The Sweet Potato Butterfly
Acraea acerata in Ethiopia

Ecology and economic importance

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Abstract

The sweet potato butterfly (*Acraea acerata* Hew.) has become an important pest on sweet potato in Southern Ethiopia in the last two decades. This thesis deals with its ecology and economic importance in Southern Ethiopia.

The insect is indigenous to this area where it feeds on both native wild *Ipomoea* species and the introduced sweet potato (*I. batatas*). However, its performance was better on the new host, sweet potato. The small *A. acerata* populations on the scattered patches of the native *Ipomoea* species evidently contribute little to the population dynamics of *A. acerata* in sweet potato fields.

Several parasitoid species attack the immatures of *A. acerata*. Larvae are attacked by two parasitic wasps and a parasitic fly while a third parasitic wasp kills the pupae. Late instar larvae die from *Beauveria bassiana* infection. Mortalities inflicted by the natural enemies were usually low and they did not seem to act in a direct density dependent way. Enemies thus appear to have little effect during high population density. However, they may play a role in keeping the population at low density for a longer period.

The insect breeds throughout the year with six discrete generations per year, which form generation cycles. An analysis of stage specific mortalities and recruitment rates from eighteen generations showed that no density dependent mortality operated in egg-young larvae, young larvae-old larvae and old larvae-pupa stages. Density dependent mortality, however, operated in the interval pupa-adult and there was strong density dependence in recruitment rate. A probable reason for this finding is adult emigration from high-density populations. Butterfly population densities are temporally autocorrelated with the partial autocorrelation function showing a positive one-generation lag and a negative two-generation lag which suggests that population regulation is a second order process with density dependence acting in the adult stages. A more detailed analysis, however, showed that larval density affects recruitment in the same generation, i.e. with almost no lag.

A strong positive correlation was found between larval tent density, extent of defoliation and yield loss and the correlation was stronger for early than for late harvests. However, delayed harvesting did not reduce yield loss significantly. It is recommended to use insecticides at larval densities exceeding 4 tents/m^2 during the first three months after planting. It is proposed that assessment of *A. acerata* damage should be based on young larvae density because they are easy to count, better correlated with yield loss and surveying at this development stage leaves enough time to decide on control measures.

Key words: *Ipomoea, Acraea*, population dynamics, natural enemies, yield loss, host plants.

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The present thesis is based on the following papers which are referred by their roman numerals

I. Azerefegne, F. 1999. Oviposition, development and adult emergence in the sweet potato butterfly, *Acraea acerata* Hew. (Nymphalidae: acraeinae). Manuscript.

II. Azerefegne, F. 1999. Larval performance of the sweet potato butterfly (*Acraea acerata* Hew.) on *Ipomoea* species. Submitted.

III. Azerefegne, F. and Solbreck, C. 1999. Effects of parasitoids and pathogens on the populations of the sweet potato buttefly, *Acraea acerata* Hew. Manuscript.

IV. Azerefegne, F. and Solbreck, C.1999. Population dynamics of the tropical butterfly *Acraea acerata* Hew. (Nymphalidae: Acraeinae): a defoliator of sweet potato. Manuscript

V. Azerefegne, F. 1999. Yield loss of sweet potato caused by the sweet potato butterfly (*Acraea acerata* Hew. Nymphalidae: Acraeinae) in Ethiopia. Submitted

Introduction

Sweet potato (*Ipomoea batatas*) is grown throughout the tropics for its edible tuberous root and ranks seventh among all food crops world wide in terms of annual total production (FAO, 1984). It is used as a human staple food, animal feed, and an industrial raw product for starch extraction and fermentation, and various processed products (cf. Chalafant, 1990). Although the plant is adapted to both low and high input agricultural systems, it is extremely important in subsistence farming systems. Tolerance to drought, high yield per unit area, ease of establishment from vine cuttings, and production with little input in terms of fertilisers and pesticides, are some of the features which have made sweet potato cultivation very attractive among the resource poor farmers.

The damage by arthropod pests is one of the constraints which limits the production of sweet potato world-wide (Horton, 1989). Recently, 270 insect and 17 mite species were listed as pests of sweet potato in the field and in storage around the world; of these the *Cylas* weevil species are the most damaging (cf. Chalafant *et al.*, 1990). Since most sweet potatoes are produced in low input agricultural systems, losses due to insects may often reach 60-100% (Chalafant *et al.*, 1990). Much of sweet potato entomology has focused on the sweet potato weevils. Vine and root tunnelling by the weevils reduce root yield and contaminate it with rotting bacteria and fungi. Most importantly, terpenoids (Sato *et al.*, 1981) produced in response to weevil feeding make the slightly damaged roots unpalatable.

Numerous species of insects also feed on the above ground parts of sweet potato. Several species of tortoise and leaf beetles (Chrysomelidae), the sweet potato hornworm (*Herse convolvuli*, Sphingidae) and the sweet potato butterfly (*Acraea acerata*) are common insects which defoliate sweet potato (Smit *et al.*,1997; Hill, 1983). Being foliage feeders, these insects have previously been considered as less important pests.

The sweet potato butterfly (*Acraea acerata*)

The association between the sweet potato butterfly, *Acraea acerata* Hew. (Lepidoptera: Acraeinae) and sweet potato is relatively new because sweet potato is of American origin (Austin, 1988), and the plant was introduced to Africa about 500 years ago by European explorers (Yen, 1982). *A. acerata* is native to Africa and it feeds on native *Ipomoea* species. On sweet potato, it has an "occasional pest" status in East, Central and West Africa (Lefèvre, 1948; Le Pelly, 1959; Nyiira, 1982; Janssens, 1982; Hill, 1983; Smit and Matengo, 1995; Anioke *et al.*, 1995; Anioke, 1996). *A. acerata* is found throughout the Afrotropical region except for savannah areas as it is believed to be dependent upon a certain level of moisture (Larsen, 1991).

Adult butterflies are aposematic with an orange and black colour pattern and avoided by avian predators. The unpalatability of *Acraea* species is due to cyanide compounds, which are exuded when the butterflies are handled roughly (Owen, 1971; Larsen, 1991). Many *Acraea spp.* feed on plants containing cyanogenic compounds and the larvae may selectively take up these cyanoglucosides from their food plant although they can metabolically synthesise them (Raubenheimer, 1989; Larsen, 1991). *Ipomoea* species, the food plants of *A. acerata*, are toxic and known to contain different kinds of alkaloids (Steward and Keeler, 1988; Amor-Prats and Harborne, 1993) and cyanogenic compounds (Arago, 1972; Seigler, 1976; Ghazi *et al.*, 1989) which might be sequestered by the larvae and used in defence.

The butterfly deposits its eggs in clusters on sweet potato leaves. Larvae hatch within a week and young larvae form loose protective tents on leaves while feeding underneath. The first 2-3 instars form cohesive groups whereas the older larvae disperse and feed solitarily. The early instars (I-III) scrape one surface of the leaf and the mesophyll leaving the other epidermis intact, whereas the late instars (IV and V) chew the whole width of leaves. Pupation takes place on the plant or on the soil. The insect has several generations per year (Hill, 1983; Smit *et al.*, 1997).

Several species of natural enemies kill immatures of *A. acerata*. Although eggs are not parasitised, larvae are attacked by *Glyptapanteles acraeae* Wlkn. (Braconidae), *Charops sp.* (Ichenumonidae), *Meteorus sp.* (Braconidae) and *Zenillia var* Curran. (Tachinidae), *Carcelia normula* (Tachinidae) and pupae by *Brachymeria spp.* (Chalicididae) (Lefèvre, 1948; Subukino, 1987; Lugojja, 1996). In addition, two pathogenic fungi *Beauveria sp.* and *Isaria sp.*, are known to cause larval diseases (Lefèvre, 1948; Smit *et al.*, 1997; Lugojja, 1996).

Sweet potato production in Ethiopia and the sweet potato butterfly problem

In Ethiopia, sweet potato is cultivated in the east, south and south-west part of the country. The production is intense in Welayita (Sodo), which is situated in North Omo, Southern Ethiopia (Fig. 1). It is one of the most densely populated parts of the country. About 2.6 million people live in North Omo and its surroundings and they depend on 267,870 hectares of farmland (Central Statistics Authority, 1996). Production is subsistence and farmers grow various kinds of crops. A typical farm will grow cereals (maize, sorghum and teff), legumes (horse beans, haricot beans, peas), root and tuber crops (cassava, potato, sweet potato, taro, yam) and perennial crops like coffee and enset.
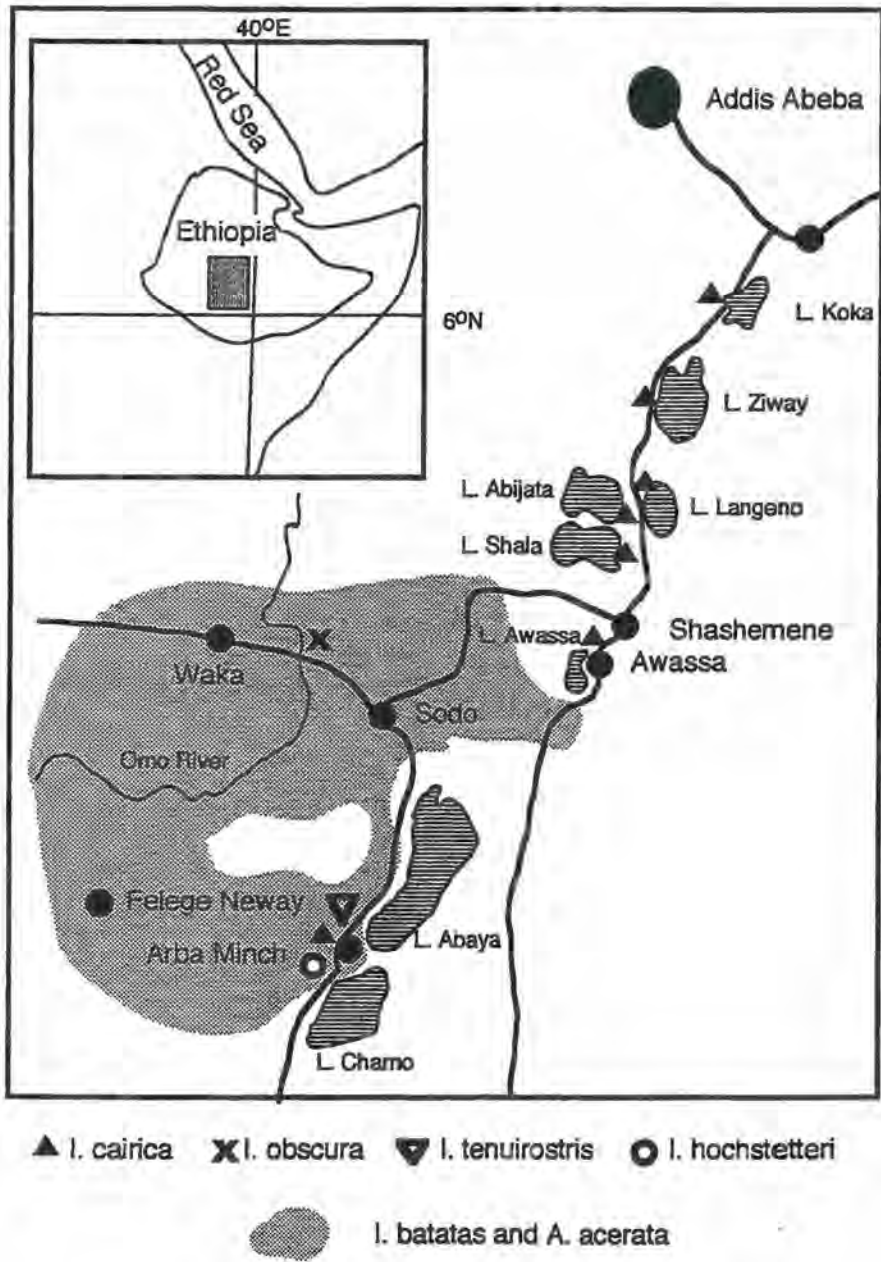
Figure 1. Distribution of *Ipomoea* species and *Acraea acerata* in Southern Ethiopia.

Sweet potato is a strategic crop in that it serves as a security and fall back when the food reserves from cereals dwindle. Some farmers in this area mainly depend on sweet potato for two to three months every year. Production is for home consumption although some farmers sell a part of their harvest. Planting is on small parcels of land (0.1-0.3ha) and no insecticides or artificial fertilisers are used. Many farmers practice successive plantings throughout the year. However, the end of the rainy season (September and October) is the main planting period during which time relatively larger plots are devoted to sweet potato production.

One of the main threats to sweet potato production in Southern Ethiopia is defoliation by the sweet potato butterfly *(A. acerata)* and the insect is considered as the most important pest of the crop. During the last two decades, Southern Ethiopia has experienced several local outbreaks. *A. acerata* is common in Welayita and its surroundings at elevations of 1500 to 2200m representing the entire altitudinal range over which the crop is cultivated. However, the butterfly is usually more abundant at higher altitudes (1800-2100m) (Chernet, 1993; personal observations).

The adoption of continuous planting which resulted in overlapping of crops has been implicated in favouring the build up of *A. acerata* population (Chernet, 1993). A survey was conducted among 162 farmers in Welayita concerning changes in cultural practices that might have lead to the increased frequency of outbreaks (Azerefegne, unpublished). Farmers responded that October and May were the planting months 15-20 years ago, October being the main planting time. Nowadays most farmers have adopted successive planting schemes during August-October and March-May. Only 35.8% of the farmers plant twice a year while the others plant 3-6 times. The current average frequency of planting is four times a year. The increase in the frequency of planting is triggered by the introduction of new high yielding and early maturing varieties. All farmers found the two newly introduced varieties (locally known as Gadisa and FAO) superior to the cultivars they used earlier. Despite all the problems they encounter with the sweet potato butterfly farmers want to maintain the present system of production. The only time farmers do not plant is during the periods of heavy rains especially in those areas with water logging problem. All farmers claim that sweet potato grown in the rainy period gives low tuberous root yield. However, farmers maintain sweet potato during the rainy period and the dense foliage will be used as planting material for the coming main planting period.

There is no report of any sweet potato resistant variety against *A. acerata*. Observations made in several countries indicate that all varieties of sweet potato will be completely defoliated during outbreaks (Ndamage *et al.*, 1992; Chernet, 1993; Smit *et al.*, 1997). However, there could be variations between varieties in their tolerance to defoliation and compensation for the lost yield.

The insect is easily controlled by any of the contact or stomach poison insecticides (Chernet, 1993; Girma, 1994; Smit *et al.*, 1997). However, most sweet potato growing farmers in Africa can not afford to buy insecticides and sprayers due to the low value of the crop. In Ethiopia, the Ministry of Agriculture provides insecticides during outbreaks. Farmers mainly depend on traditional methods of controlling *A. acerata* which involve handpicking of young larval nests, application of ash and manure (Smit *et al.*, 1997; Leblanc, 1993; personal observations). However, the need for constant vigilance to remove nests before larvae disperse makes it difficult to practice the handpicking method of control during high population density. In addition, it has to be applied on a regional level to avoid immigration of butterflies from nearby farms.

The relationship between defoliation and yield loss in sweet potato is poorly known for most sweet potato defoliating insects and there are no estimates of losses caused by *A. acerata*. It is generally believed that severe defoliation has a temporary effect on root yield for which the plant compensates by a longer period of growth (Chalafant *et al.*, 1990). Nevertheless, *A. acerata* has been observed to cause extensive damage. Complete crop failure and lack of planting material as a result of extensive defoliation is a common experience in Eastern African countries (Lefèvre, 1948; Smit *et al.*, 1997; personal observations).

Dynamics of tropical insect populations

Insect population studies from the tropics are still underrepresented in the ecological literature. There is a severe shortage of studies containing data on stage mortalitites and recruitment rates. This is evident, for example, from Stiling's (1988) review of key factors and density dependence and later in Cornell and Hawkins' (1995) extensive review of mortality factors in insect populations. How do populations change on an inter and intrageneration basis? What does the demographic structure of tropical insects look like? Which factors and processes affect the rate of population change most? Tropical insect populations, which were earlier believed to be more stable than temperate ones, seem to fluctuate no less than their counterparts in the temperate region, at least for those parts of the tropics which are seasonal (Wolda, 1978, 1983). Some species, however, do not fluctuate much. Ehrlich and Gilbert (1973) showed that the abundance of the butterfly *Heliconius ethilla* was remarkably constant in Trinidad. Some species of *Charaxes* butterflies were also found to be rather constant in Sierra Leone, but Owen and Chanter (1972) considered this finding as exception; in their experience tropical butterflies fluctuate widely in abundance.

Many tropical insects, especially those of agricultural pests, undergo generation cycles with a period of roughly one generation (Knell, 1998). Theory suggests that such types of dynamics can arise both from intraspecific competition and from the influence of natural enemies (Godfray and Hassel, 1989, Knell, 1998). However, empirical data are scarce and the causes and extent of fluctuations of tropical insect populations are poorly investigated.

Aims of the study

The present study has dual aims: ecological and practical. It describes and analyses the life history, enemy and host plant relationships and population dynamics of a tropical butterfly. How does the population fluctuate and what factors and processes determine fluctuation patterns? It also describes and analyses the pest status of *A. acerata* with the aim of developing better pest management methods.

Results and discussion

Life history of *A. acerata*

The insect breeds throughout the year with about six discrete generations. Females lay their eggs in single layered batches of approximately 160 eggs (I) on the underside of sweet potato leaves. Oviposition takes place on young plants with few leaves as well as on older vines with many leaves. Most eggs were found on the middle leaves along the vine. This oviposition behaviour helps the larvae to avoid feeding on the tough older leaves and the young small leaves. Hatching takes about a week.

Larvae pass through five instars (I). In the first three instars larvae feed gregariously whereas in the last two they disperse and feed solitarily. Larval development is of shorter duration in males than in females. Larval developmental lasts about 10 days longer in rainy than in dry periods (I). The difference in larval developmental periods in the field does not seem to be caused by temperature variations, as the temperatures of both the rainy and dry periods during the observation periods were not different. Pupation takes place on the foliage or on the ground. Pupation under clods of soil and in cracks is more frequent during dry periods. The pupal stage lasts about seven days. Adults emerge during the daytime and mating was observed during the afternoons. The adults are short lived with a maximum life span of nine days (I).

Host plants and *A. acerata* distribution

The present study shows that *A. acerata* larvae can survive and develop well on *I. tenuirostris* and *I. cairica*, both native species, as well as on the introduced *I. batatas* (II). Although sweet potato is an introduced plant, it supports the development of *A. acerata* larvae better than the wild indigenous *Ipomoea* species on which the insect has presumably been feeding prior to the introduction of sweet potato. *A. acerata* larvae do not feed on all *Ipomoea* species which are indigenous to the country. One example is *I. hochstetteri*, which is the most apparent and abundant species in areas where the insect is naturally distributed. Similarly, the introduced *I. indica* and *I. purpurea* are widely distributed in

tropical Africa and the insect has had extended contact with these plant species but *A. acerata* does not utilise them.

Although larval performance of *A. acerata* on *I. cairica* is equivalent to that on *I. tenuirostris* in the laboratory experiment, it is not utilised in the field. *A. acerata* eggs were frequently observed on both *I. tenuirostris* and sweet potato but not on *I. cairica*. Females of many butterfly species fail to accept some plants that are suitable for larval development (cf. Jaenkie, 1990). The reason why the abundant and widely distributed *I. cairica*, being suitable for larval development, is not used in the field is not yet known, but it probably has to do with oviposition behaviour.

The distribution of the insect overlaps with the distribution area of the two wild *Ipomoea* species, *I. tenuirostris* and *I. obscura*, as well as with the intense sweet potato cultivation area in Southern Ethiopia (II). The insect utilises different *Ipomoea* species in different habitats. At relatively high altitudes (1800-2000m a.s.l.) of Southern Ethiopia, where sweet potato production is intense, the insect was exclusively found on this crop. Along lakes Abaya and Chamo (both at 1200m a.s.l.) it was observed to feed on *I. tenuirostris* despite the fact that this is the least abundant *Ipomoea* species. Around Omo River (760m a.s.l.) the insect feeds on *I. obscura*. The population density of *A. acerata* in its natural habitats was low at any time. The low level of *A. acerata* population on the scattered patches of the native *Ipomoea* species evidently contributes little to the population dynamics of *A. acerata* in sweet potato fields.

Enemies

Several species of enemies attack immatures of *A. acerata* (Fig. 2). Two parasitic wasps, *Glyptapanteles acraeae* (Wilkinson) (Braconidae) and *Charops sp.* (Ichneumonidae) and one tachinid fly, *Carcelia sp.*, attack the larvae. The tachinid, is different from *C. normula* which is identified as *A. acerata* larval parasitiod in many African countries and it is probably an undescribed species (N. Wyatt pers. Comm). Pupae are killed by *Brachymeria albicrus* (Chalcididae). The pathogenic fungus *Beauveria bassiana* (Balsamo) Vuillemin (Moniliaceae) also attacks larvae. No parasitoids were found attacking the eggs of *A. acerata*, but disappearance of eggs was frequent in the field. A predatory bug *Macroraphis acuta* (Pentatomidae) was identified as egg predator. This species also feeds on larvae and pupae of *A. acerata*. No vertebrate predators were observed on this presumably aposematic insect

There is overlap between the different parasitoids in the time of attack and death on larvae (Fig. 1). *G. acraeae* young host larva. The host is killed usually in the fourth instar. *Charops sp.* attacks the second instar and emerges somewhat later than *G. acraeae*, mainly from fifth instar host larvae. *Carcelia sp.* attacks older larvae than the two hymenopterous parasitoids. It was hatched from third to fifth instar field collected larvae. Some *Carcelia sp.* emerge from last instar host larvae

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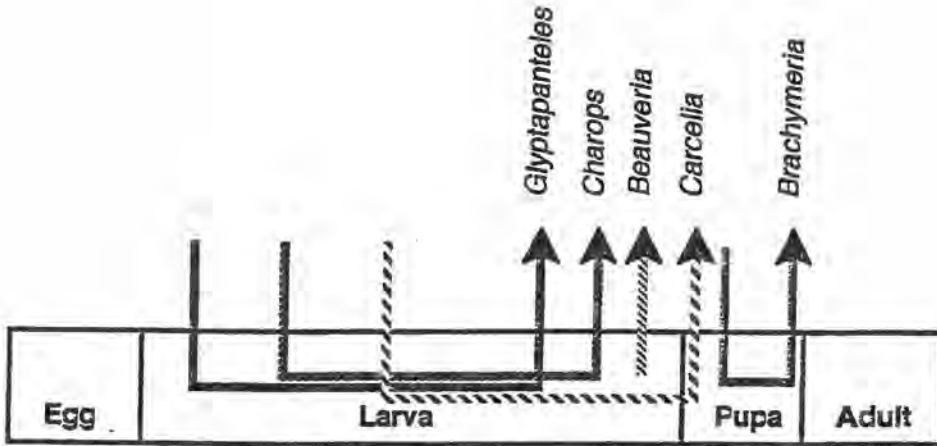but the majority emerge from host pupae. *B. albicrus* is confined to the pupal stage.

Figure 2. Sequence of attack and emergence by the parasitoids and appearance of *B. bassiana* In tehlife cycle of *A. acerata*.

Enemies seem to be of little importance in determining rates of change in *A. acerata* populations (III). No direct density dependent effects of *G. acraeae*, *Charops sp.*, *B. bassiana* and *Carcelia sp.*, could be found nor could any lagged effects of these enemies be detected (III). However, they sometimes show increased mortality during population lows suggesting that they possibly play a role in causing longer and deeper population valleys.

Population dynamics

A. acerata populations develop with discrete generation cycles (Knell, 1998). It breeds during all seasons with about six generations per year but without clear seasonal trend. There are large variations in population density between generations and years. Population fluctuations are about two to three orders of magnitude. However, population change is gradual and there are long periods (five generations) of either continuous growth or decline.

Butterfly population density is temporally autocorrelated with the partial autocorrelation function showing a positive one-generation lag and a negative two-generation lag (IV). Stepwise multiple regression showed that densities in two previous generations could explain the present population density of

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two previous generations could explain the present population density of butterflies (logN(t)=-0.350+1.497logN(t-1)-0.780logN(t-2) (R^2(first step)=71.2%, R^2(second step)=87.2%, df 15, 2). The other developmental stages showed the positive one lag only (IV).

No density dependent factor seems to operate during the period from egg to pupa. Density dependent processes, however, operate late in life affecting pupal-adult survival and recruitment. A curvilinear relationship between pupal and adult population densities suggests that direct density dependence acts in the upper interval of pupal densities and inverse density dependence in the lower range (IV).

Recruitment rate is also strongly density dependent. This effect is probably mainly a result of density dependent emigration. Lowered recruitment rate at high population density is possibly also affected by competition among larvae; food shortage or low food quality at high larval density is likely to result in small size butterflies with lowered fecundity.

The PACF analysis of butterfly densities suggested that in the *A. acerata* population negative feed back operates with a two-generation lag (IV). However, more detailed analyses looking at how recruitment rate is related to all five intra generation developmental densities measured (egg, young larvae, old larvae, pupae, adults) revealed that recruitment rate is affected by density of old larvae in the very same generation and that densities in earlier generations make no contribution. In the present case it appears that the PACF analysis does not give a correct picture of the lag structure, whereas the analysis of within generation survival and recruitment rate suggests a feed back mechanism of much shorter lag (cf. Royama, 1997).

Rainfall has significant effects on survival during both egg-pupa and pupa-adult intervals, but in opposing ways. In larvae survival decreases with rainfall, whereas it increases for the pupa-adult period. The former effect is probably the result of heavy rains directly killing larvae, but the latter effect is less easily explained. It seems that extreme weather conditions cause significant disturbances in *A. acerata* system.

The present study suggests that adult behavior and the recruitment process constitute the key to population regulation in *A. acerata*. Natural enemies seem rather inefficient in perturbing or regulating the system (Azerefegne and Solbreck, 1999). The *A. acerata* system is thus similar to some recently described systems dominated by bottom up effects in combinations with weather disturbances (eg. Solbreck, 1995).

Defoliation of sweet potato by *A. acerata* and yield loss

Two peaks of larval density were observed during the 5 to 6 month cropping cycle representing two successive insect generations. The insect population density varied between the growing seasons studied. High densities were observed during the 1995-96 and 1997-98, with 7-10 and 6-12 larval tents/m^2, respectively in the first generation. The 1996-97 season had the lowest density of larvae; less than 0.1 larval tents/m^2 at any time (V).

During 1995-96 and 1997-98, insect feeding caused considerable leaf damage as well as reduction in ground cover. The difference in the ground cover between the protected and unprotected plots reached a maximum of 28 % in 1995-96 and 14 to 53% in 1997-98. Likewise, the proportion of leaves showing signs of *A. acerata* feeding ranged from 79-90% during these two years of high insect population density. On the other hand, the very few larvae observed in 1996-97 did not reduce the ground cover.

Defoliation of sweet potato plants by *A. acerata* resulted in significantly lower yields of tuberous roots of sweet potato (V). Tuber losses of 31-53% were recorded in farmers' fields in years with high insect population density. Delaying harvesting did not reduce the loss in root yield. Defoliation by *A. acerata* also reduced the biomass of sweet potato tops (V). This difference was observed in all farms during the early harvests. The non-significant differences between protected and unprotected treatments at some sites for late harvests indicate that the crop can compensate for part of the foliage loss given enough time and favourable growing conditions. It seems that compensation through delayed harvesting is more likely for tops than for the root yield.

Complete artificial defoliation caused significant yield reductions irrespective of the age of sweet potato at defoliation but defoliation at earlier stages (6 and 8 weeks) seems to result in higher levels of root yield loss (Fig. 1). Removal of half of the leaves seems to be serious on eight week old sweet potato plants but was not statistically different from the non-defoliated plots. The complete defoliation treatment resulted in lower biomass of sweet potato tops for all ages. However, neither complete nor 50% defoliations resulted in a statistically significant reduction of tops compared with the non-defoliated plots (V).
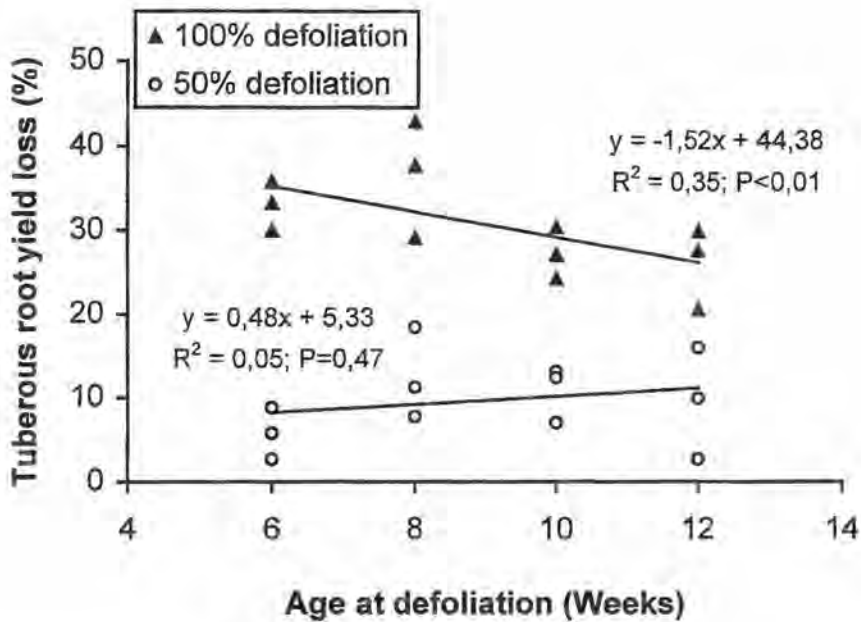
Figure 1. Effect of artificial defoliation on root yield of sweet potato

Proportion of infested hills, infested leaves, ground cover loss and larval tent density were used to evaluate extent of defoliation. Proportion of infested hills reached 100% at all sites during the years with high insect density making this variable unsuitable for expressing intensity of defoliation. Ground cover, leaves infested and larval tent density are more variable measures which are correlated to yield loss. However, larval density of the first generation was better correlated with leaf damage and yield loss for both early and delayed harvests and explained about 76% and 66% of the yield variation in early and late harvests respectively (V). Yield loss was not significantly correlated with total larval density of both generations.

Protection measures carried out during high insect densities were found to be profitable even though the price of sweet potato was very low in the area. Two sprays of insecticides applied during the periods with young larvae resulted in significantly higher yields and economical gain. The use of insecticides is recommended at larval densities exceeding 4 tents/m^2 during the first three months after planting. It is proposed that assessment of *A. acerata* damage should be based on young larval density. Larval tents are easy to locate, count, and surveying at this development stage leaves enough time to decide on control measures.

Conclusion

Unlike the commonly used approach to insect pest studies, which mainly deals with selecting best methods of control, the present study focused on basic ecological processes of population dynamics in order to understand pest status and as a basis to developing control mechanisms. Such an approach hopefully has double merits; it contributes to our ecological knowledge and it aids in improving future management practices. Most insect ecological studies are based in temperate region studies and tropical studies are severely underrepresented in the literature. Many tropical systems also have the advantage of being able to generate abundant data within short periods. We collected a life table for *A. acerata* encompassing eighteen full generations within three years, which is equivalent to about two decades' census in temperate regions. Tropical systems are thus important testing grounds for ecological theories.

Defoliation of sweet potato is economically important, but leaf damage has to pass a threshold to cause detectable loss. Thus farmers give little attention to low larval densities as they cause slight defoliations and insignificant yield losses. Farmers and crop protection personnel only struggle to contain the insect during the outbreak phase. The population dynamics study showed that population decline and build up are gradual processes taking place over several generations. It is, therefore, important to monitor the insect population at all times for prompt control measures. Moreover, control strategies should include the destruction of the population at the low densities to avert their build up. Larval tents are easy to detect and the traditional control method of constant removal carried out at low densities on a large area can probably keep the population to a level that will not cause economic damage.

A. acerata populations develop with discrete generation cycles comprising about six generations per year. The mechanism creating theses cycles is not known and needs further study. Natural enemies evidently contributed little to population regulation of *A. acertata*, and no other density dependent factors operated during the early stages of *A. acerata* development. However, population regulation takes place late in the life and during the recruitment process. This probably means that adult behaviour is the key to understanding regulation in *A. acerata* population. In other words we need to further our understanding about the mechanisms regulating emigration and oviposition. Weather factors also seem to be important in perturbing the population and they are also in need of further study. The *A. acerata* population seems to be affected by few main factors. This in combination with slow population growth make the prospects for developing useful prediction models bright.

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Acknowledgements

Oviposition, development and adult emergence in the sweet potato butterfly, *Acraea acerata* Hew. (Nymphalidae: Acraeinae)

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Abstract

The biology of *A. acerata* is described based on studies in sweet potato fields in Southern Ethiopia. Eggs are laid in batches of about 160 eggs on the underside of leaves. Most of the ovipositions are on the middle leaves along the vine, whereas the lower and top three leaves were avoided. In the laboratory it took 7-8 days for eggs to hatch. Larvae passed through five instars. Larvae in instars I-III fed gregariously, whereas instars IV-V were solitary. Male larvae developed faster than female larvae, demanding about 18 and 19 days, respectively. Pupation took place either on the plant or on the soil. Pupae hatched in seven days. In the laboratory total development from egg to adult took 34 days. However, in the field both egg and larval development were of longer durations resulting in a total development time of 40-50 days from egg to adult. Furthermore, larval development is more extended during the rainy periods.

Introduction

Insect pests are major constraint on the production of sweet potato (*Ipomoea batatas*. The sweet potato weevils *Cylas spp.* have been considered as the most serious pests of the crop globally. Recently, however, the sweet potato butterfly (*Acraea acerata*) has gained increased importance in many African countries (Nyiira, 1982; Subukino, 1987; Leblanc, 1993; Anioke *et al.*, 1995; Smit and Matengo, 1995; Anioke, 1996; Smit *et al.*, 1997)

In Southern Ethiopia the insect causes repeated defoliations of sweet potato and is considered as the most important pest of the crop. During the last decade, Southern Ethiopia has experienced several local outbreaks. Because of outbreaks hitherto being sporadic and localised, scientific investigations have been few and little information is available regarding the biology of *A. acerata* in Ethiopia. The insect is indigenous to the area and it also feeds on native wild *Ipomoea* species such as *I. tenuirostris* and *I. obscura* (Azerefegne, 1999). Sweet potato is, however, the preferred and the most important host. In this study, oviposition behaviour, developmental time of the different developmental stages, and emergence of adults of *A. acerata* were reported.

Materials and Methods

The field studies were made in Welayita (7° 00' N, 37° 56' E), Southern Ethiopia, in an area with a history of repeated outbreaks of *A. acerata*, whereas the laboratory studies were conducted at Awassa College of Agriculture (7° 05' N, 38° 29' E).

Data for this study were collected from field plots used in a study on population dynamics of *A. acerata* (Azerefegne and Solbreck, 1999). Starting in October 1994 to December 1998, each month, a new 100m^2 plot of sweet potato was established from vine tips (40-45cm) using a recently introduced sweet potato variety, Koganesengan, which is most preferred by farmers in the areas having large problems with *A. acerata*.

Sweet potato leaves were searched for presence of egg batches. The location of egg batches (upper or lower side of the leaves), the number of eggs per clutch as well as the number of clutches per leaf were recorded. The number of leaves on the vine and the position (leaf number) of the leaf on which the egg batch was deposited were recorded. The numbering of the leaves is from the base to the tip of the vine; thus leaf number one is the oldest leaf at the base.

The development time of eggs was determined by collecting butterflies and placing them in cages enclosing two hills of sweet potato plants free of prior infestation. The plants were inspected daily and new egg clusters were collected and transferred to the laboratory where they were reared in petri dishes (Ø9cm) at ambient conditions (temperature range: 22°C-28°C; relative humidity range: 42-52%). Some of the egg batches were left in the field and inspected for date of hatching.

Larvae reared in the laboratory were supplied with fresh sweet potato leaves daily until pupation. The head capsule width across the eyes of twenty larvae from each instar was measured with the aid of a micrometer eyepiece fitted to a binocular microscope with 30x magnification. Pupae were sexed using the position of genital slits (Lawson and Doudu, 1984), weighed one day after pupation and kept in separate dishes until adult emergence. Female butterflies were dissected one day after emergence and the number of mature ova was counted as a measure of potential fecundity. The duration of pupal development was recorded by daily inspection of laboratory bred insects. The time of adult eclosion was observed for every hour during the day. Time needed for larval development in the field was determined by daily follow up of field deposited eggs during four periods (August 1997 to September 1997, October 1997 to November 1997, March 1998 April 1998, June 1998 to July 1998).

Rainfall and temperature data were obtained from Welayita, Sodo Meteorological Station. The maximum and minimum daily temperatures were recorded at 1.5m above the ground. Mean daily temperature was calculated by averaging the minimum and maximum temperatures for the day.

Results

Oviposition and eggs

One day old butterflies contained 185±7.6 (mean±S.E., N=39) mature eggs. The total number of eggs may reach 800 eggs per female. Females lay their eggs in single layered batches on the leaves of sweet potato. The majority of the eggs (97.4%, N=344 batches) were laid on the underside of the leaves. A single leaf may receive up to four batches but the majority of the leaves with eggs (80.9%) had only one batch and leaves with more than two batches did not account for more than 6% percent of the ovipositions (N=121) (Fig. 1a). A batch can have more than 400 eggs (Fig. 1b) but the mean number of eggs/clutch was 161.4±8.3 (mean±S.E., N=72). Oviposition took place on young plants with few leaves as well as on older vines with many leaves. Vines having a range of 8 to 57 total leaves were used for egg laying. Most eggs were found on the middle leaves along the vine (Fig. 1c) and the lower as well as the upper two to three leaves were consistently avoided.

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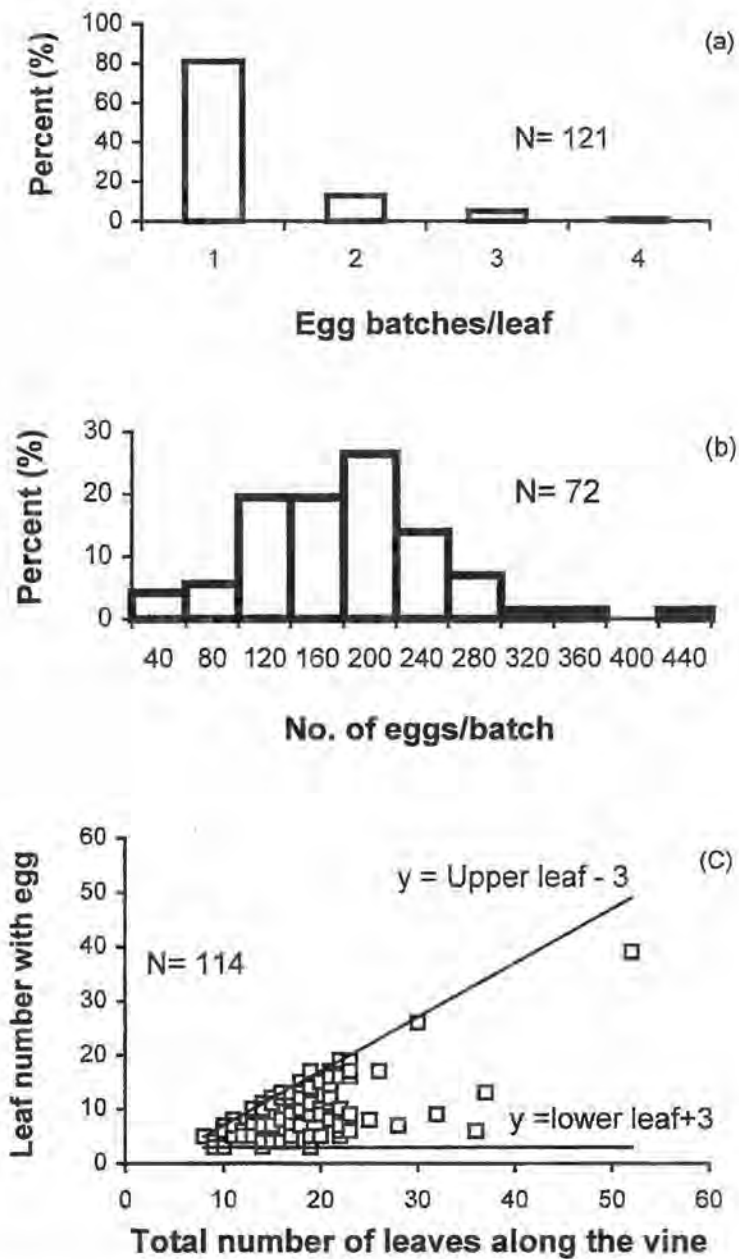
Figure 1. Oviposition of *Acraea acerata*. a) Distribution of egg batches on leaves, b) distribution of egg batch sizes, and c) distribution of egg batches along vines.

It took 7.7±0.1 (mean±S.E., N=55 batches) days in the laboratory for *A. acerata* eggs to hatch. In the field it took one to two days more (9.4±0.1, mean±S.E.; N=50 batches). Almost all field collected egg batches (98%, N=165) hatched successfully when reared in the laboratory and very few eggs failed to hatch within the batches.

Larva

There are five larval instars with characteristic head capsule widths. The growth between the consequent instars followed a constant ratio (table 1). Larvae are covered by setae. The first instar larvae can be distinguished by their fine unbranched setae, whereas instars II-V bear branching spines, as in larvae of *A. terpsicore* (=*A. eponina*) (Matanmi and Hassan, 1987; Ewete, 1990). The full-grown larvae reached a size of 25-29mm (N=50 observations).

Table 1. Size of *Acraea acerata* larval instars

Instars	Head capsule width (mm) (N=20)	Growth ratio
I	0.319±0.01	
		1.63
II	0.521±0.02	
		1.65
III	0.859+0.05	
		1.65
IV	1.412±0.05	
		1.55
V	2.188±0.06	

± = Standard deviation

The first two to three instars feed gregariously on the leaves of sweet potato. They construct loose webs under which they feed. They scrape one surface of the leaf and the mesophyll leaving the epidermis of the other side intact, whereas the late instars (IV and V) which are solitary chew the whole width of leaves. During outbreaks the new emerging leaves will be repeatedly grazed as soon as they appear which may result in death of vines. Food shortage in the laboratory rearings caused cannibalism whereby final instar larvae were observed feeding on newly formed pupae.
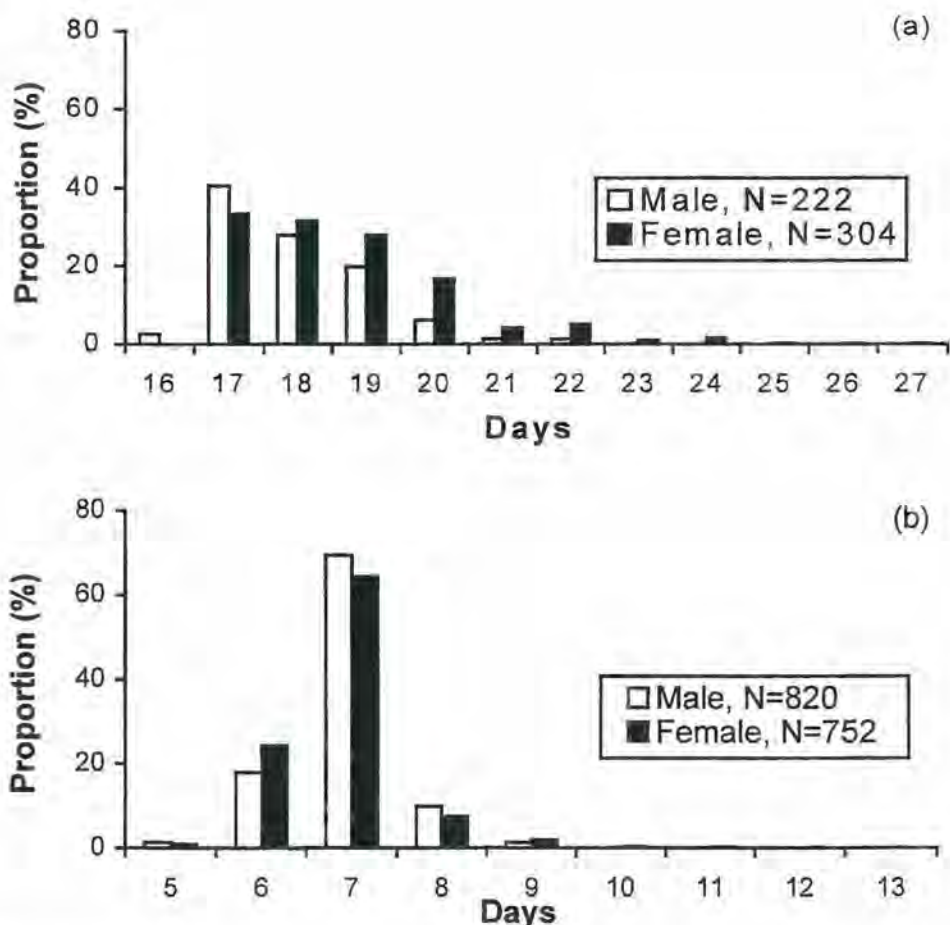
Figure 2. Distribution of developmental times of a) larvae and b) pupae of *A. acerata* in the laboratory

Larval development was of shorter duration in males (18.0±0.2 days, mean±S.E.; N=14 batches) than in females (19.3±0.2 days, mean±S.E.; N=16 batches) (t=4.30, P<0.001) (Fig. 2a). Larval development took longer time in the field (table 2) and with considerable variation between the different observation periods. Mean durations of 25, 35, 27, and 35 days were observed for the four observation periods. Two of these periods had lower rainfall, about 170mm in two months, while the other two periods were rainy (about 400mm). Variations in temperature between the four observation periods were small which indicate that the differences were not merely temperature effects.

Table 2. Development of *A. acerata* larvae in the field

Observation period	Day air temperature (°C)			Rainfall total (mm)	Rainy days	Days to pupation	
	Maximum range	Minimum range	Mean			range	mean
Aug. 1997-Sep. 1997	19-27	7-16	18.7±1.2	177.2	32	19-33	25.3±3.6 (216)
Oct. 1997-Nov. 1997	20-28	12-17	19.3±1.2	497.6	42	25-44	35.7±4.6 (275)
Mar. 1998-Apr. 1998	23-31	13-18	21.5±0.9	172.7	32	22-37	27.9±3.3 (290)
Jun. 1998-Jul. 1998	18-26	12-16	19.9±1.1	400.6	43	19-46	35.2±7.1 (318)

Number in parentheses indicate the number of larvae observed and ± is standard deviation.

Pupa

Larvae do not move far for pupation. Pupation took place in various kinds of places; on the foliage, on plant debris, on the soil, on clods and inside deep cracks of soil. However, most pupae were found on the foliage. At high population densities larvae seem to have a stronger tendency to move away from defoliated plants and pupate on the ground and among plant debris. Pupation under clods of soil and in cracks was more frequent during dry periods; some pupae were recovered as deep as 30 cm. The pupal stage lasted about 7 days (Fig. 2b), and there was no significant difference between male and female pupae. Female pupae were heavier than male ones (100.9 ± 1.7mg, mean$\pm$S.E.; N=16 batches, for females; and 78.6 ± 1.1mg, mean$\pm$S.E.; N=14 batches for males; t=11.22, P<0.001).

The adult butterfly

The butterfly is aposematically coloured with orange and black. There is another colour form with less bright orange colour but this is infrequent at all times of the year. The adults are weak fliers and usually fly close to the ground. They stay on the vegetation or on the ground when it is hot, windy and cold. There was no difference in wing span between males and females. Wing spans of both sexes ranged from 30mm to 44mm with means of 40.1 ± 0.3 (mean$\pm$S.E., N=111) and 39.0 ± 0.4 (mean$\pm$S.E., N=112) for females and males, respectively. Both males and females feed on flowers of many plants such as *Bidens pilosa, Tagetes minuta, Croton macrostachys, Guizotia scabra* and *Solanum tuberosum*. The longevity of the butterfly in captivity ranged from 2 to 9 days.
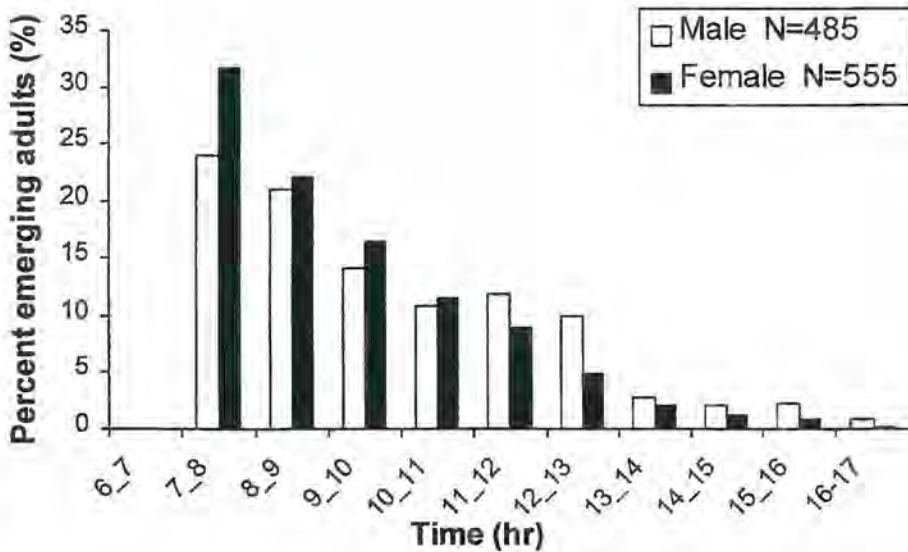

Figure 3. Distribution of emergence times of adult *Acraea acerata*

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Adults emerged during daytime with the majority emerging before noon (Fig. 3). The proportion of adults emerging in the afternoon was less than 10%. Mating in the field was only observed in the afternoons (> 30 observations). The genital plate of mated butterflies had a sphragis, a stiff plug deposited by males during mating which is most probably used to preclude further mating.

Discussion

A. acerata like other members of subfamily Acrainae lay their eggs in clusters reaching several hundred eggs, the largest clusters of any butterflies (Larsen, 1991). *Acraea* larvae are gregarious and often cause local defoliation of their food plants. High fecundity, clutch egg laying and larval aggregation, traits also possessed by *A. acerata*, are life history characteristics of many outbreaking species (Hunter, 1995). Sudden population outbreaks are also common in other *Acraea* species and some species have become threats to crops. For example, *A. terpsicore* (=*A. eponina*) (Dudou and Lawson, 1983; Lawson and Dudou, 1984; Matanmi and Hassan, 1987) defoliate tossa jute in Nigeria and Ghana. *A. violae* Fab. was reported to be a pest on a number of gourds (Cucuribitaceae) in Sri Lanka and India (D'Abrera, 1985).

Sweet potato is a creeping perennial plant, which continues to produce new leaves until harvest. However, old leaves are shed in succession from base of the stem upward during the period that follows the initiation of the tuberous roots (Hahn and Hozyo, 1984). Oviposition on the middle leaves probably has advantages for larval feeding and survival. Because of this behaviour the first instar larvae avoid feeding on the old tough leaves as well as on the young small leaves which do not provide enough food and force them to move soon. The fully developed middle leaves can sustain a larval colony at least to the end of the first instar.

There are conflicting reports with regard to the number of larval instars in *A. acerata*. Investigations elsewhere claimed that there are 5 to 7 larval instars (Smit et al., 1997). The related species *A. terpsicore* (=*A. eponina*) was reported to pass through 4 (Matanmi and Hassan, 1987) and 5 & 6 instars (Lawson and Duodu, 1984; Ewete, 1990). In our study, all the larvae we reared completed their development with five instars. The regular growth ratio of the successive head capsule widths indicates that no instar had been overlooked.

Larval development was shorter in the laboratory than in the field. The faster development in the laboratory could be attributed to constant renewal of food. But, larval development was also more extended during the rainy periods. There was no large variation in air temperature between the four periods when development time was measured under field conditions. There were, however, large differences in amount of rainfall and number of rainy days. The slower

larval development during rainy periods was probably a result of the few sunshine hours.

It is reported that for pupation caterpillars crawl away from the crop and climb any convenient support such as tall grass or a wall bordering the sweet potato field; and pupate in a vertical position often several meters from the ground (Hill, 1983; Smit *et al.*, 1997). Such behaviour was not observed in this study. Pupation could be on the foliage, plant debris and on the ground, however, most of the pupae were found on the foliage. Pupation on the ground, which has not been described before, was common during dry periods.

The diurnal pattern of adult emergence and mating in *A. acerata* is similar to that in the related species *A. terpsicore (=A. eponina)* (Matanmi and Hassan, 1987). Adult *A. eponina* emerged only during the daylight hours from 06.30 to 10.30 and mating usually occurred in afternoons at 15.00 to 19.00. On another study males of *A. terpsicore* emerged earlier than females during the day (Duodu and Lawson, 1989), however, there was no difference in the pattern of emergence between male and female of *A. acerta*. Protandry in *A. acerata* is not because of differences in adult emergence but a result of male larvae developing faster than female ones. The early emergence of males in *A. terpsicore* enables this sex to dry and become active before females emerge (Duodu and Lawson, 1989). Early emergence could have a selective advantage in male *Acraea* (Duodu and Lawson, 1989) because females mate only once which is enforced by the presence of sphragis (Pierre, 1985).

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Larval performance of the sweet potato butterfly (*Acraea acerata* Hew.) on *Ipomoea* species

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Abstract

Larvae of the sweet potato butterfly, *Acraea acerata*, develop not only on sweet potato but also on various wild *Ipomoea* species in Ethiopia. To investigate the role of different potential host plants larval performance was compared on three wild indigenous *Ipomoea* species, two wild introduced Ipomoeas as well as sweet potato, *I. batatas*. Larvae fed and developed successfully on two of the native species, *I. cairica* and *I. tenuirostris*, whereas larvae refused to feed on the abundant native *I. hochstetteri*. Both introduced species, *I. indica* and *I. purpurea* were unsuitable; larvae refused to feed on the former species and had extremely low survival on the latter one.

I. batatas was a better host plant than both *I. cairica* and *I. tenuirostris*; larvae survived better and pupae became larger resulting in more fecund female butterflies. Differences were, however, small between larvae raised on *I. cairica* and *I. tenuirostris*. No statistically significant difference was found between the hosts when days needed for development was compared. Nevertheless, in southern Ethiopia, wild *A. acerata* populations were not found on *I. cairica* but only on *I. tenuirostris* and *I. obscura*, a plant on which larval performance was not tested.

Introduction

The sweet potato butterfly, *Acraea acerata* Hew. (Lepidoptera: Acraeidae) is a species native to Africa with an "occasional pest" status in East & Central (Lefèvre, 1948; Le Pelly, 1959; Nyiira, 1982; Janssens, 1982; Hill; 1983; Smit and Matengo, 1995) and West Africa (Anioke *et al.*, 1995; Anioke, 1996). In Southern Ethiopia, however, it is considered as the most important pest of sweet potato.

The association between *A. acerata* and sweet potato is relatively new because the origin of sweet potato is in, or near, north western America (Austin, 1988), and the plant was introduced to Africa about 500 years ago by European explorers (Yen, 1982). The insect is indigenous to Ethiopia where it feeds on native plants. It is evidently specialised on plants in the family Convolvulaceae mainly in the genus *Ipomoea*. Larvae have been reported to feed on *I. tenuirostris* Choisy., *I. lilacina* Blume, *I. kentrocarpa* A. Rich., *I. wighiti* Choisy., and *Lepistimone owariense* Hall.; all in Convolvulaceae (Lefèvre, 1948; Matanmi and Hassan, 1987; Smit *et al.*, 1997; Subukino, 1997). Claims that larval food plants include Poaceae, Cucuribitaceae and Solanaceae (Larsen, 1991) are suspect because larvae have never been observed feeding on any other species than *Ipomoea* even at times of high population density and food limitations in Ethiopia (Azerefegne, unpublished data).

The purpose of this study was to investigate the importance of various *Ipomoea* species as larval host plants for *A. acerata*. If wild Ipomoeas are suitable and abundant alternative host plants they may be important reservoirs for *A. acerata* populations. Larval performance of *A. acerata* was experimentally tested on six *Ipomoea* species, three wild native, two wild introduced and the cultivated sweet potato. The native species commonly grow in habitats used by the sweet potato butterfly, and the introduced wild species are very common throughout tropical Africa (Verdcourt, 1963).

Larval development time and survival, pupal weight and potential fecundity expressed as number of mature ova per female were the life history traits used to evaluate the suitability of the host plants. Furthermore, field surveys were conducted in order to ascertain whether the natural distribution of the insect matches the distribution of the plants found suitable in the laboratory tests.

Materials and methods

Ipomoea species growing near the Rift Valley lakes of Ethiopia, possible habitats for *A. acerata*, were surveyed during 1996 to 1998 for the presence of *A. acerata*. The visits included the surroundings of Koka dam, Langeno, Shala, Abijata,

Awassa, Abaya, Chamo lakes and Omo River. Lakes Abaya and Chamo, and Omo River were visited 8 times while the other lakes were visited more than 12 times. The surveys were confined along the main roadsides from Arba Minch to Addis Ababa in case of the lakes and the surroundings of the Omo River Bridge on the road from Sodo to Waka (Fig. 1).
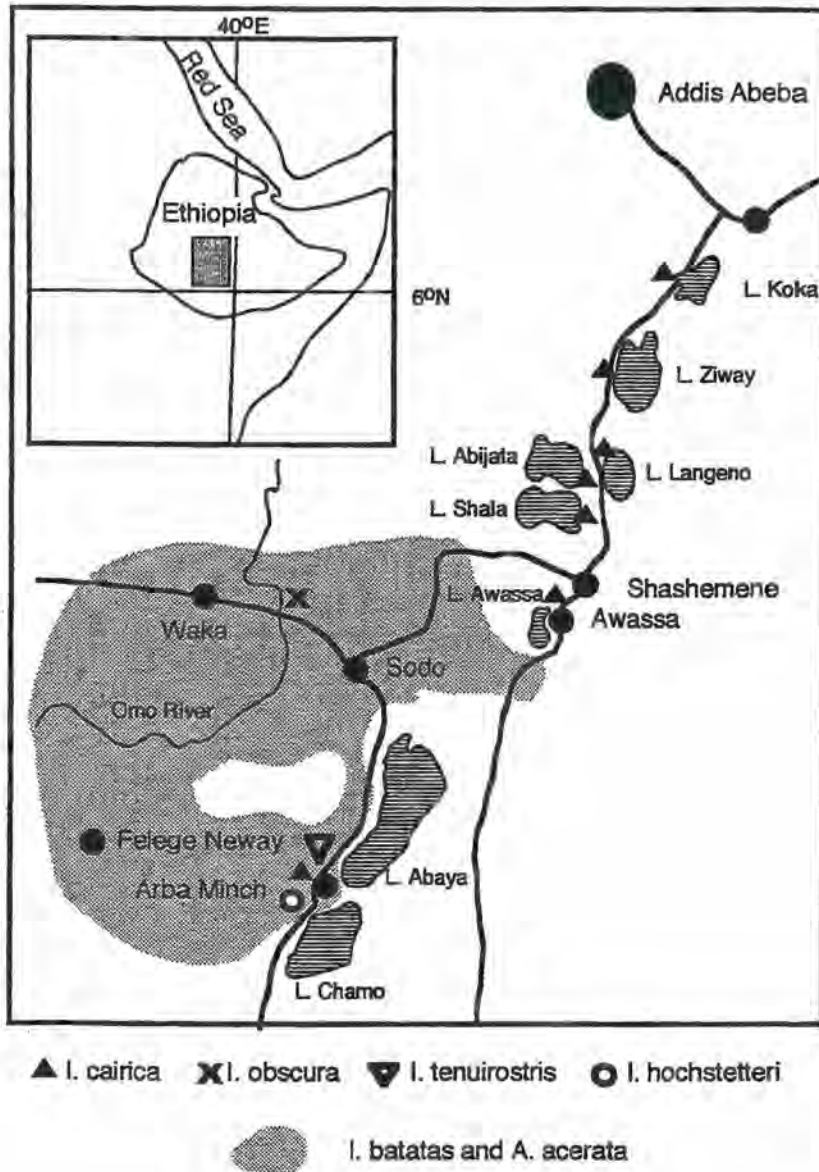

Figure 1. Distribution of *Ipomoea* species and *Acraea acerata* in Southern Ethiopia.

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An experiment was carried out at Awassa College of Agriculture, Ethiopia to investigate the suitability of the potential host plants for larval growth and survival. Three introduced and three indigenous species of *Ipomoea* which are common in the Welayita area , where *A. acerata* causes serious problem on sweet potato, were tested (Table 1). Sweet potato (*Ipomoea batatas* (L.) Lam.) was represented by a recently introduced variety, Koganesengan, which is the most preferred variety by farmers in Welayita. *I. cairica* (L.) Sweet, *I. indica* (Burm.) Merr. and *I. purpurea* (L.) Roth. were collected from Awassa, whereas *I. hochstetteri* House and *I. tenuirostris* Choicy were brought from Arba Minch and planted at Awassa. The tested plants where grown in the same plot and were not fertilised or irrigated.

Leaves of sweet potato with *A. acerata* eggs were collected in September, 1998 from Welayita (Sodo) (Fig. 1) and taken to the laboratory for hatching. Newly hatched larvae were randomly assigned to the different plants to be tested. For each plant species there were more than ten egg clusters and each egg cluster had more than 200 eggs. Larvae were fed with detached fresh leaves from the middle part of the vine. Leaves were changed every day until pupation. The rearing was conducted under ambient conditions (temperature range: 21°C-28°C; relative humidity range: 38-50%). Data on mortality were taken from clusters which became established, i.e. started to feed on the new leaves. Larvae in clusters were allowed to be in the same group through the first instar. Because older larvae are known to cannibalise at higher density, larvae were divided to a maximum of 30 per petri dish during the second instar and to about 15 for the third instar and 10 for the last two instars.

Pupae were sexed (Lawson and Duodu, 1984), weighed one day after pupation and kept in separate dishes until adult emergence. The female butterflies were dissected and the number of ripe ova was counted as a measure of potential fecundity.

Mean values for the different life history traits measured were calculated for larvae of each egg cluster. Clutch means were used as independent observations and subjected to analysis of variance. Means of the clutch means were separated using Tukey's pairwise comparison (Zar, 1984).

Results

Distribution of the insect in relation to *Ipomoea*

I. cairica has the widest distribution among the studied *Ipomoea* species. It was observed to grow along the shores of all Rift Valley lakes in varying densities. The middle Rift Valley Lakes; Abijata, Shalla and Langeno, had scarce vegetation of *I. cairica*, whereas at the other lakes it grows abundantly. *I.*

hochstetteri and *I. tenuirostris* were most common along the two southern lakes; Abaya and Chamo. In this area, *I. hochstetteri*, a perennial that creeps on tall trees sometimes reaching more than 10 meters, was the most apparent and abundant species. The density of *I. tenuirostris* was lower than both *I. hochstetteri* and *I. cairica*. *I. obscura* (L.) Ker-Gawl. was observed growing along the Omo River (Fig. 1). The two introduced species, *I. indica* and *I. purpurea* are also widely distributed in areas where *A. acerata* is abundant but they are more common in towns and cities, growing around fences and wastelands.

The distribution of the insect overlaps with the distribution area of the two wild *Ipomoea* species, *I. tenuirostris* and *I. obscura*, as well as with the intense sweet potato cultivation area in Southern Ethiopia. The insect utilises different *Ipomoea* species in different habitats. At relatively high altitudes (1800-2000m a.s.l.) of Southern Ethiopia, where sweet potato production is intense, the insect was exclusively found on this crop. Along lakes Abaya and Chamo (both at 1200m a.s.l.) it was observed to feed on *I. tenuirostris* despite the fact that this is the least abundant *Ipomoea* species. Around Omo River (760m a.s.l.) the insect feeds on *I. obscura*. Recently a sparse population of the insect was observed around Awassa (1700m a.s.l.). *I. cairica*, which *A. acerata* does not seem to use in the field, is the dominant *Ipomoea* species around Awassa. The appearance of the insect at Awassa could be due to the increased production of sweet potato in home gardens, and there is a possibility that butterflies from Welayita area could reach Awassa during periods of high population density.

The population density of *A. acerata* in its natural habitats was observed to be low at any time. There were six visits between 1996-1998 near the lake Abaya and we counted not more than 10-15 butterflies at a transect walk of about 200 meters. On the other hand, the butterfly population could reach several thousands in sweet potato fields of equivalent area in Southern Ethiopia (Azerefegne and Solbreck, 1999). *A. acerata* does not inhabit all areas of sweet potato production in the country. For example, there is no report of the insect from the Eastern highlands where sweet potato is intensively grown.

Larval performance

Of the six *Ipomoea* species tested, larvae of *A. acerata* completed development on sweet potato (*I. batatas*) as well as on two wild native *Ipomoea* species, *I. cairica* and *I. tenuirostris* (Table 2). However, all larvae refused to feed on the native *I. hochstetteri* (Table 1). Larvae initiated feeding on *I. purpurea* but very few reached the pupal stage and none of them became adult. Not a single larva initiated feeding on *I. indica*. Larvae survived significantly better on sweet potato than on either *I. cairica* or *I. tenuirostris* (Table 2), but there was no significant difference between the two latter species.

Table 1. Common *Ipomoea* species in Southern Ethiopia and utilisation by *A. acerata*.

Plant species	Origin	Feeding initiation (laboratory)	Feeding in the field
I. batatas	Introduced	Yes	++
I. tenuirostris	Indigenous	Yes	+
I. obscura	Indigenous	Not tested	+
I. cairica	Indigenous	Yes	—
I. purpurea	Introduced	Yes	—
I. hochstetteri	Indigenous	No	—
I. indica	Introduced	No	—

Feeding in the field: ++ = highly used; + = commonly used; __ = not used

Male larvae pupated approximately one day before females on all hosts. Both male and female larvae developed faster on sweet potato than on either *I. tenuirostris* or *I. cairica* but the difference is not statistically significant (Table 2).

Female pupae were heavier than male ones on all hosts. Furthermore, female pupae from *I. batatas* were much heavier than those from *I. cairica* or *I. tenuirostris* (Table 2), whereas there was no significant difference between pupae from *I. cairica* and *I. tenuirostris*. No differences in weight were found between the male pupae from *I. batatas*, *I. cairica* and *I. tenuirostris*. The lowest pupal weight was from the two surviving individuals on *I. purpurea*.

Relationship between pupal weight and potential fecundity

Dissections showed that females already one day after emergence had well developed eggs. There was a significant positive correlation between weight of pupae and potential fecundity (Fig. 2). Because slopes of the regression lines did not differ between the three hosts, all data were pooled. The combined data set shows that about 60% of the variation in potential fecundity can be explained by variation in the weight of pupae.

Table 2. Performance of *A. acerata* on *Ipomoea* species

Plant species	Time to pupation (days)		Fresh weight of pupae (mg)		Survival to pupa (%)
	Male	Female	Male	Female	
I. batatas	18.0±0.17(14)a	19.3±0.23(16)a	78.6±1.1(14)a	100.9±1.7(16)a	40.9±1.9(11)a
I. tenuirostris	18.7±0.19(22)a	20.0±0.18(22)a	74.6±1.3(22)a	94.9±1.5(22)b	24.7±2.6(20)b
I. cairica	18.9±0.24(24)a	20.0±0.28(23)a	72.6±1.5(24)a	96.5±1.4(23)b	21.8±2.7(27)b
I. purpurea	19.5±0.50(2)*	—	44.3±1.4(2)	—	0.2±0.1(4)
I. hochstetteri	—	—	—	—	0
I. indica	—	—	—	—	0

Means followed by the same letter within the column are not significantly different according to Tukey's pairwise comparison at 5% probability. Number in parentheses denote number of egg clusters used to calculate means and ± is standard error of the mean. * Only two larvae survived from two clusters of eggs on *I. purpurea* and the data from this host is not included in the analysis of variance.
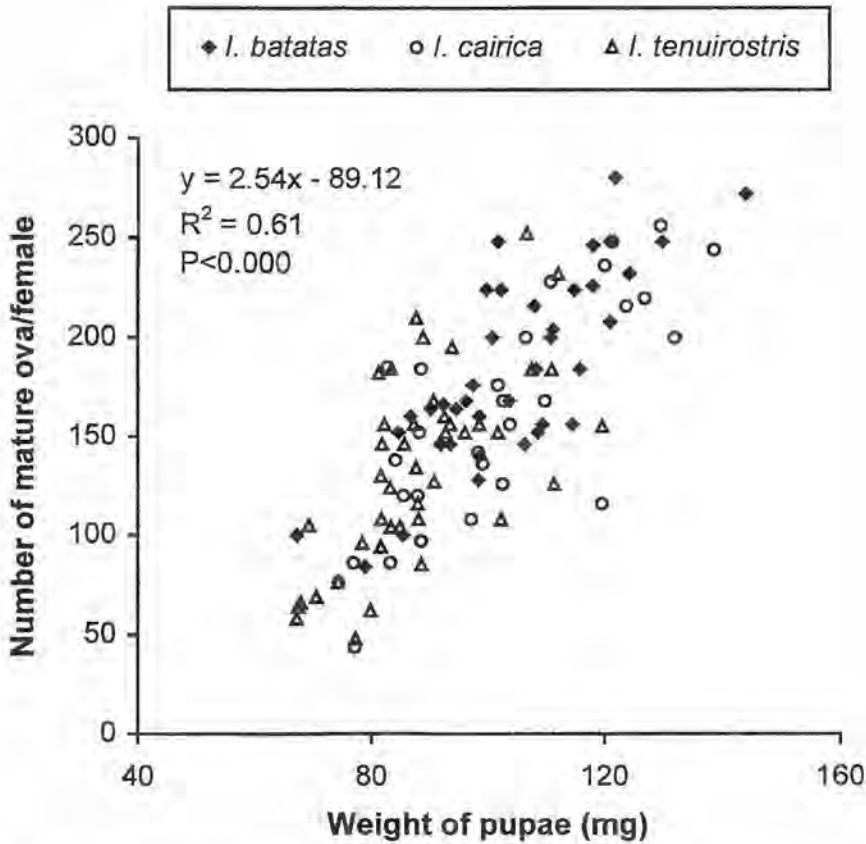
Figure 2. Relationship between weight of pupae and reproductive potential in *A. acerata*

Discussion

A. acerata larvae are evidently restricted to feeding on *Ipomoea* species and probably some other Convolvulaceae as indicated by Matanmi and Hassan (1987). The areas with frequent outbreaks of the insect are characterised by a high diversity of crops but larvae were never observed feeding on any crop except sweet potato even at times of high population density. This study shows that *A. acerata* larvae can survive and develop well on *I. tenuirostris* and *I. cairica*, both native species, as well as on the introduced *I. batatas*. Insect performance, however, seems to be better on sweet potato with regard to the life history traits measured. *A. acerata* larvae do not feed on all *Ipomoea* species which are indigenous to the country. *I. hochstetteri* is the most apparent and abundant species in areas where the insect is naturally distributed. Despite our several attempts to rear the larva on this plant, not a single larva initiated feeding. Furthermore, when fourth and fifth instar larvae were transferred from sweet potato to *I. hochstetteri* leaves all of them died.

The insect does not seem to accept any other introduced *Ipomoea* species than *I. batatas*. The introduced *I. indica* and *I. purpurea* are widely distributed in tropical Africa and the insect has had extended contact with these plant species but it does not utilise them.

Acceptance of a food plant under laboratory conditions does not necessarily mean that the insect utilises the plant in the field. Although larval performance of *A. acerata* on *I. cairica* is equivalent to that on *I. tenuirostris* in the laboratory experiment, it is not utilised in the field. Females of many butterfly species fail to accept some plants that are suitable for larval development (cf. Jaenkie, 1990). For instance, *Papilio machaon* females rejects several available plant species that are nearly as suitable for offspring survival as the normal host (Wiklund, 1975). The reason why *I. cairica*, being abundant, widely distributed and suitable for larval development, is not used in the field is not yet known, but it probably has to do with oviposition behaviour. Not a single egg cluster was observed in the field on *I. cairica* in any of the places surveyed. At Awassa, where the different *Ipomoea* species were grown for laboratory test, *A. acerata* eggs were frequently observed on both *I. tenuirostris* and sweet potato but not on *I. cairica*. It should also be noted that larval responses to *I. cairica* were different in another study. Lefèvre (1948) was not able to rear a single larva to pupal stage on *I. cairica* even in the laboratory. It thus appears that there is geographical variation in the plant with regard to larval suitability or possibly in larval responses.

Although sweet potato is an introduced plant, it supports the development of *A. acerata* larvae better than the wild indigenous *Ipomoea* species on which the insect has presumably been feeding prior to the introduction of sweet potato. Larvae developed faster and grew bigger on *I. batatas*. The regression of fecundity on weight of pupae resulted in similar slopes for all *Ipomoea* species which indicates that similar weights of pupae coming from any of the host plants give rise to butterflies with equivalent number of eggs. Thus, sweet potato fed larvae which produced heavier pupae are expected to produce adults with more eggs. High performance of the insect on sweet potatoes could be one of the reasons for the frequent outbreaks of the insect in areas where the crop is intensively grown. Another likely contributing factor is that, unlike the wild hosts which grow in patches, the cultivation of sweet potato throughout the year over large areas provides a continuous supply of host plants.

Ipomoea species like *I. tenuirostris* and *I. obscura*, which grow in the proximity of the main sweet potato production area, can potentially serve as reservoirs of the insect population. It is known that during periods with high population density migratory displacement may take place (Larsen, 1991). This has two interesting aspects. First, it raises the question whether reservoirs produce high enough number of colonisers for sweet potato fields. Second, it raises the question of gene exchange between the feeding types on sweet potato and the native species.

The low population size of *A. acerata* in the scattered patches of the native *Ipomoea* species probably contributes little to the population dynamics of *A. acerata* on sweet potato fields. Occasionally, the population of the insect becomes very low in sweet potato fields (Azerefegne and Solbreck, 1999). At such times a small number of colonies of the insect on the native host species can serve as foci of population build up for sweet potato fields. However, it should pass through several generations on sweet potatoes to reach population levels that can cause significant damages. On the other hand, migration of the insect from sweet potato to wild hosts back and forth provides abundant gene flow. Sweet potato being the most abundant *Ipomoea* species and being more or less intensively grown, with on average, higher nutritious (nitrogen) value than indigenous species would select feeding behaviours that discriminate against other potential plants, based on whatever cue(s) that this is unique for sweet potato.

Avoidance of some of the *Ipomoea* species does not seem to be a result of differences in physical structures like hairiness and shape of leaves. *A. acerata* larvae were observed feeding on sweet potato with various leaf shapes from entire ovate to digitately lobed leaves, similar to *I. cairica*. Hairiness does not seem to deter *A. acerata* larvae from feeding or ovipositing either. Glabrous leaves of sweet potato and pubescent leaves of *I. tenuirostris* were eaten to equal extent by larvae and utilised by ovipositing butterflies in the field. Hence it is likely that failure of larvae to feed on various *Ipomoea* species is due to unsuitable plant chemistry.

One of the possible means of managing insect pests is with the use of resistant varieties. Studies carried out in East African countries showed that all tested sweet potato varieties succumb to feeding by *A. acerata*. (Ndamage *et al.*, 1992; Smit *et al.*, 1997). Our observations in Southern Ethiopia indicate that cultivars, recently introduced or those which have been in use for several decades, are all defoliated to the same extent by *A. acerata*. The presence of complete resistance in some *Ipomoea* species, however, suggests that resistance against *A. acerata* or other leaf feeding insects might be possible through hybridisation of sweet potato with related species. This method has been tried to develop resistance against sweet potato weevils (*Cylas* species), and a hybrid between sweet potato and *I. trifida* showed less damage by the weevils (Takagi and Opena, 1988).

Acknowledgements

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Effects of parasitoids and pathogens on populations of the sweet potato butterfly, *Acraea acerata* Hew.

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Abstract

The sweet potato butterfly, *Acraea acerata*, is an important pest of sweet potato in Southern Ethiopia. Its larvae are attacked by three parasitoid species viz *Glyptapanteles acraeae* (Wilkinson) (Braconidae), *Charops sp.* (Ichneumonidae), and *Carcelia sp.* (Tachinidae), and the pathogenic fungus *Beauveria bassiana* (Balsamo) Vuillemin (Moniliaceae), whereas pupae are parasitized by *Brachymeria albicrus* (Klug) (Chalcidoidea). Mortalities imposed by the parasitoids and the pathogen are described and analysed based upon a three year sampling program, encompassing eighteen host generations. Mortalities inflicted were usually low or very low, and no direct density dependent effects could be found. The enemies generally seem to be of little importance in reducing high density host populations. At low population levels, however, enemy effects sometimes increase, possibly causing longer and deeper population valleys.

Introduction

The sweet potato butterfly, *Acraea acerata* Hew. (Nymphalidae: Acraeinae), is regarded as an occasional pest on sweet potato, *Ipomoea batatas* (L.) Lam. in Western (Anioke *et. al.*, 1995; Anioke, 1996) and most of Eastern Africa (Someren and Rogers, 1926; Le Pelly, 1959; Nyiira, 1980; Janssens, 1982; Hill, 1983; Smit and Matengo, 1995). In some parts of East Africa, however, such as Rwanda (Leblanc 1993) and Southern Ethiopia (Girma, 1994), it has become a major pest. In Ethiopia, the major pest status is of fairly recent origin; outbreaks have mainly occurred during the last few decades (Azerefegne, unpubl.).

A. acerata is indigenous to Ethiopia where it occurs on both sweet potato and on some wild *Ipomoea* species (Azerefegne, 1999a). Eggs are laid in clusters on host plant leaves where the first three larval instars feed in groups under protective webs. Fourth and fifth instar larvae disperse and feed solitarily. The insect pupates on the plant or on the ground, and the slow-flying aposematically coloured butterflies emerge after about one week. One generation is completed in about 6-7 weeks, and the insect produces about six generations per year (Hill, 1983; Smit *et al.*, 1997; Azerefegne and Solbreck, 1999). Population densities of *A. acerata* fluctuate several orders of magnitude, but changes are gradual and it takes several generations for populations to build up to outbreak levels following low population levels (Azerefegne and Solbreck, 1999).

The natural enemies constitute one of the potentially important factors affecting the population dynamics of *A. acerata*. Several enemy species are known to attack the immatures of *A. acerata* in East Africa (Lefèvre, 1948; Lugojja, 1996; Smit *et. al.*, 1997). In Southern Ethiopia four parasitoid species, viz *Glyptapanteles acraeae* (Wilkinson) (Braconidae), *Charops sp.* (Ichneumonidae), *Carcelia sp.* (Tachinidae) and *Brachymeria albicrus* (Klug) (Chalcidoidea) have been found on *A. acerata* larvae and pupae (Azerefegne unpubl.). Furthermore, the pathogenic fungus *Beauveria bassiana* (Balsamo) Vuillemin attacks larvae. Although there are some invertebrate predators attacking the immatures of *A. acerata* the mentioned parasitoids and the pathogen seem to be the major enemies.

The role of the different natural enemy species of *A. acerata* as mortality agents has not been evaluated before. Although enemies have generally been considered as unimportant in regulating *A. acerata* populations (e.g. Smit *et al.*, 1997), there has not yet been any detailed study of their long-term effects. For example, how do mortality rates imposed by the parasitoids and the pathogen change over time and in response to host density? Based on over three years of monitoring of *A. acerata* populations and enemy attacks in sweet potato fields in Ethiopia, we here describe variations in parasitoid and pathogen imposed mortalities and analyse their possible density dependent effects.

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Materials and methods

Sampling

The study was carried out in Welayita (7° 00' N, 37° 56' E), Southern Ethiopia, from October 1994 to December 1998. This area, where sweet potato is grown throughout the year on small parcels of land, has experienced repeated outbreaks of *A. acerata* (Azerefegne and Solbreck, 1999).

The study area was a three hectare large field surrounded by Eucalyptus trees. It contained a mixture of various crops, a third of which was sweet potato. Every month throughout the year a new 100m² plot with sweet potato (variety Koganesengan) was established from vine tips (40-45cm) in this area. No insecticides were used on the study plots or on neighbouring sweet potato fields. Sampling of *A. acerata* and its enemies started when plants were one month old and ended six months after planting when the crop was harvested.

Random samples of twenty quadrates of 0.25m² crop area were taken from each plot at fifteen day intervals. Young (the gregarious instars I-III) and old (the solitary instars IV-V) *A. acerata* larvae, cocoons of *Glyptapanteles acraeae* and *Charops sp.* as well as dead *A. acerata* larvae covered by the white mycelial growth of *Beauveria bassiana* were counted. This sampling, referred to as the *in situ method*, spanned about three years and eighteen generations (for further details on plots and sampling see Azerefegne and Solbreck (1999)).

Mortality caused by enemies was also estimated by a method referred to as the *rearing method*. Third or fourth instar larvae were collected in sweet potato fields in the surroundings of the main study area and reared in the laboratory until adult emergence or until parasitoids emerged or other mortality factors became evident. In these samples mortalities caused by *G. acraeae*, *Charops sp.*, or *B. bassiana* as well as by the tachinid *Carcelia sp.* (This species, superficially similar to *C. normula*, is probably an undescribed species (N. Wyatt pers. comm)) were estimated. Mortalities caused by the former three species were thus estimated by both methods, whereas *Carcelia*-caused mortality was only estimated by the rearing method. These rearing samples covered six generations of *A. acerata*, each generation value being based on a sample size of 257-1182 host individuals. The mortality caused by each enemy species was calculated on the number of hosts entering the developmental stage on which the mortality agent acted (cf. Table 1).

Data analysis

The between-plot variation in the frame sample data (in situ method) was found to be low and accordingly the data from the different plantings (plots) were pooled. Because plots could not be established every month (dry weather conditions sometimes prohibited planting of new plots) samples were reduced on certain occasions, but in the majority of cases 5-6 plots were available resulting in a total of 100 - 120 quadrate samples on each occasion. *A. acerata* develops with generation cycles (Knell, 1998) each lasting about two months (see Azerefegne and Solbreck, 1999). The number of young and old larvae in each *A. acerata* generation was estimated by summation of the consecutive estimates in each generation curve. In a few instances where generations overlapped slightly, data were equally apportioned to the two generations. For further details see Azerefegne and Solbreck (1999).

The method used causes moderate systematic errors in the absolute estimates of the number of insects passing through each developmental stage because it assumes equal duration of each developmental stage used (a reasonable assumption but not exactly correct, cf. Azerefegne, 1999b). However, since we use data primarily to look at between generation changes in each mortality factor this poses no serious problem (but care should be taken when comparing successive mortalities during the life cycle).

The k-values were calculated in the following way (Table 1). Larval mortality caused by *G. acraeae* is assumed to be the first mortality factor acting in the interval young - old larvae. *Charops sp.* and *B. bassiana*-inflicted mortalities occur early in the interval old larva - pupa. We assume that *Charops* mortality operates first of the two, which it usually does (see Results). The two mortalities may overlap, but because both mortality rates are very low, overlap is likely to be insignificant.

The existence of density dependence was investigated using k-factors within each stage interval. K-values for each mortality factor were regressed against the log of the initial population density on which the mortality acted. Regressions were also made on densities in earlier developmental stages and in previous generations (none of which was significant). A statistically significant regression line was taken as an indication of density dependence (cf. Sibly and Smith, 1998).

The mortality data from the rearing method were also transformed to k-values. These values represent additional independent measures of mortalities caused by *G. acraeae, Charops sp.*, and *Beauveria*. These values are plotted together with the data from the previous method as a comparison, but owing to the limited number of observations no regression lines are calculated for these data. The k-values for *Carcelia sp.* were only estimated from the rearing data.

Results

Sequence of enemy attack

Glyptapanteles acraeae was hatched in the laboratory from field collected first instar larvae of *A. acerata* and thus attacks the young host larva. The host is usually killed in the fourth instar (87.8%) when the parasitoid larva leaves its host (Fig. 1 and 2). *Charops* sp. attacks the second larval instar of *A. acerata* and emerges somewhat later than *G. acraeae*, mainly from fifth instar (82.9%) host larvae (Fig. 1 and 2).

Carcelia sp. attacks older *A. acerata* larvae than the two previously mentioned parasitoids. It was bred from field collected third instar *A. acerata* larvae. Some *Carcelia sp.* emerge from last instar host larvae, but the majority (67.7%) emerge from host pupae (Fig. 1 and 2). Larvae of *A. acerata* are also killed by the pathogenic fungus *Beauveria bassiana*. *Beauveria* infected larvae usually die during the last two instars. *Brachymeria albicrus* oviposits in the pupa of *A. acerata* as it was never retrieved from rearings of field collected larvae. It also emerges from host pupae (Fig. 1 and 2).

All parasitoid species produce one parasitoid per host. The only exception is *Carcelia sp.* which in a few instances produced two flies per host.

Mortalities inflicted by enemies

Population densities of *A. acerata* fluctuated considerably during the study period with a peak in generation six followed by a decline to very low densities in generations 11-17. This is illustrated by the population curves for young and old larvae (Fig. 3A,C). In generation 20 there was a new population peak (not shown).

Population densities of *G. acraeae* and *Charops* sp. were low during the entire study period. *G. acraeae* caused mortalities never exceeded 6% of young larvae (Fig. 3B), and *Charops* inflicted mortalities never surpassed 12% of old larvae (Fig. 3D). Mortalities inflicted on the host population increased briefly in generations 12-13 when host population density was very low. No direct density dependent effects could be found for these two parasitoid species (Fig. 4A,B). *G. acraeae* even showed a weak inverse density dependent effect.

The incidence of *B. bassiana* infections was low during most of the time (Fig. 3E). There was, however, a peak in generation 11 after a long decline in host population density. No density dependent effects of *Beauveria* could be discerned (Fig. 4C). As with the two previously mentioned enemies mortality estimates by the "in situ" and "rearing" methods yielded rather similar results (Fig. 3 and 4). Mortality caused by *Carcelia sp.* was only estimated by the "rearing method" and during host generations 12-13 and 15-18. The highest mortality rate recorded

occurred in generation 12 (Fig. 3F). No density dependent effects of *Carcelia sp.* were found (Fig. 4D).

Regressions of *G. acraeae*, *Charops sp.* or *B. bassiana* k-values on densities in earlier developmental stages in the same or previous generations did not reveal any lagged density dependent effects. The combined mortalities of *G. acraeae*, *Charops* and *B. bassiana* (k21+k31+k32) did not show a significant density dependent response when regressed against log density of young larvae (Fig. 4E). Nevertheless, considering the relatively low p-value an inverse density dependent relationship cannot be ruled out.

There is only one estimate available of mortalities caused by the pupal parasitoid *B. albicrus*. In a sample of 838 pupae collected over several days during generation 20 (a population peak) of the host population 4.1% were killed by emerging *B. albicrus* (and 6.7% by *Carcelia* sp.).

Discussion

Enemy guild

The parasitoid and pathogen guild on *A. acerata* in Southern Ethiopia is similar to that observed on the insect in other parts of East Africa (Smit *et al.*, 1997). The lack of parasitoids on either eggs or adults agrees with previous findings (Smit *et al.*, 1997). The parasitoid *Charops sp.* is found in most other studies (Lefèvre, 1948; Subukino 1987; Girma, 1994; Lugojja, 1996), and *G. acraeae* and *Brachymeria spp.* have earlier been recorded from Rwanda (Lefèvre, 1948). The tachinid species *Carcelia normula*, found in Kenya and Uganda (Lugojja, 1996; Smit *et al.*, 1997), is replaced by a closely allied and probably undescribed species in Southern Ethiopia. *Beauveria* infections were earlier recorded from Rwanda (Lefèvre, 1948) and Uganda (Lugojja, 1996).

The role of predators seems to be limited. A predatory pentatomid *Macroraphis acuta*, which feeds on all immature stages of *A. acerata* was observed in the present study, but it was never common. Furthermore, *Acraea acerata* seems to lack vertebrate enemies. Members of the genus *Acraea* are generally believed to be aposematic. The butterflies are brightly coloured with tough bodies. Some species are known to contain cyanogenic compounds and many are models in mimicry complexes (Owen, 1971; Larsen, 1991).

There is considerable overlap with regard to the residence times of parasitoids inside the host (Fig. 2), which may lead to various kinds of interactions between these enemies. Nothing is known about such interactions, but considering the relatively low rates of parasitoid attack observed on *A. acerata*, it seems unlikely that e.g. competition between parasitoids will be important.

The parasitoids attacking *A. acerata* seem to have low host specificity. Both *G. acraeae* and *B. albicrus* are wide ranging species occuring far outside the distribution area of *A. acerata* suggesting that they utilize other hosts. *B. albicrus* has been reported from various other nymphalids (J. LaSalle pers. comm). *Charops sp.* also seems to attack many Lepidoptera species including *A. terpsicore (eponina)* (Dudou and Lawson, 1983; Matanmi and Hassan, 1987) although the problem of parasitoid identification leaves this question open.

Effects on *A. acerata* populations

Mortalities inflicted by the enemies of *A. acerata* are generally low, rarely exceeding 10% and usually much lower (calculated as percentage of the number of hosts entering the stage on which the mortality factor operates). Similar low rates of parasitoid attack have been reported by other authors (Lefèvre 1948; Lugojja, 1996; Smit *et al.*, 1997).

Generally, enemy populations seem slow to respond (if at all) to changes in host density. For example, *G. acraeae* populations increased somewhat during the host population peak but this did not result in increased host mortality (Fig. 3B). Slight increases in host mortality only occurred after the host populations had dwindled to very low densities (as a result of other mortality factors). This weak and lagged response by *G. acraeae* manifests itself as an inverse density dependent relationship (Fig. 4A).

None of the other enemies killing larvae shows any significant density dependent effect. It is notable, however, that there are brief increases in both *B. bassiana* and *Charops sp.* caused mortality during the host population low. The combined mortality caused by *G. acraeae*, *B. bassiana* and *Charops sp.* was not significantly density dependent, but there were indications of inverse density dependence (Fig. 4E). However, Azerefegne and Solbreck (1999) analysing the total mortality during egg and larval stages found no indication of density dependent factors operating during this phase of the life cycle.

Whereas the two parasitoid species almost always caused very low absolute mortalities, *B. bassiana* caused high mortality (33%) on one occasion. The disease incidence is evidently not related to host density, but it is reported to be prevalent during the rainy seasons (Lugojja, 1996), and the highest mortality recorded by us also coincided with a very rainy period (cf. Azerefegne and Solbreck, 1999).

Mortalities caused by enemies killing pupae were usually in the range 1-10%, but the data for these enemies were much more limited than for those killing larvae. Azerefegne and Solbreck (1999) looking at density dependent effects in this age interval found indications of a curvilinear relationship with inverse density dependence in the lower interval of insect density and direct density dependence

in the upper interval. The role of enemy-inflicted mortality in this age interval is in need of further study.

Parasitoids and the pathogen seem to have limited effects on *A. acerata* populations. As in many other butterfly species (Dempster, 1984) there is little evidence of density dependent regulation by enemies. Some uncertainty remains, however, with regard to effects of pupal enemies on *A. acerata*. Furthermore, there is a possibility that enemy-caused inverse density dependence might prolong a population low. However, presently there is no evidence of natural enemies being able to reduce *A. acerata* population to levels where sweet potato crops are not seriously damaged.

Acknowledgements

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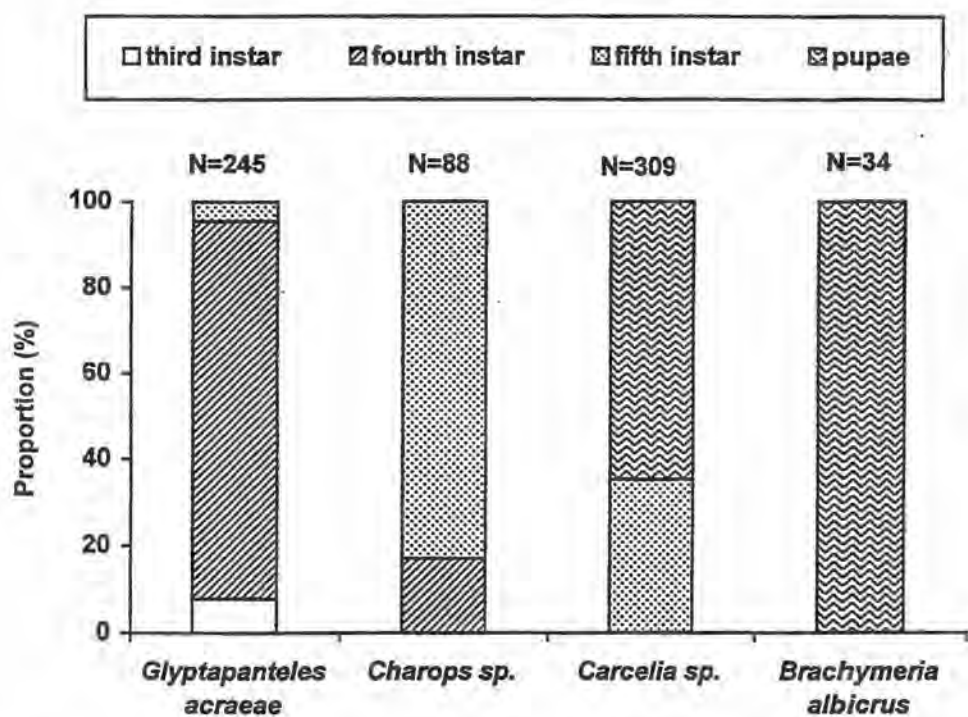
Figure 1. Stages at which parasitoids emerge from (and kill) immatures of *A. acerata*. Numbers above bars show number of parasitoids hatched.
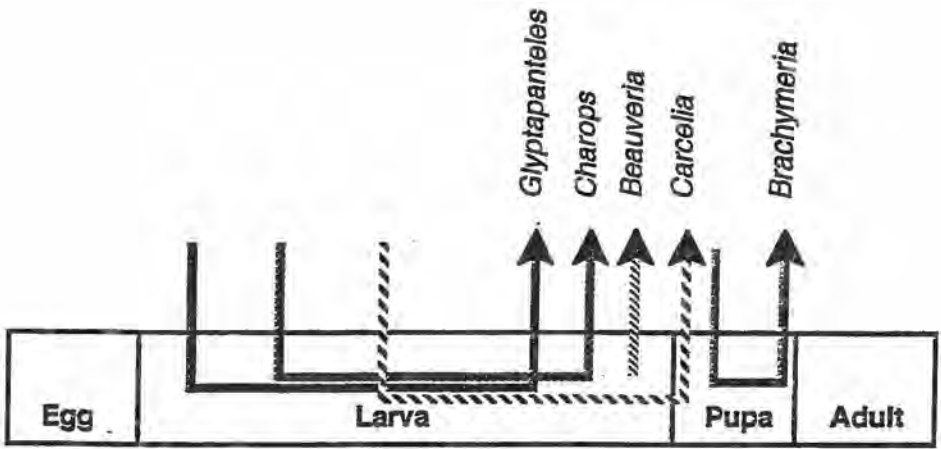
Figure 2. Sequence of attack and emergence by the parasitoids and appearance of *B. bassiana* symptoms in the life cycle of *A. acerata*.
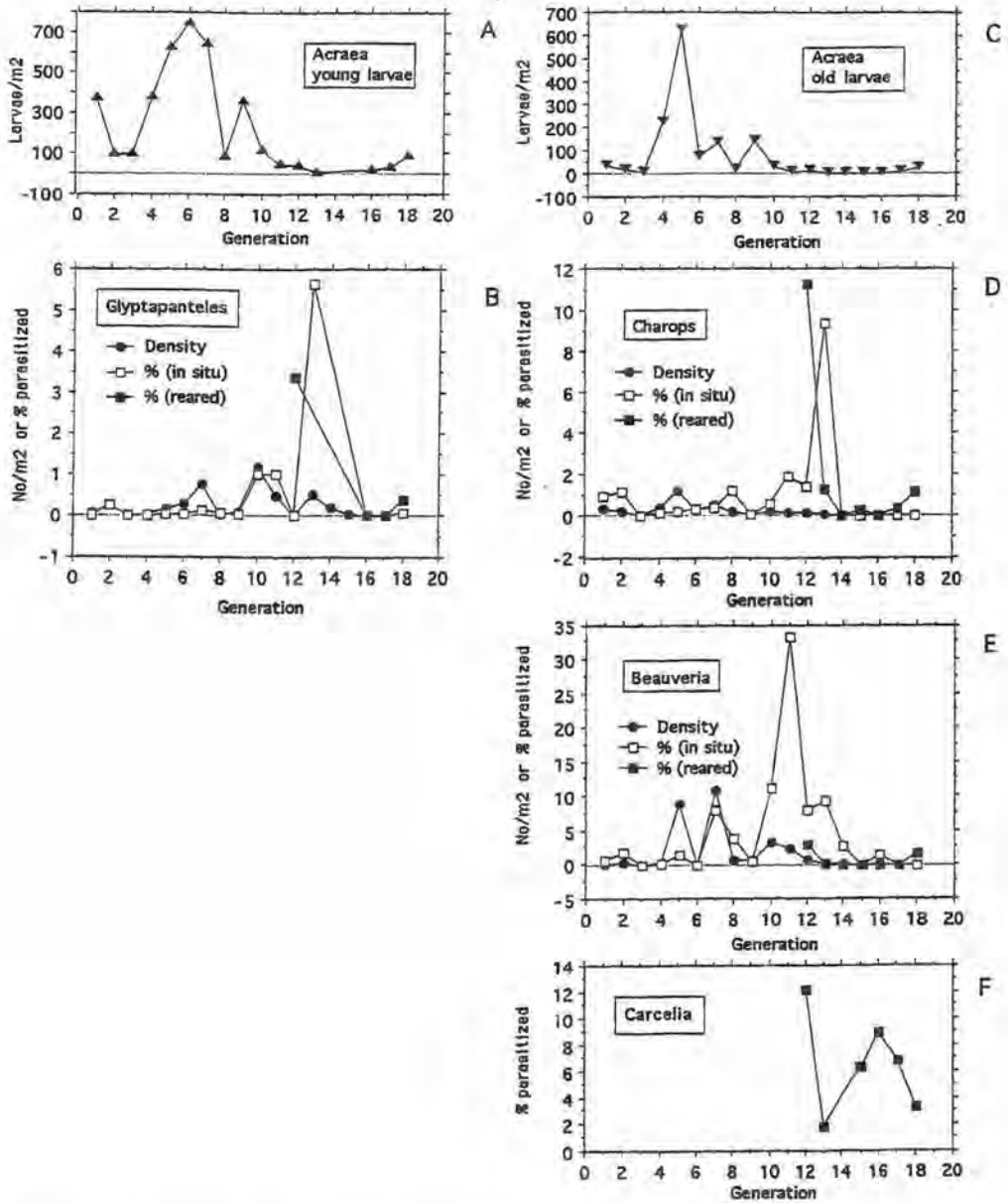
Figure 3. Density of *A. acerata* larvae over eighteen generations (October 1994 - December 1997), and densities of and percent mortality inflicted by three parasitoid species and a pathogen.

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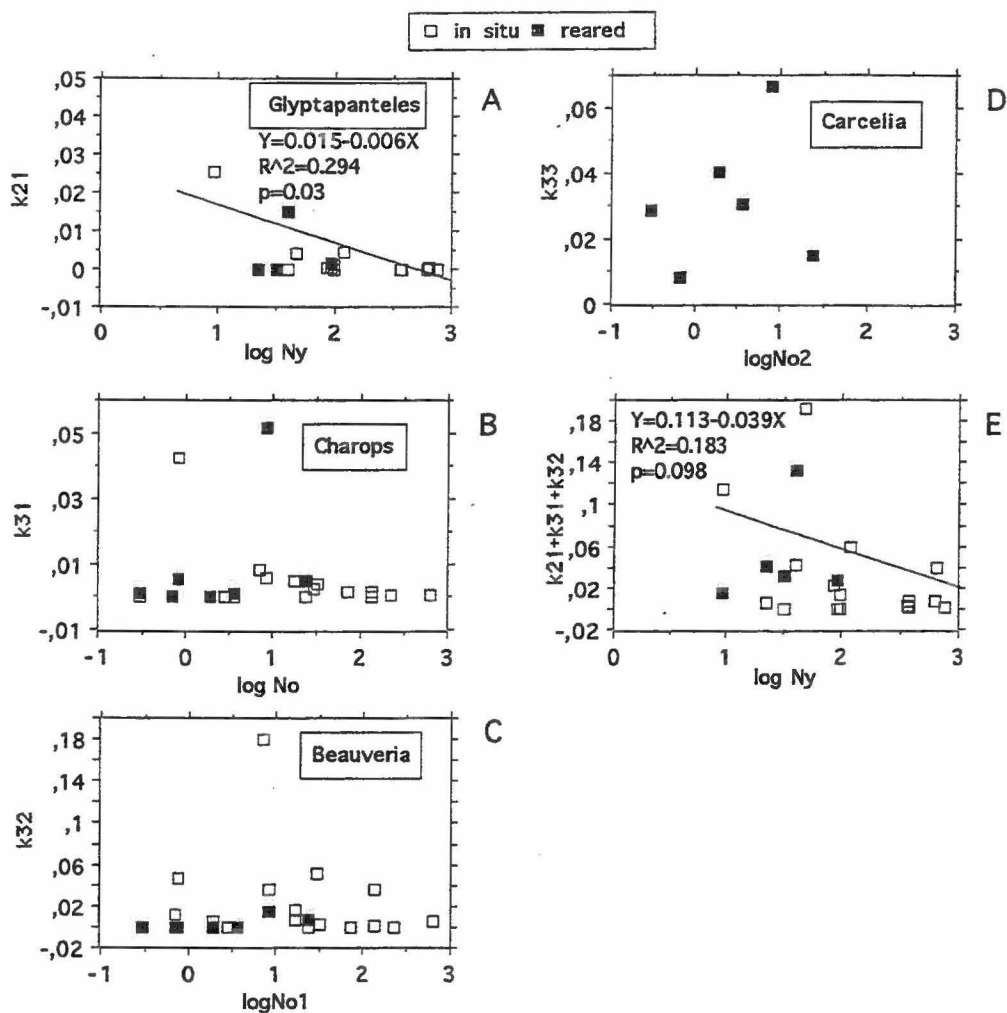
Figure 4. Mortalities, expressed as k-values, inflicted on *A. acerata* larvae in relation to host density at the time of enemy attack. For symbols see Table 1.

Table 1. Population densities measured and calculation of k-factors. Variables in bold face are directly measured.

NO ALIVE	LOG ALIVE	MORTALITIES	k-VALUE
YOUNG LARVAE Ny	log Ny		
		Glyptapanteles Ngl	k21=logNy-logNy1
Remaining after *Glyptapanteles* emergence	logNy1=log(Ny-Ngl)		
OLD LARVAE No	log No		
		Charops Nchar	k31=logNo-logNo1
Remaining after *Charops* emergence	logNo1=log(No-Nchar)		
		Beauveria Nbeau	k32=logNo1-logNo2
Remaining after *Beauveria* emergence	logNo2=log(No1-Nbeau)		
		Carcelia Ncarc 1)	k33=logNo2-logNo3
Remaining after *Carcelia* emergence	logNo3=log(No2-Ncarc)		

1) Only determined from collected and
reared larvae

Population dynamics of the tropical butterfly *Acraea acerata* Hew. (Nymphaildae: Acraeinae): a defoliator of sweet potato

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Abstract

1. The population dynamics of the sweet potato butterfly, *Acraea acerata*, was studied for three years in sweet potato fields in Southern Ethiopia in an area where farmers practice successive plantings throughout the year and do not use pesticides. Densities of eggs, young and old larvae, pupae and adults were estimated for eighteen generations.
2. The insect breeds during all seasons with about six discrete generations per year, but without clear seasonal trends in population density. Superimposed on the generation cycles are longer-term intergeneration fluctuations with an amplitude of three to four orders of magnitude. Population decline and build up are gradual processes taking place over several generations.
3. No density dependent factors seem to affect egg and larval stages, but strong density dependent processes operate in later developmental stages. Both pupal-adult survival and per capita egg production decline at high density. It seems likely that density dependent emigration of adults is an important contributing factor to both these responses.
4. Weather conditions affect mortality in two opposing ways. Rainy conditions lead to decreased survival during the egg–larval period, but to increased survival for the pupa–adult period.
5. It appears that intermittent episodes of extreme weather conditions are important in perturbing the system into domains where it is dominated by its slow endogenous dynamics, resulting in multigenerational fluctuations.

Introduction

Knowledge of insect population dynamics is to a large degree based upon studies of temperate region insects. Although there have been some serious efforts to collect data on population fluctuations of tropical insects during the last decades (Wolda, 1978, 1983), insect population studies from the tropics are still severely underrepresented in the ecological literature. In particular, there is a shortage of detailed multigenerational studies containing data on stage mortalities and recruitment rates. This is evident, for example, from Stiling's (1988) review of key factors and density dependence and later in Cornell and Hawkins' (1995) extensive review of mortality factors in insect populations.

The present study of the population dynamics of a native African butterfly, *Acraea acerata* (Hew.), was undertaken against this background of a shortage of insect population studies from the tropics. But it also has a practical aim, namely to understand the dynamics of an important and poorly known insect pest under conditions when no control measures are applied. How does population density change on an intra- or inter-generational basis? What are the mechanisms of density dependent feed back, what is the role of exogenous factors and how do these processes affect population change?

The genus *Acraea* (Nymphalidae: Acraeinae) is represented by about one hundred species in East Africa. They are toxic and aposematically coloured insects, which are adapted to a wide range of habitats from rain forest to dry open habitats (Larsen, 1991). The larva of *A. acerata* feeds on various *Ipomoea* species (Convolvulaceae) and it has become an important pest on sweet potato (*Ipomoea batatas*) in East Africa. In the Welayita region in southern Ethiopia, where we have studied *A. acerata*, the insect is indigenous, occurring on both some wild *Ipomoea* species and on sweet potato (Azerefegne, 1999a). Populations on wild plants are, however, small compared with those on sweet potato. The insect also grows faster and becomes larger, producing more eggs on sweet potato than on the wild host plant species (Azerefegne, 1999a). Sweet potato is often defoliated and *A. acerata* is regarded as the most important pest of this crop in the Welayita region.

In Welayita sweet potato is mainly produced for home consumption on small parcels of land without use of insecticides and artificial fertilisers. Accordingly populations of *A. acerata* in this area can be viewed as semi-natural, being minimally affected by control measures. Sweet potato has been grown in the region for more than one hundred years, but two important changes have taken place during the last few decades. First, the acreage under cultivation has increased substantially and second, the crop is planted repeatedly during the year. Hence the insect is now supplied with a larger and seasonally less variable food resource than before.

The butterfly deposits its eggs in clusters on sweet potato leaves. Young larvae, up to the third instar, spin loose protective webs on leaves under which they feed in groups, whereas the older larvae disperse and feed solitarily. The insect pupates on the plant or on the ground. The aposematically coloured butterfly is a slow flier. One generation is completed in about 40-50 days (Azerefegne, 1999b), and *A. acerata* breeds through all seasons producing several generations per year (Hill, 1983; Smit *et al.*, 1997). Populations of *A. acerata* as well as of other *Acraea spp.* are known to exhibit considerable fluctuations in density (Larsen, 1991; Owen, 1971).

The immatures of *A. acerata* are attacked by several species of predators, parasitoids and pathogens (Lefèvre, 1948; Lugojja, 1996; Smit *et al.*, 1997; Azerefegne and Solbreck 1999). In Ethiopia the pentatomid bug, *Macroraphis acuta* (Dallas) is a predator on all immature stages. Middle-aged larvae are killed by *Glyptapanteles acraeae* (Wilkinson) (Braconidae) while *Charops sp.* (Ichenumonidae) and *Carcelia sp.* (Tachnidae) emerges from last instar larvae. The latter parasitoid also emerges during the pupal period, along with *Brachymeria albicrus* (Chalcididae). Larvae may also die from infections of the pathogenic fungus *Beauveria bassiana* (Balsamo). Mortalities caused by these enemies in Welayita are, however, usually small or very small and none of the enemies seems to act in a direct density dependent manner (Azerefegne and Solbreck, 1999).

In this paper a broad view of the population dynamics of *A. acerata* is presented. Based upon a three year field study encompassing eighteen full generations of *A. acerata* in sweet potato plots the patterns of within and between generation population fluctuations are described and analysed. Stage-specific survival as well as recruitment rates are analysed in order to find out what factors affect population development and where in the life cycle and with what time lags density dependent processes operate (cf. Royama, 1997; Turchin, 1999).

Materials and methods

Sampling

The study was carried out in Welayita (7°00′N, 37°56′E), Southern Ethiopia, from October 1994 to December 1997, with adult sampling extending to April 1998. This area has a history of repeated outbreaks of *A. acerata*. Farmers practice successive plantings of sweet potato in small parcels of land throughout the year, with a maximum in the acreage planted during September-October, the end of the rainy season. Fields of sweet potato are interspersed with fields of numerous other crops like maize, coffee, enset, potato, sugarcane, taro and yam. Each month, over the entire study period, one new 100m² plot of sweet potato was established from vine tips (40-45cm) using a recently introduced sweet

potato variety, Koganesengan. (This variety is most preferred by farmers in the areas having large problems with *A. acerata*.) All the plots were situated within a three hectare field surrounded by Eucalyptus trees. In this field, with a mixture of various crops, approximately one ha was covered by sweet potato. The spacing between plants in rows and between rows was 0.45 and 0.5m, respectively. No fertiliser was added and weeding was by hand. No insecticides were used in the vicinity of the study plots. Sampling of *A. acerata* started when plots were one month old and ended six months after planting when the crop was harvested. Dry weather conditions sometimes prohibited planting of new plots. Thus the number of available plots was reduced to three or four on a few occasions, but in the majority of cases five or six plots were available for sampling.

Twenty randomly dispersed quadrate samples of $0.25m^2$ crop area were taken from each plot at fifteen day intervals. Data were collected on the number of egg batches, larvae, and pupae. Two larval stages, young larvae (up to the third instar), which are gregarious, and older solitary larvae (fourth and fifth instar), were discerned. The pupal counts included all pupae found on the foliage and on the soil (in crevices and on the surface) within the quadrate.

Adult population size was estimated by capture-mark-recapture. The butterflies are slow fliers and are easily caught with a butterfly net. Marking and release was carried out around noon in the above mentioned field where immature stages were sampled. The adults were marked with a dot on the underside of the forewing using a permanent marker pen. The butterflies were kept in muslin covered cages in the centre of the field until all the marking was completed. Then they were gently released to mix with the population in the field. Recapture was made two hours after release. The number of butterflies was estimated using the formula

$$N=M(C+1)/(R+1)$$ (Begon, 1979)

where N= estimated of number of butterflies, M= number of butterflies marked and released on first occasion, C= total number of butterflies captured on second occasion, and R= number of recaptured butterflies that were marked. On a few sampling occasions when butterfly abundance was very low total counts without marking were made during a four hour period.

Data analysis
The between-plot variation in the frame sample data was low and accordingly data from the different plantings (plots) were pooled. Because plots could not be established every month (see above) samples were reduced on certain occasions, but in the majority of cases 5-6 plots were available resulting in a total of 100 - 120 quadrate samples. The number of eggs was calculated by multiplying the number of egg batches by the average number of eggs in a batch (161.5$\pm$8.3 mean $\pm$ S.E., N= 72).

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All densities are expressed on a per m^2 basis. The adult population density was related to the total acreage of sweet potato in the study (and marking) area (1 ha, see above). Accordingly, the estimate obtained by mark recapture was divided by 10000.

Twenty one discrete butterfly generations were discerned during the study period, but larval and pupal estimates were only obtained from eighteen of these, and egg estimates from nineteen generations (Fig. 1). Because each generation is discerned by a generation curve, the number of individuals in each developmental stage in each generation was estimated by summation of the consecutive estimates (every fifteen days) within each curve. In a few instances where generations overlapped slightly, data were equally apportioned to the two generations. This method causes moderate systematic errors in the absolute estimates of the number of insects passing through each developmental stage. The addition of successive estimates constituting each generation rests on the assumption of equal duration of each developmental stage used (a reasonable assumption but not exactly right (Azerefegne, 1999b)). As we use data primarily to look at between generation differences this poses no serious problem, but care should be taken when comparing successive mortalities during the life cycle.

Possible intergenerational effects were analysed by calculating autocorrelation (ACF) and partial autocorrelation (PACF) functions (Turchin, 1990). Furthermore, generation survival (adults per egg) and generation recruitment rate (eggs per adult in parent generation) (cf. Royama, 1997) were calculated as was net reproductive rate expressed as Ro=adults in gen(t)/adults in gen(t-1).

For each generation, numbers alive in five developmental stages, viz. eggs, young larvae, old larvae, pupae and adults were measured. To investigate the existence of density dependence linear regressions were performed between log population density of each stage against log density in the previous stage. A significant deviation from a slope=1 was taken as an indication of the action of density dependent factors during this interval.

Using rainfall data from the Welayita National Meteorological Station, average daily precipitation was calculated for the periods when the different developmental stages of each generation occurred. The residuals from the regressions of log pupal density on egg density and log adult density on log pupal density were regressed on the rainfall data sets to investigate whether there were significant effects of rainfall on survival during these life history phases.

Results

Density changes

The *A. acerata* population developed with discrete and easily discerned generations (Fig. 1), so called generation cycles (Knell, 1998). A total of 21 butterfly generations were observed during three and a half years (October 18, 1994 - April 23, 1998), which means about six generations per year. No seasonal trends in density could be discerned (Fig. 1). Generation peaks were relatively high from late 1994 until August 1996 (highest density recorded 5263 butterflies/ha) after which density decreased drastically and remained low for about one year. During nine months in 1997 (January to September) the density of butterflies never exceeded ten individuals/ha. At the end of 1997 and in early 1998 densities increased to levels similar to those in the first year and a half of the study.

Looking at *generation totals* (Fig. 2A) the ranges of population fluctuations are about two to three orders of magnitude for egg to pupal stages but over four orders for adults. The net reproductive rate usually varies within the range 0.1-10 (Fig. 2B). Population change is thus gradual and there are long periods (up to five generations) of either continuous growth or decline.

The gradual change in population density is reflected in the autocorrelation of successive generation densities. The autocorrelation function (ACF) showed a damped sine wave pattern with an 11-14 generations (about two years) wavelength for all developmental stages (exemplified by the curve for adults in Fig. 3), but this particular wavelength is probably an artefact of the relatively short period of study.

In all immature stages the partial autocorrelation function (PACF) shows a significant positive correlation with a one generation lag only. The PACF for adult butterflies (Fig. 3), however, also displays a strong negative correlation with a two generation lag. In a stepwise multiple regression of current butterfly density ($N(t)$) on densities of butterflies in all previous generations ($N(t-1)$), $N(t-2)$, etc) current density can, to a large extent, be explained by densities in the two previous generations, $\log N(t) = -0.350 + 1.497 \log N(t-1) - 0.780 \log N(t-2)$ (R^2(first step)=71.2%, R^2(second step)=87.2%, df 15, 2).

Survival and recruitment

Generation survival and recruitment rates vary moderately over the first 8-10 generations (Fig. 2C). The population low between generations 9 and 19 (Fig. 2A) starts with a gradual decrease in generation survival over several generations (Fig. 2C). This decline is a two step process. The initial decrease is the result of egg-pupal survival decreasing, and the final decrease is due to lowered pupal-adult survival (Fig. 2C). The decrease in generation survival is being

compensated for from about generation 13 by an increase in recruitment rate. When insect density reaches the new peak at the end of the study period recruitment rate returns to previous levels.

No density dependent factors seem to operate during the period from egg to pupa (Fig. 4A). In regressions of log densities in successive developmental stages (eggs, young larvae, old larvae, pupae) none of the slopes deviates significantly *from unity*. (For log young larvae *vs* log eggs $y=0.111+0.819x$, $R^2=68\%$, $p>0.1$, log young *vs* log old larvae $y=-1.314+1.269x$, $R^2=82.7\%$, $p>0.1$, log pupae vs log old larvae $y=-0.784+0.886x$, $R^2=84.2\%$, $p>0.1$, notice that p- values refer to a test for a slope of 1.)

Density dependent processes, however, operate later in life affecting (1) pupal-adult survival and (2) recruitment. The relationship between log adult and log pupal density seems to be curvilinear, mortality being lowest at intermediate population densities (Fig. 4B). At high pupal densities adult density seems to level off, suggesting that direct density dependence acts in this upper interval of pupal densities.

Recruitment is evidently strongly density dependent. The slope of the log egg to log adult (=parents) regression is significantly smaller than unity (Fig. 4C). Butterflies hence produce considerably more eggs per capita at lower densities. (The same relationship holds if log(eggs) is plotted against log(pupae) in the previous generation ($Y=2.117 + 0.528X$, $R^2=0.465$, df 16, $p<0.01$ for slope equal to 1).

Because the PACF for adults (Fig. 3) suggested a lagged density dependent feed-back in the system, the lag structure was further investigated. Survival during (1) the egg-pupa period, (2) the pupa-adult period as well as (3) recruitment rate were regressed against population densities in the different developmental stages during previous generations (Fig. 5). This analysis gives no indications of any density dependent processes (lagged or non-lagged) operating during the egg-pupa period (Fig. 5A). The situation with regard to survival during the pupa-adult period is less clear. There is no significant correlation with densities during larval or pupal stages, but there is a significant positive correlation with both egg density in the same generation and with adult density in the previous generation (Fig. 5B). (Notice that these relationships were linear, cf. Fig. 4B. Visual inspections suggested no curvilinear relationships underlying the lack of significant effects in the other cases in Fig. 5B)

Recruitment rate, on the other hand, shows a significant negative correlation with all population density estimates back to young larvae two generations before (Fig. 5C). In a stepwise multiple regression with all previous densities, however, only adult parent density makes a significant contribution towards explaining the variation in recruitment rate ($y=2.94-0.51x$, $R^2=79.2\%$, $p<0.0001$). Removing

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parent density from the multiple regression (to avoid problems associated with the fact that parent density is used in the calculation of recruitment rate) only density of old larvae makes a significant contribution in a stepwise multiple regression explaining 68.1% of the variation in log recruitment rate (Fig. 6).

Rainfall has significant (density independent) effects on survival during both egg-pupa and pupa-adult intervals, but the two effects have opposite signs. During egg and larval stages survival is higher during dry periods (Fig. 7A), whereas for the pupa-adult period residual survival (from the curvilinear log adult *vs* log pupa regression, see Fig. 4B) is lower during dry weather conditions (Fig. 7B).

Possibly as a result of these opposing effects of rainfall, population density does not track precipitation patterns during the study period (Fig. 2A and D). The rainy season, which usually starts in March and ends in October, varied much from year to year. The long population decline from about generation ten coincides with a period of unusually heavy rains (Fig. 4D) evidently causing high larval mortality (cf. Fig. 7A), followed by a period of extreme drought associated with a strong decline in later developmental stages.

Discussion

Pattern of density change.

Density changes in *A. acerata* are characterised by (1) intrageneration large-amplitude generation cycles (Knell, 1998) and (2) intergeneration long wavelength large amplitude fluctuations extending over several generations. The occurrence of generation cycles is at first sight surprising in light of the relatively constant environment of a tropical insect. Nevertheless, this is a pattern described from several other tropical insects (Godfray and Hassell, 1989). Among the factors suggested for maintaining such a pattern are enemy effects and intraspecific competition (Godfray and Hassell, 1987; Knell, 1998). The former explanation is unlikely for *A. acerata* because mortalities inflicted by its enemies are generally small and without direct density dependence (Azerefegne and Solbreck, 1999). The latter explanation, however, seems more likely. Although the present study does not provide any evidence of intraspecific competition causing mortality among immatures, it seems to cause density dependent emigration (see below) and egg shortfall.

The long-wave intergenerational fluctuations are not uncommon among the Acraeinae of Africa. Many species of this genus are characterised by having population outbreaks following long periods of very low density (Larsen, 1991). Although population build up may seem fast on an absolute time scale, population growth on a per generation basis is evidently limited in *A. acerata*. Four to five generations were needed to reach a new population peak following a population

low. If compared on a generation time scale this tropical insect thus displays fluctuations similar to that of many temperate Lepidoptera species, where cycles often last about ten generations, and where fluctuation patterns exhibit a PACF with a positive one-generation and a negative two generation lag (Turchin, 1990).

Changes in vital rates

The mechanisms of population change in *A. acerata* were analysed by considering both survival and recruitment (cf. Royama, 1997). This analysis shows that density dependence does not operate in the interval egg - pupa (Fig. 4A), a phase in the life cycle during which most natural enemies attack. Azerefegne and Solbreck (1999), analysing the effects of various enemy species, found that none of them alone responded in a direct density dependent way (one, however, displayed weak inverse density dependence) nor did they together cause density dependence.

Although it was observed that *A. acerata* larvae consumed a large proportion of available foliage during population peaks, we found no evidence of this imposing density dependent mortality among larvae. Nor could any lagged density dependent effects be found that are expressed during the egg - pupa part of the life cycle (Fig. 5A).

Our study, however, provides strong evidence for density dependent processes being expressed late in life. The pattern of survival observed during the pupa-adult phase (Fig. 4B) suggests two effects. First, survival seems to be lower at low densities. We have no explanation for this possible inverse density dependence at low population density. Second, it appears that direct density dependence operates at high density. We think that this is the result of an increased emigration rate at high population density (but enemy effects cannot be entirely ruled out since our data on enemies affecting pupae are limited, see Azerefegne and Solbreck (1999)).

There is some anecdotal evidence for migratory movements taking place in *Acraea* spp. Larsen (1991) mentions that in *A. eponina* and *A. encedon* there are occasional well documented migrations, and concerning *A. acerata* he writes, "Population explosions sometimes occur and in these circumstances I think that migratory displacement may take place ..... Though usually a weak flier many were once seen by me flying steadfastly in the same direction at the third floor level of my hotel .."

There is also strong density dependence in recruitment rate (Fig. 5C and Fig. 6); fewer eggs per capita are laid at higher butterfly densities. This effect could also be linked to density dependent emigration. Emigration is thus likely to cause two effects. First, increased emigration at high density appears as lower "survival" in late life (pupa - adult period). Second, migratory females are likely to have a

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lowered or delayed egg production as has been shown for other Lepidoptera (Nielsen, 1961, Gatehouse and Zhang, 1995).

There is a possibility that the lowered recruitment rate at high density could partly be explained by competition among larvae. Moderate food shortage or low food quality at high larval density is likely to result in smaller pupae, and pupal size has been shown to affect fecundity in *A. acerata* (Azerefegne, 1999a) as in several other Lepidoptera (e.g. Dempster, 1983). Variations in sex ratio have also been observed in the Acraeinae (Owen, 1971; Jiggins *et al.*, 1998). In *A. acerata* Lefèvre (1948) claimed that the sex ratio changed from 1:1 during the wet season to 2:1 (females:males) during the dry season. Unfortunately, there are no sex ratio data available from the present study. Nevertheless, it is unlikely that either size or sex ratio changes could explain more than a minor part of the very large variation observed in recruitment rate (over two orders of magnitude) (Fig. 6).

Feed back and lag structure

The PACF analysis (Fig. 3) suggests that negative feedback in the *A. acerata* population operates with a two generation lag, a lag structure found in several other insect species subjected to this kind of analysis (Turchin, 1990). However, a more detailed analysis, making use of all within generation density data on *A. acerata* (Fig. 5), generates a different picture. Recruitment rate is then found to be affected by density late in the very same generation, i.e. with almost no lag at all. Densities earlier in the life cycle or in previous generations make no contribution at all towards explaining changes in recruitment rate.

What is the reason for obtaining such conflicting results? We think the PACF analysis, by using just one density measure per generation (and looking at the state variable *density*, rather than at *rates of change*), simply has poor temporal resolution. In the present case, the PACF analysis evidently gives a misleading picture of the lag structure in the system and the feed back mechanisms at work. There is a further problem with a PACF analysis in the present case. If a system is affected by an exogenous factor displaying autocorrelation (Williams and Liebhold, 1995, 1997) system feed back (endogenous dynamics) cannot be distinguished from the driving effect of the exogenous factor. In the study area, the pattern of rainfall (expressed as average precipitation per generation, Fig. 2D) is autocorrelated (with a highly significant negative feedback of lag 2) and rainfall does affect *A. acerata* populations albeit in a complicated way (Fig. 7).

Weather and disturbance

It has been claimed that population change in *A. acerata* is linked to seasonal weather patterns (Lugojja, 1996; Smit *et al.*, 1996), but our data do not point to any simple coupling of population change to season. Weather conditions, such as rainfall, evidently have important density independent effects, but the effects of rainfall during early and late life seem to be different (Fig. 7). In larvae, survival

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decreases with rainfall, whereas it increases for the pupa - adult period. The former effect is probably the result of heavy rains directly killing larvae (cf. Anioke, 1996), but the latter effect is less easily explained. One possibility is that rainfall is a hindrance to flight and accordingly reduces emigration rate.

Although the combined result of the opposing weather effects is not immediately clear, it seems that weather conditions are important in causing occasional perturbations of the population. The drastic population decline observed was evidently brought about by a sequence of extreme wet and dry conditions (Fig. 2D). Such perturbations in combination with a slow population recovery rate are likely to cause the long-wave intergenerational fluctuations observed in *A. acerata*.

Population regulation

The findings presented above suggest that adult behaviour and recruitment form the key to population regulation in *A. acerata*. This is in line with the findings from several recent papers on insect population dynamics. An earlier focus on analysing mortalities is now shifting towards giving a deeper consideration of variations in recruitment rates (Royama, 1997). Evidence of many insect species being regulated in the adult stage by changes in migratory rates and/or fecundity in response to available resources is accumulating (Gatehouse and Zhang, 1995; Ohgushi, 1999).

The population responses observed in *A. acerata*, with density feeding back on adult survival/emigration and recruitment rate with almost no lag, are likely to be highly stabilising, resulting in a population efficiently tracking the resource base. Whereas natural enemies seem rather inefficient in perturbing the system from this state (Azerefegne and Solbreck, 1999), extreme weather conditions (possibly in combination with occasional pathogen outbreaks) seem to create important disturbance regimes. The *A. acerata* system is thus similar to several recently described systems dominated by bottom up effects in combination with weather disturbance (e.g. Solbreck, 1995).

Acknowledgements

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artificial defoliation helps to understand the relative sensitivity of stages of sweet potatoes to defoliation.

Stages of crops differ in their sensitivity to defoliation. Potato is found to be less sensitive to defoliation during both late and early stages of its development (Hare, 1980), whereas, defoliation during the blooming stage causes up to 64% tuber reduction. Artificial defoliation during the early stages of sweet potato development caused higher levels of root yield loss. The stronger correlation of both early and late harvest root losses with first generation larval density in the field also emphasises the importance of early stage defoliation. Yen (1973) concluded that tuberous root reduction is stronger on sweet potatoes defoliated 2-4 months after planting. Therefore, control measures against *A. acerata* should mainly focus on young sweet potato plants.

A. acerata produces about six generations per year in Southern Ethiopia with densities fluctuating several orders of magnitude (Azerefegne and Solbreck, 1999). During the study period, the sweet potato crops were attacked by two subsequent larval generations before harvest. Population density in consecutive years differed greatly with varying effects on the yield of sweet potato. The sporadic nature of the pest with very low larval population density in some years and high density in others indicates that there is a need to establish action threshold levels to determine when insecticidal treatment is justified.

Defoliation of annual crops apparently must exceed a threshold, usually between 5 and 30% before productivity is impaired (Mattson and Addy, 1975). *A. acerata* is known to cause complete defoliation. In this study, however, we recorded a maximum of 75% damaged leaves and reduction in ground cover ranging from 14 to 37% during the two years of higher insect population density. The best correlation between insect density and yield loss was found for a specific stage of the crop development. In potatoes this relationship is known to be affected by the variety, differences in growing conditions, age at defoliation and the time allowed to recover (Cranshaw and Radcliffe, 1980; Hare, 1980; Ferro *et al.*, 1983).

Assessment of *A. acerata* damage should be based on young larval density which has several advantages. First, although leaf damage or ground cover loss were well correlated with the extent of yield loss especially for the early harvest, insect density expressed as larval tents per m^2, was better correlated with the yield loss for both early and late harvests. Second, compared to monitoring using percent plant parts damaged and ground cover loss, locating and counting the conspicuous larval tents is easy. Third, surveys at this development stage leaves enough time to decide on control measures. The lowest number of larval tents, which caused significant yield reduction during this study, was about 6 per m^2. Thus, it is proposed that larval densities of more than 4 tents/m^2 during the early growing period of sweet potato warrant insecticide treatments.

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The actual difference in weight between the protected and unprotected plots remained the same or was higher for the late harvests. Several factors could affect the recovery of crops from early season defoliation. In potatoes, recovery from early season injury was observed to be complete for late maturing varieties (Cranshaw and Radcliffe, 1980) indicating that a longer growth period may dampen defoliation effects. On the other hand, delayed harvesting may expose the roots to the attack of sweet potato weevils. Farmers in the study area start to harvest sweet potato as early as three months after planting. The farming system of the area is characterised by cultivation of several crops on small plots which calls for timely harvesting for efficient crop rotation.

Defoliation by *A. acerata* reduced the biomass of sweet potato tops. Sweet potato tops serve as animal feed and/or human food in some countries. Heavy defoliation also causes shortage of planting material during the next season. The non-significant differences between protected and unprotected treatments at some sites for late harvests indicate that the crop can compensate for part of the foliage loss given enough time and favourable growing conditions. It seems that compensation through delayed harvesting is more likely for tops than for the root yield.

Lugojja (1996) suggested that a single defoliation might not cause significant yield reduction in sweet potatoes. He observed significant yield reduction with increased frequency of defoliation, and the growth stage at which single or repeated defoliations were carried out did not significantly affect root yield. In contrast, the complete single artificial defoliation carried out in the current experiment resulted in significant yield reductions for all ages of sweet potato.

Discrepancies in the effect of defoliation on the yield reduction could be due to several factors. Together with the differences in plant variety, growing environment (weather, soil, etc), variability in yield between plants could cause large variance. Yield in sweet potato is highly variable and no two plants are alike. Vine cuttings of different sizes and from different parts of the vine have variable production potential. The tip part is the most preferred part of the vine for planting. Thus, failure to have uniform plants in a plot will lead to large experimental variation making it impossible to detect significant differences between treatments. In this experiment, all the hills were established from the 45cm tip part and 50 plants of the inner rows were harvested from each plot. The combination of uniformity in planting material and relatively large sample size reduced the error term and revealed real differences between treatments.

Yield loss due to artificial defoliation may not be directly comparable with insect defoliation. Artificial defoliation is abrupt and gives the plant a chance for uninterrupted development afterwards, which may underestimate the insect caused defoliation effect. When larval population density is high, the plant will be repeatedly grazed and the new leaves will be quickly consumed. Nevertheless,

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Artificial defoliation

Complete artificial defoliation caused significant yield reductions irrespective of the age of sweet potato at defoliation (Table 3), but defoliation at earlier stages (6 and 8 weeks) seems to result in higher levels of root yield loss. Removal of half of the leaves seems to be serious on 8 week old sweet potato plants but was not statistically different from the non-defoliated plots. The complete defoliation treatment resulted in lower biomass of sweet potato tops for all ages (Table 3). The lowest biomass of tops was recorded on late defoliated sweet potatoes. However, neither complete nor 50% defoliations resulted in statistically significant reduction of tops compared with the non-defoliated plots.

Table 3. Effect of artificial defoliation of sweet potato on tuberous root and top yield

Age at defoliation	Defoliation extent (%)	Root yield (tons/ha)	Percent reduction (%)	Tops (tons/ha)
Not-defoliated	—	43.58a	—	15.85a
6 weeks	50	41.10a	5.7	15.26a
	100	29.21b	33.0	13.42a
8 weeks	50	38.10a	12.6	15.17a
	100	27.70b	36.4	12.68a
10 weeks	50	38.88a	10.8	16.03a
	100	31.73b	27.2	14.52a
12 weeks	50	39.38a	9.6	14.16a
	100	32.27b	26.0	11.91a

Means followed by the same letter within a column are not statistically significant according to Tukey's studentized range (HSD) test at P=0.05 probability.

Discussion

Defoliation of sweet potato plants by *A. acerata* resulted in significantly lower tuberous root and top yield of sweet potato. Tuber losses in the range 31-53% and top losses of 25-36% were recorded in farmers' fields in years with high insect population density. Protection measures carried out during high densities were found to be profitable even though the price of sweet potato was very low in the area.

There is a trend towards a reduction in the percent of tuberous root yield loss by delaying harvest, but unprotected fields never fully compensated for the root loss.
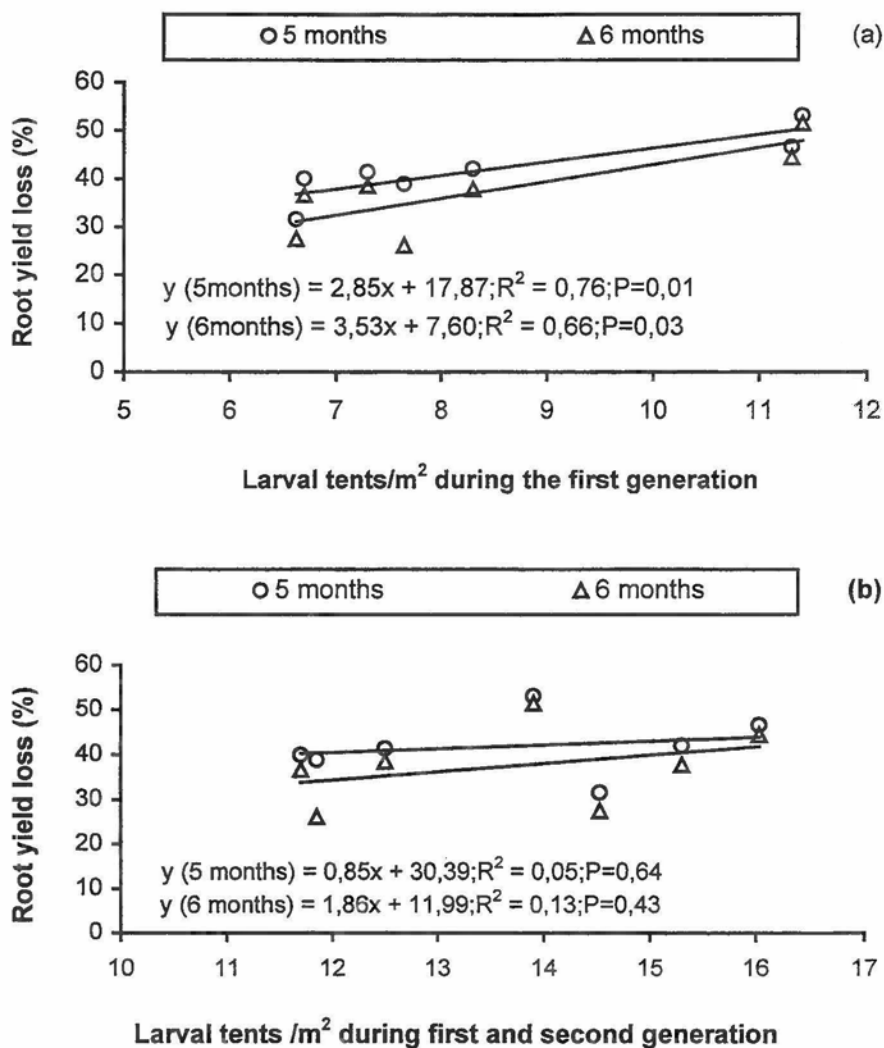
Figure 5. Relationship between larval density of *Acraea acerata* during a) first generation and b) first & second generation and tuberous root yield loss.

Cost-benefit analysis

The estimated cost of spraying a hectare twice during the growing period (316 Birr) showed that there should be a difference of 1.26 tons per hectare to make insecticide treatments economically profitable. The price of sweet potato at the nearest market was very low (30 Ethiopian Birr/100kg). Nevertheless, the use of insecticides was economically justifiable in all cases of high insect density. Profits ranged from 626 to 2669 Birr for early harvests and 762 to 3126 Birr for late harvests. The profit was higher for late harvests on all occasions except one (Table 1).
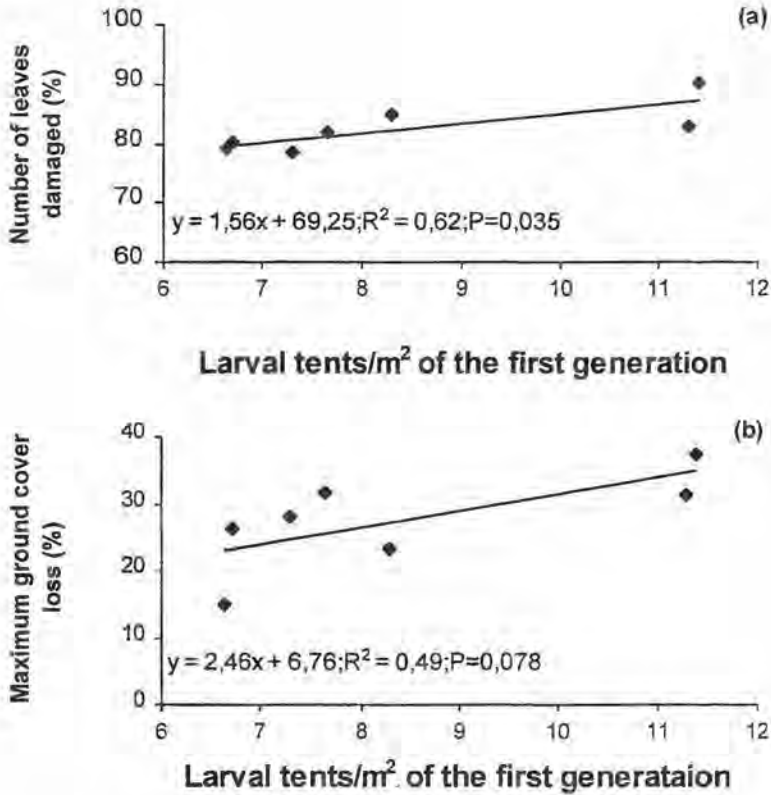
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Figure 4. Relationship between larval density and extent of defoliation on sweet potato expressed as a) number of leaves damaged and b) maximum ground cover loss.

The percentage of leaves damaged was significantly correlated with larval density during the first generation (Fig. 4a), however, the correlation with the maximum ground cover loss was not significant (Fig. 4b). Root yield loss of both early and late harvests was strongly correlated with the density of larvae during the first generation (Fig. 5a), explaining about 76% and 66% of the yield reduction in early and late harvests, respectively. Yield loss was not significantly correlated with total larval density of both generations (Fig. 5b).
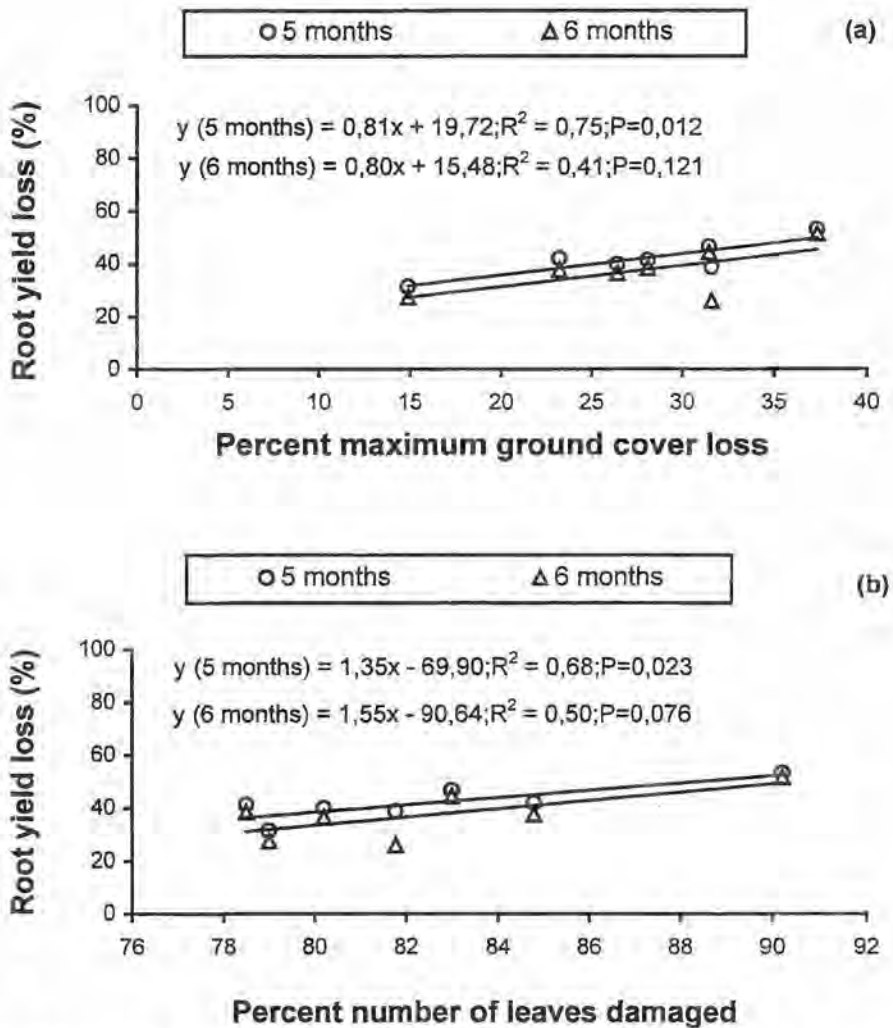
Figure 3. Relationship between a) percent maximum ground cover loss and b) percent number of leaves damaged by *A. acerata* and tuberous root yield loss.

Relationship between damage levels and yield loss

Except in 1996-97 with low insect population density, the proportion of infested hills reached 100% at all sites at some point during the growth period, which makes this variable unsuitable for expressing intensity of defoliation. The maximum difference in the percent ground cover between protected and unprotected plots is more variable and correlated with tuberous root yield loss for the five months harvest (Fig. 3a), explaining 75% of the variation in yield for unprotected plots. However, although the slope for the late harvest is similar to that of the early harvest, it is not significantly different from a zero slope. The percent yield loss was also correlated with the proportion of damaged leaves (Fig. 3b), but only significantly so for the early harvest.

In 1996-97, there was no infestation by the insect and thus there was no difference between the sprayed and unsprayed plots. The yield was lower than in the other years of the study due to drought.

The protected plots also produced a greater biomass of sweet potato tops than the unprotected plots during the 1995-96 and 1997-98 cropping seasons (Table 2). This difference was observed in all farms during the early harvests. However, for late harvests only three out of five sites in 1997-98 were significantly different.

Table 2. Biomass of sweet potato tops from plots protected and unprotected against *A. acerata*

Location (farms)	Treatment	5 months after planting		6 months after planting	
		biomass tons/ha	percent reduction	biomass tons/ha	percent reduction
1995-96 cropping season					
Abotaulto	Unsprayed	8.96a	34.8	6.85a	52.0
	Sprayed	13.29b		14.33b	
Adekoysha	Unsprayed	8.55a	32.6	9.26a	36.6
	Sprayed	13.11b		14.59b	
1996-97 cropping season					
Abotaulto	Unsprayed	6.64a	—	8.02a	—
	Sprayed	6.75a		8.26a	
Gacheno	Unsprayed	6.86a	—	7.86a	—
	Sprayed	7.41a		8.49a	
1997-98 cropping season					
Abotaulto-I	Unsprayed	3.58a	41.0	5.15a	36.7
	Sprayed	6.07b		8.13b	
Abotaulto-II	Unsprayed	4.88a	44.2	7.22a	38.4
	Sprayed	8.75b		11.70b	
Buge	Unsprayed	14.66a	33.7	21.02a	—
	Sprayed	22.10b		26.02a	
Gacheno-I	Unsprayed	7.15a	47.4	7.79a	41.9
	Sprayed	11.79b		13.37b	
Gacheno-II	Unsprayed	6.73a	41.0	6.09a	—
	Sprayed	11.40b		7.57a	

In comparison between sprayed and unsprayed treatments at each site means followed by same letter are not significantly different (F-test at $P<0.05$).

Table 1. Yield loss of sweet potatoes in farmers' fields caused by *A. acerata*

Cropping Season	Location	Treatment	5 months tuberous root yield (tons/ha)	loss (%)	profit (Eth. Birr)	6 months tuberous root yield (tons/ha)	loss (%)	profit (Eth. Birr)
1995-96	Abotaulto	Unsprayed	16.86a	41.4	2669	21.97a	38.6	3126
		Sprayed	28.78b			35.74b		
	Adekoysha	Unsprayed	10.96a	40.0	1684	15.22a	28.6	1286
		Sprayed	18.56b			21.25b		
1996-97	Abotaulto	Unsprayed	7.61a	—	—	9.03a	—	—
		Sprayed	7.35a			8.85a		
	Gacheno	Unsprayed	9.63a	—	—	11.57a	—	—
		Sprayed	9.81a			11.31a		
1997-98	Abotaulto-I	Unsprayed	5.21a	53.2	1161	8.28a	51.5	1885
		Sprayed	11.12b			17.09b		
	Abotaulto-II	Unsprayed	5.47a	46.7	880	8.58a	44.5	1401
		Sprayed	10.26b			15.45b		
	Buge	Unsprayed	12.44a	31.6	1119	17.60a	27.5	1684
		Sprayed	18.18b			24.26b		
	Gacheno-I	Unsprayed	7.59a	42.1	1062	10.18a	37.8	1349
		Sprayed	13.11b			16.36b		
	Gacheno-II	Unsprayed	5.90a	39.0	626	12.21a	26.1	762
		Sprayed	9.68b			16.53b		

In comparison between sprayed and unsprayed treatments at each site means followed by same letter are not significantly different (F-test at $P<0.05$).
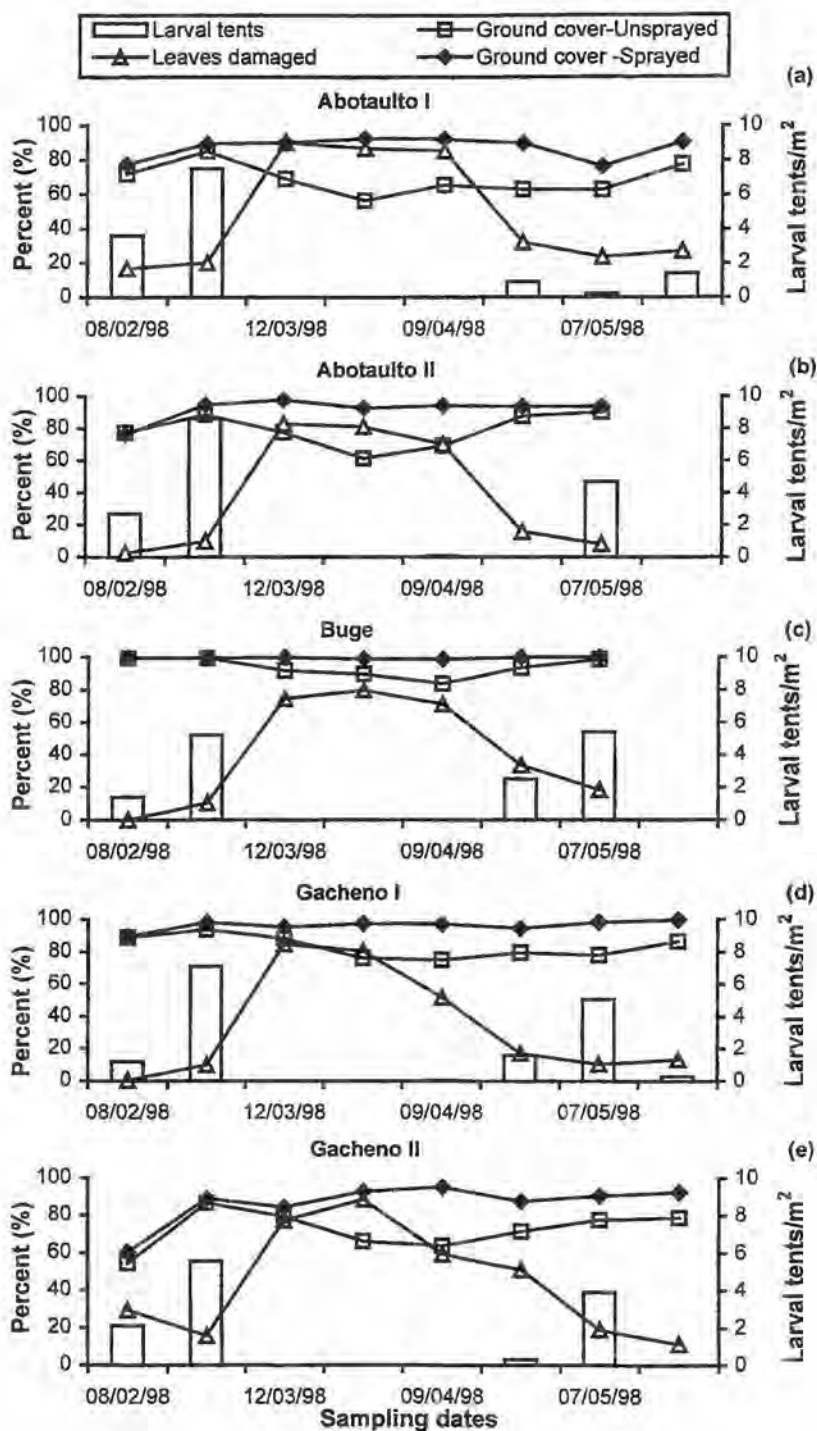
Figure 2. Density of *A. acerata* and damage on sweet potato during 1997-98 cropping season.
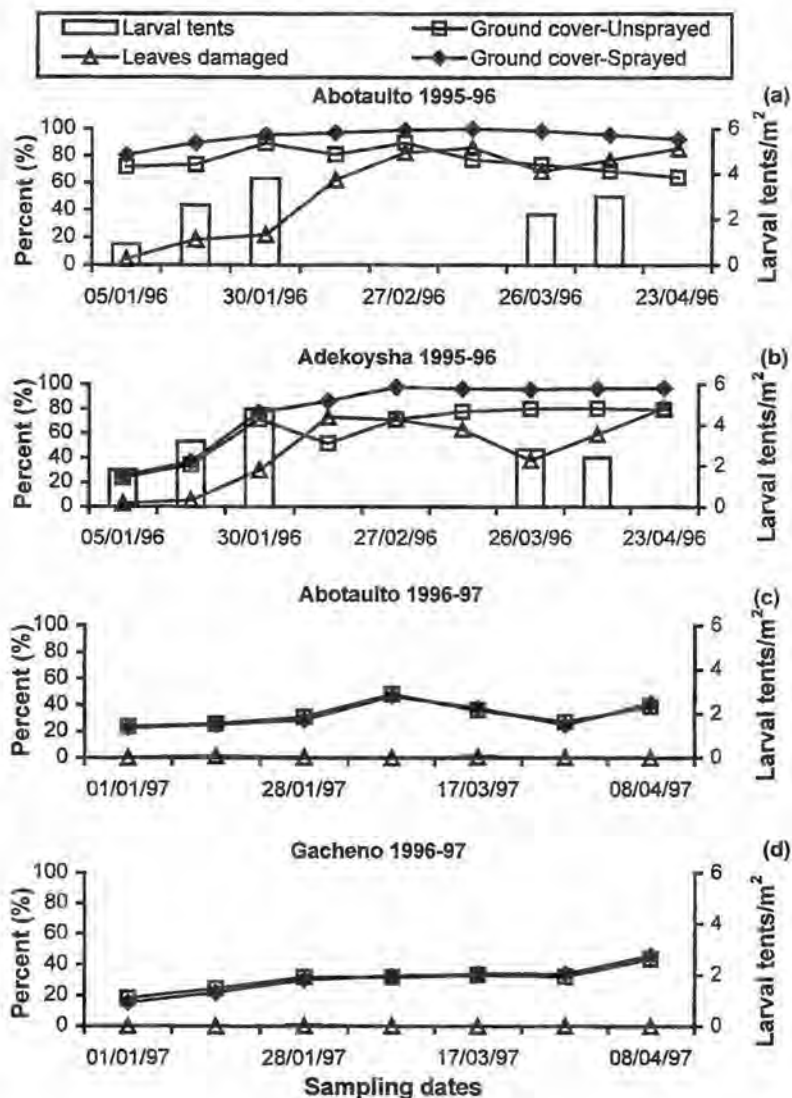
Figure 1. Density of *A. acerata* and damage on sweet potato during 1995-96 and 1996-97 cropping seasons.

Yield loss

There is considerable variation between years and locations in crop yield (Table 1). Yield ranges of 5 to 28 tons/ha for 5 month harvests and 8 to 35 tons/ha for six month harvests were recorded from the different farms. In the 1995-96 and 1997-98 cropping seasons the protected plots produced significantly more tuberous roots at all sites (Table 1). This significant difference was observed for both five and six month harvests. The percent yield reduction varied between locations from 31-53% for the five month and 26-51% for the six month harvests.

Data on the tuberous yield and tops were subjected to analysis of variance (SAS, 1996) and means were separated with Tukey's studentized range (HSD) test at p=0.05.

Results

Insect population density

Two peaks of larval density were observed during the 5 to 6 month cropping cycle representing two successive insect generations. The insect population density varied between the three growing seasons studied. High densities were observed during the 1995-96 (Fig. 1, a&b) and 1997-98 (Fig. 2) cropping seasons, with 7-10 and 6-12 larval tents/m^2, respectively in the first generation. The 1996-97 season had the lowest number of larvae when compared with the other years (less than 0.1 larval tents/m^2 at any time) (Fig. 1, c&d).

Crop damage

During 1995-96 insect feeding caused considerable leaf damage as well as reduction in ground cover (Fig. 1, a&b). The difference in the ground cover between the protected and unprotected plots reached a maximum of 28% at both sites. While the protected plots reached 100% ground coverage, the unprotected plots did not surpass 90%. At both farms the proportion of infested hills reached 100% at some time during the growing period and about 80% of the leaves showed signs of *A. acerata* feeding.

In the 1996-97 cropping season there were very few larvae (Fig. 1, c&d) and no differences in ground cover were observed between sprayed and unsprayed plots. Unlike the other two periods studied, the 1996-97 cropping season was not favourable for growth of sweet potato because of a prolonged dry period. In consequence, complete coverage of the ground was never attained at either farms at any time during the growing period.

In 1997-98 (Fig. 2) reduction of the ground cover was observed on unprotected compared with protected plots. The reduction ranged from 14 to 53 % at the different farms. As in the 1995-96 cropping season, there were larvae on all the hills. The proportion of leaves infested ranged from 79 to 90%.

Harvesting was done five and six months after planting. The inner $40m^2$ crop area in each plot was harvested. The fresh weights of tuberous roots and shoots were measured. The yield data from each site were separately subjected to analysis of variance (SAS, 1996) and the F-test value at P=0.05 was used to separate the two treatments. In addition, simple regression analyses were performed between the parameters used to express extent of damage (percent leaf damaged, ground cover loss, and larval tent density) and the yield loss at the two harvesting periods.

Crop value was estimated at 30 Ethiopian Birr/100kg by taking an average of prices obtained by eight farmers in the local market for 15 to 20kg tuberous roots. Labour cost was estimated by averaging the time spent for spraying $100m^2$ area of the crop three times. Three operators can spray one hectare in about 6 hours with a manual knapsack sprayer. With a daily wage of 10 Ethiopian Birr/day the total labour cost was estimated at 30 Ethiopian Birr/ha. The machine cost for a hectare (28 Ethiopian Birr/ha) is estimated as 4% of the initial price of a manual knapsack sprayer (700 Ethiopian Birr) on the assumption that it can be used for a minimum of 5 years on 5 hectares. The cheapest chemical, malathion 50% e.c., at the rate of 2 litres/ha is used for calculating the pesticide cost. A litre of this chemical costs 50 Ethiopian Birr. The total cost of chemical protection for one hectare per spray is accordingly estimated to be 158 Ethiopian Birr. (One US dollar is equivalent to 7.8 Birr)

Economic benefit of using insecticides is calculated as;
Profit =((Yield from protected-Yield from unprotected) x price of crop) − cost of insecticide application

Artificial defoliation of sweet potatoes at different ages after planting

This experiment was carried out at Awassa College of Agriculture Research and Farm Centre (7° 05' N, 38° 29' E), Ethiopia. The sweet potato butterfly does not cause damage to sweet potato in this area. The experimental plots were established from 45cm vine tips of the variety Koganesengan, in September 1996. No insecticide or fertiliser was used and weeding was done by hand.

The experiment was a randomised complete block design with three replications. The treatments included two levels of defoliation (50%, 100%) at 6, 8, 10, and 12 weeks after planting and a non-defoliated control. Each plot had an area of 5m x 3m with 0.5m and 0.45m spacing of plants between and within the rows, respectively. For the 100% defoliation treatments, all the leaves were removed leaving the petiole intact to imitate complete defoliation by the insect. In the 50% defoliation treatments, half of the leaves were randomly removed. After five and a half months the inner three rows, comprising 50 sweet potato hills ($11.25m^2$), were harvested from each plot and fresh tuberous roots and tops were weighed.

4

The relationship between defoliation and yield loss in sweet potato is poorly known and there is no estimate of the loss caused by *A. acerata*. It is generally believed that severe defoliation has a temporary effect on root yields for which the plant compensates by a longer period of growth (Chalafant *et al.*, 1990). This paper reports a study on sweet potato yield loss caused by *A. acerata* on farmers' fields in Southern Ethiopia. The sensitivity of sweet potato to defoliation during different developmental stages was investigated by artificial defoliation at different intervals following planting. In addition, the economic benefits of using insecticides against *A. acerata* were evaluated.

Materials and methods

Yield loss in farmers' fields

The study was carried at Welayita, (7° 00' N, 37° 56' E) Southern Ethiopia, an area with a history of repeated outbreaks of *A. acerata*. Two fields in 1995-96 and 1996-97 and five fields in the 1997-98 cropping season were selected for the study. The farms were situated within 10 km of each other. Farms were selected based on their uniformity of planting and sweet potato variety. The fields were planted in October or November. There was no history of fertiliser and herbicide use on the selected farms.

Each selected field was divided into eight adjacent plots with a size of 18m x 6m each. The two treatments, protected and unprotected, were randomly assigned. The protected plots were sprayed twice, one application for each of the two insect generations during the cropping season. Spraying was carried out when the larvae were at the young cluster stage (I to III instar) with either malathion 50% e.c. at the rate of 2 litres/ha or Lamda cyhalothrin (Karate®) 5% e.c. at the rate of 16gm a.i./ha. The selection of the insecticides depended on availability. Both insecticides gave complete control of the insect and there were no surviving larvae 72 hours after spraying.

The number of young larval clusters were counted using twenty 0.5m x 0.5m quadrates in each plot at 15-day intervals. In addition, the proportions of infested hills and damaged leaves/hill were estimated by inspection of twenty randomly chosen hills. Hills and leaves were categorised as damaged if there was any sign of *A. acerata* feeding.

The proportion of the ground covered (sensu Burstall and Harris, 1982) by the foliage was used as a measure of the extent of larval feeding. A 1m x 1m wooden frame was equally divided by strings into 100 1dm^2 units. The frame had four legs to hold it over the crop while counting the number of squares covered by the foliage. Squares with more than half of the area covered by foliage were classified as covered. In each plot ten measurements were made.

3

Yield loss of sweet potato caused by the sweet potato butterfly (*Acraea acerata* Hew. (Nymphalidae: Acraeinae)) in Ethiopia

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Abstract

Sweet potato defoliation and yield loss due to *Acraea acerata* Hew. (Lepidoptera: Acraeinae) was studied in farmers' fields in Welayita, Southern Ethiopia. Two generations of the pest attack the crop in one growing period.

Insect population density varied considerably between fields and years as did yield. In 1995-96 and 1997-98, yield loss ranged from 31 to 53% in the early harvest (5 months). Delaying harvesting did not reduce the loss in root yield. Larval density of the first generation was correlated with leaf damage and yield loss for both early and delayed harvests and explained about 76% and 66% of the yield variation in early and late harvests, respectively.

Both artificial defoliation and field studies showed that early stages of sweet potato are more sensitive to defoliation than later stages.

Protection with insecticides at high insect density was economically justifiable. Two sprays of insecticides applied during the young larval periods resulted in significantly higher yields. The study recommends the use of insecticides at larval densities exceeding 4 tents/m^2 during the first three months after planting.

It is proposed that assessment of *A. acerata* damage should be based on young larval density. Larval tents are easy to locate, count, and surveying at this development stage leaves enough time to decide on control measures.

Introduction

Sweet potato *(Ipomoea batatas* (L.) Lam.) is a chief source of carbohydrates for the resource poor farmers of third world countries. It is a major staple food for many farmers in East Africa (Smit *et al.*, 1997). In North Omo, Southern Ethiopia, sweet potato is a strategic crop in that it serves as a security and fall back when the food reserve from cereals dwindles. The period between September to November, the end of the rainy period, is the main planting time for sweet potato in this area although many farmers practice successive plantings throughout the year.

The crop is attacked by many insects, which can be divided into two main feeding groups; the borers and the defoliators. The boring sweet potato weevil *(Cylas spp.*) has been identified as the most serious insect problem of the crop. Among the defoliators there are cassid beetles, the sweet potato hawk moth and the sweet potato butterfly. The sweet potato butterfly *(Acraea acerata* Hew.) has been considered as a pest of secondary importance in many parts of Africa (Hill, 1983; Lugojja, 1996; Smit *et al.*, 1997). In Southern Ethiopia, however, it is the most serious pest of sweet potato. Frequent outbreaks have occurred during the last two decades.

The butterfly deposits eggs in clusters on sweet potato leaves. Larvae hatch within a week and young larvae form loose protective tents on leaves while feeding underneath. The first 2-3 instars form cohesive groups, whereas the older larvae disperse and feed solitarily. Pupation takes place on the plant or on the soil. One generation (egg to adult) takes about 34 days in laboratory under ambient conditions (temperature range: 21°C-28°C; relative humidity range: 38-50%) (Azerefegne, 1999). The insect has several generations per year (Hill, 1983; Smit *et al.*, 1997). Six generations in one year were observed in Southern Ethiopia (Azerefegne and Solbreck, 1999).

In most cases, the relationship between the extent of foliar damage on plants by pests and extent of yield loss is not linear. Plants produce far more leaves than needed, which enables them to tolerate some damage without showing significant yield reduction. Sparks *et al.* (1957) demonstrated that potato plants could tolerate relatively heavy defoliation at certain stages of growth without significant yield reduction, whereas moderate defoliation at other stages reduced yield considerably. Establishing the relationship between extent of damage and yield loss becomes more difficult when the plant part harvested is different from the part attacked, as in the case of sweet potato root yield. Sweet potato is a creeper, which produces a large number of leaves and continues to produce new leaves until harvest. There is mutual shading of leaves as the leaves form a dense layer near the soil surface. Hence, it is reasonable to expect that sweet potato is not sensitive to moderate levels of defoliation.
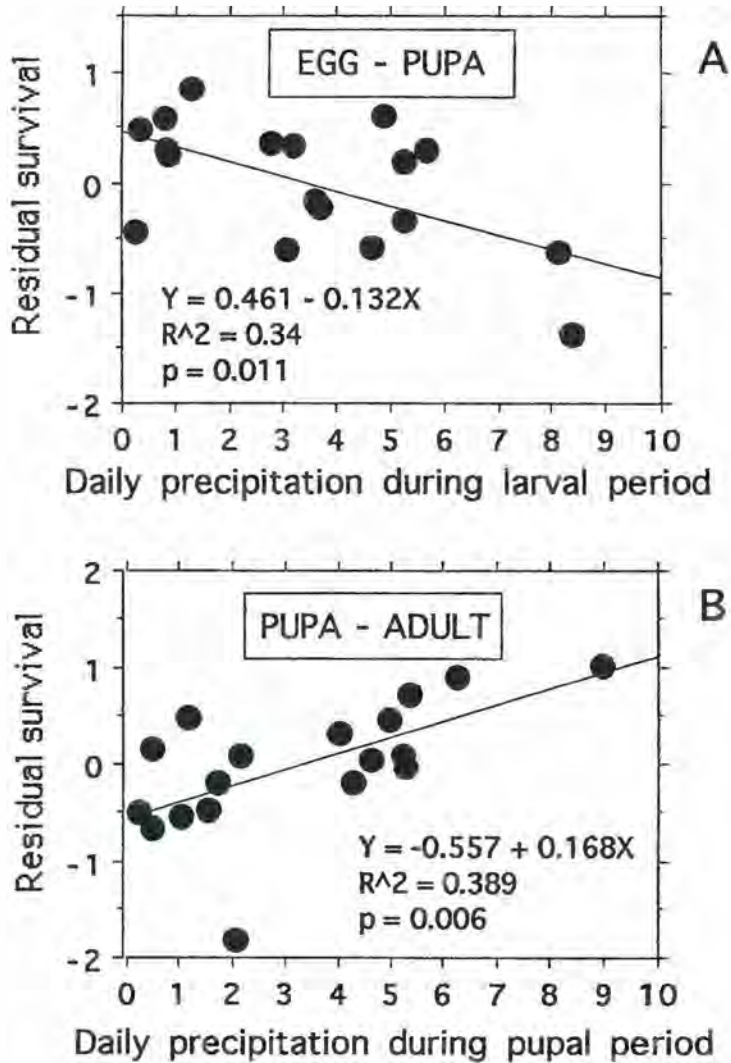
Figure 7. Correlations between average daily rainfall and residual variation in survival from (A) log pupal vs log egg densities (Fig. 4A) and (B) log adult vs log pupal density (Fig. 4B).
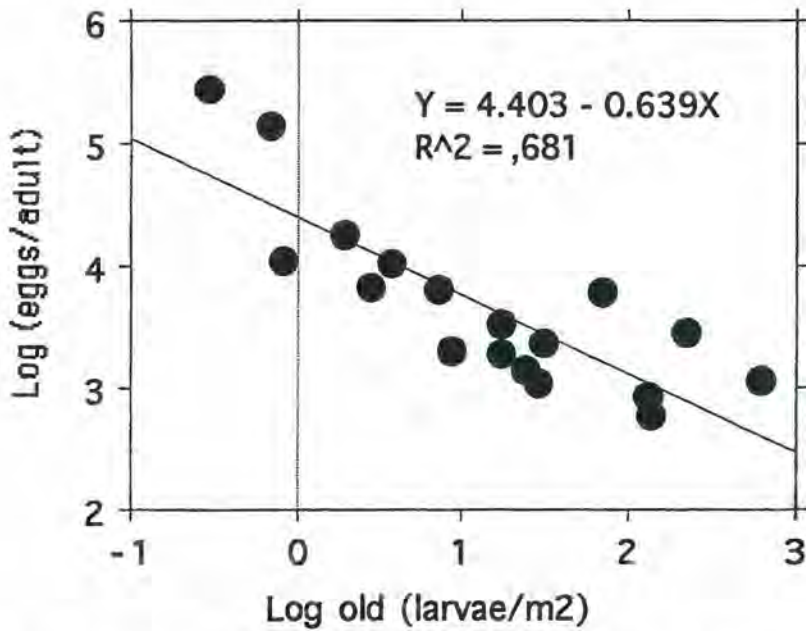
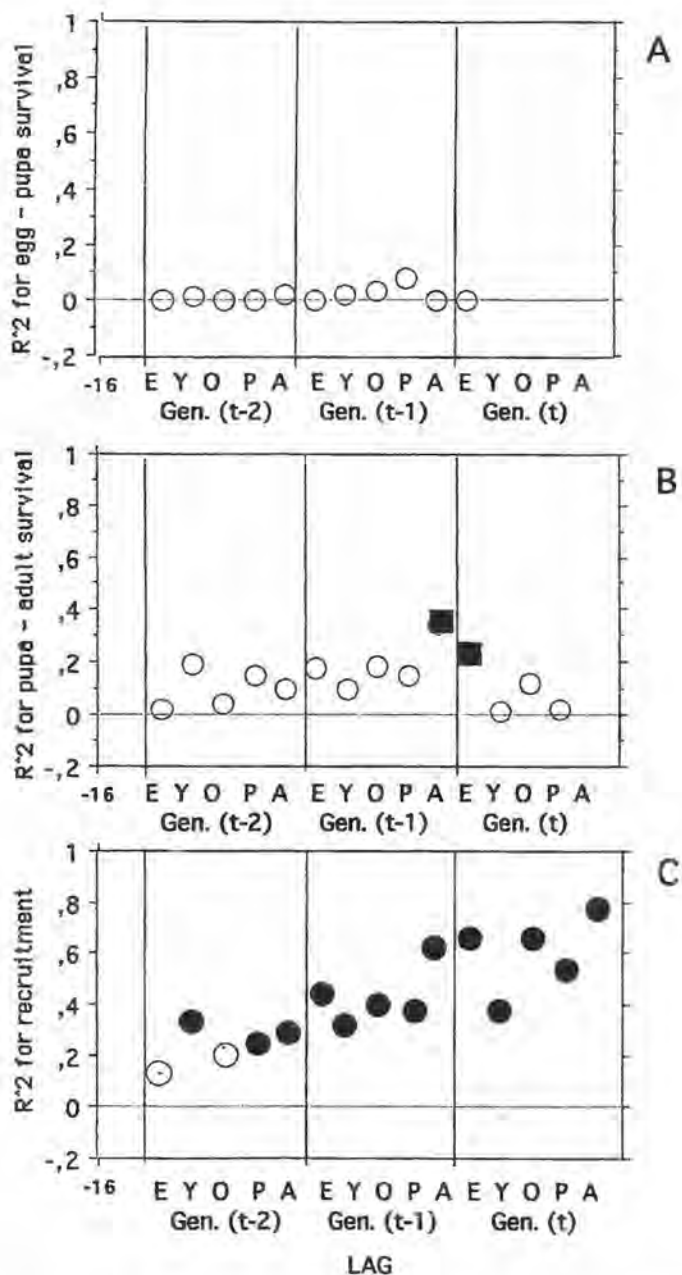Figure 6. Recruitment rate (eggs/adult) as a function of density of old larvae.

Figure 5. Coefficient of determination (R^2) from linear regressions between log population densities in five developmental stages (E=egg, Y=young larva, O=old larva, P=pupa, A=adult) in present (t) and previous generations (t-1 and t-2) and (A) log egg-pupal survival, (B) log pupal-adult survival and (C) log recruitment rate (eggs per adult). Significant (at $p<0.05$ level) positive correlations (slopes) are denoted by black squares and significant negative ones by filled circles.
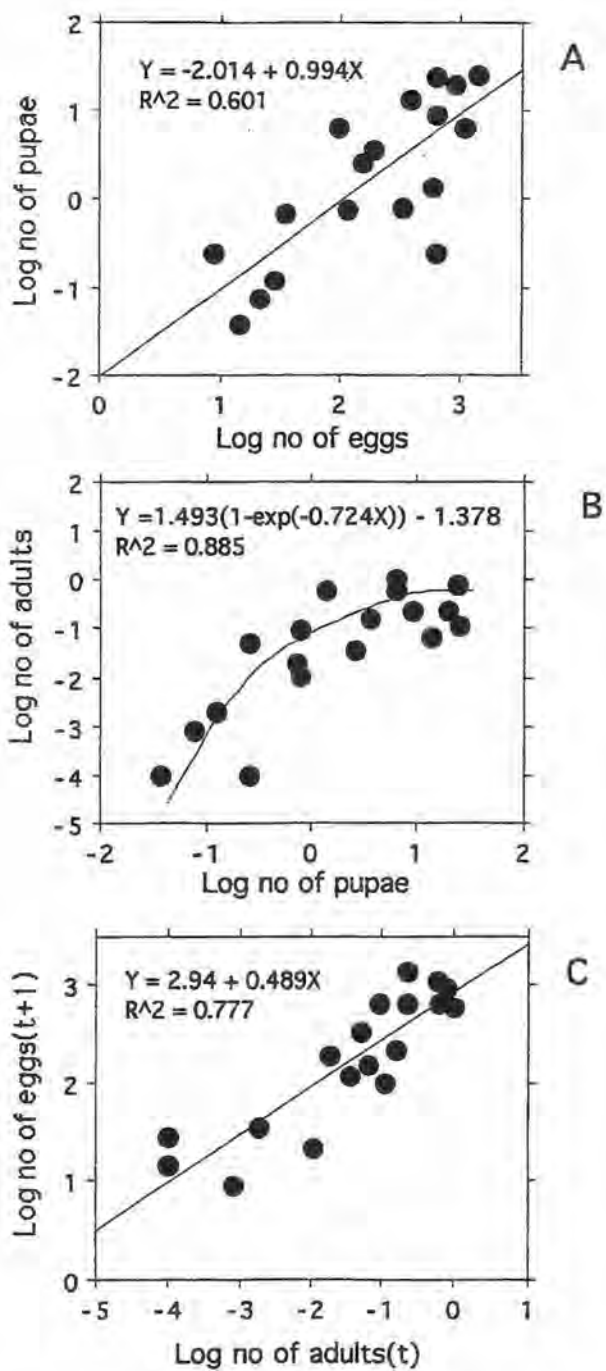
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Figure 4. Correlations between log densities in successive developmental stages (eggs, pupae, adults in generation (t) and eggs in generation (t+1)).
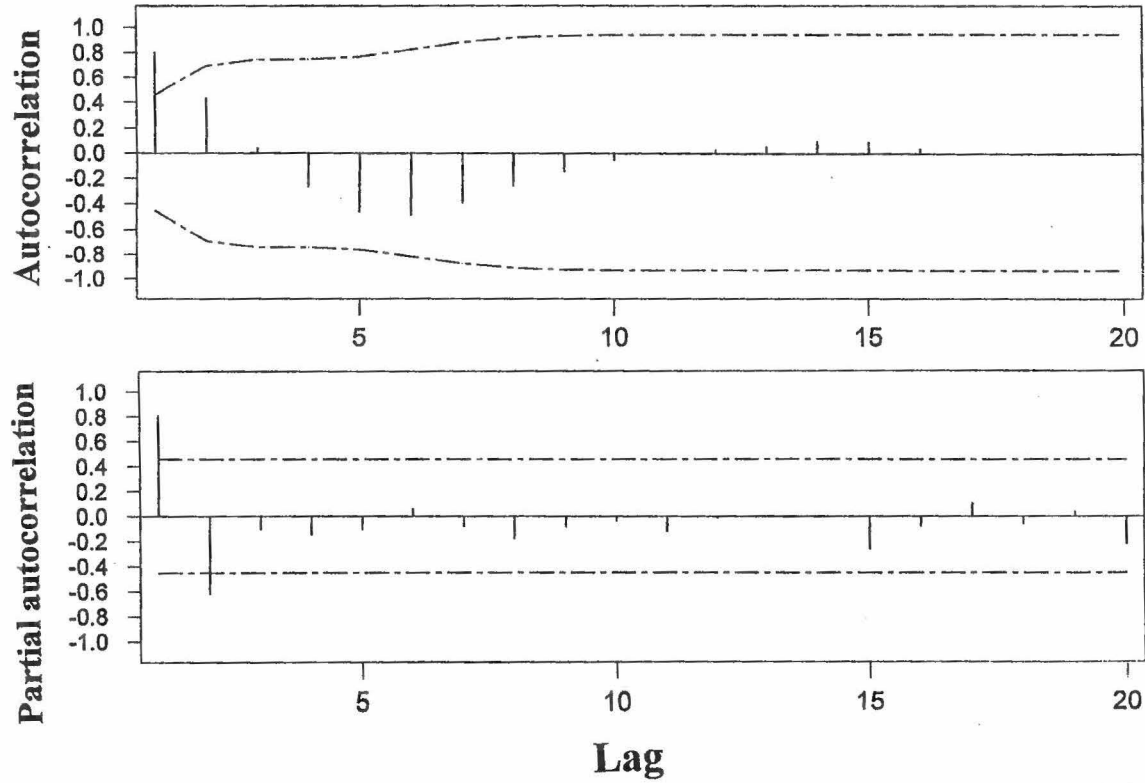
Figure 3. Autocorrelation (ACF) and partial autocorrelation (PACF) functions for generation totals of adult *A. acerata*. Dotted lines indicate approximate 95% confidence limits.
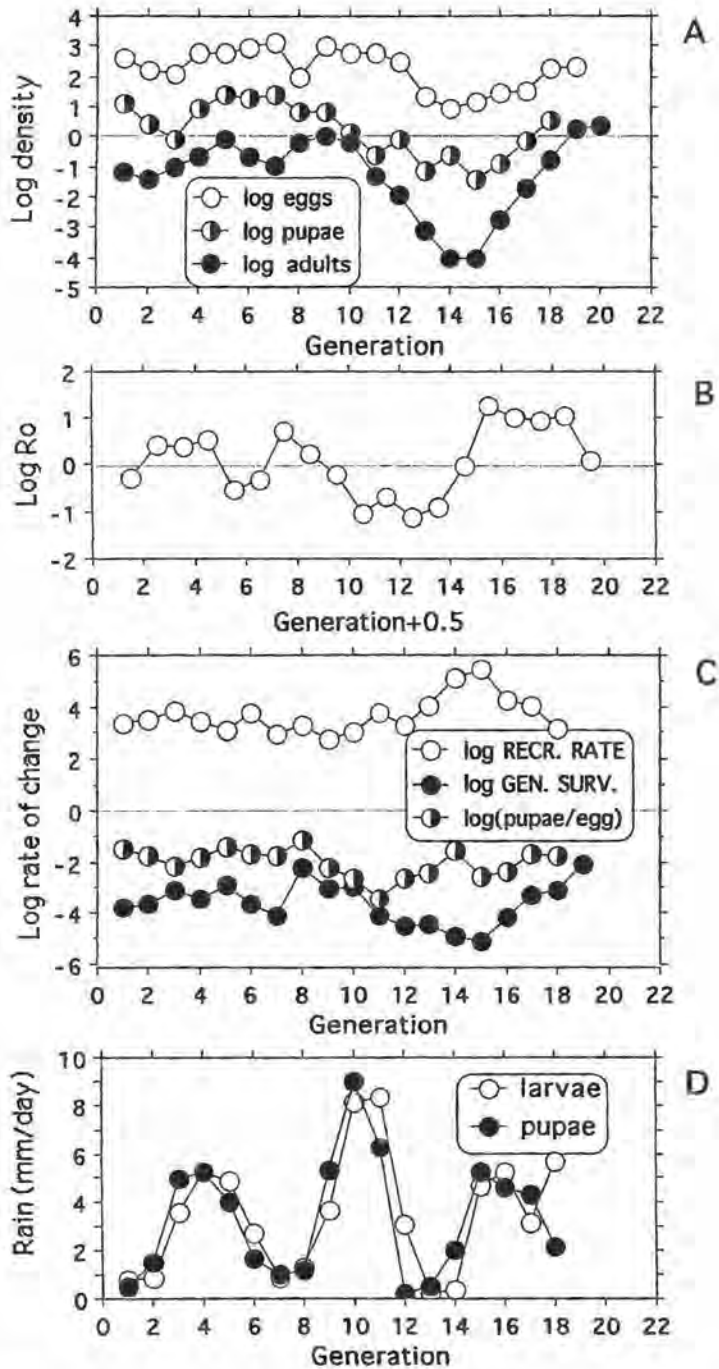
Figure 2. Generation totals of *A. acerata* A) egg, pupal and adult population densities, B) net reproductive rate Ro C) recruitment rate, generation survival and survival until pupal stage, and D) average daily rainfall during larval and pupal periods for each generation.
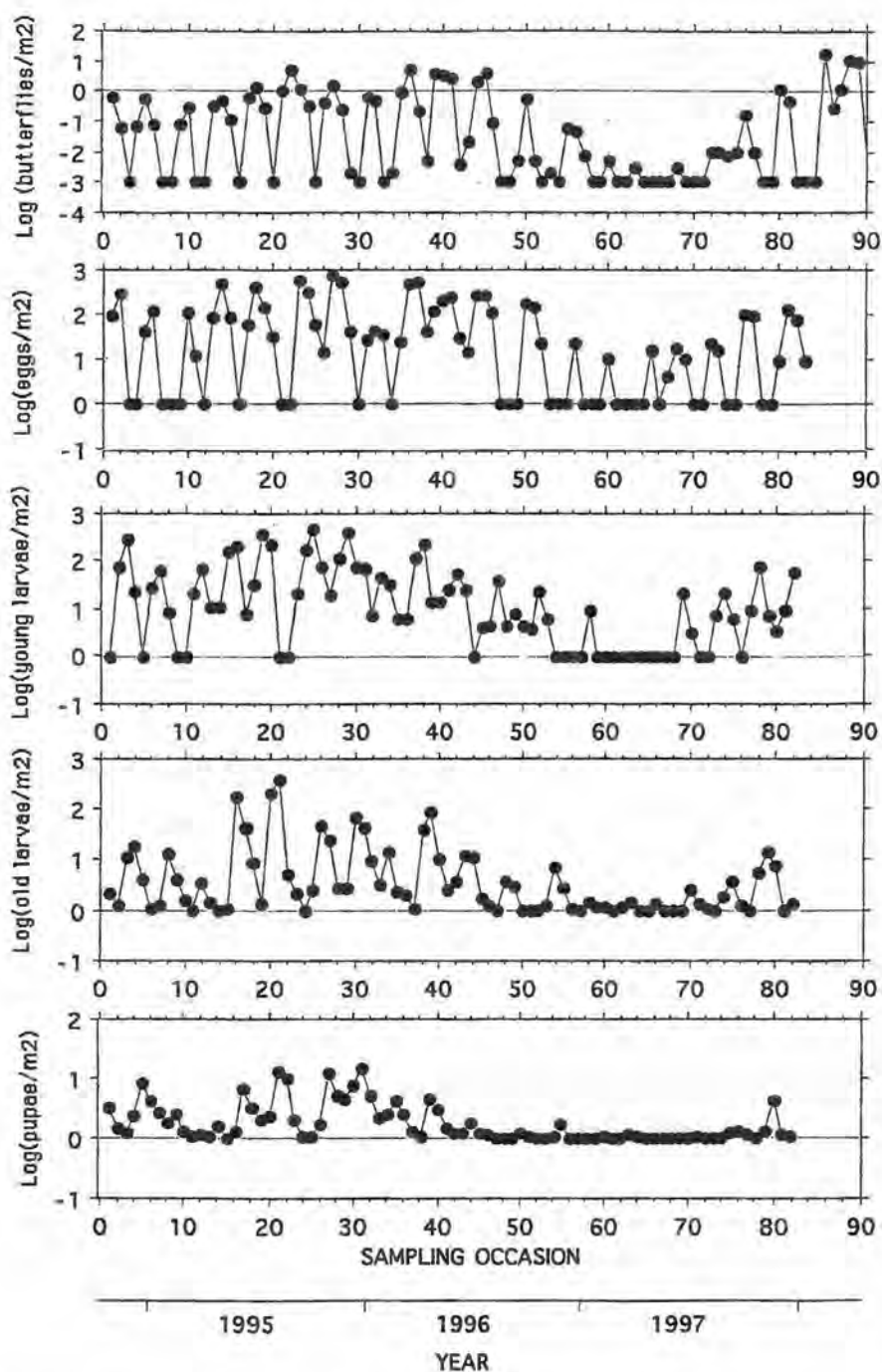
Figure 1. Population densities of *A. acerata* adults, eggs, young and old larvae and pupae at fifteen day intervals from Dec 1994 to January 1997 (April 1998 for adults).

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