes yellowish. It gradually darkens, prior to transformation to the adult (Reinhard 1923).

The pupa is ca. 5 mm long by 1.5 mm wide (Reinhard 1923, Sutherland 1986^{a}). The length of the pupal period varies with temperature, from 5 to 11 d (Table 4; Mullen 1981).

d. Adult

At the end of the pupal stage, the pupal skin splits down the back beginning near the head. The new adult pulls its head and then its legs out of the old skin. As soon as the legs become hard they are used to push the skin off the rear of the body.

The partially exposed hind wings are wrinkled at first, but, after a short period of time, body fluids flow into them, expanding them to their full length beyond the elytra, in which position they remain until hardened. The wings are then folded in the normal position under the elytra.

The newly transformed adult is almost white and rather helpless. A minimum of 4 d is required before it is able to cut a passageway to the surface of the potato and emerge.

The adult weevil (Asian subspecies) is black in color with a reddish brown prothorax (Gonzales 1925, Trehan & Bagal 1957, Rajamma 1983, Sutherland 1986[a]). The elytra and head are black and the legs are reddish-brown and black (Kalshoven 1981, Sutherland 1986[a]).

Body size and antennal structure differ in males and females. The adult female is usually smaller than the male (5.8 x 1.5 mm compared with 6.1 x 1.6 mm, for the male; Rajamma 1983). Body size, however, is not a reliable criterion for sex determination, since it varies significantly in nature (Gonzales 1925, Trehan & Bagal 1957).

The sexes can be separated reliably on the basis of differences in the size and shape of the 10th antennal segment (Fig. 6).

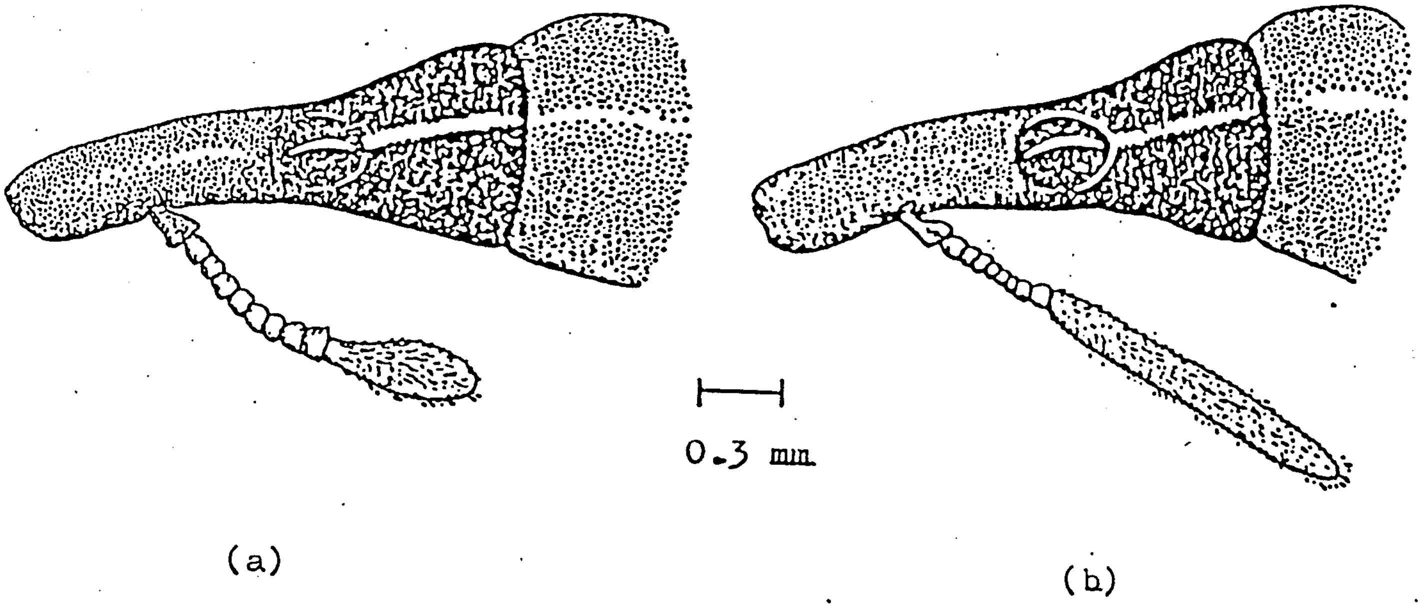

Figure 6. Head and antenna of adult *Cylas formicarius* (F.) (Coleoptera: Curculionidae). (a) female and (b) male. Source: Sutherland 1986^a.

2.1.4. Feeding habits and crop damage

Adult weevils feed on the exposed parts of the sweet potato plant, including the foliage, vine, stem, and tuber (Reinhard 1923, Gonzales 1925, Cockerham et al. 1954, Trehan & Bagal 1957, Kalshoven 1981, Rajamma 1983, Sutherland 1986[a]), although the tuber is the preferred food source (Reinhard 1923, Gonzales 1925, Cockerham et al. 1954).

The adult weevil feeds on the tuber surface, particularly if it is shaded (Reinhard 1923). On tubers, the damage appears as patches of shallow feeding punctures (Reinhard 1923). Females also deposit eggs, which are usually covered with frass, on the tubers.

On the vine, the adult weevil feeds by gnawing rather than by making distinct punctures; on the stems, petioles and leaf veins the feeding scars often run together or overlap (Cockerham et al. 1954).

The larvae feed inside the tubers and underground inside the lower portions of the stems by tunnelling into them (Trehan & Bagal 1957, Cockerham et al. 1954, Rajamma 1983). The tunnels inside the tubers follow a zig-zag pattern (Reinhard 1923, Rajamma 1983).

The tunnels are usually closed with excreta or remains of food materials (Rajamma 1983); feeding rarely occurs in open tunnels.

The level of damage that results depends on the parts of the plant that are attacked. Damage to above ground stems, vines and foliage is usually not significant, in contrast to underground damage, especially to the tuber, which can be devastating. The greenish black color and bitter taste of infested tubers containing terpenoids (Akazawa et al. 1960, Uritani et al. 1975, Sato et al. 1977) make them unfit for human and animal consumption (Rajamma 1983, Raman 1989).

In addition to attacking tubers in the field, losses of sweet potatoes in storage to the SPW are also significant (Rajamma 1983, Raman 1989).

The level of damage both in the field and in storage ranges from 5 % to 90 % (Sutherland 1986[a], Raman 1989). Loss of production was found to be 10 % to 20 % in Hawaii (Sherman & Tamashiro 1954), 60 % in Papua New Guinea (Szent-Ivany 1958), 60 % to 70 % in Malaysia (Ho 1970), 16% to 80 % in India (Rajamma 1983), 12 % to 90 % in Africa (Alverez 1987) and 5 % to 20 % in China (Lu et al. 1989). Therefore, loss of yield caused by the SPW can be one of the main limits on production (Raman 1989, Horton & Ewell 1991).

2.1.5. Reproduction

Sexual attraction in SPW has been claimed to be poorly developed, since in the laboratory males were found to show no response to the presence of females (Reinhard 1923). Recent studies, however, have shown that the males are attracted to sex pheromones released by the females (Nottingham et al. 1986). These pheromones are released only when the females have found and fed upon an appropriate host.

Copulation takes place after both sexes have fed on a tuber; it occurs several times (Reinhard 1923). During copulation, the weevils remain relatively motionless. If disturbed, however, the female immediately begins to crawl, either carrying the male with her or separating (Reinhard 1923).

At first the eggs are laid inside the vines, and then, when the tubers develop, inside them (Reinhard 1923). The female can lay eggs in all parts of the tuber, in especially prepared cavities. The egg cavities are usually wider, but shallower than the feeding punctures, and are oriented obliquely.

After digging out the cavity, the female turns around and inserts the tip of the abdomen, which moves from side to side. Eventually the ovipositor is protruded into the cavity and an egg is laid (Reinhard 1923). Adults mate within 3 to 5 d of emerging (Subramanian 1959) and after feeding (Reinhard 1923).

2.1.6. Factors affecting infestation by SPW

Infestation of sweet potato crops by SPW is affected directly and indirectly by the age of plants, type of soil, season, especialy rain fall, elevation, source of the weevils, and the cultural techniques being used.

The age of plants influences the level of infestation by SPW (O'Hair 1991). This reaches a peak at the same time as storage root formation and development, which starts as early as 28 DAP and reachs its peak between 56 and 84 DAP (Wilson & Lowe 1973, Wilson, 1982).

Soils with a higher clay content tend to shrink when dry and form cracks through which weevils can enter and reach underground tubers (Hahn & Leuschner 1982, Eusebio 1983, O'Hare 1991). When this occurs, high infestations are common, as has been documented in Papua New Guinea (Bourke 1985). Soil pH also affects the level of SPW infestation, high weevil infestation being associated with high soil acidity (pH 4.6 to 5.5), and low infestation with low soil acidity (pH 8.6 to 9.5; Abella 1982). Thus, applying lime to adjust soil pH to approximately neutral is often suggested as part of a weevil control program.

Infestation by SPW is claimed to be low at high altitudes, since the lower temperatures slow the developmental rate of SPW (Eusebio 1983); however, the situation may be reversed if there is a long dry season. Consequently, high damage to tubers usually occurs in highland regions during longer than usual dry seasons. For example, the dry season of 1954 in Bena-Bena, Goroka, and Chimbu subdistricts of the eastern highland region of Papua New Guinea, coincided with devastation of the sweet potato crop, and resulted in food shortages (Zsent-Ivany 1958, Anas 1960).

Infestation may also be a symptom of poor farm practices, such as allowing the spread of the SPW from a previous crop, from adjacent alternative hosts, or from infected planting materials. It is also affected by poor land preparation, failure to hill-up the plants, and by late harvesting (Franssen 1934, Kalshoven 1981, O'Hare 1991).

2.2. ROLE OF INTERCROPPING IN FOOD PRODUCTION

2.2.1. Definitions

Intercropping is a form of multiple cropping in which two or more crops are planted simultaneously in the same field (Andrews & Kassam 1976). Thus, cropping is intensified in both time and space, as is inter-specific competition (Andrew & Kassam 1976, Roy & Braun 1983, Gomez & Gomez 1983, Francis 1986). Consequently, achieving success requires a higher level of management skills than in a monocropping system.

Intercropping may be classified into mixed intercropping (no distinct rows), row intercropping (single rows), strip intercropping (several rows) and relay intercropping (overlapping in time) (Andrews & Kassam 1976, Roy & Braun 1983, Gomez & Gomez 1983, Francis 1986).

Intercropping is commonly practiced by subsistence farmers in tropical developing countries, at all levels of agricultural technology (Andrews & Kassam 1976, Gomez & Gomez 1983)

Traditionally, two or more crops are grown on the same field, primarily to achieve optimal use of space, diversify the range of products, and reduce risk in the face of a crop failure (Gomez & Gomez 1983).

Today, with the increasing loss of agricultural land and soil degradation, intercropping is being recognized as a way to enhance efficiency and conserve soil (Gomez & Gomez 1983).

2.2.2. Status

Intercropping has long been recognized as a way in which farmers in the tropics and subtropics, with limited land resources, can more effciently and economically produce food and cash crops (Beets 1982, Kass 1978, Willey 1979, Roy & Braun 1982). It now plays a significant role in the production of staple crops in Africa (Okigbo & Greenland 1976, Steiner 1982), Latin America, and Asia (Harwood & Price 1976, Gomez & Gomez 1983).

The significance of intercropping in developing countries is apparent from the large area of land that is devoted to this cropping system. In Africa, for example, almost 80 % of cultivated land is intercropped (Steiner 1984), and this is probably also the case for much of Latin America and Asia, where most staple crops are produced in intercropping systems.

The type of intercropping and species used varies with geography and culture. For example, 98 % of cowpeas in Africa, and more than 60 % of maize and beans in Latin America, are grown in crop mixtures (Francis <u>et</u> <u>al</u>. 1976); whereas in Asia, especially India, 5 to 6 % of rice, and 70 to 80 % of other crops, are grown as mixtures (Kass 1978). The commonest intercropped plants in Asia include upland rice, sorghum, millet, maize, rainfed wheat, and soybean.

Even though intercropping is prevalent in tropical areas where farms are small and farmers lack capital (Roy & Braun 1982, Liebman 1987), some farmers in temperate regions who have large farms and adequate capital are starting to practice intercropping, for a range of reasons. Such farmers may be using intercropping to solve problems of soil depletion and contamination (Poincelot 1986), which are often associated with long periods of monoculture agriculture.

Monoculture agriculture is characterized by a heavy dependence on petrochemical energy for operating farm machinery, and on synthetic fertilizers and pesticides (Hill & Ramsay 1977). Extensive use of energy has increased food production (Horwith 1985, Power & Follett 1987), but it has also resulted in changes in farming methods (Horwith 1985, Power & Follett 1987, Altieri 1987, Poincelot 1986), and a decrease in energy efficiency (Hill & Ramsay, 1977).

Monoculture tends to degrade the environment by accelerating soil erosion, increasing the potential for depleting or degrading ground water resources, reducing the quality of surface water, and using up fossil energy resources (Power & Follett 1987). It also causes health hazards and pest problems as a result of the wide use of pesticides and fertilizers (Poincelot 1986), and supplementary fertilization may be unable to compensate for the drop in yield (Power & Follett 1987).

As a result of energy related problems, including increased costs, environmental damage and health hazards, some farmers in developed countries have become motivated to practice intercropping.

Estimation of the percentage of crops that are planted as intercrops in various countries are given in Table 5.

Table 5. Percentage of cultivated land under intercrops in selected countries

Country	Main crop	% Intercropped	Intercrop[1]	References[2]
Dominican Rep.	Maize	> 40%	b,s,*	1
El Salvador	Maize	--	b,s,*	1
Jamaica	Maize	50 %	*	1
Mexico	Maize	20 %	*	1
Brazil	Rice	6 %	*	1
	Maize	11 %	*	1
	Bean	80 %	*	4
Paraguay	Beans	33 %	*	1
	Sweet potato	10 %	*	1
	Maize	10 %	*	1
Venezuela	Rice	16 %	*	1
	Maize	33 %	*	1
	Bean	20 %	*	1
	Cassava	20 %	*	1
	Cotton	50 %	*	1
Columbia	Bean	90 %	*	4,8
Guatemala	Bean	73 %	*	4
Bhutan	Potato	40 %	m,b	7
Indonesia	Maize	--	*	1
	Rice	--	*	1
Pakistan	Wheat	--	*	1
	Barley	--	*	1
	Cotton	--	*	1
Cent.African Rep.	Cotton	25 %	*	1
	Coffee	33 %	*	1
	Cassava	20 %	*	1
Senegal	Groudnuts	25 %	*	1
	Millet	25 %	*	1
Nigeria	Cowpeas	99 %	*	2
	Groundnut	95 %	*	2
	Melon	93 %	*	2
	Millet	90 %	*	2
	Cocoyam	86 %	*	2
	Cotton	80 %	*	2
	Maize	76 %	*	2
Uganda	Maize	84 %	*	3
	Bean	81 %	*	3,5
	Pigeon peas	76 %	*	3
	Coffee	63 %	*	3
	Cowpeas	62 %	*	3
	Goundnut	56 %		3
Malawi	Malawi	90 %	m	6,8

1) b = bean; s= sorghum; m= maize; * other crops

2) 1 = FAO, 1973; 2. Francis, 1986; 3. Okigbo & Greenland, 1976; 4. Francis *et al.*, 1976; 5. Osiru, 1982; 6. Edje, 1982; 7. Roder *et al.* 1992; 8. Coaker 1990.

2.2.3. Advantanges and disadvantanges

The advantanges of intercropping that are likely to appeal to subsistence farmers include: the possibility of obtaining a higher yield, reduced risk of total crop failure, enhanced resource use, reduced fertilizer and pesticide requirement, absorption of excess farm labor, and improved nutrition (Gliessman 1985, Vandermeer 1990).

The posibility of achieving a greater yield from the limited area available is often the main reason why more and more farmers are choosing to intercrop (Kass 1978, Liebman 1987, Gliessman 1985). Total yield per area is usually greater in intercropped systems, even though the individual species invariably yield more in monocultures (Trenbath 1974, Hardwood & Price 1976, Willey 1979, Gliessman 1985). The greater total yield in intercropping occurs if the relative yield total (RYT), which is the sum of the intercropped yield divided by yields of monoculture crops, is greater than 1.0 (Gliessman, 1985).

Not all the intercropping systems, however, achieve RYT's greater than 1.0. Trenbath (1986), for example found that among 572 comparisons of crop mixtures, only 66 % had RYT's close to 1.0, indicating no distinct advantage to these mixtures in terms of yield. On the other hand, 20 % of the mixtures had RYT's greater than 1.0, ranging up to 1.7, indicating a distinct advantage over the monocultures. Only 14 % had RYT's less than 1.0, indicating distinct disadvantages.

In addition to yield advantages, intercropping may reduce economic loss because of the failure of a particular crop within the system. Even when the RYT is close to 1 (e.g., shows no increased yield over the monoculture), the other benefits of intercropping, such as lower energy costs and less pest problems, will serve to make intercropping competitive with the monoculture system (Harwood & Price 1976, Willey 1979, Horwith 1985, Liebman 1987, Gliessman 1985).

Available light, water and nutrient resources may also be used more efficiently in intercropping systems (Liebman 1987). Thus, because total densities are usually higher in such systems, more light can be intercepted early in the growing season. This has been demonstrated for mixtures of maize and mungbean, peanut or sweet potato (Liebman 1987). Moreover, because intercropped plants have non-synchronous patterns of canopy development and different maturation times, the leaf area produced over the growing season is greater and therefore able to intercept more light than are monocultures (Liebman 1987).

One outcome of the increased canopy cover is that a greater proportion of available soil water is channelled through the crops as transpiration, rather than being lost as evaporation from the soil surface. Futhermore, increased canopy coverage can also increase penetration of rainfall into the soil, and decrease soil erosion by lessening the impact of rain and wind on the soil surface. This has been documented, for example, with maize intercropped with cassava (Lal 1986, 1989).

Intercropping of plants with different rooting patterns permits greater exploitation of a larger volume of soil and improves access to relatively immobile nutrients. As a result, intercropped plants tend to absorb more nutrients than those in monocultures (Horwith 1985, Liebman 1987).

In addition, intercropping with legumes may enhance nutrient availability for the non-legume crop, e.g., maize with soybean, cowpea or mungbean. The legumes may provide both additional nitrogen through their mutualistic association with nitrogen-fixing bacteria such as Rhizobium (Nicol 1935, Gomez & Zandstra 1977, Horwith 1985), and phosphorous through their mutualistic association with vesicular arbuscular mycorrhizal (VAM) fungi (Hetrick 1984). The mutualistic associations, especially those involving VAM, may also occur with non-legume intercrops (Chiariello et al. 1982). Such relationship can reduce the need for imported nutrients, whether as manures or synthetic fertilizers.

Intercropping may increase or reduce pest populations. Reduction mechanisms include the provision of physical barriers to the pest's ability to find suitable hosts (Litsinger & Moody 1976, Perrin 1977); the production of chemicals that disrupt the searching behaviour of the pest and provide associational resistance (Perrin 1977); and the provision of shelter and alternative food sources for predators and parasites (Litsinger & Moody 1976, Perrin 1977, Horwith 1985, Liebman 1987). By taking up excess available nutrients, especially nitrogen, intercropping may prevent the main crop from becoming more attractive to pests, such as through the accumulation of free amino acids and sugars in the plant tissue.

Intercropping can affect the development of diseases, nematodes and weeds (Litsinger & Moody 1976, Liebman 1987). Thus, a susceptible crop planted between a resistant crop may be protected from a disease by the interception of the inoculum (Liebman 1987). Also, the microclimate provided by the intercrop may be less or more favorable for disease development (Litsinger & Moody 1976, Liebman 1987). Some crops are known to excrete substances that are toxic to nematodes, thereby lowering the incidence of infection in susceptible hosts (Liebman 1987).

The more complete canopy and plant cover associated with intercropping is also an effective way to control weeds (Litsinger & Moody 1976, Liebman 1987). In these ways, intercropping can reduce the need for pesticides in crop production, and so reduce production costs.

Because intercropping requires more labor and management than monoculture (Andow 1983, Gomez & Gomez 1983, Liebman 1987), it can absorb excess farm labor (Gomez & Gomez 1983). Consequently, intercropping is likely to be most profitable in labor intensive production systems (Andow 1983, Hare 1986; Liebman 1987).

There are, however, some disadvantanges. These include yield reduction of the main crop, loss of productivity during drought periods, and high labor inputs in regions where labour is scarce and expensive (Gliessman 1985).

It is well documented that in most cases the main crop in an intercropping system will not reach as high a yield as in a monoculture, because there is competition among intercropped plants for light, soil nutrients and water (Willey 1979, Fordham 1983, Gliessman 1985). This yield reduction may be economically significant if the main crop has a higher market price than the other intercropped plants.

Another disadvantange that is likely to occur is the higher cost of maintainance, in particular, weeding, which may have to be done by hand. This is not a serious problem in countries where excess farm labor is cheap, but for countries lacking such a labour force, intercropping will result in increased costs. Furthermore, harvesting of one crop may cause damage to the others (Gliessman 1985). Finally, the increased canopy cover may result in a microclimate with a higher relative humidity conducive to disease outbreaks, especially of fungal pathogens (Gliessman 1985).

2.3. EFFECTS OF INTERCROPPING ON INSECT PESTS

Intercropping can result in a significant reduction of insect pest problems within agroecosystems (Altieri & Letourneau 1982, 1984, Cromatie 1983, Perrin 1977, Altieri & Liebman 1986). This occurs because intercropping may disturb the insect's activities and development, make the host less available, and enhance the development of the pest's natural enemies.

The activities that are affected include the rate of colonization, movement, and development (Perrin 1977, Altieri & Liebman 1986). The main ways in which intercropping has significant effects on insect populations are explained below.

2.3.1. Rate of colonization

Intercropping affects the rate of insect colonization by disturbing the visual and olfactory responses that are employed by many insects in searching for suitable host plants (Cromatie 1983, Ferro 1987). As a result, they do not easily recognize and locate suitable hosts that are dispersed amongst other vegetation (Cromatie 1983, Kareiva 1983).

Colonization of large, closely spaced fields of the same crop is likely to be more efficient than if the fields are small and widely spaced. Thus, colonization by insects may be less intense when the agroecosystem contains a relatively low proportion of food useable by the particular insect pest (Cromatie 1983).

a. Visual effects

In an intercropping system, host plants are usually scattered among other crop plants, so that the plant is camouflaged by the non-host crop (Perrin 1977, Cromatie 1983). Consequently, for a pest that is flying over the field, intercropping makes host recognition more difficult (Perrin 1977).

b. Olfactory effects

Intercropping of host and non-host plants may produce a mixture of odors that fill the air and so mask the smell of host plants and disorient insect pests as they attempt to locate their hosts (Perrin 1977, Cromatie 1983). As a result, intercropping makes it more difficult for insects to find their host plant, and so results in less plant damage. For example, when cabbages are intercropped with tomato, they are sometimes protected against flea beetle infestation (Burroughs 1982). Also, certain intercropped species release chemicals that repel and antagonize insect pests of other crops. For example, the diamond-back moth, *Plutella xylostella*, causes less damage on cabbage intercropped with tomato, as the tomato odors repel the moth and so reduce colonization on the cabbage crop (Buranday & Raros 1975).

Some insect species, however, may be attracted to the mixed odor produced by particular combinations of intercropped plants (Kayumbo 1976). Therefore, to avoid the undesired result of increasing insect pests as a result of intercropping, careful consideration must be given in selecting the species to be intercropped (Burroughs 1982).

c. Diversionary host effects

In intercropping, the combination of crop plants may shift insect feeding to the more tolerant or less valuable crop, or the pest may colonize one particular crop in a mixture, thereby protecting and reducing the feeding damage to the more economically valuable crops, which may be more susceptible (Perrin 1977, Cromatie 1983). In this way, economic losses can be decreased.

The intercropped plants may function as diversionary hosts for a particular pest (Cromatie 1983). This may involve careful timing of planting so that the particular growth stage of the intercrop that is most attractive to the pest is present at the time when the main crop is most susceptible (Perrin 1977).

2.3.2. Development

The degree of shading and the nature of cultural practices often differ between multiple and monoculture systems, and this usually affects the crop micro-climate, which may become less or more favourable for a particular insect pest (Suryatna & Harwood 1976). Also, the confusing olfactory and visual stimuli received from hosts and non-hosts may disrupt normal feeding and mating behaviours (Tahvanainen & Root 1972). In addition, the pests that are associated with a particular crop combination might disperse elsewhere because of the low quality of food obtained from the intercropped plants. This may interfere with the insects' growth and development (Kareiva 1983), and, as a result, the population of insects, as well as the crop damaged, will be low .

2.3.3. Dispersal

Intercropping affects the movement of both adult and larval stages of insect pests because it may provide a physical barrier that prevents their dispersal (Perrin 1977, Cromatie 1983). For example, tall intercrops grown as rows between shorter crops may, by reducing air flow, cause more insect pests to settle than if the air flow were uninterupted (Litsinger & Moody 1976). Moreover, as a physical barrier, intercropping may be valuable in reducing colonization, thus preventing high infestation and crop damage (Cromatie 1983). For example, the cabbage rootfly, *Delia radicum*, can be impeded from laying its eggs in fields that have a cover of clover (Burroughs 1982).

2.3.4. Abundance of natural enemies

By providing a more diverse environment, intercropping may create more favorable conditions for natural enemies, both in terms of numbers and diversity (Perrin 1977, Cromatie 1983). This may occur through the provision of essential resources for predators and parasites, and so enable them to obtain all of their requirements near to the pest population, rather than having to seek it farther away (Cromatie 1983). Important resources include food, cover and alternative prey (Way 1977).

Intercropping provides more pollen and nectar sources, which may attract natural enemies and increase their reproductive potential (Kareiva 1983, Altieri 1987). Moreover, it may increase ground cover, which favors certain predators such as carabid and staphylinid beetles, and increase the diversity of herbivorous insects that can serve as alternative food sources for natural enemies. Therefore, creating an environment suitable for a diversity of insect species will help prevent the loss of beneficial insects (predators and parasitoids) when their main hosts are in low numbers (Altieri 1987). In these various ways, intercropping can indirectly support the beneficial insects that prey on the pests (Burroughs 1982, Flint 1990).