HOST-PARASITOID INTERACTIONS OF *ELDANA SACCHARINA* (LEPIDOPTERA: PYRALIDAE) IN *CYPERUS PAPYRUS*

by

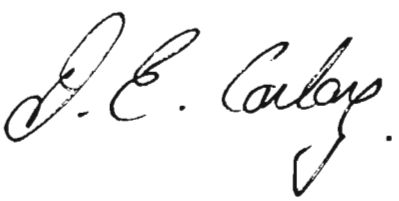
DESMOND EDWARD CONLONG

Submitted in partial fulfilment of the
requirements for the degree of
Doctor of Philosophy
in the Department of Zoology and Entomology
University of Natal
Pietermaritzburg
1994

PREFACE

This study was completed at the South African Sugar Association Experiment Station Entomology Department. The author was registered with the Department of Zoology and Entomology, University of Natal, Pietermaritzburg from February 1992 until December 1994. Professor Michael J. Samways supervised the work.

These studies represent original work by the author and have not been submitted in any form to another university. Where use was made of the work of others, it has been duly acknowledged in the text.



D. E. CONLONG

CONTENTS

FIGURES

TABLES

ACKNOWLEDGEMENTS

The enthusiastic and objective supervision of this work by Dr A.J.M. Carnegie, previously Head of the Entomology Department, South African Sugar Association Experiment Station (SASEX) and Prof. M.J. Samways led to the submission of the thesis.

The SASEX entomology field teams helped complete most of the field work needed, and the local Umfolosi Pest and Disease team, under the control of Julius de Lange, completed that not done by the SASEX teams. They are all thanked for their diligence and patience.

Mr E. Harrison, owner of the farm Palm Ridge on which the study site was situated, is warmly thanked for his co-operation and enthusiastic interest during and after the field work was completed.

SASEX provided interest free loans for registration of the project with the University of Natal for this degree, for which I am grateful.

My family are especially thanked for their patience while this study was completed. Their understanding is greatly appreciated.

ABSTRACT

Since becoming a pest in graminaceous crops in Africa, the African sugarcane stalkborer Eldana saccharina Walker has been the subject of much study. Its very cryptic habits have precluded more commonly available control measures being used against it. Biological control is regarded as a viable control option, but the apparent paucity of parasitoids in graminaceous crops leads to E. saccharina being regarded as lacking parasitoids, and thus not a good candidate for biological control in the classical sense. In contrast, this project argues that interactions in indigenous hosts of E. saccharina had been ignored, and that classical biocontrol principles and basic ecological theory could be applied by the discovery, collection and introduction of parasitoids from its indigenous habitat to its newly adapted habitat, sugarcane.

The habitat offered by Cyperus papyrus L. was shown to be heterogenous both temporarily and spatially. Umbels, from young through mature to senescent, were available in the same proportion for colonisation throughout the year. Umbels with sexual reproductive stages (seeds) were present from early spring into late summer, and provided an additional component to the already heterogenous environment. Young umbels, in addition, developed from rhizomes in an environment regarded as sub-optimal for photosynthesis, until they reached the canopy.

All stages of umbels were attacked by E. saccharina, but larvae were only found in rays of umbels and in the apex of the culm, which was the meristematic area for rays, both high nutrient areas. Young umbels were never found with borer pupae, only smaller larvae, indicating that E. saccharina development matched growth of young umbels until they reached canopy height. Also, the majority of borings found were occupied, indicating that infestation of young umbels was recent. All stages of E. saccharina development were found in mature umbels, which were also most abundant at any one time. Numerous empty borings were found in addition to those occupied, indicative of past occupation by E.

saccharina. Very few young larvae were found in old umbels, the majority of life stages found being pupae or empty pupal cases, and also many empty borings, showing that old umbels were not suitable for E. saccharina development.

A guild of parasitoids which comprised Orgilus bifasciatus Turner, the most common parasitoid of small and smaller medium E. saccharina larvae, Goniozus indicus Ashmead the most common parasitoid of larger medium and large larvae, and an entomogenous fungus Beauveria bassiana (Bals.) Vuill. attacking all life stages of E. saccharina was found. Three uncommon parasitoids of smaller E. saccharina were also found, viz. Bassus sublevis (Granger), Iphiaulax sp. and Venturia sp. The former three natural enemies were instrumental in depressing a major outbreak within two months of it being observed and then maintaining the host population at a lower level in C. papyrus. G. indicus and B. bassiana were most effective during the summer and autumn months, and O. bifasciatus most effective during the winter months.

This study supports the hypotheses that the apparent paucity of parasitoids and lack of biological control success thus far against E. saccharina in sugarcane has been because very little was known about its ecology and biology in its numerous indigenous host plants, and that studies of the latter factors coupled with ecological theory could enhance biological control programmes against this borer. As more indigenous host plants are investigated in the same way as has been done with C. papyrus, more will become known of natural enemies of E. saccharina. Parasitoid guilds could be selected, even from rare parasitoids in the more stable indigenous habitats, which would provide control in the unstable habitat of sugarcane.

CHAPTER 1

GENERAL INTRODUCTION

1.1 ELDANA SACCHARINA AS A SUGARCANE PEST IN AFRICA

The African sugarcane stalkborer, Eldana saccharina Walker (Lepidoptera: Pyralidae), is indigenous to Africa where it occurs in numerous wetland sedges (Girling, 1972; Atkinson, 1979, 1980). It has been a pest of graminaceous crops on this continent for over 100 years, as it was first described in 1865 from sugarcane in Sierra Leone (Walker, 1865). Since then it has spread through west to east Africa, and southwards down the east coast to the southern Natal and Transkei coasts (Girling, 1972, 1978; Atkinson, 1980; Atkinson et al., 1981; Conlong, 1986; Leslie, 1986). The northern range could be extended past Girlings (1972) 15°N, as I have recently received correspondence from Egypt (Sayed Abd Elurahab Morad, pers. comm., 1990) where this insect is now being studied.

Eldana saccharina has been a major pest of sugarcane in South Africa (Carnegie, 1974), and of sugarcane, maize (Kaufmann, 1983; Bosque-Perez and Mareck, 1991) and to a lesser extent sorghum (Waiyaki, 1968; Girling, 1972) in East and West Africa.

Only since 1965 has intensive entomological research on the pest been developed (Betbeder - Matibet, 1981), despite a paper reporting its basic biology following an outbreak in southern African sugarcane by Dick (1945). Girling (1972, 1978) published the first comprehensive results of research in Ugandan sugarcane. This was followed by Waiyaki (1974(a)) in Tanzania and Carnegie (1974) in South Africa. In 1977, work on E. saccharina in the sugarcane growing areas of the Ivory Coast, Mali and Upper Volta in West Africa was commenced (Cochereau, 1980; Betbeder - Matibet, 1981). Scheibelreiter (1980) was commissioned to investigate, from 1970 to 1978, several sugarcane stem

borers and their distribution in cane at Asutsuare and Komenda in Ghana. This study included an analysis of their economic importance and natural enemies. E. saccharina was the fourth most common of the six lepidopteran stalk borers found. Sampson and Kumar (1983, 1985) then followed with their work on E. saccharina in sugarcane in southern Ghana.

In terms of papers published, the insect has been most studied in southern African sugarcane. Since 1973, the distribution, behaviour and biology of E. saccharina in sugarcane has been described by Carnegie (1974), Atkinson (1980, 1982), Atkinson and Carnegie (1989), Atkinson and Nuss (1989) and Leslie (1990). Its incidence and spread are described by Carnegie et al. (1976), Carnegie (1977), Smaill (1978), Carnegie and Smaill (1980), Atkinson et al. (1981), Paxton (1982) and Carnegie and Leslie (1990).

Crop loss caused by E. saccharina in South African cane has been estimated as 0,1% yield loss with every 1% of stalks damaged (Smaill and Carnegie, 1979), and in Swaziland cane as a 1% loss of recoverable sugar for every 1% of internodes bored (King, 1989). Waiyaki (1968) quotes crop loss figures for Tanzanian cane as 3,5% sugar loss in 100 joints bored from one author, and 0,35% sugar loss in 15% joints bored by another. His own estimate is a decrease in brix of 0,332% for each 1% increase in joints bored (Waiyaki, 1974(b)). In the Ivory Coast, Cochereau (1982) estimated a 0,5% loss in weight of sugar for each 1% of nodes bored. Crop loss estimates of E. saccharina in sugarcane are not consistent. Cane variety, growing conditions and climate all affect cane yield, making quantifiable crop losses difficult to determine.

The progress in its control in South Africa has been reviewed by Carnegie (1981, 1982). Aspects of chemical control have been reported by Heathcote (1984), and cultural control by Carnegie and Smaill (1982), Paxton (1983), Atkinson (1984) and McCulloch (1989). Sugarcane resistance studies have been done by Nuss and Atkinson (1983), Nuss et al. (1986), Bond (1988) and Nuss (1991).

Biological control has received much attention. Originally efforts concerned arthropod predators in sugarcane fields (Leslie, 1977, 1981, 1982, 1986, 1988; Leslie and Boreham, 1981), but subsequently, more emphasis was placed on insect parasitoids (Carnegie and Leslie, 1979; Conlong and Hastings, 1984; Conlong et al., 1984, Carnegie et al., 1985; Graham and Conlong, 1988; Conlong et al., 1988, Conlong, 1990). Most recently, pathogens have also been investigated as potential biocontrol agents. These include nematodes (Spaull, 1988, 1990), entomogenous micro-organisms (Jacobs, 1989) and genetically engineered bacteria (Herrera and Thompson, 1989).

The need for biological control of pyralid borers in Africa was recognised twenty two years ago by Mohyuddin and Greathead (1970). This conclusion was based on the cryptic behaviour of pyralid borers such as E. saccharina and the unsatisfactory performance of pesticides tested against them. Unfortunately, these authors and those cited by them, confined their searches for natural enemies to graminaceous crops where the insect was a pest, with very little time spent on the natural host plants of E. saccharina. The continued emphasis on searching graminaceous crops for parasitoids continued in West Africa (Nagarkatti and Rao, 1975; Girling, 1980; Scheibelreiter, 1980; Cochereau, 1980, 1982; Betbeder-Matibet, 1981). Further, in all these studies involving parasitoids of E. saccharina, none followed the significantly important seasonal changes in the insect's biology relative to the crop. They were all inventory type surveys done over short periods of time.

1.2 ELDANA SACCHARINA IN ITS NATURAL HABITAT IN AFRICA

The above approaches are contrary to the advice of biocontrol authorities such as De Bach (1964), Huffaker (1971), and van den Bosch et al. (1982), who advocate searching the "home (or natural host) range" of the pest for natural enemies. Girling (1978) reviewing all available records (dating from 1900), found that E. saccharina occurred in wild plants in all habitable areas south of the Sahara. Only in the latter half of the 1960's was it noticed as an increasingly

important pest of graminaceous crops. Atkinson (1980) records it as an insect primarily of the sedges (Cyperaceae). In his review of the host plants of E. saccharina in Africa and especially South Africa, he recorded only eight crop plants among the 29 plants listed. Of the remainder, 15 were sedges and the rest wild grasses. Eldana saccharina appears only recently to have extended its host range into graminaceous crops, especially in East and southern Africa. Its natural host range was initially indigenous sedges and wild grasses.

This observation is not surprising. Pemberton and Williams (1969), in their review of the distribution, origin and spread of sugarcane pests, found that of the approximately 1300 insect species found feeding on sugarcane worldwide, in any one country on a continent, 75% of the species are indigenous. It is thus only on islands, where local faunas have produced few pests (Pemberton and Williams, 1969), that classical biological control principles as described by van den Bosch et al. (1982) can be applied. This is because insect sugarcane pests on islands are exotic to the islands, and the island's limited indigenous insect species do not adapt readily to crop plants (Pemberton and Williams, 1969). Examples include Mauritius and Hawaii, where 84% of the insects feeding on sugarcane are alien.

In contrast, by 1950 southern African sugarcane had at least thirty three indigenous species feeding on it (Dick, 1950). Subsequent to Dick's paper, Leslie (1986) added two additional pests, Numicia viridis Muir (Homoptera: Tropiduchidae) and an unidentified species of Margarodes sp. (Homoptera: Margarodidae). Perkinsiella saccharicida Kirkaldy (Homoptera: Delphacidae) is the only exotic pest recorded (A.J.M Carnegie, 1991, pers. comm.)

1.3 KNOWN INSECT COMMUNITIES IN THE NATURAL AND ADOPTED HABITATS OF ELDANA SACCHARINA

The importance of knowing of an insect's ecology in its natural habitat, especially its interaction with natural enemies in this habitat, is stressed by

Waage and Hassell (1982) and Cock (1986). Such information can be used to predict the best agents available or used retrospectively to explain successes or failures in biological control programmes. Furthermore, Waage and Hassell (1982) stress that fundamental research and theory are of enormous value in identifying what kind of information is necessary for the evaluation of biological control. Theory and practice stand to benefit from detailed studies of pest and parasitoid before, during and after introduction.

Despite these suggestions, the only seasonal study of E. saccharina in its natural habitat has been completed by Leslie (1986). He investigated its arthropod predators in the sedge Cyperus immensus C.B.Cl. and in mature sugarcane fields in Natal.

The present study has concentrated on the pest-parasitoid interactions of E. saccharina in another sedge recorded as an indigenous host, Cyperus papyrus L. In many thousands of sugarcane stalks searched, no parasitoids of consequence have been found. Conversely, in C. papyrus, these recent investigations have revealed a complex of seven parasitoids attacking the larval instars of E. saccharina (Conlong et al., 1988). This complex of natural enemies exert varying levels of control of E. saccharina in C. papyrus during different seasons (Conlong, 1990). These two facts are further evidence that original hosts for E. saccharina are indigenous.

1.4 BIOLOGICAL CONTROL OF ELDANA SACCHARINA

Classical biological control involves the control of species which are not indigenous to the area where they have become regarded as a pest. Their pest status comes from their ability to escape their natural population controlling factors in this new area. If these controlling factors can be identified in its area of origin, they can be introduced into the area where their host is a pest, and in this way control it (De Bach, 1964; van den Bosch et al., 1982).

Because E. saccharina is a pest in its country of origin, it has been regarded as being an unsuitable candidate for classical biological control. However, its cryptic biology and behaviour in crops has reduced the effectiveness of the more conventional chemical control measures (Girling, 1972; Moyhuddin and Greathead, 1970; Heathcote, 1984). This had led to biological control remaining an option, not only further north in Africa, but also in southern Africa.

Eldana saccharina has always been an insect of African wetland sedges and large grasses (the habitat of origin). The recent invasions of graminaceous crops represents the new habitat. Earlier biocontrol work investigated the new habitat of graminaceous crops for control agents, when they should have been searching the habitat of origin. The original habitat may conceivably be home to new agents not yet discovered.

1.5 A BIOLOGICAL CONTROL APPROACH AGAINST ELDANA SACCHARINA IN SOUTHERN AFRICAN SUGARCANE

Since 1981, the emphasis placed on the biological control of E. saccharina by the South African Sugar Association Experiment Station (SASEX) has been considerable (Carnegie, 1987). Two approaches have been followed (Conlong and Hastings, 1984). The one, which is quite separate from the classical approach, is to import likely parasitoids of similar borers in other parts of the world. If these accept E. saccharina as a host in the laboratory, then they are mass reared for release into selected sugarcane fields and their performance assessed. This approach of controlling an indigenous pest with introduced natural enemies, is regarded as a possible option by Carl (1982), Ehler (1990) and Waage (1990), who cite examples of it working in a variety of crops, including sugarcane, on numerous pest species. The most successful of these have involved candidate enemies from congeneric host species from other geographic areas (Ehler, 1990). However, there is much debate on these introduction strategies. Both Waage (1990) and Ehler (1990) review the arguments. The second approach is more broad based and any suitable natural

enemies which are available are released into the field, with the hope that at least one effective species will establish on the host (Ehler, 1990). Table 1 lists the exotic parasitoid species (i.e. those never before recovered from E. saccharina) that have been tested against E. saccharina by SASEX using this approach, which has not yet yielded results.

Table 1. Exotic parasitoids tested against Eldana saccharina in South Africa.

EGG PARASITOIDS			
Parasitoid	**Natural Host**	**Host Plant**	**Source**
HYMENOPTERA			
Trichogrammatidae. Trichogramma pretiosum Riley	Heliothis sp. (Noctuidae)	Cotton	USA, 1971
T. braziliensis Ashmead	H. zea (Boddie), Diatraea sp. (Pyralidae)	Cotton Sugarcane	Colombia, 1980.
T. semifumatum Perkins	Diatraea sp.	Sugarcane	Colombia; 1980.
T. perkinsi Girault	Diatraea sp.	Sugarcane	Colombia; 1980.
T. australicum Girault (= T. chilonis Ishii)	Argyroploce schistaceana Snellen	Sugarcane	Colombia, Taiwan; 1980, 1983, 1986, 1987.
T. evanescens Westwood	Ostrinia nubilalis (Hubner)	Maize	Germany, Switzerland; 1984.
Trichogrammatoidea armigera	H. armigera (Hubner)	Cotton	India; 1978.
T. cryptophlebia Girault	Cryptophlebia leucotreta Meyr. (Olethreutidae)	Citrus	Zebediela, SA; 1990.

Scelionidae Telenomus sp.	Diatraea sp.	Sugarcane	Bolivia; 1984, 1986.
LARVAL PARASITOIDS			
DIPTERA (Tachinidae)			
Sturmiopsis inferens Tns.	Chilo infuscatellus Sn. (Pyralidae)	Sugarcane	India; 1977.
Paratheresia claripalpis Wulp.	Diatraea sp.	Sugarcane	Brazil, Colombia, West Indies; 1978, 1985, 1986, 1987, 1991.
Metagonisty-lum minense Tns.	Diatraea sp.	Sugarcane	Brazil, Colombia, West Indies; 1978, 1985, 1986, 1987.
Palpozenilla diatraeae Tns.	Diatraea rufescens Box	Sugarcane	Bolivia; 1984, 1986.
Lixophaga diatraeae Tns.	Diatraea saccharalis (F.)	Sugarcane	Trinidad; 1987.
Lydella sp.	Eoreuma loftini (Dyar) (Pyralidae)	Maize	USA; 1991.
HYMENOPTERA			
Braconidae Cotesia (=Apanteles) flavipes Cameron	Diatraea sp., Chilo partellus Swinhoe. (Pyralidae)	Sugarcane, Maize	Brazil, Pakistan, USA; 1978, 1983, 1985, 1991.
Allorhogas pyralophagus Marsh	E. loftini, Diatraea sp.	Sorghum halepense (L.) Pers., sugarcane, maize	Trinidad, USA; 1984, 1985.
Rhaconotus roslinensis Lal.	Chilo sp., Bissetia steniella (Hampson)	Sorghum, sugarcane	USA; 1985, Originally Pakistan.

Macrocentrus prolificus Wharton	Diatraea sp., E. loftini	Sugarcane	USA; 1985.
Iphiaulax (=Digonogastra) kimballi Kirkland	Diatraea sp., E. loftini	Sugarcane, maize, sorghum	USA; 1985.
Ichneumonidae Mallochia pyralidis Wharton	E. loftini	Sorghum, sugarcane	USA; 1985.
PUPAL PARASITOIDS			
HYMENOPTERA			
Ichneumonidae Xanthopimpla stemmator Thunb.	Chilo sacchariphagus (Bojer) (Pyralidae)	Sugarcane	Mauritius; 1984, 1988.
Eulophidae Tetrastichus howardi	C. suppressalis (Walker)	Rice	Philippines; 1988.

The classical approach has also been followed, but to a lesser degree. Table 2 lists the parasitoid species which have been collected from and tested against E. saccharina in sugarcane in South Africa.

Host identification of many of the parasitoids imported from other African countries have in some cases been questionable. With the larval parasitoids in particular, the host could easily have been Sesamia calamistis Hamps. (Lepidoptera: Noctuidae) rather than E. saccharina, and which is also a common stalk borer in sugarcane and maize. This may be why Descampsina sesamiae Mesnil (Diptera: Tachinidae) was not successful against E. saccharina, from which it was apparently reared in Ghana and Nigeria. Further investigations revealed that D. sesamiae larvae were encapsulated by E. saccharina larvae.

Table 2: Reported indigenous parasitoids of Eldana saccharina imported from other African countries and those from indigenous host plants in southern Africa tested against E. saccharina in South African sugarcane.

EGG PARASITOIDS		
Parasitoid	**Source**	**Host Plant**
HYMENOPTERA		
Trichogrammatidae Trichogramma sp.	Ivory Coast, 1980	Maize
Trichogrammatoidea eldanae Viggiani	Ivory Coast, 1980, 1981, 1984	Maize
Scelionidae Telenomus applanatus Bin and Johnson	Ivory Coast, 1980, 1981, 1982.	Maize
LARVAL PARASITOIDS		
DIPTERA (Tachinidae)		
Descampsina sesamiae Mesnil	Ghana, Nigeria; 1975, 1981, 1983, 1984.	Maize, sugarcane
Schembria eldana Barraclough	Natal South Africa; 1982-1985	Cyperus papyrus umbels
HYMENOPTERA		
Bethylidae Goniozus indicus Ashmead (= G. natalensis Gordh)	Natal South Africa, Malawi, Botswana; 1981-	C. papyrus and C. dives umbels
Braconidae Orgilus bifasciatus Turner	Natal South Africa; 1981-	C. papyrus and C. dives umbels and sugarcane
Bassus sublevis (Granger) (=Agathis sp.)	Natal South Africa; 1981-	C. papyrus, C. dives, C. fastigiatus and sugarcane
Ichneumonidae Venturia sp. (=Chriodes sp.)	Natal South Africa; 1986-	C. papyrus, C. dives and sugarcane

Iphiaulax sp.	Natal South Africa; 1981-	C. papyrus, C. dives and sugarcane

More convincing evidence that the "classical" approach could work has come from indigenous host plant surveys completed in South Africa. Four of the six larval parasitoids found in wetland sedges on E. saccharina, viz. Orgilus bifasciatus, Bassus sublevis, Venturia sp. and Iphiaulax sp. (Table 2), have more recently being found on this host in sugarcane (Anon., 1992). These recoveries were made without purposeful introductions of these parasitoids into sugarcane.

The discovery of and development of rearing techniques for Goniozus indicus (Conlong et al., 1988), also from wetland sedges (Table 2), led to its initial establishment at two sites in sugarcane in Natal (Anon., 1987). The development of efficient mass rearing techniques followed (Graham and Conlong, 1988). Subsequently, in each succeeding annual SASEX Progress Report, its establishment in different sugarcane fields was recorded. Establishment, however, occurred only where the current crop was standing, and the apparent spread of this parasitoid was restricted to adjacent fields. When the current crop was harvested, the parasitoid population was destroyed. This has retarded the parasitoids large-scale geographical establishment.

Recent surveys of former sugarcane release sites have resulted in the recovery of E. saccharina parasitised by G. indicus. In the first case, releases had stopped 12 months previously, and cane was harvested once in that period (Conlong, 1991). The most recent recovery was from a field which had the last release of G. indicus in November 1989, thirty one months previously. During that period, cane in that field was harvested three times.

However, it took at least a hundred generations for Lixophaga diatraeae Tns.(Diptera: Tachinidae) to change its status from an incidental parasitoid to an important controlling factor of the Barbadian sugarcane stalk borer Diatraea saccharalis Fabricius (Lepidoptera: Pyralidae) (Carl, 1982). This situation, despite

the isolated recoveries so far, may be applicable to the G. indicus - E. saccharina association in sugarcane. The time interval for the latter association may however be longer, because G. indicus has biological characteristics of a K-strategist (Conlong, et al., 1988), while L. diatraeae is biologically closer to an r-strategist.

The arguments presented show that a biocontrol approach against E. saccharina, based on slightly modified classical principles, is feasible. Also, investigations of E. saccharina - parasitoid interactions in indigenous host plants such as C. papyrus, will provide solutions to its biological control in sugarcane.

REFERENCES

Anonymous, 1987. Entomology Department Progress Report 1986/1987 (Unpublished). South African Sugar Association Experiment Station, Private Bag X02, Mt Edgecombe, Natal. 4300.

Anonymous, 1992. Entomology Department Progress Report 1991/1992 (Unpublished). South African Sugar Association Experiment Station, Private Bag X02, Mt Edgecombe, Natal. 4300.

Atkinson, P.R., 1979. Distribution and natural hosts of Eldana saccharina Walker in Natal, its oviposition sites and feeding patterns. Proceedings of the South African Sugar Technologists Association 53: 111 -115.

Atkinson, P.R., 1980. On the biology, distribution and natural host-plants of Eldana saccharina Walker (Lepidoptera: Pyralidae). Journal of the entomological Society of southern Africa 43: 171-194.

Atkinson, P.R., 1982. Phenology of Eldana saccharina Walker in Natal and the use of light traps to monitor the distribution and abundance of the insect. Proceedings of the South African Sugar Technologists Association 56: 90 - 94.

Atkinson, P.R., 1984. Seasonal cycles of Eldana Borer in relation to available control measures. Proceedings of the South African Sugar Technologists Association 58: 165 - 167.

Atkinson, P.R. and Carnegie, A.J.M., 1989. Population dynamics of the sugarcane borer, Eldana saccharina Walker (Lepidoptera: Pyralidae), in Natal, South Africa. Bulletin of entomological Research 79: 61 - 80.

Atkinson, P.R. and Nuss, K.J., 1989. Associations between host-plant nitrogen and infestations of the sugarcane borer, Eldana saccharina Walker (Lepidoptera: Pyralidae). Bulletin of entomological Research 79: 489 - 506.

Atkinson, P.R., Carnegie, A.J.M. and Smaill, R.J., 1981. A history of the outbreaks of Eldana saccharina Walker in Natal. Proceedings of the South African Sugar Technologists Association 55: 111 - 115.

Betbeder - Matibet, M., 1981. Eldana saccharina Walker. Borer of the stalks of sugarcane in Africa. L'Agronomie Tropicale 36: 279 - 293.

Bond, R.S., 1988. Progress in selecting for Eldana resistance. Proceedings of the South African Sugar Technologists Association 62: 129 - 133.

Bosque-Perez, N.A. and Mareck, J.H., 1991. Effect of the stem borer Eldana saccharina (Lepidoptera: Pyralidae) on the yield of maize. Bulletin of entomological Research 81: 243 - 247.

Carl, K.P., 1982. Biological control of native pests by introduced natural enemies. Biocontrol News and Information 3: 191 - 200.

Carnegie, A.J.M., 1974. A recrudescence of the borer Eldana saccharina Walker (Lepidoptera: Pyralididae). Proceedings of the South African Sugar Technologists Association 48: 107 - 110.

Carnegie, A.J.M., 1975. Report on a visit to Ghana, West Africa, 14 - 24 June, 1975. Internal Report 21/75 (Unpublished). SA Sugar Association Experiment Station, 14 July, 1975.

Carnegie, A.J.M., 1977. Current situation regarding the borer Eldana saccharina Walker (Lepidoptera: Pyralididae). Proceedings of the South African Sugar Technologists Association 51: 24 - 26.

Carnegie, A.J.M., 1981. Combating Eldana saccharina Walker: a progress report. Proceedings of the South African Sugar Technologists Association 55: 116 - 119.

Carnegie, A.J.M., 1982. Current research programme against Eldana saccharina Walker (Lepidoptera: Pyralidae). Proceedings of the South African Sugar Technologists Association 56: 95 -98.

Carnegie, A.J.M., 1987. A biological control programme for the Eldana borer. Sugarcane Spring 1987 Supplement: 4 - 6.

Carnegie, A.J.M. and Leslie, G.W., 1979. Attempts at the biological control of Eldana saccharina Walker (Lepidoptera: Pyralididae). Proceedings of the South African Sugar Technologists Association 53: 116 - 119.

Carnegie, A.J.M. and Smaill, R.J., 1980. The incidence of moth borers in South African sugarcane during the 1979/80 season. Proceedings of the South African Sugar Technologists Association 54: 154 -157.

Carnegie, A.J.M. and Smaill, R.J., 1982. Pre-trashing of sugarcane as a means of combating the borer Eldana saccharina Walker. Proceedings of the South African Sugar Technologists Association 56: 78 -81.

Carnegie, A.J.M. and Leslie, G.W., 1990. Eldana saccharina (Lepidoptera:

Pyralidae): Ten years of light trapping. Proceedings of the South African Sugar Technologists Association 64: 107 -110.

Carnegie, A.J.M., Leslie, G.W. and Lindley, M.E.O., 1976. Incidence and spread of the borer Eldana saccharina Walker (Lepidoptera: Pyralididae). Proceedings of the South African Sugar Technologists Association 50: 34 - 39.

Carnegie, A.J.M., Conlong, D.E. and Graham, D.Y., 1985. Recent introductions of parasitoids against Eldana saccharina Walker (Lepidoptera: Pyralidae). Proceedings of the South African Sugar Technologists Association 59: 160 - 163.

Cochereau, P., 1980. The sugar cane African borer Eldana saccharina Walker (Lepidoptera, Pyralidae, Gelenchiinae): studies on populations and parasites. Entomology Newsletter 8: 6 - 7.

Cochereau, P., 1982. Observations on the borer Eldana saccharina Walker (Lep.: Pyralidae) in maize and sugarcane in Ivory Coast. Proceedings of the South African Sugar Technologists Association 56: 82 - 84.

Cock, M.J.W., 1986. Requirements for biological control: An ecological perspective. Biocontrol News and Information 7: 7 - 16.

Conlong, D.E., 1986. Search for Eldana saccharina and its parasitoids in sugarcane and natural hosts at the East Pondoland Sugar Project, Transkei (23 - 26/6/86). Internal Report 8.1.45 (267) (Unpublished), 25 July 1986. South African Sugar Association Experiment Station, Private Bag X02, Mt Edgecombe, Natal. 4300.

Conlong, D.E., 1990. A study of pest - parasitoid relationships in natural habitats: an aid towards the biological control of Eldana saccharina (Lepidoptera: Pyralidae). Proceedings of the South African Sugar Technologists Association

64: 111 - 115.

Conlong, D.E., 1991. Monitoring of Previous Parasitoid Release Fields. SASA Experiment Station, Internal Report 8.1.45 (6) (Unpublished). South African Sugar Association Experiment Station, Private Bag X02, Mt Edgecombe, Natal. 4300. 4pp.

Conlong, D.E. and Hastings, H., 1984. Evaluation of egg parasitoids in the biological control of Eldana saccharina Walker (Lepidoptera: Pyralidae). Proceedings of the South African Sugar Technologists Association 58: 168 - 172.

Conlong, D.E., Graham, D.Y. and Hastings, H., 1988. Notes on the natural host surveys and laboratory rearing of Goniozus natalensis Gordh (Hymenoptera: Bethylidae), a parasitoid of Eldana saccharina Walker (Lepidoptera: Pyralidae) larvae from Cyperus papyrus L. in Southern Africa. Journal of the entomological Society of southern Africa 51: 115 - 127.

Conlong, D.E., Graham, D.Y., Hastings, H. and Leslie, G.W., 1984. Rearing parasitoids and their hosts for the biological control of Eldana saccharina Walker. Proceedings of the South African Sugar Technologists Association 58: 159 - 164.

De Bach, P., 1964. Biological Control of Insect Pests and Weeds. Chapman and Hall, London.

Dick, J., 1945. Some data on the biology of the sugarcane borer (Eldana saccharina Wlk.). Proceedings of the South African Sugar Technologists Association 19: 75 - 79.

Dick, J., 1950. Sugarcane entomology in Natal, South Africa. Proceedings of the International Society of Sugarcane Technologists 7: 377 - 394.

Ehler, L.E., 1990. Introduction strategies in biological control of insects. In Mackauer, M., Ehler, L.E. and Roland, J. (Eds.). Critical Issues in Biological Control. Intercept. Andover, Hants.

Girling, D.J., 1972. Eldana saccharina Wlk. (Lepidoptera: Pyralidae), a pest of sugarcane in East Africa. Proceedings of the International Society of Sugarcane Technologists 14: 429 -434.

Girling, D.J., 1978. The distribution and biology of Eldana saccharina Walker (Lepidoptera: Pyralidae) and its relationship to other stem borers in Uganda. Bulletin of entomological Research 68: 471 - 488.

Girling, D.J., 1980. Eldana saccharina as a crop pest in Ghana. Tropical Pest Management 26: 152 - 156.

Graham, D.Y. and Conlong, D.E., 1988. Improved laboratory rearing of Eldana saccharina (Lepidoptera: Pyralidae) and its indigenous parasitoid Goniozus natalensis (Hymenoptera: Bethylidae). Proceedings of the South African Sugar Technologists Association 62: 116 -119.

Heathcote, R.J., 1984. Insecticide testing against Eldana saccharina Walker. Proceedings of the South African Sugar Technologists Association 58: 154 - 158.

Herrera, G. and Thompson, J.A., 1989. Biological control of Eldana saccharina using cloned Bacillus thuringiensis genes. 1. Cloning of delta-endotoxin DNA sequences from B. thuringiensis 234. Proceedings of the South African Sugar Technologists Association 63: 189 - 191.

Huffaker, C.B., 1971. Biological Control. Proceedings AAAS Symposium on Biological Control, Boston, Mass. Plenum, New York.

Jacobs, S.J., 1989. Micro-organisms as potential biological control agents of Eldana saccharina Walker (Lepidoptera: Pyralidae). Proceedings of the South African Sugar Technologists Association 63: 186 -188.

Kaufmann, T., 1983. Behavioural biology, feeding habits, and ecology of three species of maize stem borers: Eldana saccharina (Lepidoptera: Pyralidae), Sesamia calamistis and Busseola fusca (Noctuidae) in Ibadan, Nigeria, West Africa. Journal of the Georgia entomological Society 18: 259 - 272.

King, A.G., 1989. An assessment of the loss in sucrose yield caused by the stalkborer, Eldana saccharina, in Swaziland. Proceedings of the South African Sugar Technologists Association 63: 197 - 201.

Leslie, G.W., 1977. The toxicity of some agrochemicals to Pheidole sp. (Hymenoptera: Formicidae) a common ant in Natal cane fields. Proceedings of the South African Sugar Technologists Association 51: 21 - 23.

Leslie, G.W., 1981. The macro- arthropod community of sugarcane fields and of Cyperus immensus stands. Proceedings of the South African Sugar Technologists Association 55: 120 - 126.

Leslie, G.W., 1982. A study of egg predators of Eldana saccharina Walker (Lepidoptera: Pyralidae). Proceedings of the South African Sugar Technologists Association 56: 85 - 87.

Leslie, G.W., 1986. The arthropod predators of Eldana saccharina Walker (Lepidoptera: Pyralidae), their identification and relative importance. Unpublished M.Sc. Thesis. Department of Entomology, University of Natal, Pietermaritzburg.

Leslie, G.W., 1988. The identification and importance of predators of Eldana saccharina (Lepidoptera: Pyralidae). Proceedings of the South African Sugar Technologists Association 62: 124 - 128.

Leslie, G.W., 1990. The influence of dead leaf material on the oviposition behaviour of Eldana saccharina (Lepidoptera: Pyralidae) in sugarcane. Proceedings of the South African Sugar Technologists Association 64: 100 - 102.

Leslie, G.W. and Boreham, P.F.L., 1981. Identification of arthropod predators of Eldana saccharina Walker (Lepidoptera: Pyralidae) by cross-over electrophoresis. Journal of the entomological Society of southern Africa 44: 381 - 388.

McCulloch, D.J., 1989. The feasibility of cutting rainfed cane at a younger age on the north coast of Natal. Proceedings of the South African Sugar Technologists Association 63: 206 - 208.

Mohyuddin, A.I. and Greathead, D.J., 1970. An Annotated list of the parasites of graminaceous stem borers in East Africa, with a discussion of their potential in biological control. Entomophaga 15: 241 - 274.

Nagarkatti, S. and Rao, V.P., 1975. Biology of and rearing technique for Sturmiopsis parasitica (Curr.)(Diptera, Tachinidae), a parasite of graminaceous borers in Africa. Bulletin of entomological Research 65: 165 - 170.

Nuss, K.J., 1991. Screening sugarcane varieties for resistance to eldana borer. Proceedings of the South African Sugar Technologists Association 65: 92 - 95.

Nuss, K.J. and Atkinson, P.R., 1983. Methods used to measure the susceptibility of sugarcane varieties to Eldana saccharina Walker. Proceedings of the South African Sugar Technologists Association 57: 92 - 94.

Nuss, K.J., Bond, R.S. and Atkinson, P.R., 1986. Susceptibility of sugarcane to the borer Eldana saccharina Walker and selection for resistance. Proceedings of the South African Sugar Technologists Association 60: 153 - 155.

Paxton, R.H., 1982. Eldana borer (Eldana saccharina): the results of surveys. Proceedings of the South African Sugar Technologists Association 56: 99 - 103.

Paxton, R.H., 1983. Pest and disease control committees - the first year of operation. Proceedings of the South African Sugar Technologists Association 57: 95 -98.

Pemberton, C.E. and Williams, J.R., 1969. Distribution, origins and spread of sugarcane insect pests. In Williams, J.R., Metcalfe, J.R., Mungomery, R.W. and Mathes, R. (Eds.), 1969. Pests of Sugarcane. Elsevier Publishing Company, Amsterdam.

Sampson, M.A. and Kumar, R., 1983. Population dynamics of the stem-borer complex on sugar-cane in Southern Ghana. Insect Science and Application 4: 25 - 32.

Sampson, M.A. and Kumar, R., 1985. Life history, development and behaviour of Eldana saccharina Walker on sugar-cane in southern Ghana. Insect Science and Application 6: 135 - 143.

Scheibelreiter, Von G.K., 1980. Sugarcane stem borers (Lep.:Noctuidae and Pyralidae) in Ghana. Zeitschrift fur angewandte Entomologie 89: 87-99.

Smaill, R.J., 1978. Mill yard surveys of the lepidopterous cane borers Eldana saccharina Walker and Sesamia calamistis Hampson. Proceedings of the South African Sugar Technologists Association 52: 139 - 142.

Smaill, R.J. and Carnegie, A.J.M., 1979. The situation regarding Eldana borer (E. saccharina Walker) during 1978/79 and assessments of crop loss. Proceedings of the South African Sugar Technologists Association 53: 108 - 110.

Spaull, V.W., 1988. A preliminary evaluation of entomogenous nematodes to control the African sugarcane stalkborer Eldana saccharina (Lepidoptera: Pyralidae). Proceedings of the South African Sugar Technologists Association 62: 120 - 123.

Spaull, V.W., 1990. Field tests to control the pyralid, Eldana saccharina, with an entomogenous nematode, Heterorhabditis sp. Proceedings of South African Sugar Technologists Association 64: 103 - 106.

Van den Bosch, R., Messenger, P.S. and Guttierrez, A.P., 1982. An Introduction to Biological Control. Plenum, New York.

Waage, J.K., 1990. Ecological theory and the selection of biological control agents. In Mackauer, M., Ehler, L.E. and Roland, J. (Eds.). Critical Issues in Biological Control. Intercept. Andover, Hants.

Waage, J.K. and Hassell, M.P., 1982. Parasitoids as biological control agents - a fundamental approach. Parasitology 84: 241 - 268.

Waiyaki, J.N., 1968. The biology and control of the principle Lepidopterous borers associated with sugar cane at the Tanganyika Planting Company, Arusha Chini. Miscellaneous Report No. 653 (Unpublished). Tropical Pesticides Research Institute, Arusha, Tanzania.

Waiyaki, J.N., 1974 (a). Laboratory observations on the biology of Eldana saccharina Walker, a pest of sugarcane in the northern region of Tanzania. Proceedings of the International Society of Sugarcane Technologists 15: 439 - 443.

Waiyaki, J.N., 1974 (b). The ecology of Eldana saccharina Walker, and associated loss in cane yield at Arusha-Chini, Moshi, Tanzania. Proceedings of the International Society of Sugarcane Technologists 15: 457 - 462.

Walker, P., 1865. List of specimens of Lepidopterous insects in the collection of the British Museum. British Museum (Natural History). Part 32. Suppl. Part 2: 632 - 633.

CHAPTER 2

STUDY AREA

2.1 GEOGRAPHICAL LOCATION

Population fluctuations of Eldana saccharina Walker, and its parasitoid and pathogen complexes, were monitored at a lake fringed with Cyperus papyrus L. on the farm Palm Ridge (28° 20'S, 32° 14'E). The lake is on the western side of the national road (N2), 13 km from Mtubatuba northwards towards Hluhluwe in Kwazulu-Natal, South Africa. It lies on an unnamed tributary of the Nsane River, which flows into the Nyalazi River. This river is a major fresh water source for False Bay, which is part of Lake St. Lucia. The elevation of the study site was 46 m above mean sea level (a.m.s.l.), and it occurred on the western fringe of the Zululand (or Mozambique) Coastal Plain, which at this point, is about 23 km wide.

2.2 CLIMATIC PARAMETERS

The study site was in an area regarded as transitional between the tropical and subtropical climatic regions (Stuckenberg, 1969; van Dijk, 1971). Being on the Zululand Coastal Plain, the climate was also influenced by the proximity of the sea and, in particular, the warm Agulhas current. Climatological data was been obtained from the Riverview Meteorological Site (Station No. 339/357, 28° 27'S, 32° 12'E, 46m a.m.s.l.) which is 13 km south of the study site.

2.2.1 Temperature

The subtropical nature of the climate is reflected in the mean annual variation in temperatures collected over 23 years (Figure 1). The mean monthly maximum temperature at Riverview ranged from 23.5°C to 30.4°C, with January being the hottest month. The coolest months were June and July, with mean

minimum temperatures of 12°C. The mean annual maximum and minimum temperatures are 26.9°C and 17.1°C respectively. There was a 6.9°C difference in the mean maximum summer and winter temperatures, and a 9.1°C difference in the mean minimum summer and winter temperatures at Riverview.

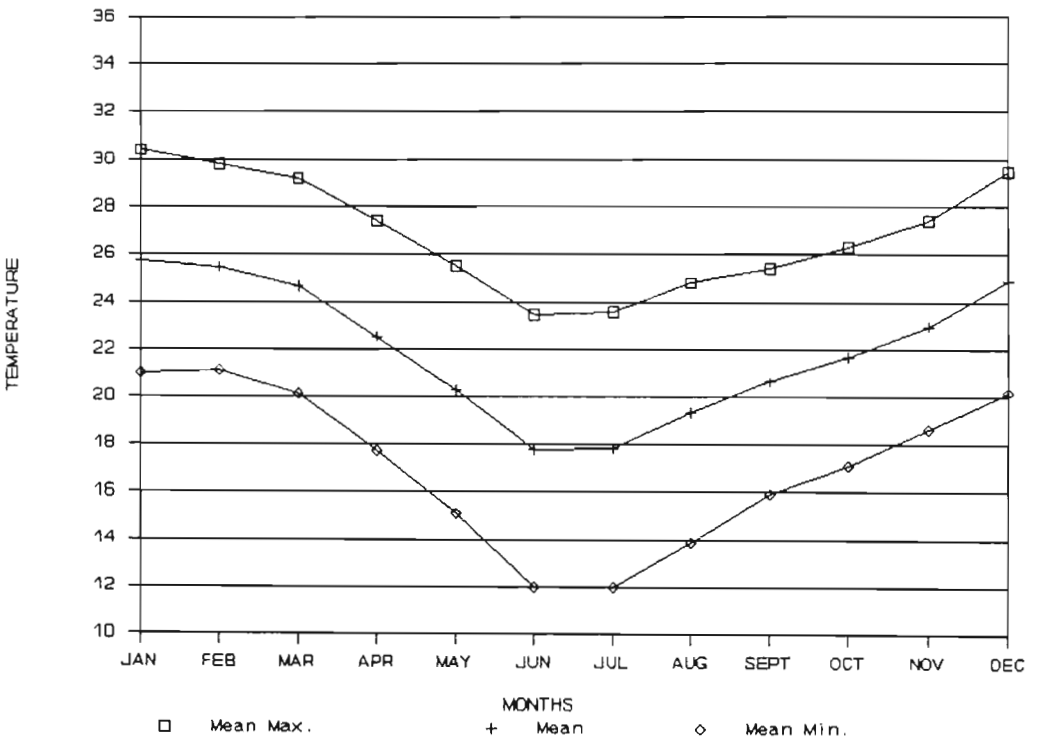


Figure 1. The long term mean annual variation in temperatures (over 23 years) at the Riverview Meteorological Site.

2.2.2 Rainfall

The mean annual rainfall for the period 1932 - 1977 on the farm Palm Ridge was 909 mm (Taylor, 1982). However, at Riverview the annual long term mean (over 23 years) was 950.5 mm. Sixty-five percent of this rainfall occurred during the spring and summer months from September to February. The winter months were thus not dry, as rain fell in every month of the year. The wettest month was February (146.9 mm) and the driest was July (35.7 mm). These long-term rainfall data are presented in Figure 2.

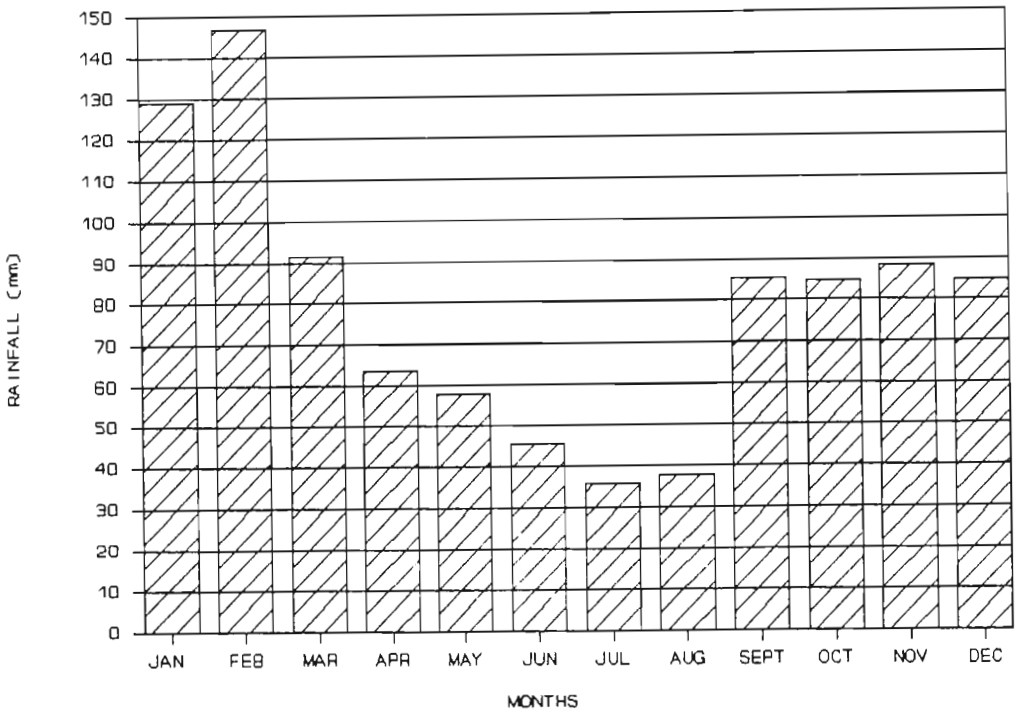


Figure 2: The long term annual variation in rainfall (over 23 years) recorded at the Riverview Meteorological Site.

Figure 3 compares the monthly rainfall recorded at Riverview during the years of the study, with the long-term average. During 1985 and 1987, rainfall was 21.7% and 70.7% above the long-term annual total respectively. During 1986, it was 34.6% below. The study period was drier than these figures imply however, as in 22 of the 33 months of the study the rainfall was below average, while in only 11 months was the rainfall above the long-term monthly mean. The high rainfall figures were normally caused by unexpectedly severe storms. For example, the exceptionally high September 1987 rainfall was caused by a cut off low pressure system over Natal, which sucked in moist air from over the Indian Ocean (Durban Met. Office, 1993, pers. comm.)

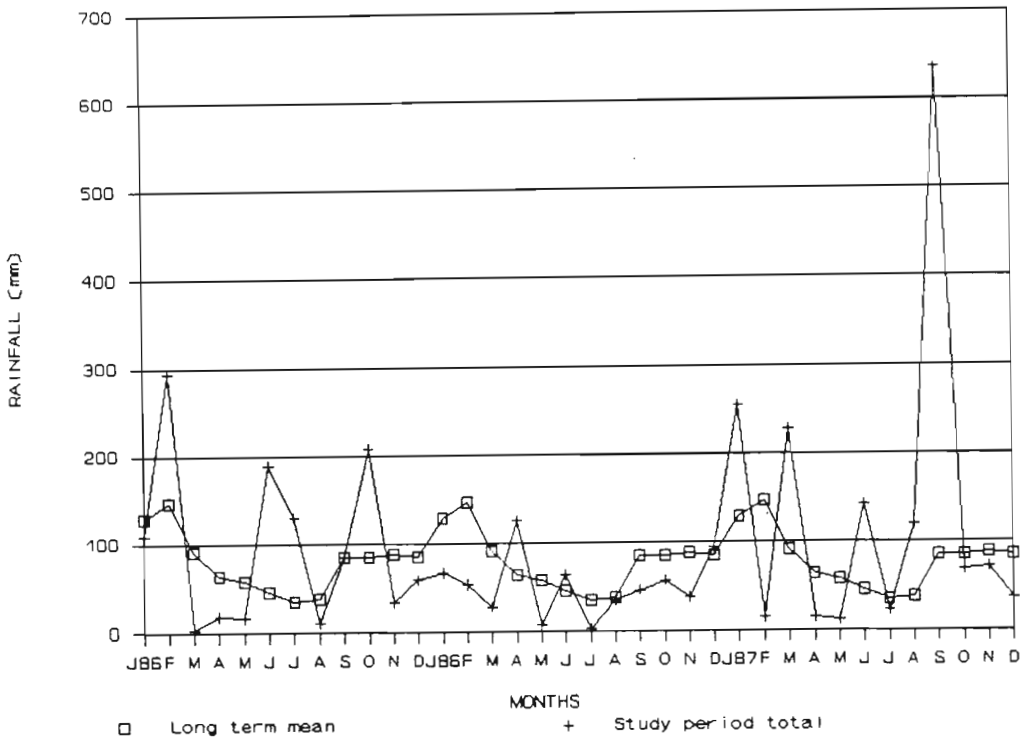


Figure 3: Long term annual rainfall variation and that recorded during the study (1985 - 1987) at the Riverview Meteorological Site.

2.2.3. Relative Humidity

Recordings of long-term relative humidity trends at Riverview, show that this area was humid, averaging 80% at 08h00 and 60% at 14h00 throughout the year. The most humid mornings occurred from March to May (83%) and the least humid in December (76%). February and November had the highest afternoon humidities (65%), and July the lowest (54%). The largest daily differences occur during winter, especially in July (25%). In summer, especially November (12%), these differences were least. Figure 4 shows the long-term relative humidities recorded at Riverview.

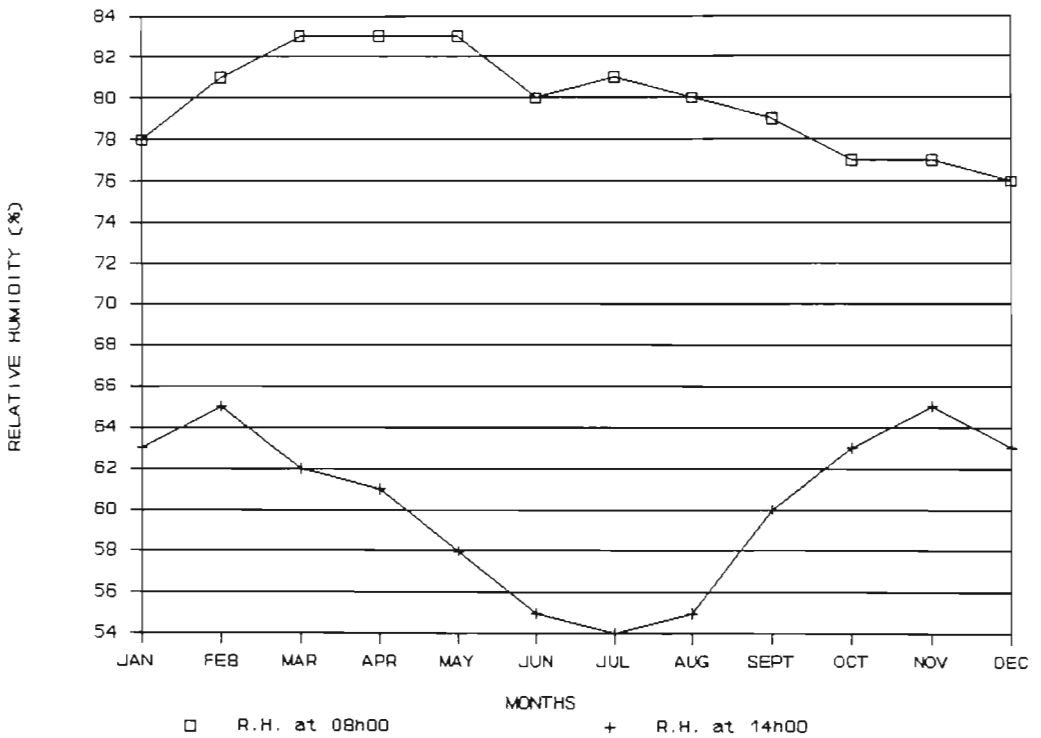


Figure 4: The long term relative humidities recorded at the Riverview Meteorological Site.

2.3. VEGETATION

The centre of the lake comprising the study site was open water. Cyperus papyrus was the dominant emergent macrophyte between the water and the lake shore. The C. papyrus had localised areas of Phragmites communis Trin. on its landward side. The wetland area of the lake was fringed by trees, with Ficus sur Forssk., Halleria lucida L., Bridelia micrantha (Hochst.) Baill. and the palm, Phoenix reclinata Jacq. being dominant. In the drier zone, there were scattered clumps of the sedge Cyperus sexangularis Nees. A mown grass break separated the trees from cultivated sugarcane fields, which dominated the surrounding landscape.

REFERENCES

Stuckenberg, B.R., 1969. Effective temperature as an ecological factor in southern Africa. Zoologica Africana 4: 145 - 198.

Taylor, W.M., 1982. The climatology of the St. Lucia area. In Taylor, R.H. (Ed.), St. Lucia Research Review. Unpublished Proceedings of the Symposium held at Queen Elizabeth Park, Pietermaritzburg, 16 February, 1982. Natal Parks Game and Fish Preservation Board, P.O. Box 662, Pietermaritzburg, 3200.

Van Dijk, D.E., 1971. The zoocartographic approach to Anuran ecology. Zoologica Africana 6: 85 -118.

CHAPTER 3

PHENOLOGY OF CYPERUS PAPYRUS AND ITS SUITABILITY AS A HABITAT FOR ELDANA SACCHARINA

3.1 INTRODUCTION

Cyperus papyrus is the largest sedge in the world, normally attaining a height of between 3 m and 4 m and sometimes up to 10 m at high elevation sites (Thompson et al., 1979). This emergent macrophyte is dominant in much of the permanent swamp, which covers 85 000 km^2 in Africa (Thompson and Hamilton, 1983). It occurs largely in tropical central and eastern Africa, extending to 29°S (Jones and Muthuri, 1985) in decreasing clumps along the subtropical coastal plain of South Africa. C. papyrus grows best in shallow lake systems with slow response times during wet seasons and which are not subject to flash floods. Thus, C. papyrus only establishes where seasonal flood regimes do not exceed 3 m in amplitude (Thompson et al., 1979). It follows that stands of C. papyrus generally establish in restricted wetland areas which are not subject to large water level fluctuations or much wave action (Thompson, 1976[a]; Gaudet, 1977; Thompson et al., 1979). Once established, however, it forms large mats which exclude all but a few other plant species (Gaudet, 1977).

The terminology used to describe the morphology of C. papyrus follows that of Thompson et al. (1979). It consists of a rhizome, covered by brown sheathing scale leaves or bracts. Stubby roots emerge from the ventral portion of the rhizome, and culms emerge from the dorsal surface. These green culms are sheathed with scale leaves at their bases and bear umbels at their apex. When culms are young and short, umbels form a bud sheathed by bracts which open as the culm grows, revealing numerous green bracteoles.

A number of authors divided umbels into "age classes", depending on their

stage of development (Thompson et al., 1979; Jones and Muthuri, 1985; Breen and Stormanns, 1989; Muthuri et al., 1989). Because of the presence of all of these ages at any one time, umbels themselves are heterogenous both spatially and temporarily.

Cyperus papyrus is a major indigenous host for the African sugarcane stalkborer, Eldana saccharina (Atkinson, 1980). The study of parasitoid-pest-indigenous host plant interactions is considered important in determining the success of controlling indigenous pests biologically (Conlong, 1994). A study of the phenology and seasonal abundance of C. papyrus umbels is therefore important, as it provides baseline data needed for further study on the population dynamics of E. saccharina. Possible clues may also be identified which could contribute to its control in sugarcane.

3.2 SEASONAL ABUNDANCE OF UMBEL TYPES

3.2.1 Materials and methods

Sampling was done monthly for two years, in successive quadrats moving from the wetland edge deeper into the wetland until a minimum of five quadrats had been surveyed. Quadrats measured 8 m along the margin, and 4 m into the wetland (32 m^2). Thompson et al. (1979), using nested quadrats, determined that quadrats 20 - 40 m^2 (2m by 10-20 m) were adequate to detect most of the variability in biomass and productivity determinations of C. papyrus.

All the umbels within a quadrat were harvested and divided into:

1) young umbels - those in which the bracteoles were green and had not opened beyond 45°.
2) mature umbels - those which had green bracteoles opened beyond 45°. This umbel category was subdivided into:
   - those containing no reproductive structures;
   - those containing reproductive structures with seeds;

- those containing reproductive structures from which the seeds had been shed.

3) old umbels - those with bracteoles opened beyond 45°, but containing no chlorophyll, and brown in colour.

The proportion of each umbel type to the total number of umbels collected per quadrat was calculated as a percentage. The percentage was transformed into arcsin values. Results thus approached a normal distribution, which allowed statistically significant comparisons of umbel proportions and phenology.

3.2.2 Results

Figure 5 shows the proportion of major umbel types (young, mature and old) at each sampling date over the study period. During this period, the most common umbel class was always the mature class, comprising just over 50% of umbels at the start of the study and increasing to 60% at the end of sampling. There was no significant difference between the proportion of young and old umbels in samples. Young umbels comprised, on average, 20% of the sward throughout the sampling period. In contrast, old umbels were around 30% at the start of the study, and decreased to just below 20% at the end of sampling. The mature umbel contribution to the sward was always significantly greater than the contribution by the young and old umbels.

The umbels bear reproductive structures with flowers and seeds, and shed seeds at different times of the year. Figure 6 shows the times when these stages were recorded on the young umbels, and Figure 7, the times of these stages on the mature umbels.

Reproductive structures were borne on young umbels from October until December 1985, and then again from August until December 1986. In both years, the highest proportion of these (around 16%) was recorded from mid September until early October. No young umbels had shed seed at any time

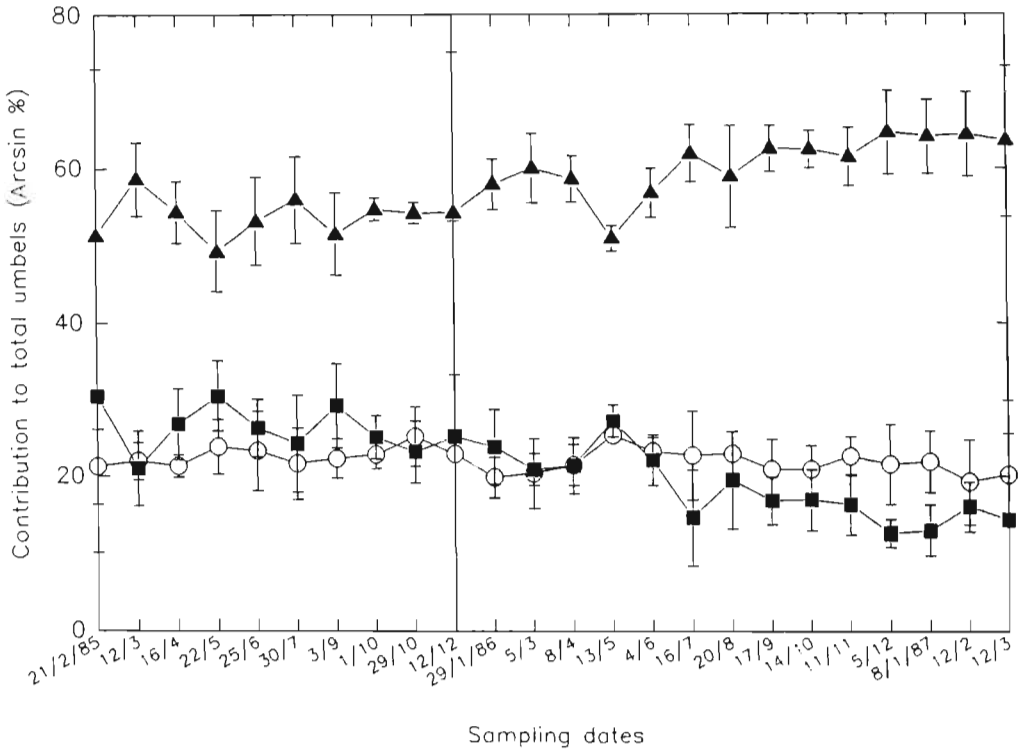


Figure 5: The proportion of young (○—○), mature (▲—▲) and old umbels (■—■) present in the above ground standing crop of C. papyrus sampled during the study period (┃ = 95% confidence limits).

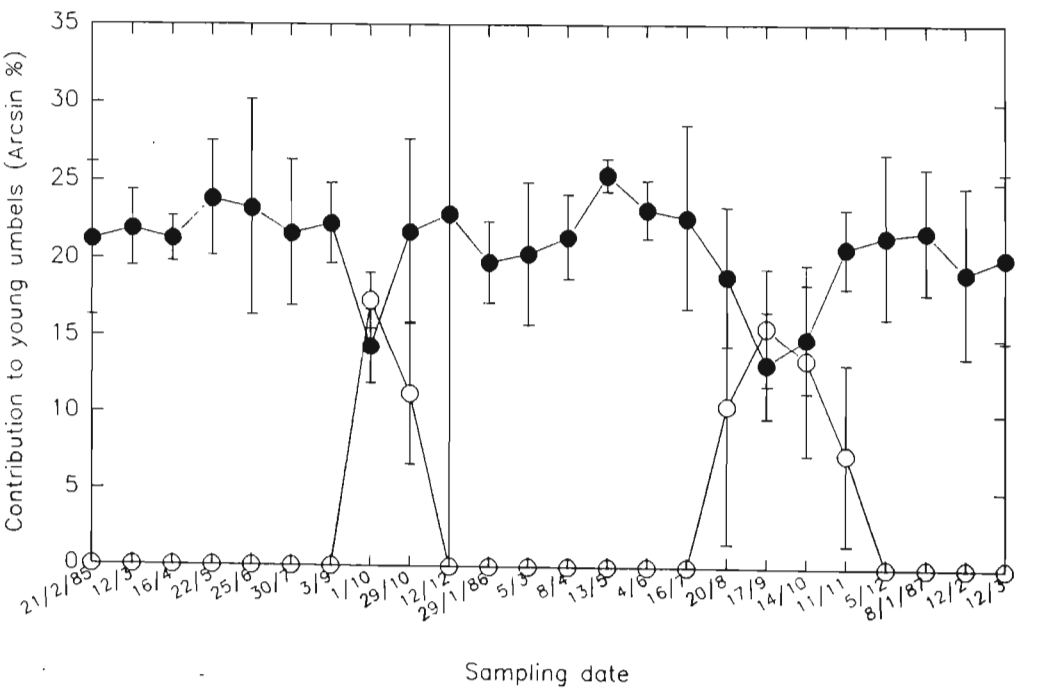


Figure 6: The proportion of young umbels bearing no reproductive structures (●—●), and those bearing seeds (○—○) in C. papyrus umbels sampled during the study period (┃ = 95% confidence limits).

during the study (Figure 6).

Mature umbels started bearing reproductive structures in early September 1985, and the last of these were recorded at the end of March 1986 (Figure 7).

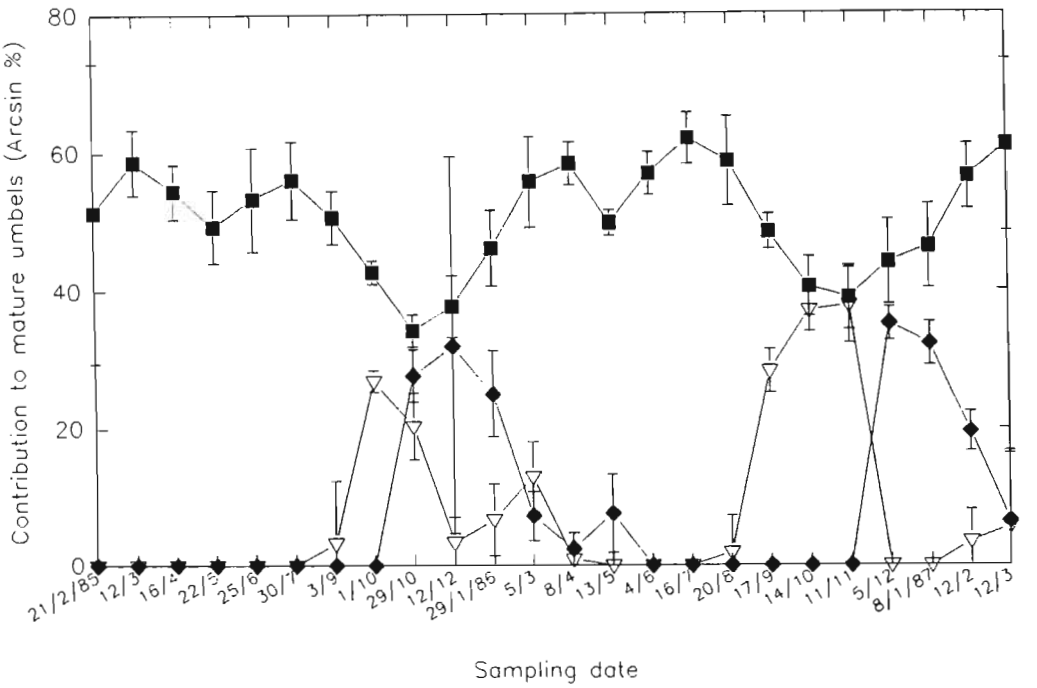


Figure 7: The proportion of mature umbels bearing seeds (▽—▽), those which had shed their seeds (◆—◆) and those bearing no reproductive structures (■—■) in C. papyrus umbels sampled during the study period (I = 95% confidence limits).

The highest proportion (21%) of mature umbels bearing reproductive structures was recorded in early October 1985. A similar trend followed in 1986, with the first umbels bearing reproductive structures recorded in August, reaching its highest proportion in October/November (38%). When sampling stopped in March 1987, a small proportion of these were still recorded (5%). Seed shed was recorded in the mature umbels, because reproductive structures with no seeds were first found at the end of October 1985, reaching a peak in mid December (30%), and were last found in mid May 1986 (2%). Later that year, they were recorded in November, peaked in December (38%), and, at the completion of sampling in March 1987, a small proportion were still found (5%;

Figure 7).

When sexual reproductive umbel stages were found, the proportion of umbels with no reproductive structures decreased, (Figures 6 and 7), which indicated that at these times there was no increased production of umbels, but rather a partitioning of resources within them.

3.3 DISCUSSION

The lack of a seasonal cycle in the production of new umbels and senescence of old umbels of C. papyrus recorded during this study period was not unexpected, nor was the constancy of the relative numbers of young, mature and old umbels. It had been recorded before by workers on this tropical wetland plant (Thompson et al., 1979; Jones and Muthuri, 1985; Muthuri et al., 1989). Also, the C. papyrus monoculture recorded during the study was not unusual, as tropical swamp habitats demand extreme specialisation of plants growing in them, which greatly reduces the diversity of the flora (Thompson, 1976[a]). Because of its location and very productive vegetative growth (Thompson et al., 1979), C. papyrus is long lived and regarded as a stable habitat for herbivores, because all its plant parts are present at all times and in constant numbers. C. papyrus stands are subject to "self-thinning", a density dependent mechanism regulating the number of umbels present per unit area (Muthuri et al., 1989).

The C. papyrus habitat, however, is itself quite diverse, both biotically and abiotically. Jones and Muthuri (1985) determined that more than 90% of the photosynthetically active radiation was intercepted by the upper part of the canopy, where the majority of mature green umbels were situated. Young umbels developing from rhizomes thus spend half of their lifespan in a region of low light intensity, while elongating to reach the canopy (Breen and Stormanns, 1989). During this time rays of umbels are tightly enclosed in bracts. Once umbels reach the canopy, rays are fully expanded. In addition, air temperatures are 4 to 5 °C lower in mid height under the canopy when compared with

ambient temperature (Jones and Muthuri, 1985).

Even though all above authors followed the population structure and phenology of umbels for up to one year, none mentioned the existence of a sexual phase of C. papyrus reproduction. During this study it occurred in the spring and summer months (September to April) of both years sampled. This phase of the sedge's growth has important implications not only for propagation of C. papyrus for fuel purposes in the Third World (Jones, 1983), but also because seeds produced a new habitat which could be exploited by phytophagous insects. Also, when seeds were lost from umbels, there was a loss of nutrients from the plant. Thompson (1976)[(b)] cited work of Boyd (1970), who found that up to 40% of nitrogen and phosphorus in Typha was translocated to its fruits (seeds), and stated that even though C. papyrus fruits store less of these nutrients, fruit shedding nevertheless represented a considerable nutrient export from the plant itself. The presence of seeds also changed the shape of the umbel, and in this way masked visual signals which natural enemies of phytophagous insects may use to locate their hosts (Hattingh, 1991; Tumlinson et al., 1993).

The effect of rainfall on production of mature and old umbels was very evident. In the first year of sampling (February 1985 to February 1986), rainfall was below the long term mean in 8 of the 12 months, while in the second year of sampling (March 1986 to March 1987) it was only below the long term mean in 4 of the 12 months sampled (Figure 3). Improved growing conditions brought about by increased rainfall was reflected in the increase in mature umbels during the latter part of the sampling period, and fewer old umbels found during that time. This indicated a decrease in rate of senescence of mature umbels.

3.4 CONCLUSION

It is evident that many habitats were available in C. papyrus stands. Umbels themselves, sampled over two seasons, provided a diverse habitat as they grew,

which could be exploited by phytophagous insects. This diversity was caused by both growth of culms bearing umbels and expansion of bracteoles as umbels matured. Seasonal seed production changed the shape of umbels, and caused a translocation of nutrients within umbels affected, and possibly a loss of nutrients to umbels when seeds were shed. The effect of shading by mature umbels on temperature and light intensity under them changed the environment between the top of the canopy, within the canopy and below it considerably. The effect of drought, which stressed plants, and the better rainfall year, which allowed C. papyrus to grow more vigorously, were also factors determining diversity of habitats within the umbels.

REFERENCES

Atkinson, P.R., 1980. On the biology, distribution and natural host plants of Eldana saccharina Walker (Lepidoptera: Pyralidae). Journal of the entomological Society of southern Africa 43: 171 -194.

Boyd, C., 1970. Chemical analyses of some vascular aquatic plants. Archiv fur Hydrobiologie 67: 78 - 85.

Breen, C.M. and Stormanns, C-H., 1989. Observations on the growth and production of Cyperus papyrus L. in a sub-tropical swamp. Thirty-fourth Congress of the International Association for Theoretical and Applied Limnology, Munich, 13-19 August, 1989. Unpublished presentation of the Institute of Natural Resources, Univerity of Natal, Pietermaritzburg.

Conlong, D.E., 1994. A review and perspectives for the biological control of the African sugarcane stalkborer Eldana saccharina Walker (Lepidoptera: Pyralidae). Agriculture, Ecosystems and Environment 48: 9 - 17.

Gaudet, J.J., 1977. Natural drawdown on Lake Naivasha, Kenya, and the formation of papyrus swamps. Aquatic Botany 3: 1 - 47.

Hattingh, V., 1991. Comparative Feeding and Foraging Behaviour of the Biocontrol Agents Chilocorus spp.. Unpublished Ph D Thesis, Department of Zoology and Entomology, University of Natal, Pietermaritzburg.

Jones, M.B., 1983. Papyrus: a new fuel for the Third World. New Scientist 99: 418 - 421.

Jones, M.B. and Muthuri, F.M., 1985. The canopy structure and microclimate of papyrus (Cyperus papyrus) swamps. Journal of Ecology: 73: 481 - 491.

Muthuri, F.M., Jones, M.B. and Imbamba, S.K., 1989. Primary productivity of papyrus (Cyperus papyrus) in a tropical swamp; Lake Naivasha, Kenya. Biomass 89: 1 - 14.

Thompson, K., 1976[a]. Swamp development in the headwaters of the White Nile. In Rzoska, J. (Ed.). The Nile, Biology of an Ancient River. W. Junk, The Hague.

Thompson, K., 1976[b]. The primary productivity of African wetlands with particular reference to the Okavango Delta. In Nteta D.N. (Ed.). Proceedings of the Symposium on the Okavango Delta and its Future Utilisation. August 30th to September 2nd, 1976. National Museum Gaborone, Botswana.

Thompson, K. and Hamilton, A.C., 1983. Peatlands and swamps of the African continent. In Gore, A.J.P. (Ed.), Ecosystems of the World. Elsevier, Amsterdam, Netherlands.

Thompson, K., Shewry, P.R. and Woolhouse, H.W., 1979. Papyrus swamp development in the Upemba Basin, Zaire: studies of population structure in Cyperus papyrus stands. Botanical Journal of the Linnaean Society 78: 299 - 316.

Tumlinson, J.H., Lewis, W.J. and Vet, L.E.M., 1993. How parasitic wasps find their hosts. Scientific American 266: 100 - 106.

CHAPTER 4

ELDANA SACCHARINA ON CYPERUS PAPYRUS

4.1 INTRODUCTION

In 1942, Weber first proposed that umbels of Cyperus papyrus provided a suitable habitat for a variety of insects. His hypothesis was based on the fact that in vast regions such as the Sudd swamps of the Sudan, umbels, which normally touched one another "ten or more feet" above the water surface, would have an arthropod fauna forced to nest on the plants since no soil was exposed. Of particular interest to him were bases of umbels, where numerous bracteoles (rays) "come together to form a dense mass one or two inches thick".

While passing through the Sudd by steamboat for four days in July 1939, Weber (1942) collected nine arthropod orders from umbels which brushed against the boat, and also from boat lights in the evenings. In his collection were eight species of ants, individual locusts from vast swarms, unidentified Lepidoptera and parasitic Hymenoptera adults and arachnids.

Thornton (1957) expanded on Weber's (1942) study, by describing the succession of animals which occurred as umbels grew, matured and eventually died. From May to June 1954 and again in January 1955, Thornton collected arthropods from his C. papyrus study site on the Upper White Nile. Umbels for his study were divided into similar age classes to those described in Chapter 3. He did not, however, recognise umbels bearing reproductive structures. His study showed fauna of umbels to be congregated at umbel bases, confirming the observations of Weber (1942).

The most common orders collected by Thornton (1957) on young umbels were Thysanoptera, Homoptera (mostly aphids) and Diptera (mostly larvae). Those

more common in older young and mature umbels were Acarina, Hymenoptera (mostly ants), Heteroptera, Homoptera and Coleoptera. As umbels matured and aged, Araneida and Psocoptera (Corrodentia) became more abundant. In all, he collected 16 arthropod orders. However, of more importance to the present study, were his records of Lepidoptera (mostly larvae) and Hymenoptera parasitoids, particularly Goniozus sp., which usually attack lepidopterous larvae (Thornton, 1957). He recognised that C. papyrus umbels are sites of an intricate food web, the pattern of which changed as the umbel grew, matured and died.

No further work was published on insect/C. papyrus interactions until E. saccharina became a pest in graminaceous crops of East Africa (Girling, 1978) and South Africa (Atkinson, 1980). Both these authors identified a large range of indigenous host plants of E. saccharina, which included many Cyperaceae. Atkinson (1979) identified oviposition sites and feeding patterns of E. saccharina on another cyperaceous host, Cyperus dives Delile, and mentioned C. papyrus as another possible major indigenous host plant in this paper.

It was only when the biological control programme against this borer was expanded in South Africa (Carnegie, 1982) that the biology of E. saccharina in C. papyrus was studied in any detail. The interactions of the borer and its parasitoids in this habitat were described (Conlong et al., 1984; Conlong et al., 1988) and its oviposition and feeding habits in C. papyrus discussed (Conlong, 1990). However, in none of these studies was the extent of boring by E. saccharina in C. papyrus reported, nor were population fluctuations in different umbel types documented. This Chapter aims to address these shortcomings.

4.2 MATERIALS AND METHODS

4.2.1 Impact of E. saccharina on umbels of C. papyrus

All umbels, once harvested and sorted into their age categories (Chapter 3), had their rays, ray bases, associated bracts and umbel-bearing culms searched for

borer damage. If umbels which were bored contained any immature E. saccharina stages, other borers and/or their parasitoids, they were classed as "occupied". These umbels were placed in a separate pile and counted once all of that age class in that quadrat had been searched. The number was recorded. Umbels that were bored but contained no stalkborers and/or parasitoids were treated in the same way, as were unbored umbels, until those of all age classes in all quadrats had been searched and counted.

Umbels that were bored with borings occupied, those with borings unoccupied and those that were unbored were totalled for each age class of each quadrat. The percentage contribution of each category of boring to the total number of a certain age class of umbels sampled per quadrat was then calculated. The mean of each boring category in each umbel age class at each sampling date was determined. Percentages were transformed using arcsin values, so that data approached normal distribution. This allowed use of statistical methods such as 95% confidence limits (Elliott, 1983). These transformed values were used as the basis for Figures presented in this Chapter.

This procedure gave a measure of damage caused by E. saccharina to each umbel age category of C. papyrus which was encountered, and to the status of E. saccharina infestations during the study.

4.2.2 Age structure and population fluctuations of E. saccharina in C. papyrus umbels

In any umbel age class, when immature stages of borers and/or their parasitoids were found, they were identified as far as possible and placed individually in numbered vials containing laboratory prepared diet medium (to identify the umbel type and quadrat from which they were collected). These were kept in the laboratory until adults of either borers or their parasitoids had emerged. In addition, on the basis of their size at collection , E. saccharina larvae found were subjectively assigned to one of three larval sizes: small, medium and large. The

former size included first and second larval instars, the middle category third and fourth, and the latter fifth and sixth. The instar classification was based on that of Atkinson (1980).

The population structure of E. saccharina found in each umbel type at each sampling date could then be calculated in a similar way as done for infestations in sugarcane, i.e. E. saccharina/100 umbels (e/100 umbels) as opposed to e/100 stalks. However, as animal populations are aggregated to some degree, their distributions are generally not normally distributed and thus some form of transformation of raw data was needed. This allowed statistical methods associated with the normal distribution to be applicable to the data (Elliott, 1983).

4.3 RESULTS

4.3.1 Impact of E. saccharina on C. papyrus umbels

All umbel types showed signs of boring, irrespective of their proportion in the standing sward. Of the major umbel types, young ones showed least damage, especially in autumn and winter months (March to September) for both years sampled (more than 75% of umbels unbored, Figure 8). During spring and summer months (October to March of both years), borer damage increased, with numbers of undamaged young umbels dropping to between 55% and 65% of those sampled (Figure 8). The proportion of empty borings found in young umbels was generally below 5%, with no significant differences recorded during the study (Figure 8). In both years, most borings found in this umbel type were occupied, with significantly more occupied borings (30% and 25% respectively) found in October than in the preceding late winter months (10% and 5% respectively). The occurrence of occupied borings in young umbels during autumn and winter periods of both years rarely increased above 15%, while during spring and summer months it was generally greater than 20% (Figure 8).

A greater amount of borer damage was recorded in mature umbels. However, a similar summer/winter trend in damage to that found in young umbels,

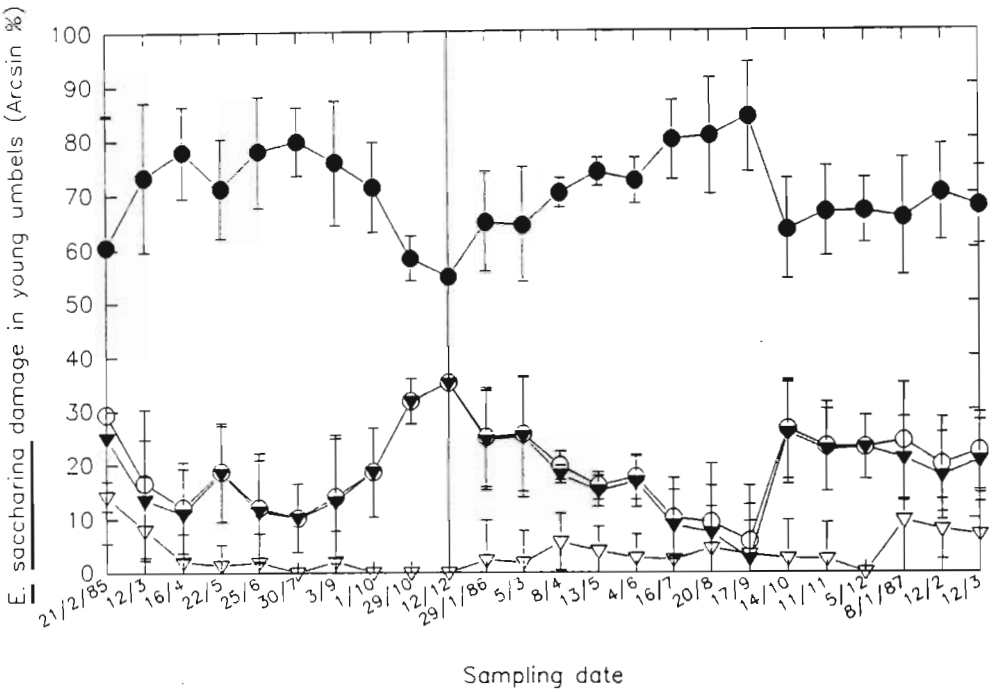


Figure 8: The extent and seasonal fluctuations of borer damage in young umbels collected during the study period (●——● unbored umbels;○——○ bored umbels;▾——▾ bored umbels containing borers and/or parasitoids;▿——▿ umbels with empty borings; I = 95% confidence limits)

especially during the first year of study, was evident. Figure 9 shows unbored mature umbels increased significantly from around 40% in February 1985 and January 1986, to approximately 65% in October in both years of the study. In January 1987 the lower proportion of unbored mature umbels was not evident.

In contrast to the extent of borings in young umbels, the proportion with empty borings was not significantly different from those with occupied borings in the mature category. However, during autumn and winter months there were significantly more mature umbels with empty borings (30%) than with occupied borings (15-20%). The converse was true during mid-summer (December/ January 1986 and December 1987) when those occupied increased to 40 and

25% respectively of mature umbels sampled, while those with empty borings dropped to 25% and 10% respectively (Figure 9).

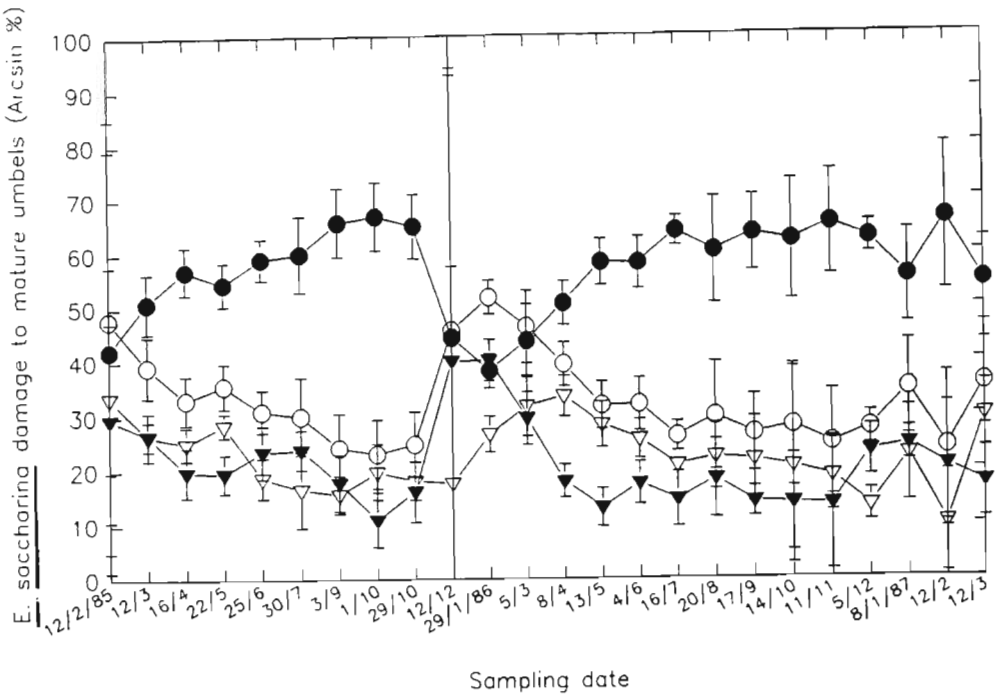


Figure 9: The extent and seasonal fluctuations of borer damage in mature umbels collected during the study period (●——● unbored umbels; ○——○ bored umbels; ▾——▾ bored umbels containing borers and/or parasitoids; ▿——▿ umbels with empty borings; I = 95% confidence limits).

The extent of damage in old umbels was similar to that recorded in mature ones, except that the least proportion of unbored umbels (40%) was recorded in March 1986 (Figure 10), one month after the same category recorded in mature umbels (Figure 9). Proportions of old umbels with occupied and empty borings recorded during the study were opposite to the same components recorded in young umbels. Umbels with occupied borings in this case were generally below 10%, with no significant differences recorded during the study. The proportion of old umbels with empty borings was generally greater than 20%, reaching a

peak of 60% in April of 1986, which was significantly greater than the proportions of the same recorded during the two winter periods on either side of this summer (Figure 10). Damage decreased as the study progressed.

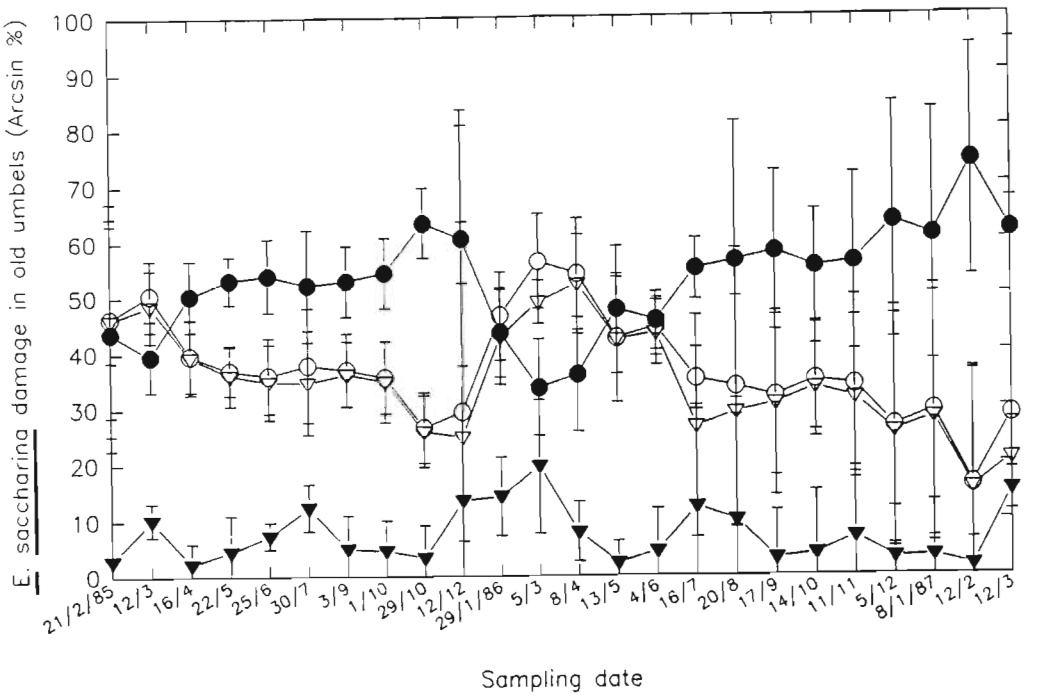


Figure 10: The extent and seasonal fluctuations of borer damage in old umbels collected during the study period (●——● unbored umbels; ○——○ bored umbels; ▼——▼ umbels containing borers and /or parasitoids; ▽——▽ umbels with empty borings; I = 95% confidence limits).

In Chapter 3 it was recorded that reproductive structures, or seeds, were present between August and December on young (Figure 6) and mature umbels (Figure 7), and again in mature umbels, at a lower level, from January to March. Seed set was from October to March in mature umbels, with another smaller peak being recorded in May of 1986 (Figure 7). Even though these categories of young and mature umbels were not common, they were found and used by insects, and thus could be regarded as an important part of the insect's habitat.

When seeds were first recorded during 1985 in young umbels, 20% of them already had occupied borings. This increased to just below 40% when the last of this class were recorded (Figure 11). During the next year, borings increased to 20% of umbels searched in this age class. At no time were empty borings found. There was no significant difference in the proportion of occupied borings in this category of young umbels (Figure 11), when compared to young umbels with no reproductive structures (Figure 8). Levels of infestation increased similarly in these two categories.

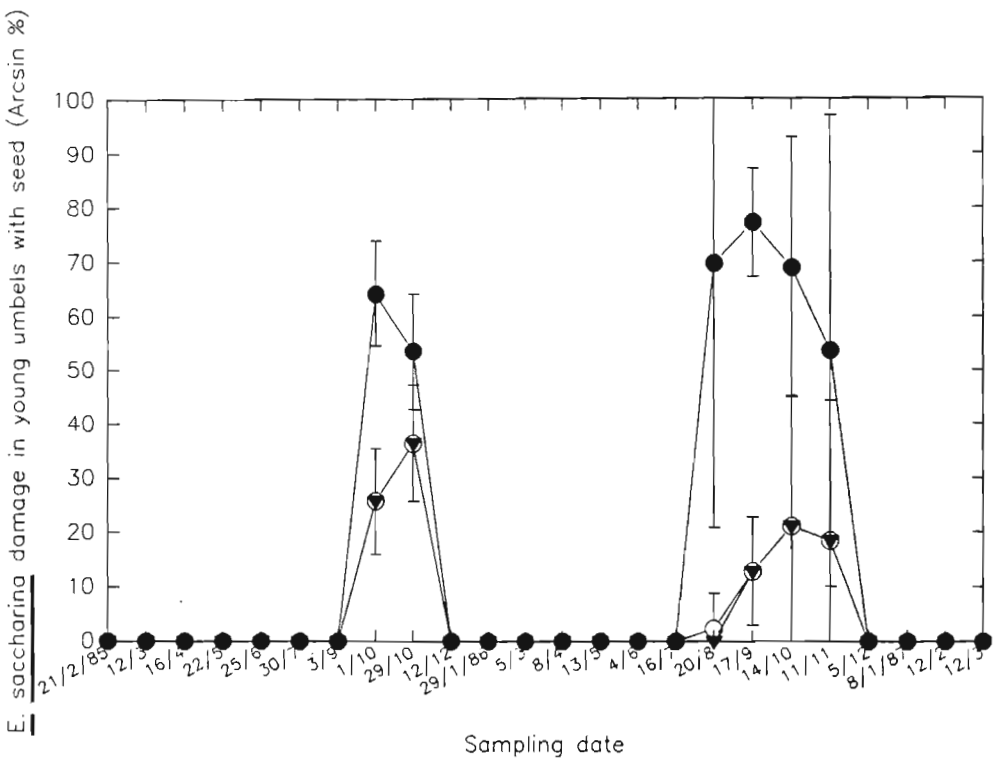


Figure 11: The extent and seasonal fluctuations of borer damage in young umbels with seeds collected during the study period (●——● unbored umbels; ○——○ bored umbels; ▾——▾ umbels containing borers and /or parasitoids; ▿——▿ umbels with empty borings; I = 95% confidence limits).

Damage in mature umbels with seeds followed a similar trend (Figure 12). Occupied borings were found with the first reproductive structures. When the last umbels of this category were found in 1985, 40% of umbels had occupied borings. Throughout this category's presence, the proportion of old borings was

significantly less than the proportion of occupied borings, reaching a peak of 5% one month after the first reproductive structures were found (Figure 12). In subsequent infestations of this category, proportions were not as high, reaching 20% in occupied borings, and 10% in empty borings. There was no significant difference between these two boring categories.

In October 1985, mature umbels with seeds had significantly more occupied borings (Figure 12), than those of their counterparts with no seeds (Figure 9). Subsequently though, both umbels types exhibited the same proportions bored.

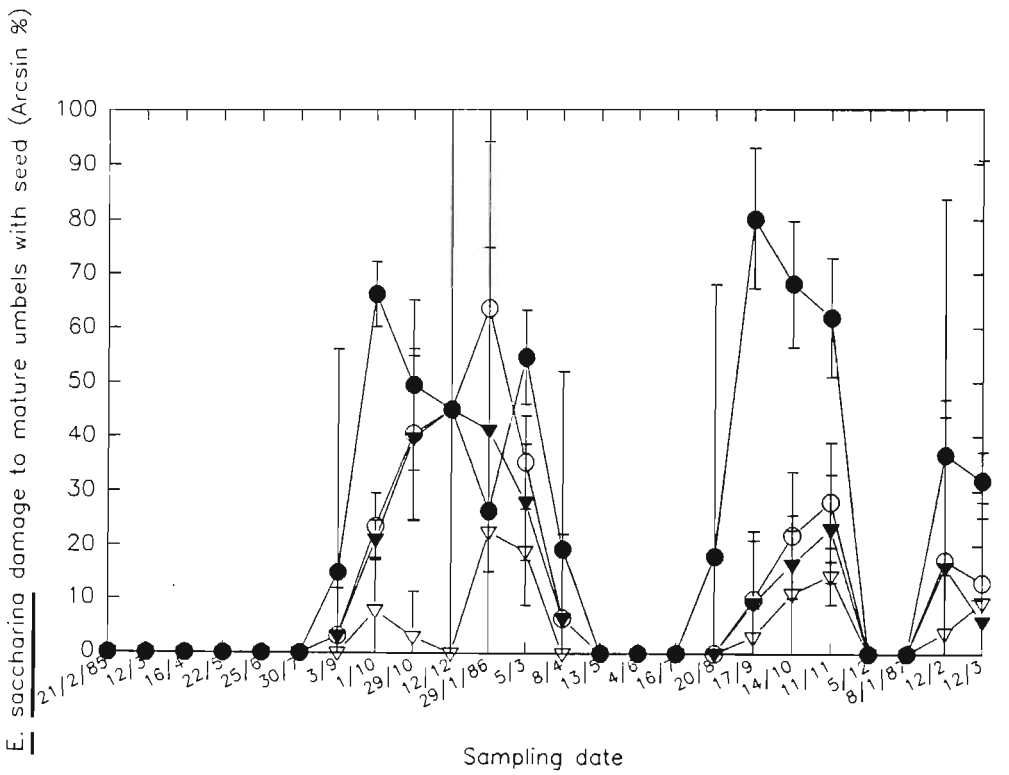


Figure 12: The extent and seasonal fluctuations of borer damage in mature umbels with seeds collected during the study period (●——● unbored umbels; ○——○ bored umbels; ▼——▼ umbels containing borers and /or parasitoids; ▽——▽ umbels with empty borings; I = 95% confidence limits).

As expected, mature umbels which had shed their seeds were found only in late October 1985 and early December 1986, two and four months respectively after the appearance of fresh seeds. The proportion of occupied borings (30%; Figure 13) found in late October 1985, when the first mature umbels which had

shed seed were found, was significantly greater than the proportion of empty borings (5%). However, differences ceased to be significant in subsequent samplings (Figure 13). Most occupied borings were recorded in December 1985 (50%). The month afterwards, empty borings reached their peak (45%). The significance of these damage levels in different umbel types will become evident in the next section, when actual borer infestations are presented.

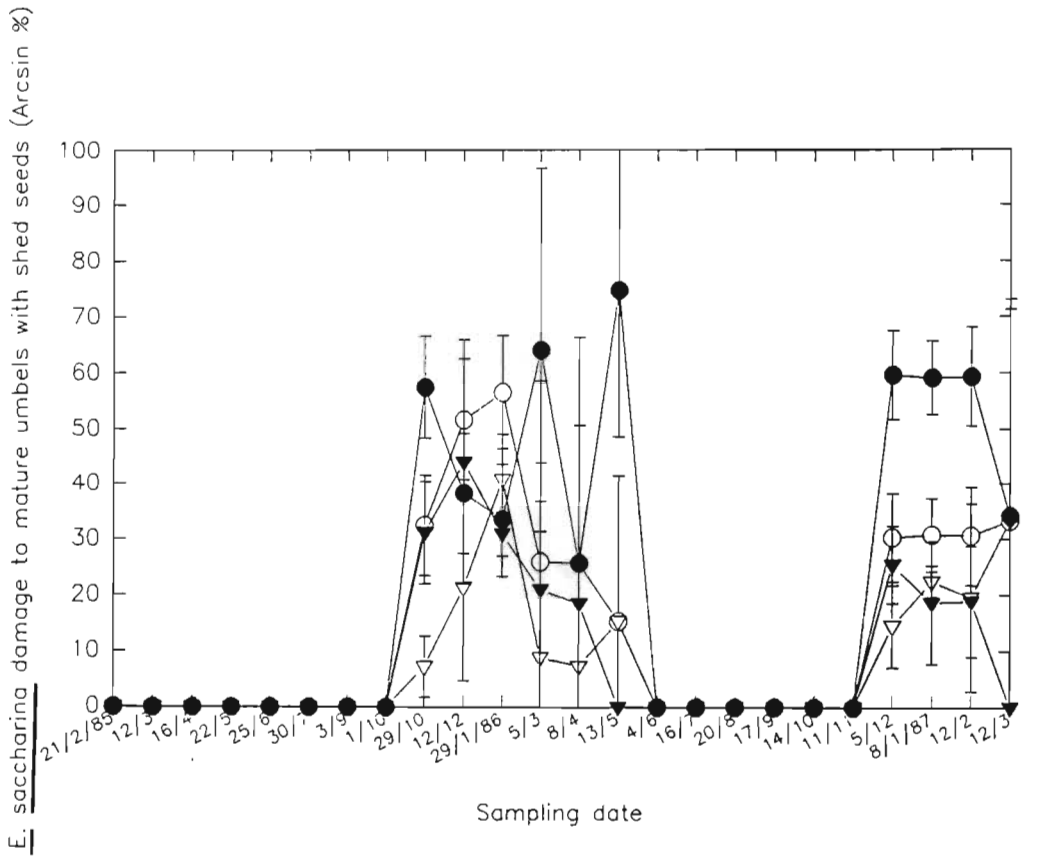


Figure 13: The extent and seasonal fluctuations of borer damage in mature umbels with shed seeds collected during the study period (●——● unbored umbels; ○——○ bored umbels; ▼——▼ umbels containing borers and /or parasitoids; ▽——▽ umbels with empty borings; I = 95% confidence limits).

4.3.2 Age structure and population fluctuations of E. saccharina in C. papyrus umbels

4.3.2.1 Young umbels

Figure 14 shows population and age structure fluctuations of E. saccharina

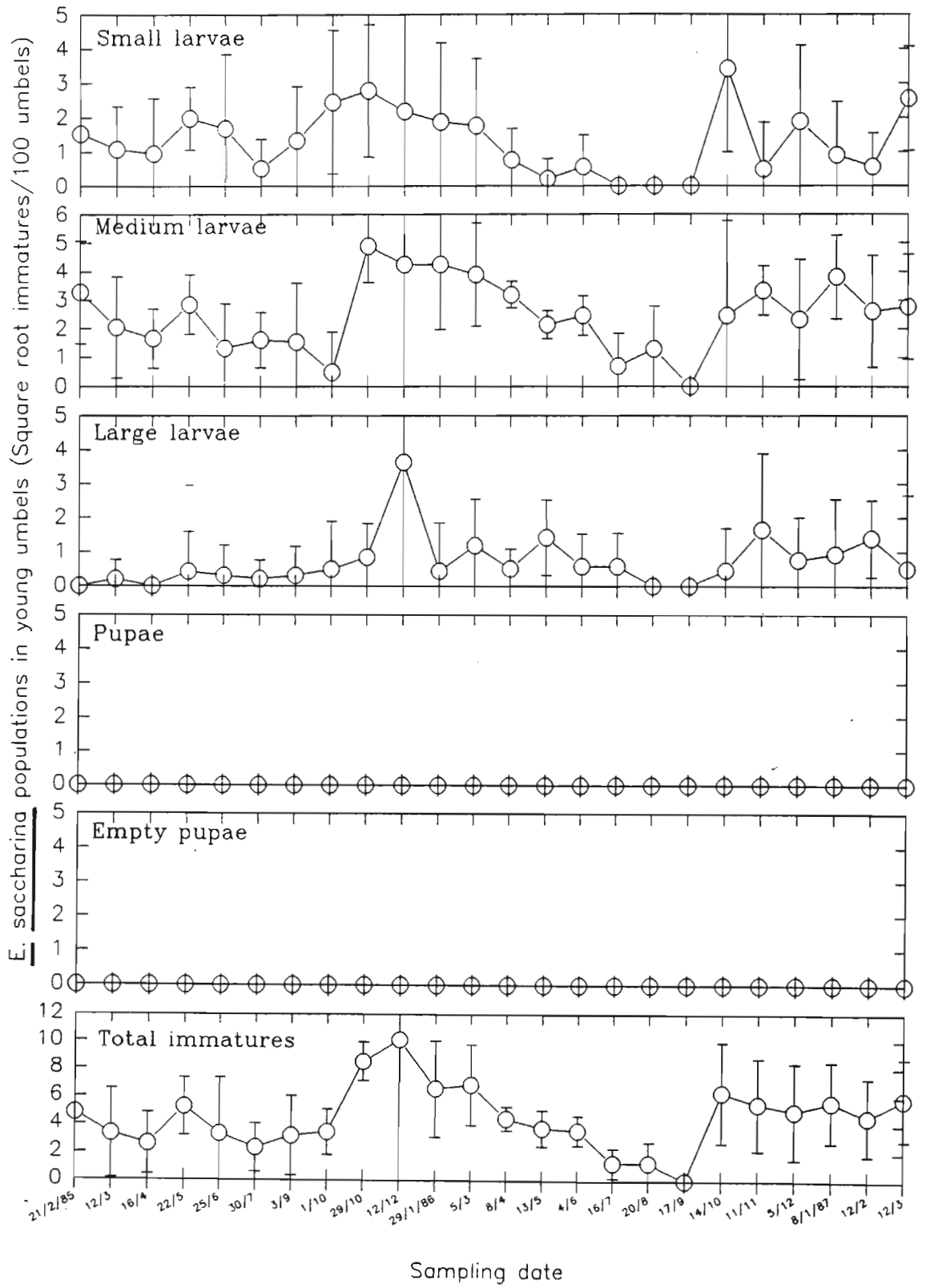


Figure 14: Age structure and population fluctuations of different aged immature life stages of E. saccharina found in young umbels sampled during the study period (I = 95% confidence limits).

found in young umbels. The population generally reflected damage recorded in this class (Figure 8). Highest immature populations were found from October 1985 until March 1986 (8 per 100 umbels). Similar levels were found over the same period the next year. The lowest populations were found during the autumn and winter months of April to September of both seasons sampled (4 per 100 umbels).

It is of importance to note that no pupae or empty pupae were found in this class (Figure 14). Very few large larvae were recorded, generally less than 1 per 100 umbels during autumn and winter months, and just over 1 per 100 during spring and summer months. The bulk of the immature population comprised small and medium sized larvae, with the latter contributing to the population a little more than the former (4 per 100 umbels compared with 2 during the summer months, and 2 per 100 umbels compared to 1 in the winter months). During June to September 1986, larval populations were very low, with no small larvae recorded over that period. Medium larvae were not present in September, and large larvae were not found in August and September. Peaks in small, medium and large larvae generally followed in consecutive months, especially from early October to December 1985.

4.3.2.2 Young umbels with seeds

These umbels were seasonal (Figure 9), and when present, were infested by borers (Figure 11). The only borer found was E. saccharina, and its age structure was similar to that found in young umbels, with no pupae and empty pupae found, less than 1 large larva per 100 umbels, between 1 to 3 small larvae per 100, and from 1 to 5 medium larvae per 100 respectively (Figure 15). Populations were generally higher during early spring in these umbels (October to November 1985, and September to October 1986; Figure 15) than in plain young umbels (Figure 14). During September 1986, small and medium larvae were found in the former.

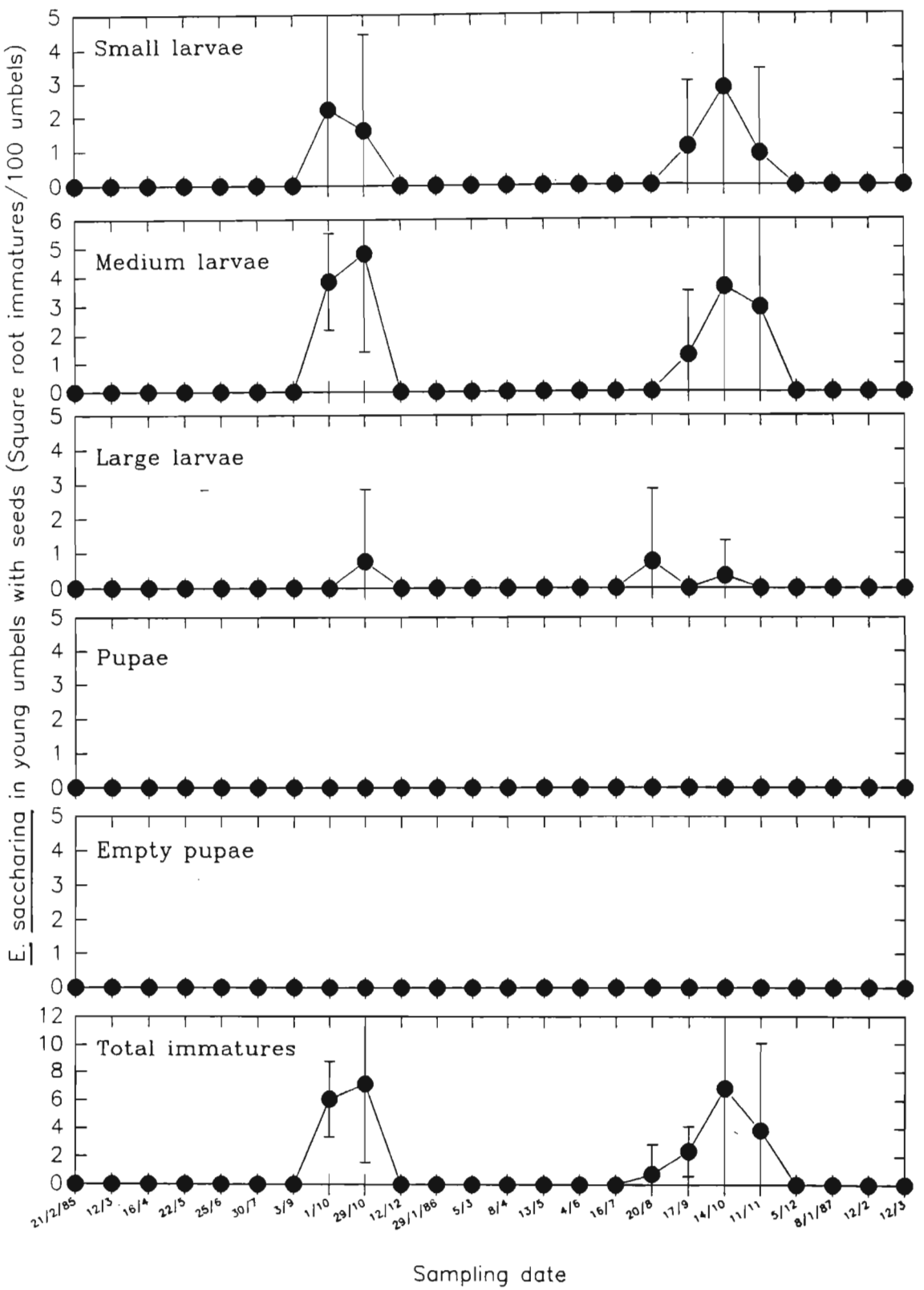


Figure 15: Age structure and population fluctuations of different aged immature life stages of E. saccharina found in young umbels with seeds sampled during the study period (I = 95% confidence limits).

4.3.2.3 Mature umbels

This age-class was most heavily attacked by borers, and had highest populations of immature E. saccharina life stages of all umbel types sampled(Figure 16). This was not surprising, as mature umbels comprised 60% of the total sampled during the study period (Figure 5).

During the first spring and summer period (October to March 1985), the total immature population also peaked, but at a very much higher level (16 per 100 umbels) than those found in young umbels. During autumn and winter months, populations were significantly lower (4 to 8 per 100 umbels) than summer peaks. No immature stage peak was recorded during the 1986/1987 spring and summer period.

In this umbel type, all immature stages of E. saccharina were present (Figure 16). Very few small instar larvae were found. Significant peaks were recorded in June and July 1985 (just below 2e/100 umbels), and again in February and March 1987 (1e/100 umbels).

Medium instar larvae were more common. Their winter populations remained around 3 per 100 umbels for 1985. They dropped significantly to 1 per 100 in early October 1985. By January 1986 the largest population was recorded (5 per 100 umbels). The population then dropped to 1 per 100 by May 1986, where it remained until December 1986 and January 1987 when it increased significantly (at 95% confidence levels) to 3 per 100 umbels. The population level of this class of E. saccharina larva was significantly higher (at 95% confidence levels) during the first year of sampling than in the second (Figure 16). However, population trends during both years were similar, with fewer medium larvae collected during winter months, and with populations building up in spring and summer months.

Populations of large larvae peaked at the same time as those of small and

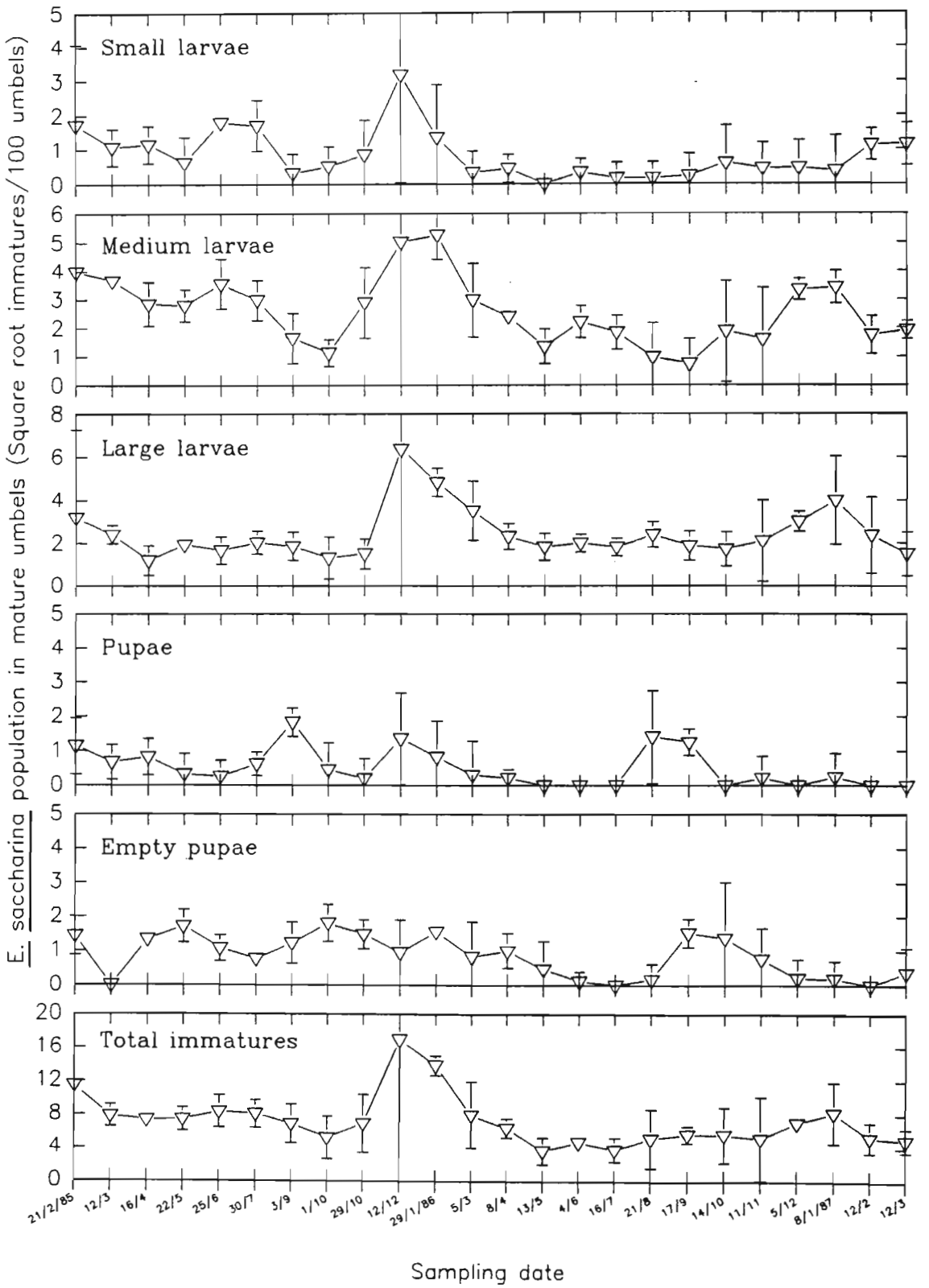


Figure 16: Age structure and population fluctuations of different aged immature life stages of E. saccharina found in mature umbels sampled during the study period (I = 95% confidence limits).

medium larvae. Six per 100 umbels were recorded in December 1985 and January 1986, which was significantly higher than the population recorded during preceding and succeeding autumn and winter months (Figure 16). The second summer peak was lower than the first. There was no significant difference in populations collected between the two years, however.

The pupal population was as low as that of small larvae. It peaked in September 1985 and 1986, reaching 2 per 100 umbels searched. This was significantly higher than the preceding autumn and winter months of both years. Peaks of just over 1 per 100 umbels recorded in December 1986 and January 1986 had very large confidence levels assigned to them, and can thus be disregarded as being not significantly different from the generally lower levels (less than 1 per 100 umbels) recorded during intervening periods. From May until July, October and December 1986, and February and March 1987, no pupae were found in mature umbels searched. Numbers of pupae found in August and September of the first year of sampling were in most cases significantly more than those found during the second year.

Empty pupae never exceeded 2 per 100 umbels, and highest and lowest numbers were always collected one month after peaks and troughs of unemerged pupae respectively (Figure 16). One would expect to find a correlation of peaks for successively older immature stages found as one sampled through seasons. This is not apparent in this umbel type.

4.3.2.4 Mature umbels with seeds

Figure 17 shows that E. saccharina immature stages were found in this class one month after the first umbels with seeds became apparent (Figure 7). Peak immature populations occurred in October 1985 and 1986 (7 per 100 umbels in both years). Even though umbels with seeds were present from December 1985 to April 1986, and in January and February 1987 (Figure 7), no E. saccharina immature stages were found (Figure 17).

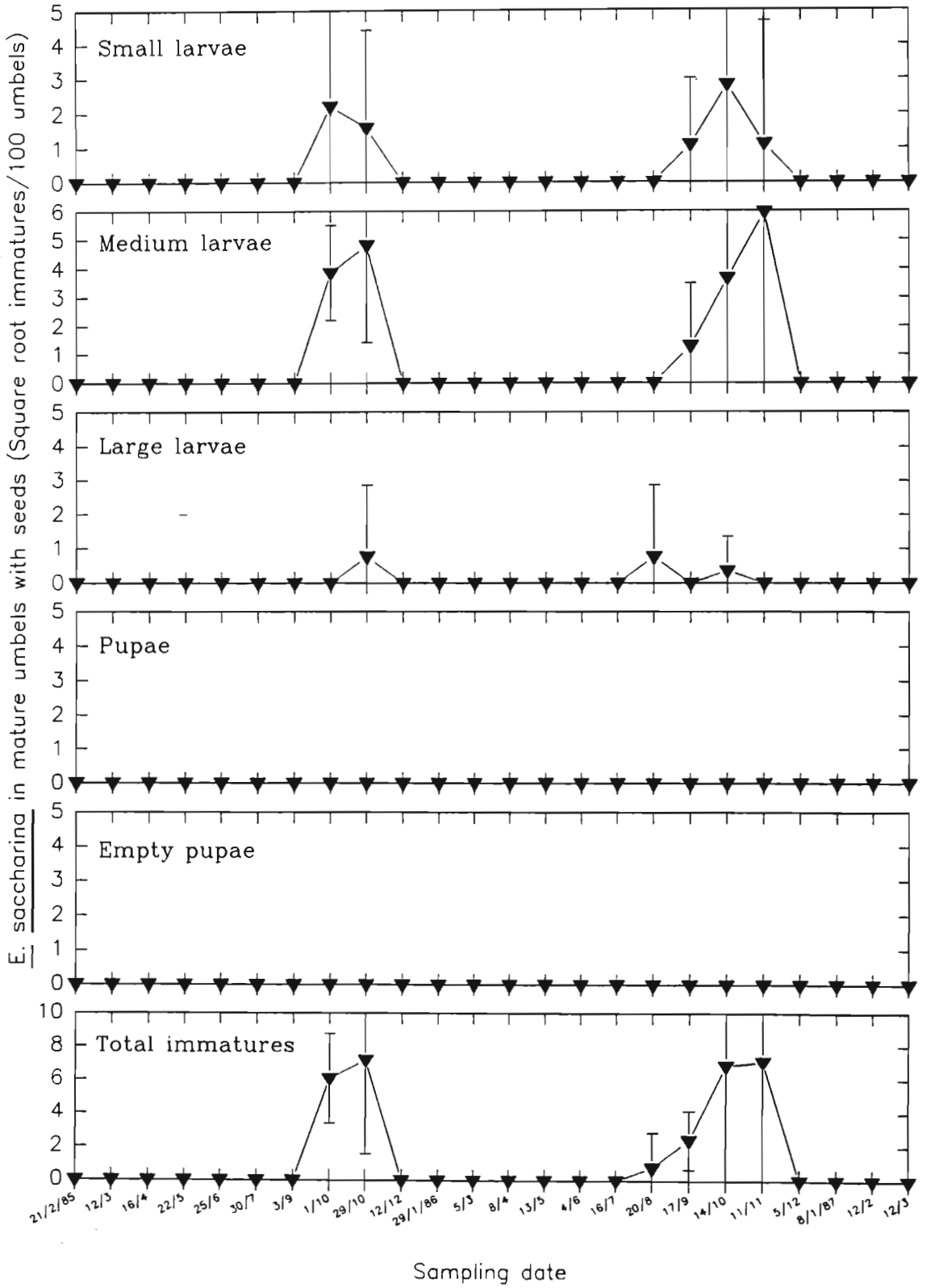


Figure 17: Age structure and population fluctuations of different aged immature life stages of E. saccharina found in mature umbels with seeds sampled during the study period (I = 95% confidence limits).

It appears that immature populations in these umbels peaked before those found in mature umbels (Figure 16). This is not the case though, as immature populations in mature umbels with seeds (Figure 17) increased only to levels of immature stages found in mature umbels at that time (Figure 17). There were no significant differences between the two populations at similar times during the year.

As was the case in the two categories of young umbels (Figures 14 and 15), no pupae or empty pupae were found (Figure 17). Populations of large instar larvae were very low (1 per 100 umbels at the end of October 1985 and end of August 1986, and less than 1 per 100 in October 1986).

Medium larvae were the greatest contributors to the population. At the end of October 1985 their population stood at 5 per 100 umbels, which again was no different to similar populations at the same time in mature umbels.

Small instar larvae peaked a month before peaks of medium instar larvae (Figure 17) in both years sampled, reaching 3 per 100 umbels on both occasions. This type of growth is expected. However, absence of peaks after the same time period in the large larval population is puzzling, as is the absence of pupae.

4.3.2.5 Mature umbels with seeds shed

All immature stages of E. saccharina were found in these umbels (Figure 18). When the first umbels with shed seeds were found in October 1985 and December 1986 (Figure 7), resident immature stages were present (Figure 18). The population of immature stages peaked at the same time (Figure 18) as those in mature umbels (Figure 16). This was not unexpected as the proportion of umbels with shed seed was greatest at these times (Figure 7). However, total immatures found over these periods were significantly fewer in mature umbels with shed seeds (Figure 18), than in those without (Figure 16).

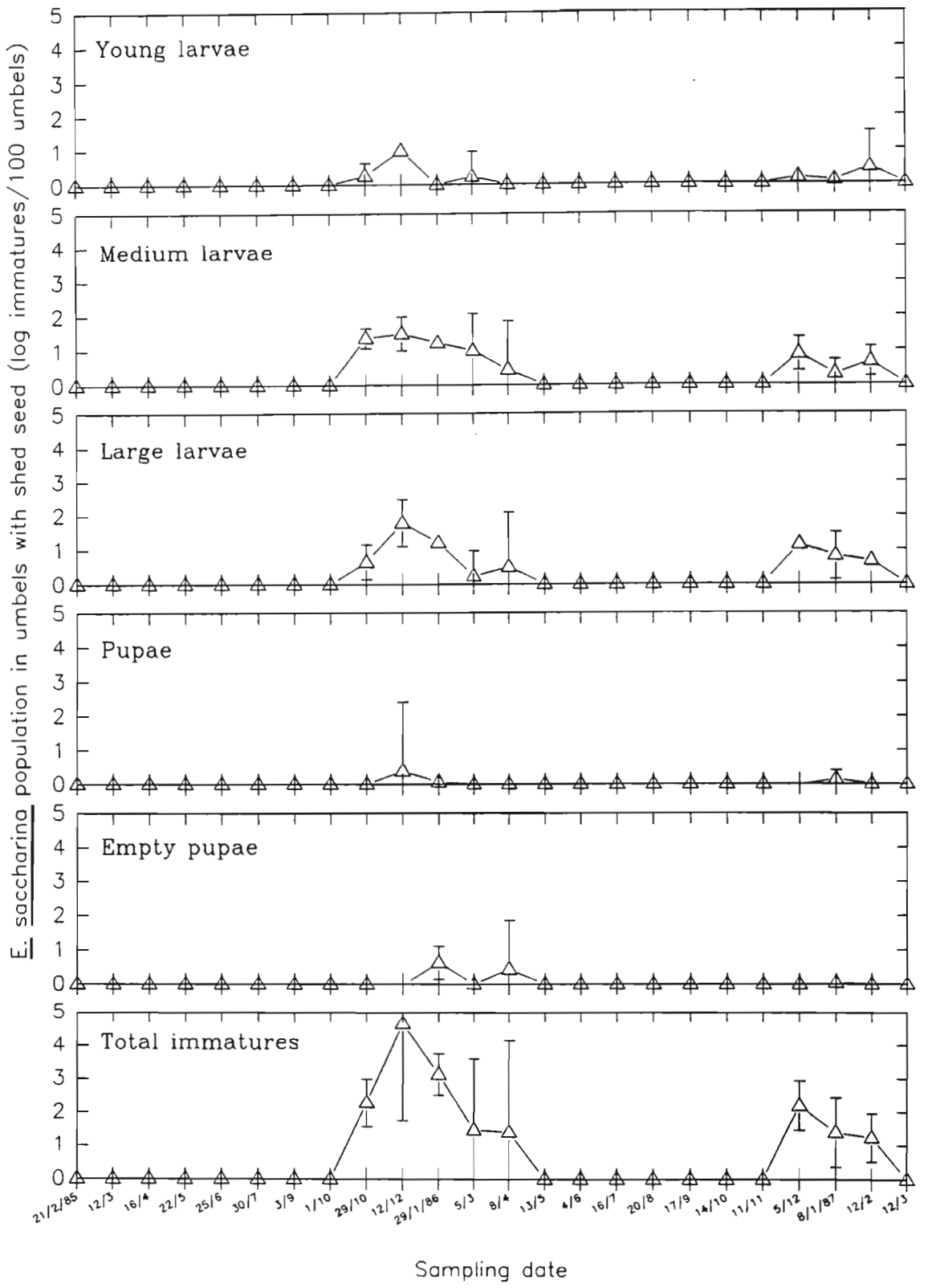


Figure 18: Age structure and population fluctuations of different aged immature life stages of E. saccharina found in mature umbels with shed seeds sampled during the study period (I = 95% confidence limits).

Even though their populations were very low, the presence of pupae (less than 1 per 100 umbels in December 1985 and early January 1987) and empty pupae (in January and early April 1986, Figure 18) indicated that this umbel type was older than mature umbels with seeds. This is supported by the significantly greater numbers of larger instar larvae found. Similar numbers of medium larvae were found, but young larval populations never exceeded 1 per 100 umbels (December 1985, Figure 18), another indication of the age of umbels.

4.3.2.6 Old umbels

All immature stages of E. saccharina were found in this age class. The population of total immatures followed that recorded in mature umbels, with a peak in population of 7 per 100 umbels during the summer of 1985/86 (December to April, Figure 19). This was significantly higher than in the period preceding this summer (3 per 100), and at certain periods succeeding that summer (2 per 100; Figure 19). Interestingly, the high summer peak was not recorded early in 1985, nor in the summer of 1986/87.

The age structure of immatures found here was opposite to that found in young umbels. Pupae and empty pupae made up the bulk of immatures found, right through the study period. Following the summer peak of 3 per 100 umbels, pupal numbers dropped, and no pupae were collected after April 1986, except for 1 per 100 in August 1986 (Figure 19). During the winter period preceding the summer peak, pupae were never at a level greater than 1 per 100 umbels. The peak of empty pupae occurred one month after the peak of pupae (Figure 19). More empty pupae than live pupae were always found, even during the second year of sampling when no live pupae were found.

Larval populations were generally lower than in greener living umbels. Very few young larvae were found (less than 1 per umbel), and these were found on only four occasions: February, June-July and end October 1985, and early November 1986 (Figure 19).

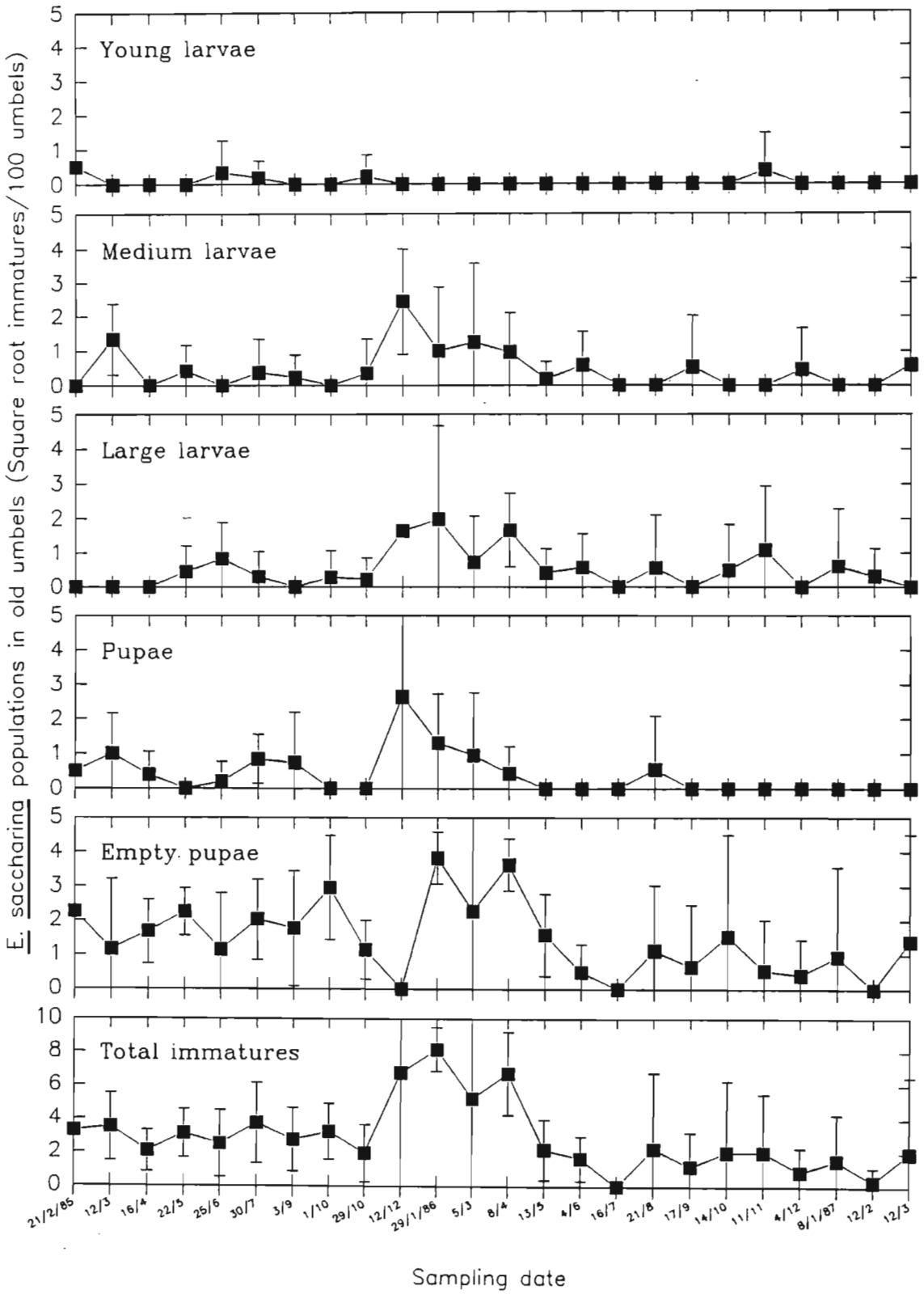


Figure 19: Age structure and population fluctuations of different aged immature life stages of E. saccharina found in old umbels sampled during the study period (⌶ = 95% confidence limits).

The medium instar population peaked one month after young instar peaks (1 per 100 umbels in March, <1 per umbel in July, 3 per 100 umbels in early December 1985 and <1 per umbel in December 1986). The summer period of 1985/86 was when this age class was most abundant (>1 per 100 umbels).

Populations of large larvae generally peaked one month after medium instar peaks were recorded: 1 per 100 umbels in June 1985, 2 per 100 in January 1986, and the following small peaks of not more than 1 per 100 in August, November 1986 and January 1987. None of these differences was significant.

4.4 DISCUSSION

4.4.1 Impact of E. saccharina on C. papyrus umbels

The historical study of Weber (1942) recognised that C. papyrus umbels would have a unique arthropod fauna. He hypothesised that umbels provided an ideal habitat for a variety of insects because they formed a "platform" which allows free passage of arthropods between one umbel and another. This, however, only refers to mature umbels. Thornton (1957) realised that all types of umbel formed habitats, and he followed the faunal succession through young, mature and old umbels. However, most of the arthropods he looked at were sap suckers or predators.

The present study showed that E. saccharina occurred and fed on all umbel stages, from young below the mature umbel canopy through the mature stage to the senescent stage. This borer therefore did not only respond to the continuous spatial habitat which mature umbels provided, but also exploited young umbels. As E. saccharina attacked C. papyrus rhizomes (Conlong, 1990), it is not surprising that young umbels were chosen as suitable oviposition sites, because between their rays, they provide concealed oviposition conditions favoured by E. saccharina (Waladde, 1983).

It is well known that phytophagous insects respond to nutrient status of plants (Mc Neill and Southwood, 1978; Crawley, 1989). Droughted plants, or plants stressed in other ways, are known to be prone to insect attack because of a change in their nutrient status (Mattson and Haack, 1987). Atkinson and Nuss (1989) demonstrated the difference in growth rate of E. saccharina in stressed and unstressed sugarcane. The latter food source allowed E. saccharina to develop more slowly than in the former, because the nutrients in the latter were not as freely available as in the former. In addition, Carnegie (1981) has implicated excess nitrogen fertilizer applications with increased E. saccharina populations in sugarcane.

The relationship between E. saccharina damage and C. papyrus nutrient status, especially nitrogen, illustrates the above clearly. A number of authors have analysed different living portions of C. papyrus plants to determine nutrient budgets and flow for various limnological studies. Others have more recently analysed the component parts of C. papyrus for nutrient availability for insects. Nitrogen in particular, is important for insect nutrition (Mc Neill and Southwood, 1978), and the higher nitrogen content of umbels, compared with the culm, can increase their use by insects. Table 3 summarises the nitrogen contents of components of C. papyrus as determined by various authors.

Atkinson (1980) identified feeding sites of E. saccharina on its indigenous cyperaceous hosts as being in peduncles of inflorescences (= umbels), and beneath bracts of rhizomes. This was confirmed by Conlong (1990), who found E. saccharina in umbels and rhizomes (when these were not submerged) of C. papyrus. Further, Conlong (1990), after detailed examination of many umbels, illustrated that E. saccharina adult females laid eggs on papery bracts at the base of mature umbels and also in young umbels which had not opened. This cryptic oviposition behaviour is controlled by sensillae on the ovipositor of the female, which stimulate inhibition of oviposition unless the ovipositor is in a narrow hidden place (Waladde, 1983). Upon hatching, young larvae bored into basal portions of rays adjacent to bracts on which eggs were laid. As larvae

grew too big for rays, they bored into the top of the culm, in the meristematic area of ray bases. Borings were hardly much larger than larvae found in them. E. saccharina were never found in supporting tissue of the culm itself. This supporting tissue also formed the inner core of the rhizome. A softer outer core

Table 3: The nitrogen content (% dry weight) of components of Cyperus papyrus, as determined by various authors.

Author	Umbels			Culm	Rhizome	
	Young	Mature	Old		Cortex	Medulla
Lind & Visser (1962)		1.71		0.49		
Gaudet (1977)		1.74			1.29	
Atkinson & Nuss (1989) Dried swamp 22/5/84.	2.5	2.37	1.77		2.82	
Wet swamp 22/5/84	1.81	0.85			1.17	
Dried swamp 3/7/84	2.46	1.82	1.7		2.07	
Wet swamp 3/7/84	1.68	1.29	0.63		1.17	
Conlong (1990)					1.37	0.49

was found in the rhizome from which rootlets and bracts developed. E. saccharina larvae were found only in this outer region of the rhizome (Conlong, 1990). The boring sites described are regions of high nitrogen content (Table 3) and confirmed the preference of E. saccharina larvae for high nutrient areas as feeding sites. However, because rhizomes were often flooded, E. saccharina impact and population fluctuations on umbels only were followed.

The higher levels of damage recorded during the first full summer season compared to the second summer season, in all umbel types, was a consequence of the drought experienced during the first year. For the period October 1985 to March 1986, rainfall was considerably below the long term mean for five of

the six month period (Chapter 2). In the similar period of 1986/87, rainfall was below average for only three months, and very considerably higher than the long-term mean in the remaining months (Chapter 2). It is well known that plants not subjected to stress are less favoured as feeding sites than plants under stress (Mattson and Haack, 1987). The above results substantiate this. The sudden improvement in food quality of umbels, as a consequence of drought, could additionally have triggered the outbreak of E. saccharina which caused the increased damage measured, thus inflating the rate of increase beyond the point at which E. saccharina escaped natural enemy control (Crawley, 1989).

4.4.2 Age structure and population fluctuations of E. saccharina in C. papyrus umbels

All stages of umbels found in the C. papyrus standing crop were attacked by E. saccharina. The summer population peak of immature stages reported by Conlong (1990) occurred in all umbel types sampled. However, not all stages were present in the different umbel stages.

The populations found in the young umbels (both with and without seeds) were indicative of new infestations. Very few empty borings were found, and immature stages comprised mostly the smaller and medium size larvae. No pupae or empty pupae were found.

This is not surprising, as Thompson (1976) stated that C. papyrus umbels have an "active" life of 100 days. Similar measurements were made by Breen and Stormanns (1989). Culm initiation to maximum culm height in the canopy took 55 days. After a further 45 days umbels started to die. Senescence occurred rapidly after 100 days. Their study suggested that about half the life span of the culm and umbel, as it grew to reach the canopy (which intercepts 90% of incident solar radiation), was spent in a suboptimal environment for photosynthesis, and the remaining half in the canopy, a maximum period of 120

days. As their study took place in a C. papyrus swamp close to that of the present study area (27° 30'S, 32° 15'E), it is reasonable to assume that similar growth periods of culms and umbels could be expected.

Atkinson and Nuss (1989) determined that the length of the larval and pupal period of E. saccharina (i.e. from egg hatch to emergence from the pupa) in unstressed sugarcane (0.145% N) took 80 days for males, and 91.4 days for females. In stressed cane (0.218% N), life cycles were much shorter, taking 49.7 days for males and 55.6 days for females. Under ambient temperature conditions, the egg stage would probably take 10 days. Also, as no young larvae or eggs were found on the very tightly packed young umbel spears of about 20 days old, which had emerged from rhizomes (leaving a period of about 35 days for E. saccharina to exploit), it is reasonable to assume that young umbels developed too quickly to allow development of E. saccharina pupae. These would appear only when umbels were mature. The higher (approximately 10%) nutrient content of the umbels (Table 3) compared to stressed sugarcane (Atkinson and Nuss, 1989), would have allowed the population in umbels to grow at a faster rate (Crawley, 1989). However, even this faster growth-rate is probably insufficient to allow pupal development in young umbels, as degree day determinations show (see below).

E. saccharina development through the egg stage and to the medium or early large instar larval stage, requires 423 degree days. If this is converted to the number of days needed (40) to reach these stages at the study site during November and December (when one would expect fastest growth because of warmer temperatures) it is evident that young umbels reached maturity and the canopy of the C. papyrus stand before the E. saccharina population reached maturity.

Mature umbels, which were at least 55 days old (Breen and Stormanns, 1989), had all life stages of E. saccharina present, including pupae and empty pupae. The degree days needed to complete development right through to adults were

encompassed by the living period of this umbel type, which is 120 days (Breen and Stormanns, 1989). The presence of small larvae in these mature umbels also indicates that they are suitable for oviposition by female E. saccharina. The remaining living period of this umbel type was suitable for completion of the major portion of the borer's life cycle.

As umbels aged, populations of E. saccharina diminished. Their suitability for oviposition decreased, since very few small larvae were found, and their suitability as a food source decreased, as illustrated by the large proportion of empty borings. The most common immature stage found was empty pupae. The few living large larvae and pupae found were the slower developers from mature umbels.

The influence of umbel age on population structure is further illustrated by populations found in mature umbels with seeds, and those with shed seeds. Chapter 3 showed that the former appeared before the latter, and were thus younger. The E. saccharina population was also young, as no pupae or empty pupae were found in the former, while the latter umbel type did contain pupal stages of the borer population.

However, as young, mature and old umbels were present throughout the sampling period, and E. saccharina immature stages were present at all times, the multivoltine nature of the borer population was illustrated.

4.4.3 Determinants of population fluctuations

The above two sections illustrate that E. saccharina larvae use high nutrient areas of C. papyrus as boring sites, and as a result, do not bore extensively once in these areas. These sites, because of the many rays of the umbels and bracts covering the rhizomes, provide oviposition sites suited to the oviposition behaviour of E. saccharina adult females.

In addition, all umbel stages are attacked by E. saccharina. Young umbels, because of their rapid rate of development, do not allow resident larvae to develop into pupae while they are still young and thus below the canopy of mature umbels. The pupal stage is reached only once young umbels have developed into the mature stage. Adult E. saccharina thus emerge from pupae in the canopy. This may account for the nightly mating behaviour of male and female E. saccharina on the canopy of green sugarcane leaves observed by Atkinson (1980). Mature umbels are still available for another generation of E. saccharina to develop before the umbel dies, as the presence of small larvae as well as pupae in this umbel class indicates. Once the mature umbels start dying, E. saccharina females no longer oviposit on them, and the resident larval population are generally either large or have already pupated, and/or adults have emerged from pupae.

The system just described would explain the E. saccharina population fluctuations described if C. papyrus was an annual plant, with young umbels developing in spring, maturing in summer and then dying off in autumn and winter. However, in Chapter 3 it was shown that this is not the case, as at any one time during the sampling period, there were always young, old (each making up 20% of umbels found) and mature umbels (60% of umbels found). The second option explaining the population fluctuations would be that the E. saccharina population was univoltine, with eggs being laid in early spring, maturing into larvae and then pupae in late summer, moth emergence occurring in early autumn and terminating in winter. However, this Chapter showed that this was not the case, as all life stages of E. saccharina were found at any one time. The E. saccharina population in umbels was thus multivoltine.

It is therefore surprising that the population of E. saccharina did not maintain the very high levels recorded at the commencement of the study, and also that it did not increase to the same level in the second summer sampled. The latter has to some extent been explained by the higher rainfall and thus better growing conditions experienced during the second season sampled, but rainfall itself

could not explain the sudden decrease in E. saccharina levels in the first summer sampled.

Further anomalies arise when light trap catches of E. saccharina adults from natural host plants and sugarcane are compared with E. saccharina immature stage fluctuations recorded during this project. Since 1969 SASEX has used Robinson-type light traps to monitor the presence of various crop spoilers at various locations in the sugar belt (Carnegie and Leslie, 1990). Atkinson (1982) reported three peaks of E. saccharina adults per year caught in these traps from sugarcane: in March/May, September and November/December. These peaks are clearly shown by Carnegie and Leslie (1990) for traps situated close to natural host plants and traps close to sugarcane. Means of monthly catches from all traps in sugarcane, and all traps in natural host plants, however, show that catches from sugarcane were generally ten times higher than catches from natural host plants. The largest peak commonly occurred in March/April, next highest in November/December and the lowest peak in September in both sugarcane and natural host plants. It is thus evident that these peaks are a reflection of natural population fluctuations, and not as a result of sugarcane crop management (Carnegie and Leslie, 1990). Further evidence that these are natural populations comes from recently established temperature thresholds and degree day development times for eggs, larvae and pupae (5.5°C, 118°D; 10.4°C, 618°D and 11,3°C, 160°D respectively. M. Way, 1994, pers. comm.). When these were fitted to meteorological records obtained from the Riverview Meteorological Site (which is close to the study site), using the April peak in adult numbers as starting point for oviposition, it was calculated that moths again would be produced in September and again in December and also again in April. Three generations of E. saccharina are thus produced per year.

Because the September peak is generally so small, it has become customary to speak of two peaks per year, in April and November (Carnegie and Leslie, 1990). However, this study shows that the total E. saccharina immature population in C. papyrus only showed the November population peak (Conlong, 1990). Figure

16, which shows the immature stage population fluctuations in the most common mature umbel class reflects a relatively high September pupal peak in both years sampled, and in the first year sampled, a relatively high pupal peak in December. This would more clearly reflect the adult light trap catch peaks. The autumn (April) peak though is still missing.

The life cycle characteristics described above discount the life cycle as a factor determining the population fluctuations recorded, as has the climate. Conlong (1990) has, however, implicated a guild of parasitoids and an entomophagous fungus as effective natural enemies, which initially brought the E. saccharina outbreak recorded in the first summer under control, and thereafter regulated it at a lower level. These interactions are explained in more detail in Chapter 5.

REFERENCES

Atkinson, P.R., 1979. Distribution and natural host of Eldana saccharina Walker in Natal, its oviposition sites and feeding habits. Proceedings of the South African Sugar Technologists Association 53: 111 - 115.

Atkinson, P.R., 1980. On the biology, distribution and natural host plants of Eldana saccharina Walker (Lepidoptera: Pyralidae). Journal of the entomological Society of southern Africa 43: 171 - 194.

Atkinson, P.R., 1982. Phenology of Eldana saccharina Walker in Natal and use of light traps to monitor distribution and abundance. Proceedings of the South African Sugar Technologists Association 56: 90 - 94.

Atkinson, P.R. and Carnegie, A.J.M., 1989. Population dynamics of the sugarcane borer, Eldana saccharina Walker (Lepidoptera: Pyralidae) in Natal, South Africa. Bulletin of entomological Research 79: 61 - 80.

Atkinson, P.R. and Nuss, K.J., 1989. Associations between host-plant nitrogen

and infestations of the sugarcane borer Eldana saccharina Walker (Lepidoptera: Pyralidae). Bulletin of entomological Research 79: 489 - 506.

Breen, C.M. and Stormanns, C-H, 1989. Observations on the growth and production of Cyperus papyrus L. in a sub-tropical swamp. Thirty-fourth Congress of the International Association for Theoretical and Applied Limnology, Munich, 13-19 August, 1989. Unpublished presentation of the Institute of Natural Resources, University of Natal, Pietermaritzburg.

Carnegie, A.J.M., 1981. Combating Eldana saccharina Walker: A progress report. Proceedings of the South African Sugar Technologists Association 55: 116 - 119.

Carnegie, A.J.M., 1982. Current research programme against Eldana saccharina Walker (Lepidoptera: Pyralidae). Proceedings of the South African Sugar Technologists Association 56: 95 - 98.

Carnegie, A.J.M. and Leslie, G.W., 1990. Eldana saccharina (Lepidoptera: Pyralidae): Ten years of light trapping. Proceedings of the South African Sugar Technologists Association 64: 107 - 110.

Conlong, D.E., 1990. A study of pest - parasitoid relationships in natural habitats: An aid towards the biological control of Eldana saccharina (Lepidoptera: Pyralidae). Proceedings of the South African Sugar Technologists Association 64: 111 - 115.

Conlong, D.E., Graham D.Y. and Hastings, H., 1988. Notes on the natural host surveys and laboratory rearing of Goniozus natalensis Gordh (Hymenoptera: Bethylidae), a parasitoid of Eldana saccharina Walker (Lepidoptera: Pyralidae) larvae from Cyperus papyrus L. in southern Africa. Journal of the entomological Society of southern Africa 51: 115 -127.

Conlong, D.E., Graham, D.Y., Hastings, H. and Leslie, G.W., 1984. Rearing parasitoids and their hosts for the biological control of Eldana saccharina Walker (Lepidoptera: Pyralidae). Proceedings of the South African Sugar Technologists Association 58: 159 - 164.

Crawley, M.J., 1989. Insect herbivores and plant population dynamics. Annual Review of Entomology 34: 531 - 564.

Elliott, J.M., 1983. Some Methods for the Statistical Analysis of Samples of Benthic Invertebrates. Freshwater Biological Association Scientific Publication No. 25. Titus Wilson & Sons Ltd, Kendal. ISSBN 0 900386 29 0.

Gaudet, J.J., 1977. Uptake, accumulation and loss of nutrients by papyrus in tropical swamps. Ecology 58: 415 - 422.

Girling, D.J., 1978. The distribution and biology of Eldana saccharina Walker (Lepidoptera: Pyralidae) and its relationship to other stem borers in Uganda. Bulletin of entomological Research 68: 471 - 488.

Jones, M.B. and Muthuri, F.M., 1985. The canopy structure and microclimate of papyrus (Cyperus papyrus) swamps. Journal of Ecology: 73: 481 - 491.

Lind, E.M. and Visser, S.A., 1962. A study of a swamp at the north end of Lake Victoria. Journal of Ecology 50: 609 - 613.

Mattson, W.J. and Haack, R.A., 1987. The role of drought in outbreaks of plant-eating insects. Bioscience 37: 110 - 118.

Mc Neill, S. and Southwood, T.R.E., 1978. The role of nitrogen in the development of insect/plant relationships. In Harborne, J.B. (Ed.). Biochemical Aspects of Plant and Animal Coevolution. Proceedings of the Phytochemical Society Symposium, Reading, April, 1977. Academic Press, London.

Thompson, K., 1976. Swamp development in the headwaters of the White Nile. In Rzoska, J. (Ed.). The Nile, Biology of an Ancient River. W. Junk, The Hague.

Thornton, I.W.B., 1957. Faunal succession in umbels of Cyperus papyrus L. on the Upper White Nile. Proceedings of the Royal Entomological Society of London (a) 32: 119 -131.

Waladde, S.M., 1983. Chemoreception of adult stem-borers: Tarsal and ovipositor sensilla on Chilo partellus and Eldana saccharina. Insect Science and Application 4: 159 - 165.

Weber, N.A., 1942. A biocoenose of papyrus heads (Cyperus papyrus). Ecology 23: 115 -119.

CHAPTER 5

PARASITOIDS AND PATHOGENS OF ELDANA SACCHARINA IN CYPERUS PAPYRUS

5.1 INTRODUCTION

During the early years of the current infestation of southern African sugarcane by Eldana saccharina, it was thought that no parasitoids of this borer existed in Natal (Carnegie, 1974). In addition, in the rest of Africa where this insect was a pest, very few parasitoids had been found (Mohyuddin and Greathead, 1970; Carnegie, 1974; Waiyaki, 1974; Betbeder-Matibet, 1981). These observations were not surprising, because all surveys for natural enemies had been completed in crops where E. saccharina was already a pest, and were of a short term nature (Conlong, 1994).

In 1981, the South African Sugar Association Experiment Station embarked on an intensive biological control programme against this pest. One of the approaches was to search the indigenous host plants of E. saccharina for controlling agents (Conlong, 1990). Investigations of the biology of E. saccharina in Cyperus papyrus soon revealed numerous parasitoids which both depressed the E. saccharina population, and conferred a degree of stability to this depression (Conlong, 1990). Both these characteristics are important factors determining the effectiveness of parasitoids against their hosts (Hassell and Waage, 1984).

Conlong (1990) monitored the population fluctuations of E. saccharina and two indigenous parasitoids, Goniozus indicus Ashmead (Hymenoptera: Bethylidae)(= G. natalensis Gordh, Synonymy by Polaszek and Krombein (1994)), and Orgilus bifasciatus Turner (Hymenoptera: Braconidae) as well as an indigenous entomophagous fungus , Beauveria bassiana (Bals.) Vuill., in the umbels of C. papyrus. He did not, however, analyze the interactions of these natural enemies

in the different umbel types present, nor did he report on all the parasitoids which were found in these situations (Bassus sublevis (Granger), Iphiaulax sp. (Hymenoptera: Braconidae) and Venturia sp. (Hymenoptera: Ichneumonidae) were not common, occurring at low numbers once only during the study, and will thus not be discussed further).

This chapter serves to highlight the effectiveness of natural enemies at locating and successfully parasitising their hosts in different umbel types, which form a spatially and temporarily heterogeneous habitat (Chapter 4). It will also identify reasons behind the ranking of those natural enemies as important in this guild.

5.2 MATERIALS AND METHODS

After separation of umbels found in each quadrat into their different classes (Chapter 3), and collection of different life stages of E. saccharina from different umbel classes (Chapter 4), vials containing borer life stages (or recognisable natural enemy stages) were returned to the laboratory and screened for appearance of other natural enemies.

At completion of emergences of hosts and/or parasitoids, records were collated, and percentage parasitism by different parasitoid and entomophagous fungal species on immature E. saccharina life stages per quadrat calculated. Unknown mortality, i.e. immature stages of E. saccharina which had died either at time of collection, or during screening without apparent cause, were also considered. The means of percentages from each quadrat sampled were obtained, and 95% confidence limits of the mean calculated for each sampling date (Parker, 1973).

5.3 RESULTS

In Chapter 3, the relative proportion of different umbel types to total umbel standing crop was presented and discussed. The young and mature umbel stages bearing reproductive structures (seeds) were identified as being seasonal

and thus only important as a potential food source for E. saccharina during the spring and summer months. E. saccharina, however, did not exploit these umbels any more or less heavily than umbels without reproductive structures (Chapter 4), which were present throughout the year, and thus formed the more stable portion of the habitat. In the presentation of these results, the impact of the more transient umbels with reproductive structures on abundance and effectiveness of natural enemies found attacking E. saccharina will be discussed first, followed by a discussion of the same parameters in the more stable habitat offered by umbels without reproductive structures.

5.3.1 Natural enemy impact on E. saccharina populations in young umbels with seeds

When these umbels were present, they were generally colonised by fewer than eight E. saccharina per 100 umbels. The small and medium instar larvae made up the bulk of the immature stages collected (Chapter 4 and Figure 20).

The major mortality factor of smaller larvae found in this umbel type was unknown. During the first spring period (October 1985) approximately 18% of the larvae found died of unexplained causes, and during the second spring (October 1986) 23% (Figure 20). The small and medium larvae were most affected. No unknown mortality was recorded from the few large larvae found in this umbel type.

Beauveria bassiana was the only identifiable mortality factor. Mortality due to this entomopathogen was 10% during October 1985. No mortality was recorded during the 1986 spring (Figure 21). None of the large larvae collected were attacked.

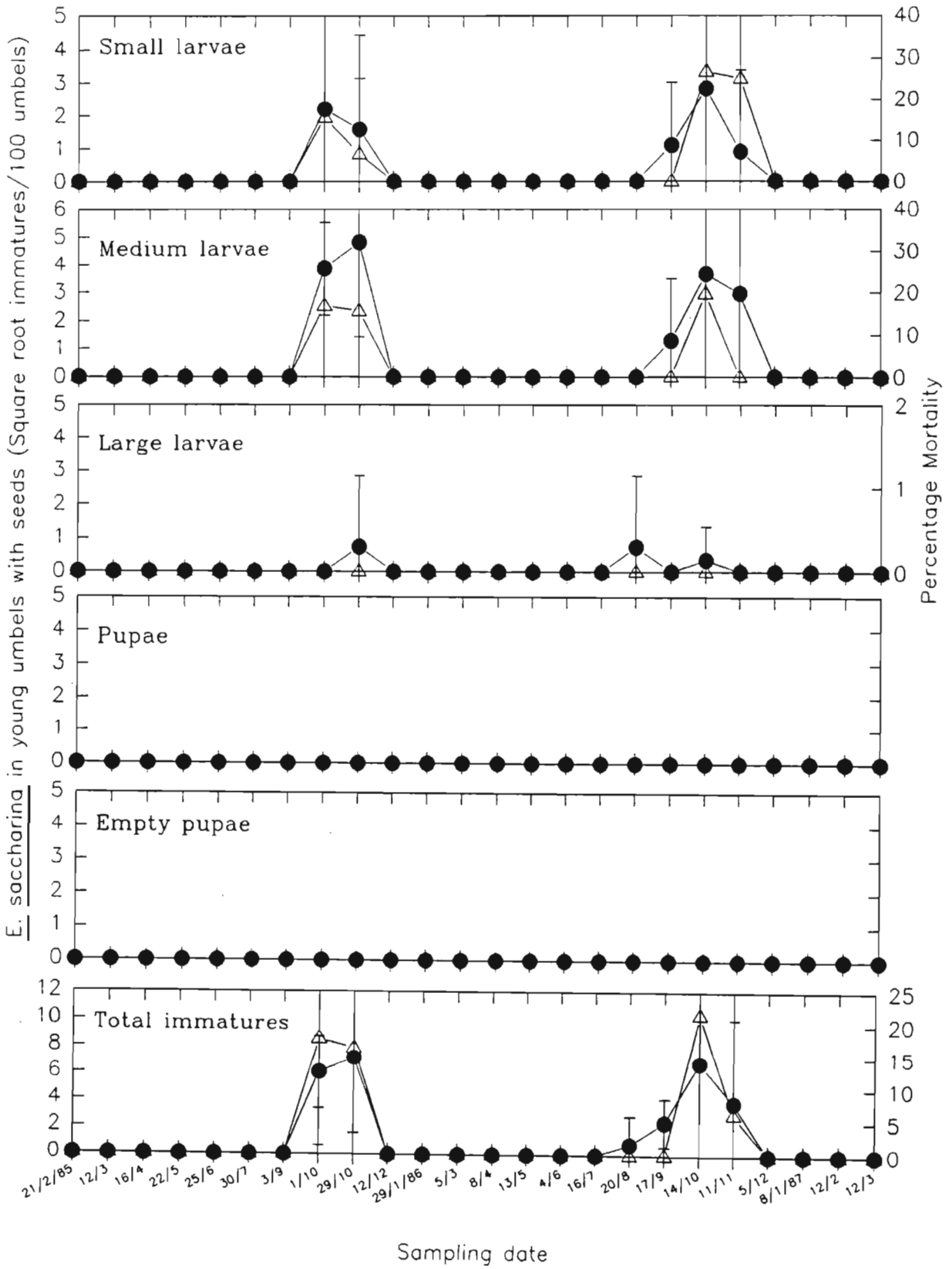


Figure 20: Impact of unknown mortality factors on the E. saccharina immature population in young C. papyrus umbels with seeds (●——● E. saccharina immature population; ▵——▵ Unknown mortality factors; I = 95% confidence limits).

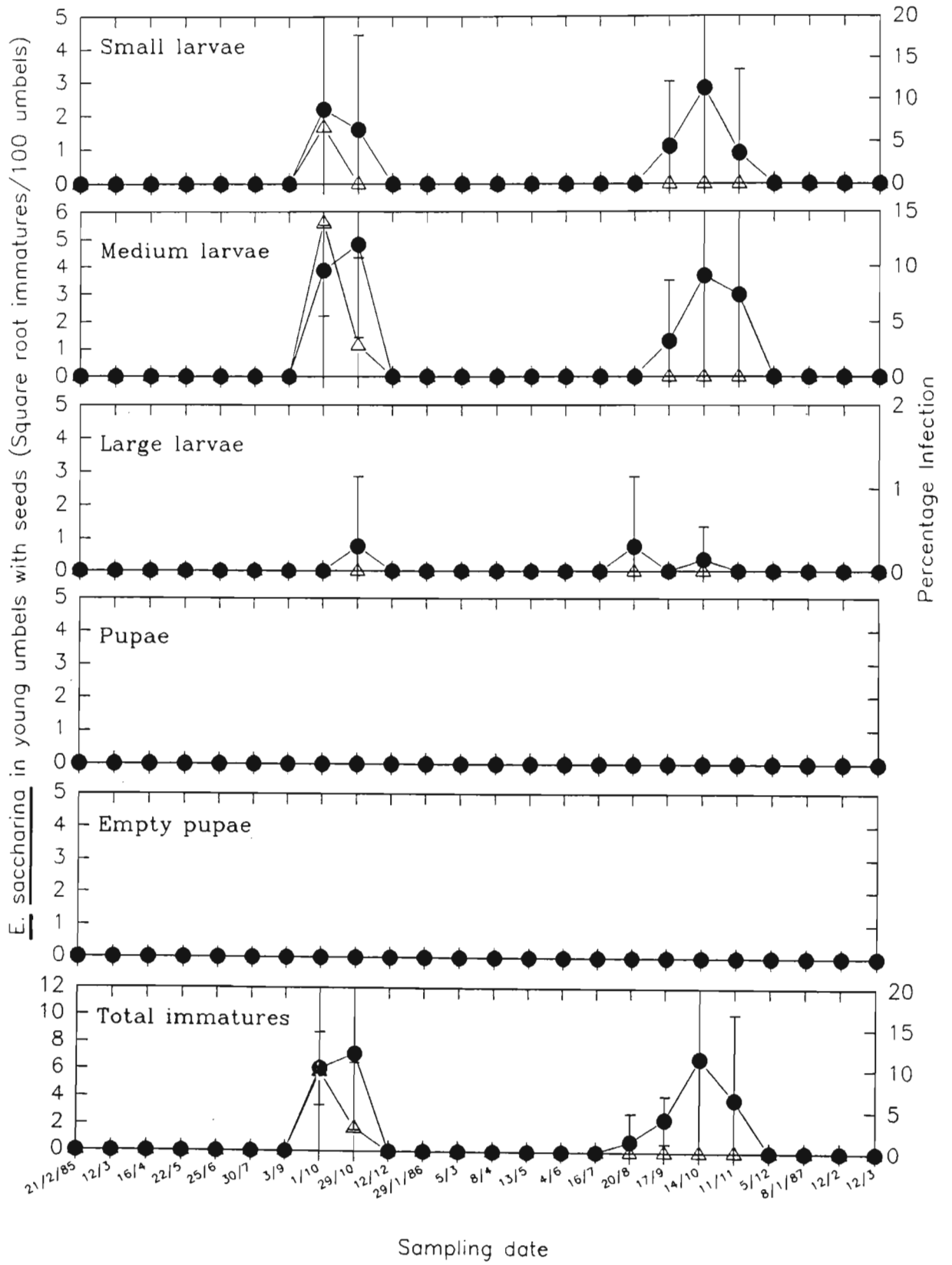


Figure 21: Impact of <u>Beauveria bassiana</u> on the <u>E. saccharina</u> immature population in young <u>C. papyrus</u> umbels with seeds (●——● <u>E. saccharina</u> immature population; ▲——▲ <u>B. bassiana</u> parasitism; I = 95% confidence limits).

5.3.2 Natural enemy impact on E. saccharina populations in mature umbels with seeds

The umbels in this age class are next youngest after young umbels (Chapter 3). This is reflected in the age structure of E. saccharina found, which was not significantly different from that found in the previous umbel age class. Very few large instar larvae were found, and no pupae or empty pupae (Chapter 4).

Unknown deaths of younger larvae were again the largest mortality factor. especially during the 1986 spring period (approximately 30%, Figure 22). During spring 1985 this mortality factor accounted for a maximum of 13% of these stages. The most adversely affected were small larvae, with in excess of 30% dying during both spring periods (Figure 22). Despite the very few large larvae found, those dying of unknown causes peaked at just below 20% in the 1986 spring period (Figure 22).

Beauveria bassiana contributed to 10% of mortality of immature stages found during the first spring sampling period, and a maximum of 5% during the second (Figure 23). Highest mortality (20%) occurred in the small larval category during the 1985 spring. No mortality was recorded in the large larval category, and less than 10% in the medium larval category (Figure 23).

Larval parasitoids were found in this umbel class. The most common was O. bifasciatus, which parasitised less than 5% of the total immature E. saccharina found during spring 1985, but 20% of those found during the second spring (Figure 24). However, the impact of this parasitoid was most obvious on the small larval component of E. saccharina (20% in both spring seasons sampled, Figure 24). Less than 5% of medium instar larvae, and no large instar larvae were parasitised.

Goniozus indicus, although not parasitising many of the total immature E. saccharina life stages in this umbel age class (less than 5%, Figure 25), did have

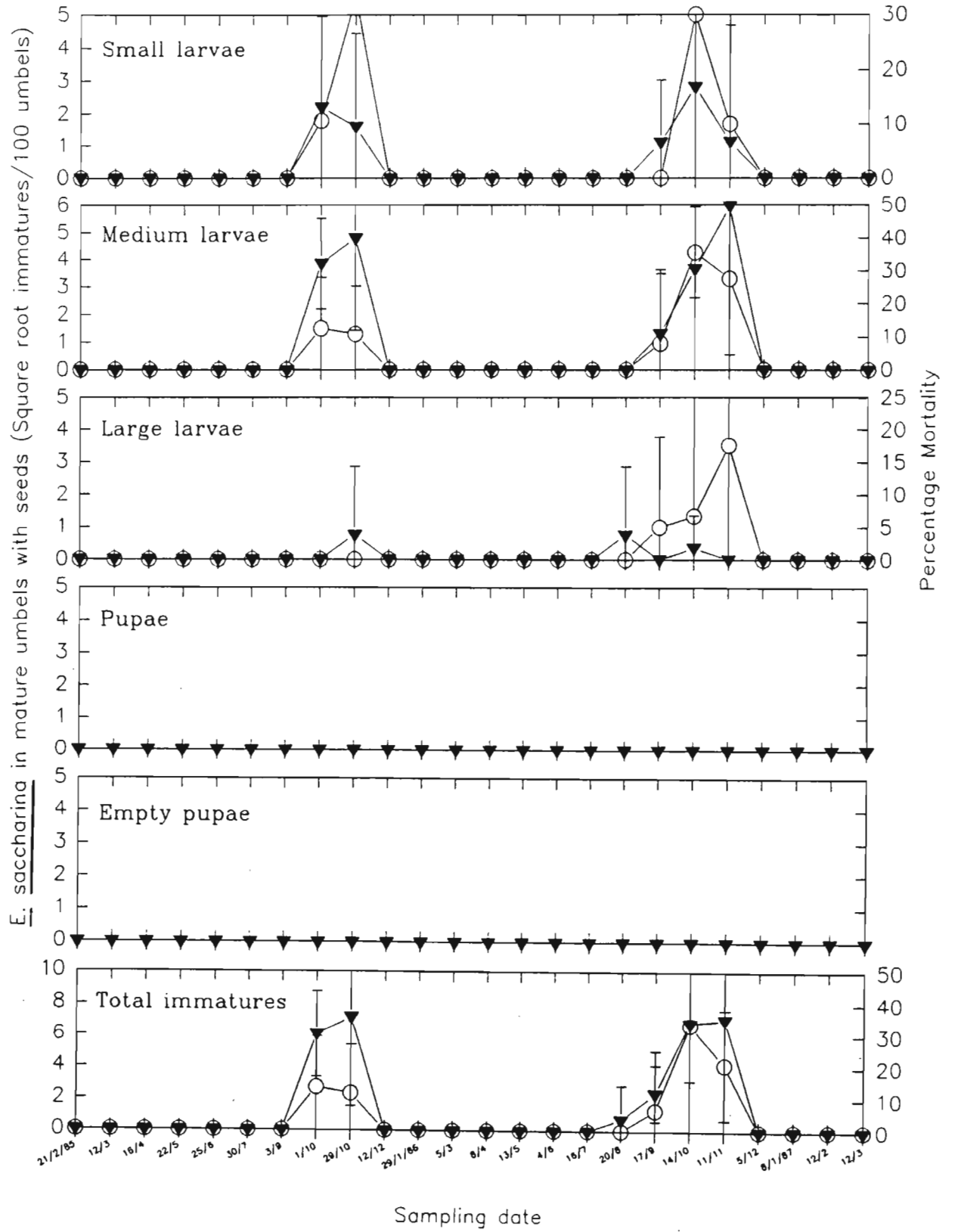


Figure 22: Impact of unknown mortality factors on the E. saccharina immature population in mature C. papyrus umbels with seeds (▼——▼ E. saccharina immature population; ○——○ Unknown mortality factors; I = 95% confidence limits).

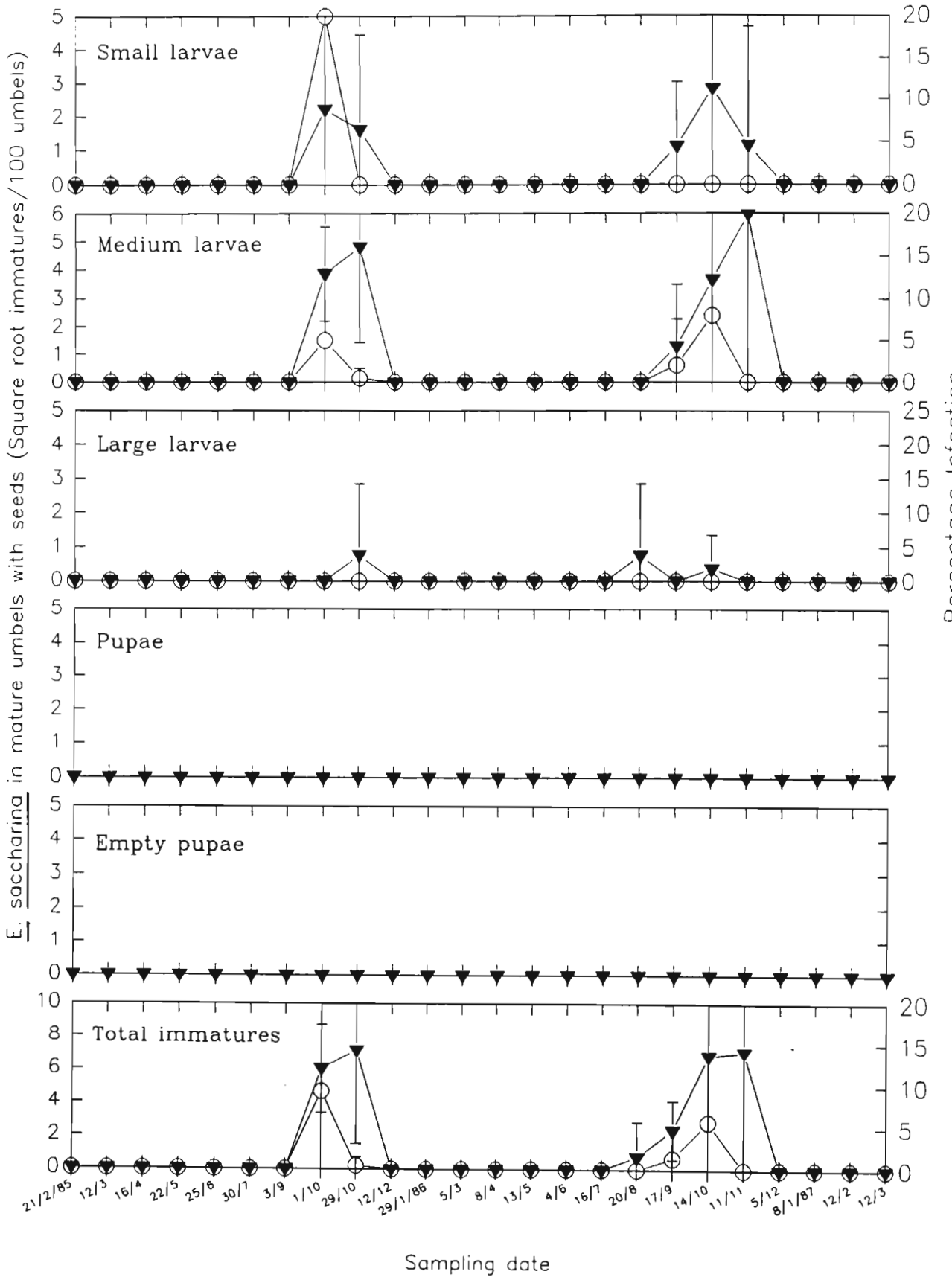


Figure 23: Impact of Beauveria bassiana on E. saccharina immature populations in mature C. papyrus umbels with seeds (▼——▼ E. saccharina immature population; ○——○ B. bassiana parasitism; I = 95% confidence limits).

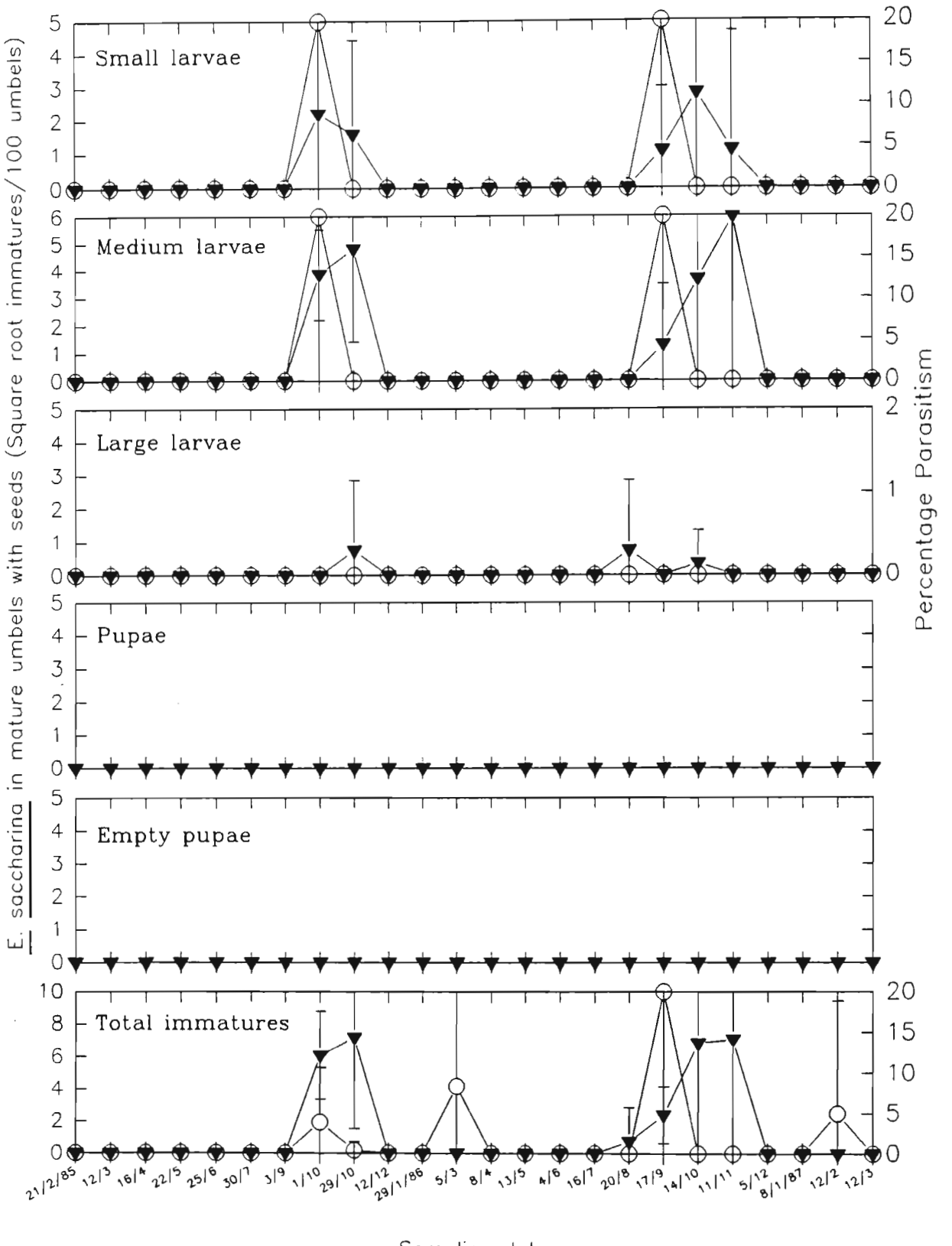


Figure 24: Impact of Orgilus bifasciatus on E. saccharina immature populations in mature C. papyrus umbels with seeds (▼——▼ E. saccharina immature population; ○——○ O. bifasciatus parasitism; I = 95% confidence limits).

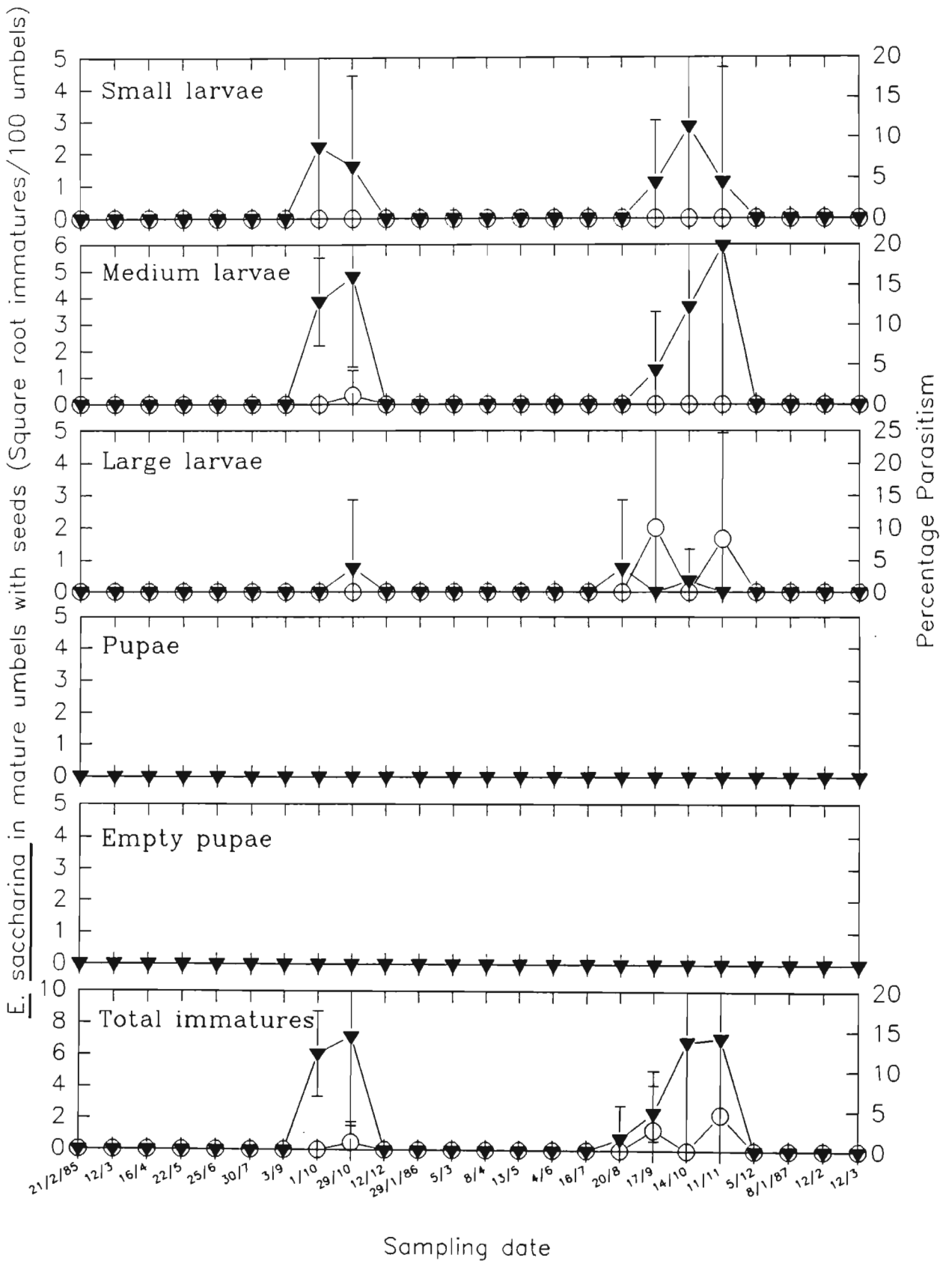


Figure 25: Impact of Goniozus indicus on E. saccharina immature populations in mature C. papyrus umbels with seeds (▼——▼ E. saccharina immature population; ○——○ G. indicus parasitism; I = 95% confidence limits).

more of an impact on the very few large larvae found, with up to 10% of these being parasitised. No small or medium larvae were attacked by G. indicus (Figure 25).

5.3.3 Natural enemy impact on E. saccharina populations in mature C. papyrus umbels with seeds shed

In Chapter 3 it was demonstrated that this was the oldest umbel age class carrying reproductive structures. It also lasted longer, with stages found from early spring through to autumn in both years of the study. The E. saccharina population also reflected the older age of this umbel age class, as pupae and empty pupae were found (Chapter 4, also Figure 26). In addition, the contribution of small larvae to the total immature population was small, while that of large larvae increased.

Goniozus indicus had the greatest impact on immature stages of E. saccharina in this umbel type. During autumn 1986, it accounted for 10% of mortality and in the second autumn (1987), 50% of all immature stages found were parasitised by G. indicus. The most heavily parasitised stage was large larvae, with 20% being parasitised in the first autumn and more than 60% in the second. Just over 2% of medium instar larvae found in December 1986 were parasitised. No parasitism by G. indicus was recorded in the young larvae and pupae categories (Figure 26).

Unknown mortality occurred most frequently in young and medium E. saccharina larvae. In the former, 15 to 25% died in the first flowering season, and a maximum of 50% of the few small larvae found in the second season died in early summer. Similarly, unknown mortality of medium larvae was low during the first flowering season (less than 15%) but much higher during the second season (between 20 and 30%, Figure 27). Six percent of large larvae died of unknown causes in December 1986. In general, this type of mortality accounted for a maximum of 10% of immature E. saccharina stages during the first

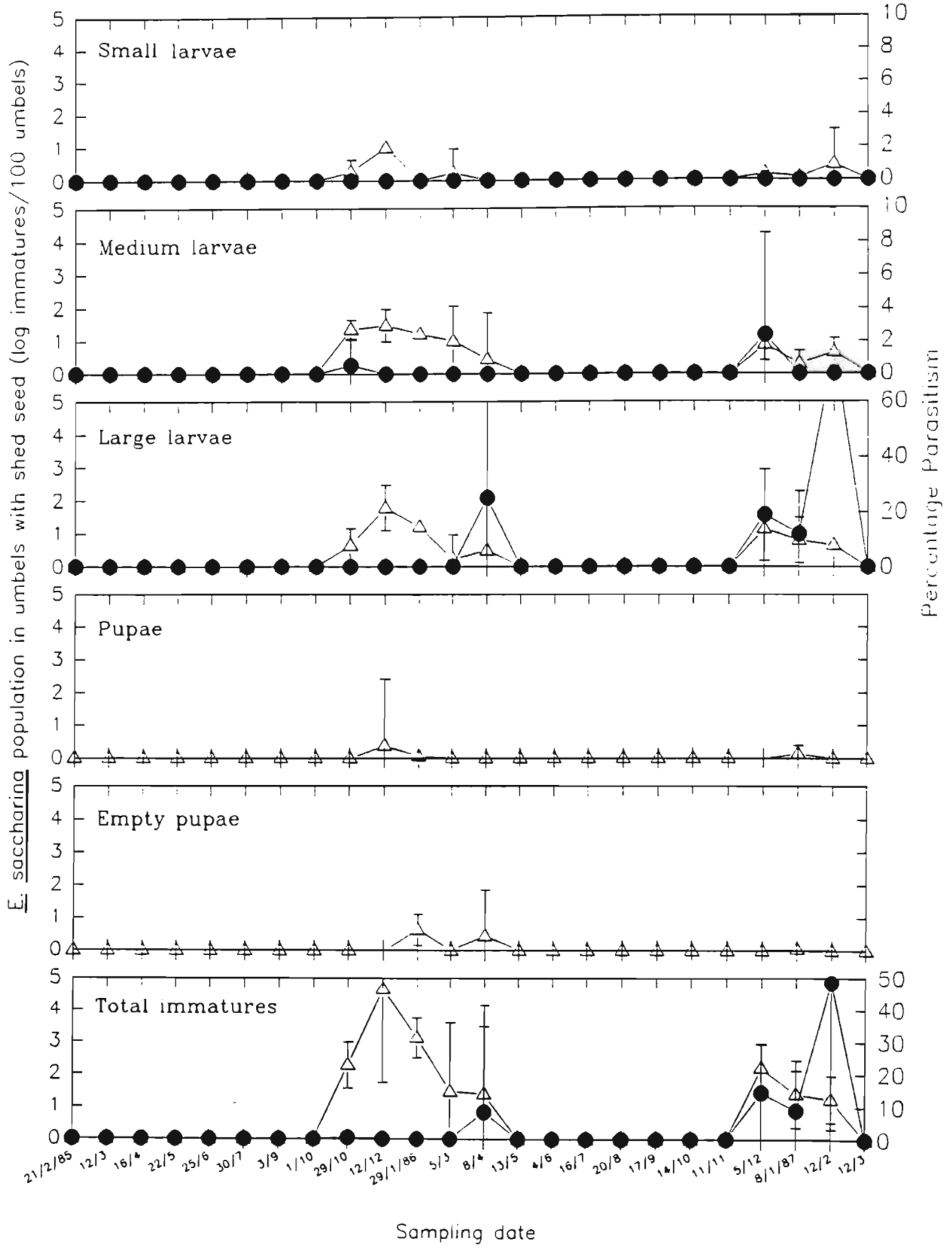


Figure 26: Impact of Goniozus indicus on E. saccharina immature populations in mature C. papyrus umbels with shed seeds (△——△ E. saccharina immature population; ●——● G. indicus parasitism; I = 95% confidence limits).

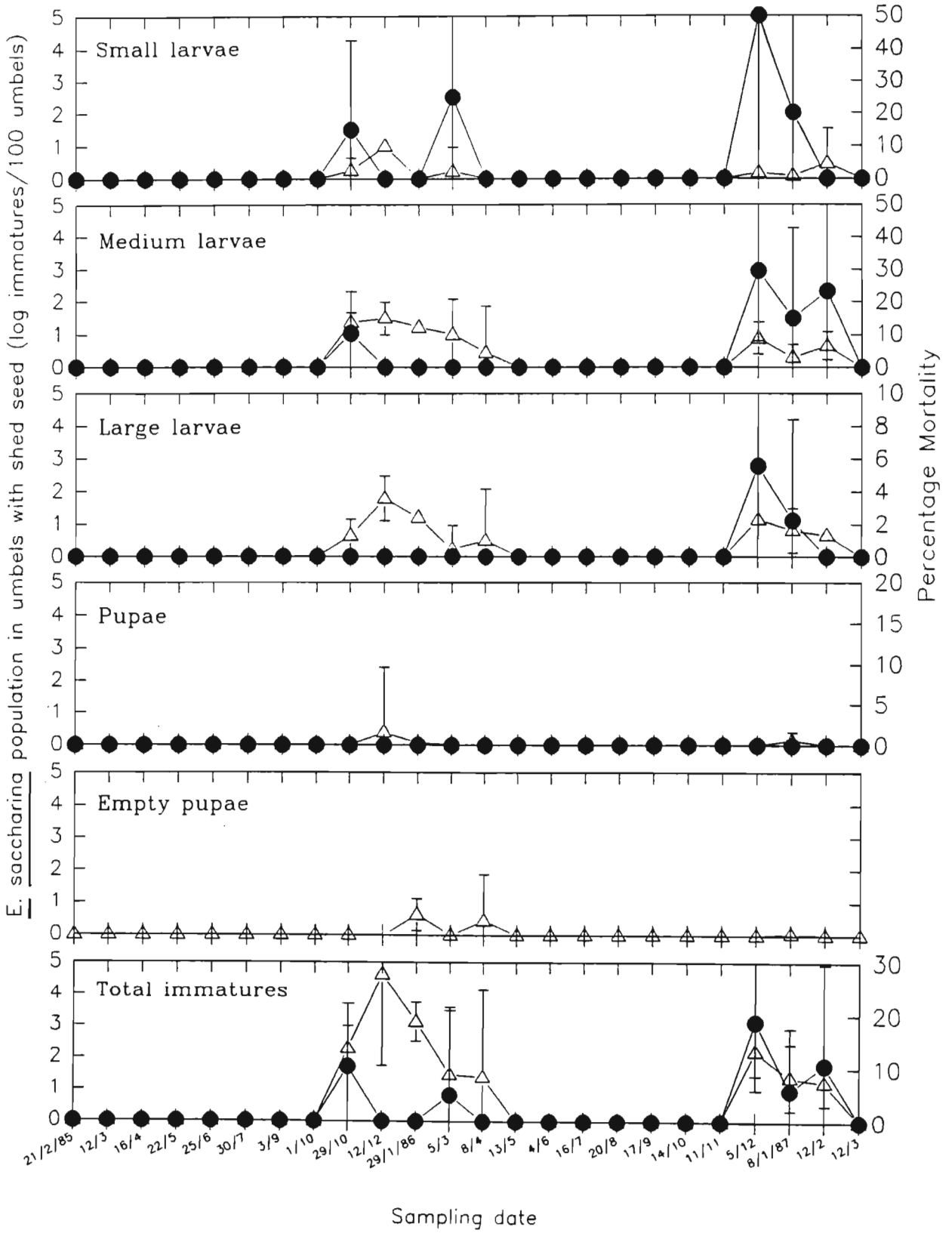


Figure 27: Impact of unknown mortality factors on E. saccharina immature populations in mature C. papyrus umbels with shed seeds (▲——▲ E. saccharina immature population; ●——● Unknown mortality; I = 95% confidence limits).

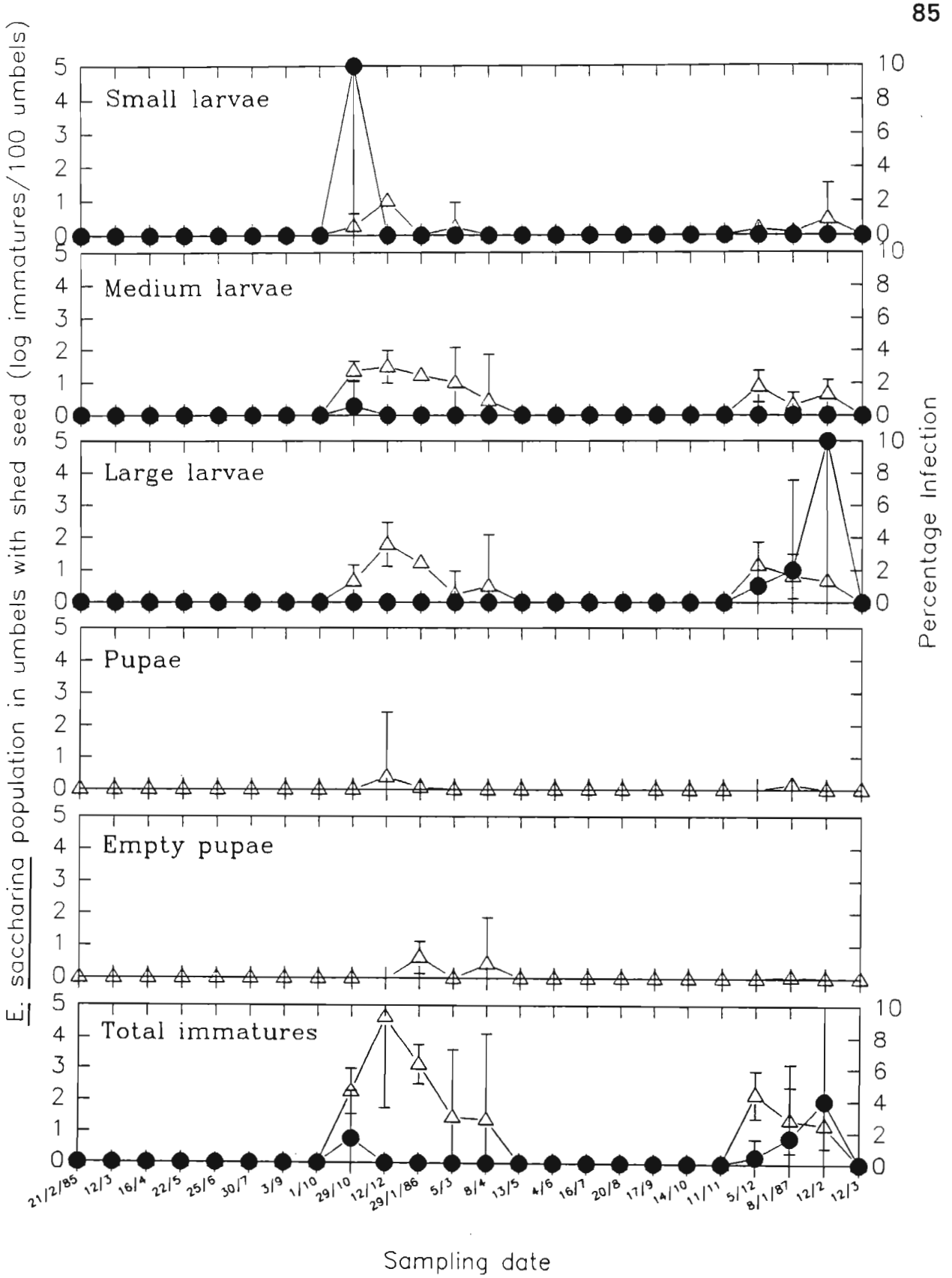


Figure 28: Impact of Beauveria bassiana on E. saccharina immature populations in mature C. papyrus umbels with shed seeds (▵——▵ E. saccharina immature population; ●——● B. bassiana parasitism; I = 95% confidence limits).

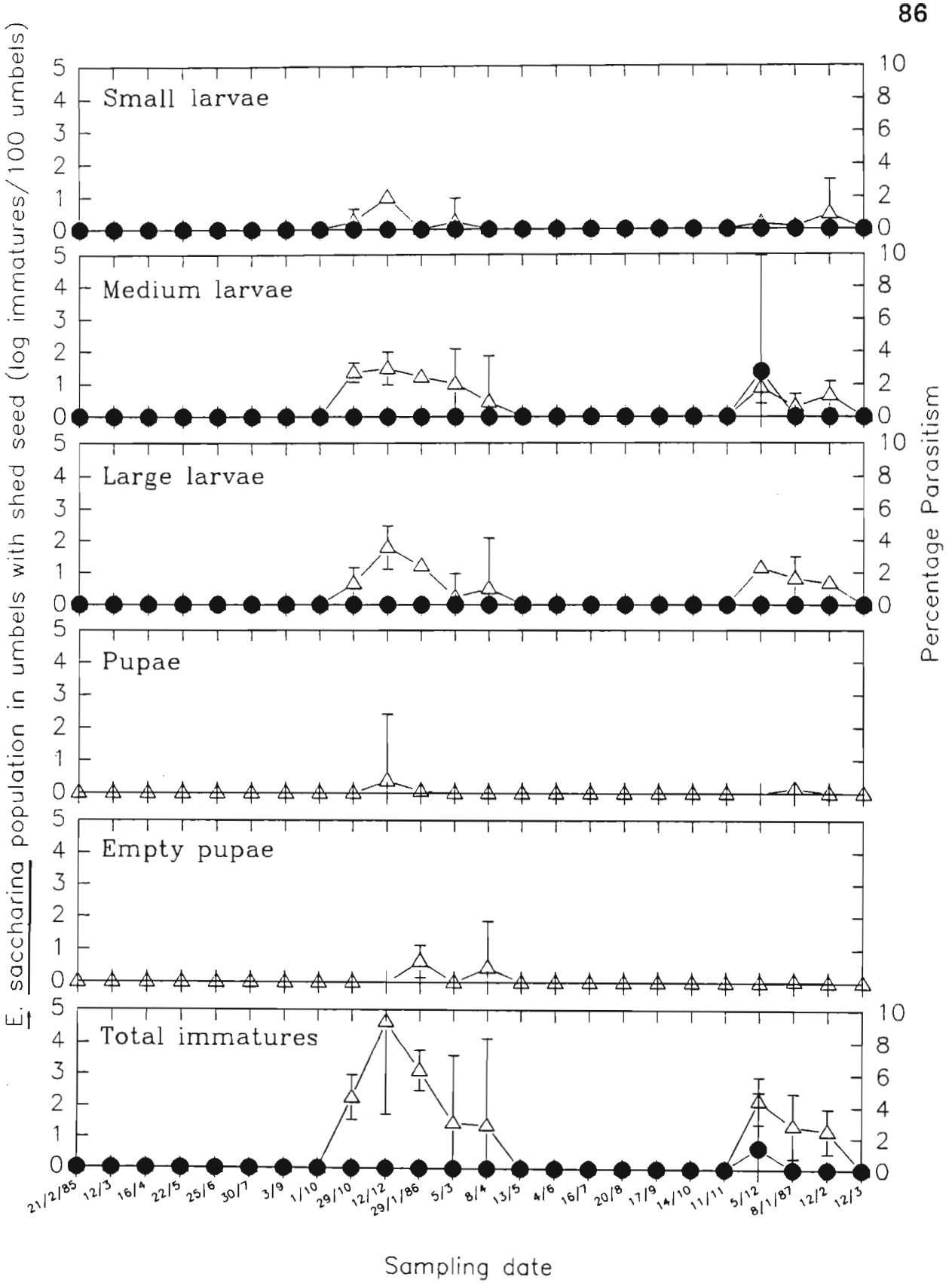


Figure 29: Impact of Orgilus bifasciatus on E. saccharina immature populations in mature C. papyrus umbels with shed seeds (△——△ E. saccharina immature population; ●——● O. bifasciatus parasitism; I = 95% confidence limits).

flowering season, and 20% during the second season (Figure 27).

Beauveria bassiana accounted for a maximum of 4% of mortality of immature E. saccharina in this umbel type. During the first flowering season, its largest impact was on small larvae (10%, Figure 28), and during the second flowering season, the large larval component was most attacked (10%, Figure 28). Again, no mortality of pupae was recorded (Figure 28).

The braconid O. bifasciatus had least impact on the E. saccharina populations of this umbel type. It was only recorded parasitising medium larvae in December 1986, when 3% of those found were parasitised. As a result, its impact on the total immature E. saccharina population was only just above 1% in December 1986 (Figure 29).

5.3.4 Natural enemy impact on E. saccharina populations in young C. papyrus umbels

This umbel type is produced in all seasons, and comprises about 20% of the total umbel standing crop (Chapter 3). As such it produced a stable habitat, which was exploited by E. saccharina. Highest populations of this borer were generally present in early spring and summer, and lowest in winter. In addition, no pupae were ever found, and the large larval population was very low. Small and medium larvae made up the bulk of E. saccharina immature stages (Chapter 4).

Again, young and medium larvae seemed most susceptible to death by unknown factors, but this mortality did not seem to influence E. saccharina populations in any way (Figure 30). Mortality of small larvae reached 50% in May and October 1985, March, October and December 1986, and March 1987. There were no marked declines of small larvae populations following these high mortalities. The 1986/87 summer population of young larvae was however kept slightly lower than the first summer, and mortality in the former was higher than

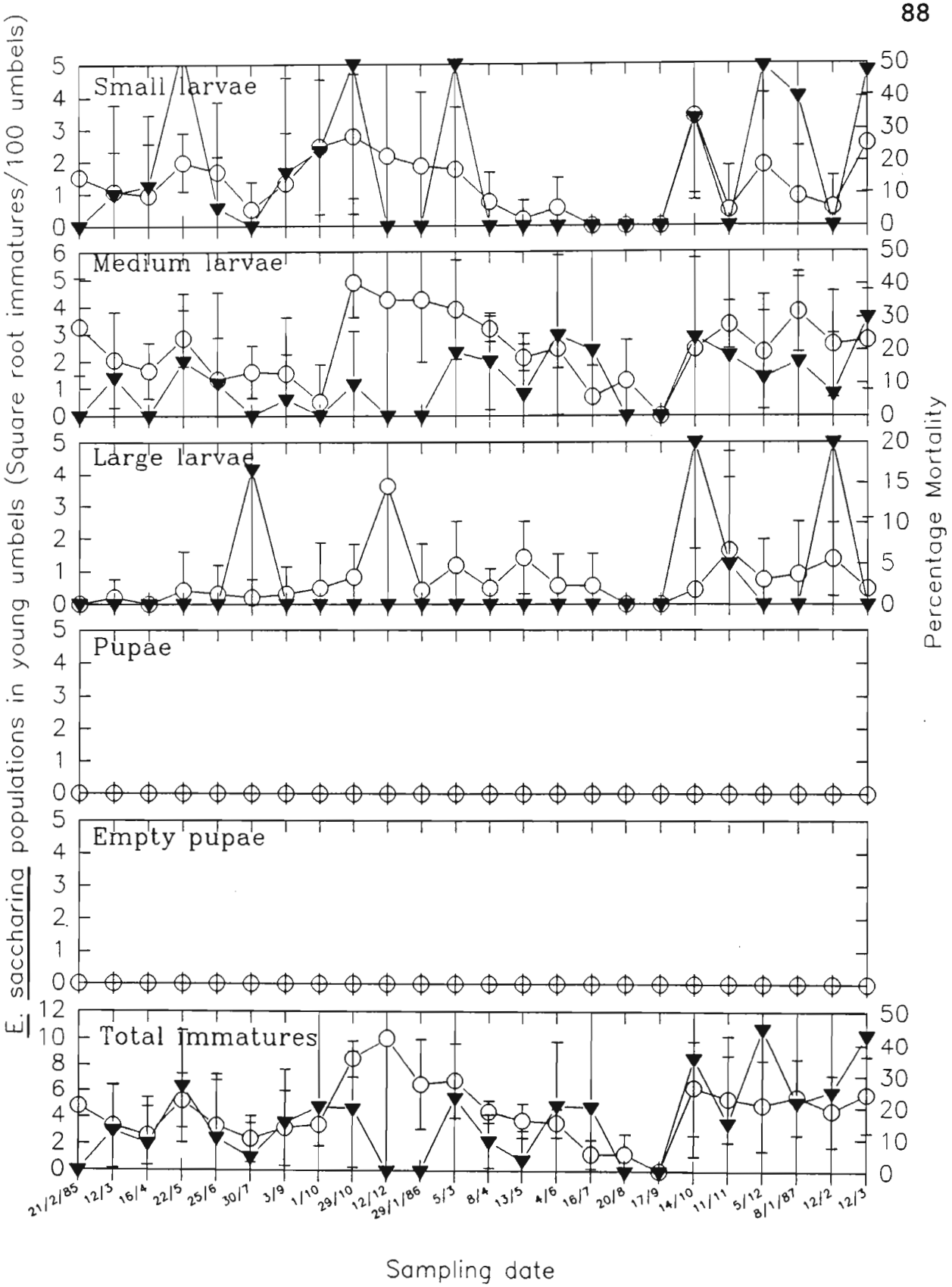


Figure 30: Impact of unknown mortality factors on E. saccharina immature populations in young C. papyrus umbels (○——○ E. saccharina immature population; ▼——▼ unknown mortality; ⌶ = 95% confidence limits).

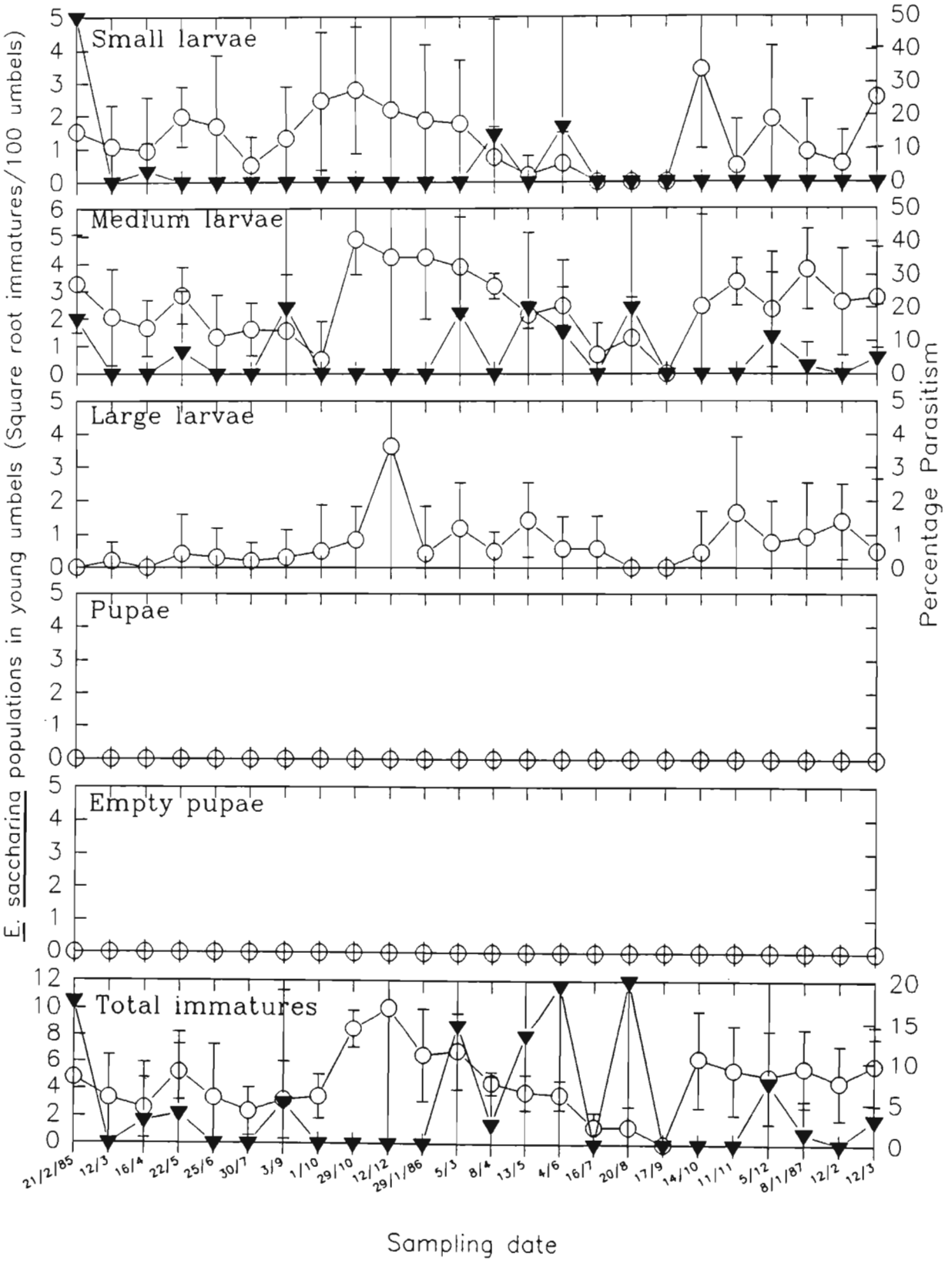


Figure 31: Impact of Orgilus bifasciatus on E. saccharina immature populations in young C. papyrus umbels (○——○ E. saccharina immature population; ▼——▼ O. bifasciatus parasitism; I = 95% confidence limits).

in the latter period (Figure 30). In general, unknown mortality followed the E. saccharina immature population, i.e. when populations were high, mortality was high, and when populations were low, mortality was low. The only exception to this was during December 1985 and January 1986, when no mortality was recorded, despite there being a fairly high E. saccharina population (Figure 30).

Orgilus bifasciatus was predominantly collected from immature E. saccharina stages during autumn and winter months in this umbel type (Figure 31). During the first period parasitism averaged 4%, and in the second period it averaged 15%. No parasitism was recorded from large larvae. Small larvae were parasitised on three occasions: February 1985 (50%), April and June 1986 (both 20%). Medium larvae were parasitised more frequently, with most parasitism occurring from March to August 1986 (approximately 15%, Figure 31), when medium larval populations declined.

Beauveria bassiana infection was generally below 10% of total immature E. saccharina stages collected in young umbels. Only at the commencement of the study (February, 1985) was parasitism above 20% recorded (Figure 32). Small and medium larvae were the only stages affected, but at different times. B. bassiana was found on small larvae in October 1985 (7%) and February 1987 (20%), while on the medium larvae it was found in February (20%), March (4%) and April 1985 (10%), in March (3%) and May 1986 (5%) and January 1987 (5%) (Figure 32).

On one occasion, in February 1987, the large larval component of the immature stages of E. saccharina was parasitised by G. indicus (20%, Figure 33). The overall impact of this parasitoid on the total immature stages was however minimal, being 4% of the stages found in February 1987 (Figure 33).

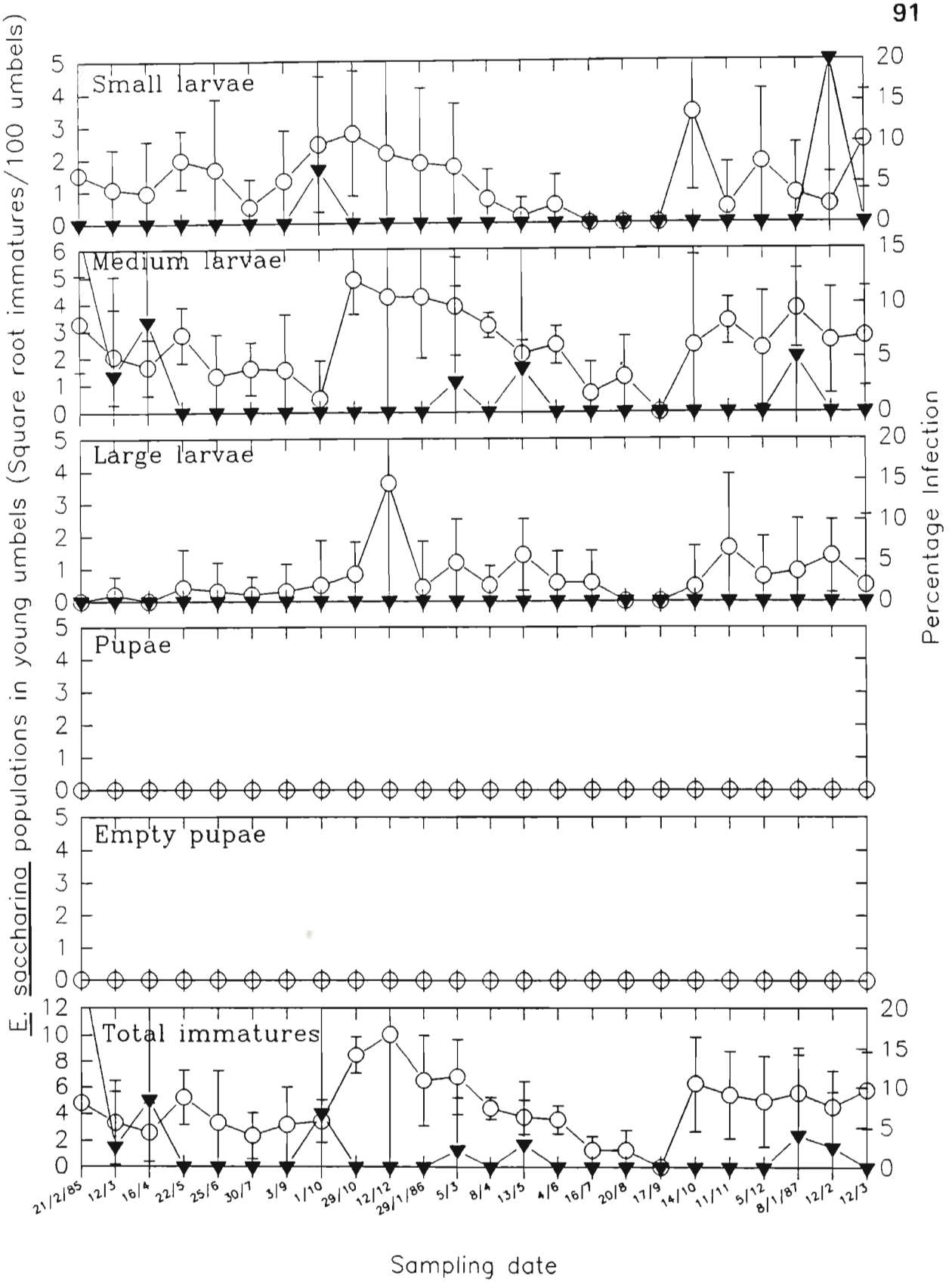


Figure 32: Impact of Beauveria bassiana on E. saccharina immature populations in young C. papyrus umbels (○——○ E. saccharina immature population; ▼——▼ B. bassiana parasitism; I = 95% confidence limits).

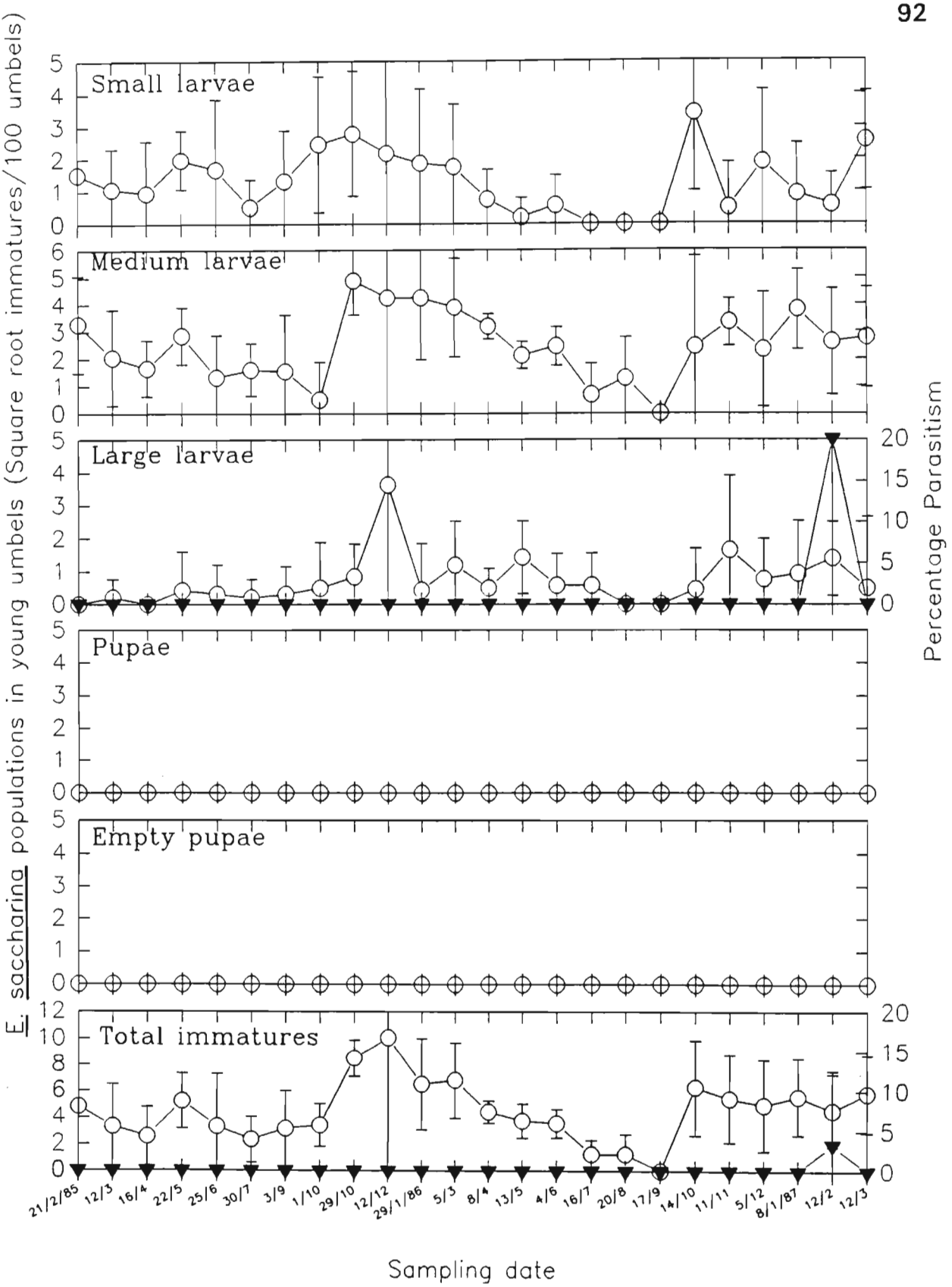


Figure 33: Impact of Goniozus indicus on E. saccharina immature populations in young C. papyrus umbels (○——○ E. saccharina immature population; ▼——▼ G. indicus parasitism; I = 95% confidence limits).

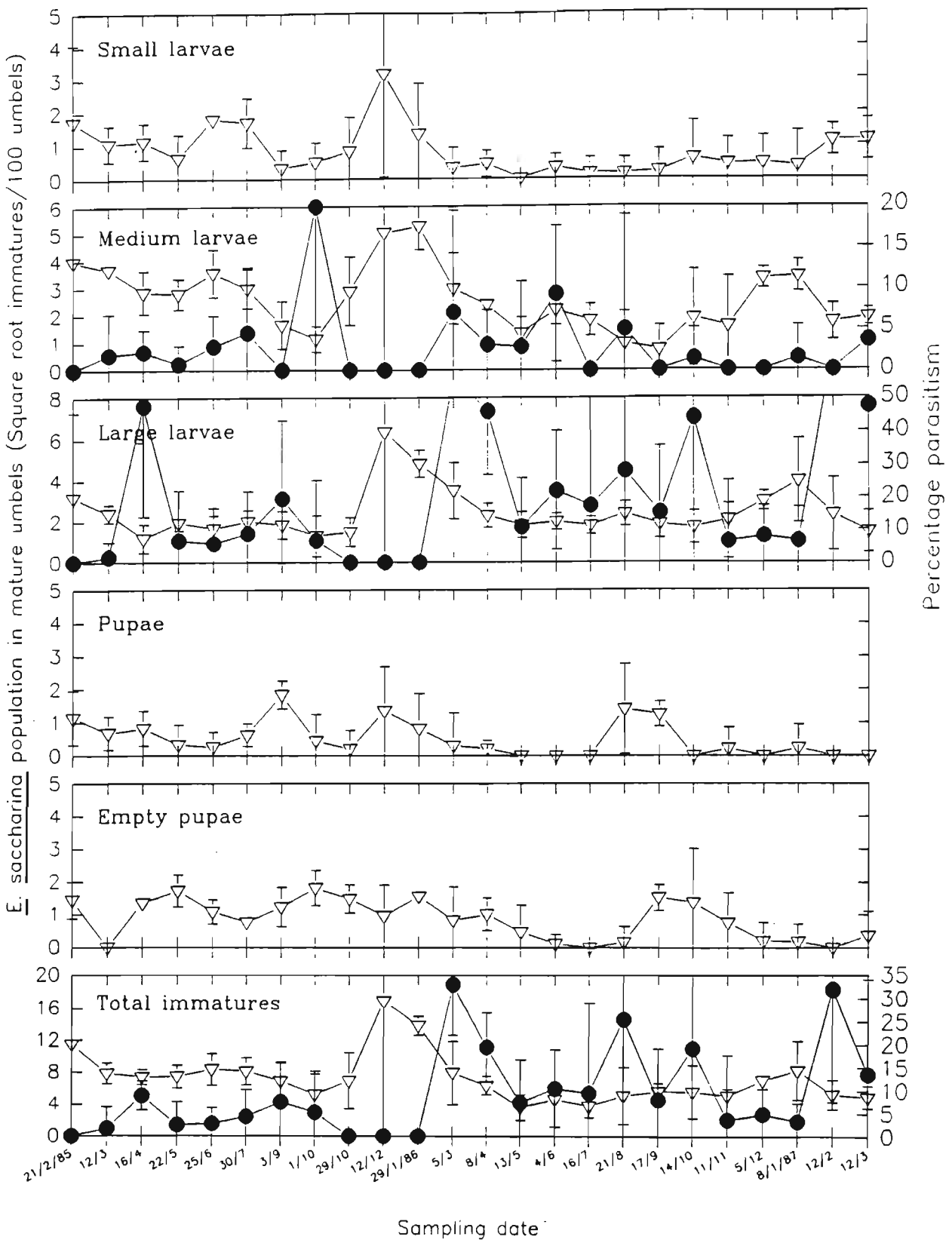


Figure 34: Impact of Goniozus indicus on E. saccharina immature populations in mature C. papyrus umbels (▽——▽ E. saccharina immature population; ●——● G. indicus parasitism; I = 95% confidence limits).

5.3.5 Natural enemy impact on E. saccharina populations in mature C. papyrus umbels

These umbels comprised the major proportion of the above ground standing crop through the two seasons sampled (60%, Chapter 3). As a result, the major E. saccharina infestations were found here (Chapter 4). All immature stages of E. saccharina were found in these umbels, with small larvae not being a major contributor to the total immature stages found.

The impact of G. indicus on total immature stages of E. saccharina was particularly marked. From February 1985 to January 1986, parasitism never increased above 10%, while the E. saccharina population did (Figure 34). However, by early February 1986 parasitism increased to 35% of immature stages found. This increase of parasitism parallelled a decrease in E. saccharina levels. Parasitism by G. indicus remained above 10% until November 1986 when it dropped to below 5% for 3 months. In February 1987 it again increased to 35%, which reduced the corresponding E. saccharina levels (Figure 34). The large larvae were most affected by parasitism by G. indicus. Peaks in parasitism usually followed, within 2 months, peaks in larval numbers. Figure 34 shows E. saccharina peaks followed by major peaks in parasitism in April 1985 (50%), March 1986 (>50%) and February 1987 (>50%). Smaller peaks were clearly evident in September 1985 and October 1986. Parasitism of medium larvae was generally below 10%; however, a large peak occurred in October 1985 (20%). This had no impact on the E. saccharina population, though (Figure 34). No parasitism by G. indicus was recorded from small larvae nor from pupae found in this umbel class (Figure 34).

Beauveria bassiana was a major mortality factor in April 1986, when just less than 30% of the total immature E. saccharina stages were infected (Figure 35). Other smaller peaks were evident, in March 1985 (10%), September 1985 (10%), September 1986 (15%) and March 1987 (8%), but these had no impact on E. saccharina populations (Figure 35). All living immature stages of E.

saccharina were attacked, but at different times of the year. Small larvae were most heavily infected in March 1985 (25%) and again in June and July 1986 (15 to 20%, Figure 35). Medium larvae were most infected in September 1985 (17%), April 1986 (>25%) and September and October 1986 (20%, Figure 35). Large larvae were most infected in February 1985 (15%), October 1985 (20%), March to May 1986 (>15%) and October 1986 (10%, Figure 35). Pupae were least infected, but levels were still higher than 10% in July 1985 and March 1986 (Figure 35). The only correlation to be found was in the period October 1985 to January 1986, when no B. bassiana was recovered, and total immature E. saccharina populations reached their peak.

Again, unknown mortality was a major factor limiting growth of small larvae. Generally, 20% died of unknown causes (Figure 36). Medium larvae were subject to less mortality (<20%) during the first year of sampling than in the second year (>20%, Figure 36). Less than 10% of large larvae died because of unknown causes, except in September and October 1986 (25 to 30 %) and March 1987 (20%, Figure 36). Pupal mortality was only recorded in April (6%) and July 1985 (10%) and again in March (15%) and August 1986 (15%). No mortality was recorded at the time of peak E. saccharina levels (December 1985, January 1986; Figure 36).

Orgilus bifasciatus parasitism recorded from total immature E. saccharina populations peaked in the winter months of June and July 1985 (5%) and June to August 1986 (5 to 15%)(Figure 37). This parasitoid's biggest impact on small larvae occurred from May until July 1985, when 20 to 30% of small larvae were parasitised. A peak of 28% parasitism was recorded in March 1986, and in August 1986 20% of small larvae were parasitised. In general, more parasitism of small larvae occurred in the first winter sampled than in the second (Figure 37). The converse was true of medium larvae. Here parasitism during the first winter (June to September 1985) averaged 5%, while for the same period the next year it varied between 10 and 30% (Figure 37). Very low parasitism of large larvae by O. bifasciatus was recorded in June 1985 (approximately 2%),

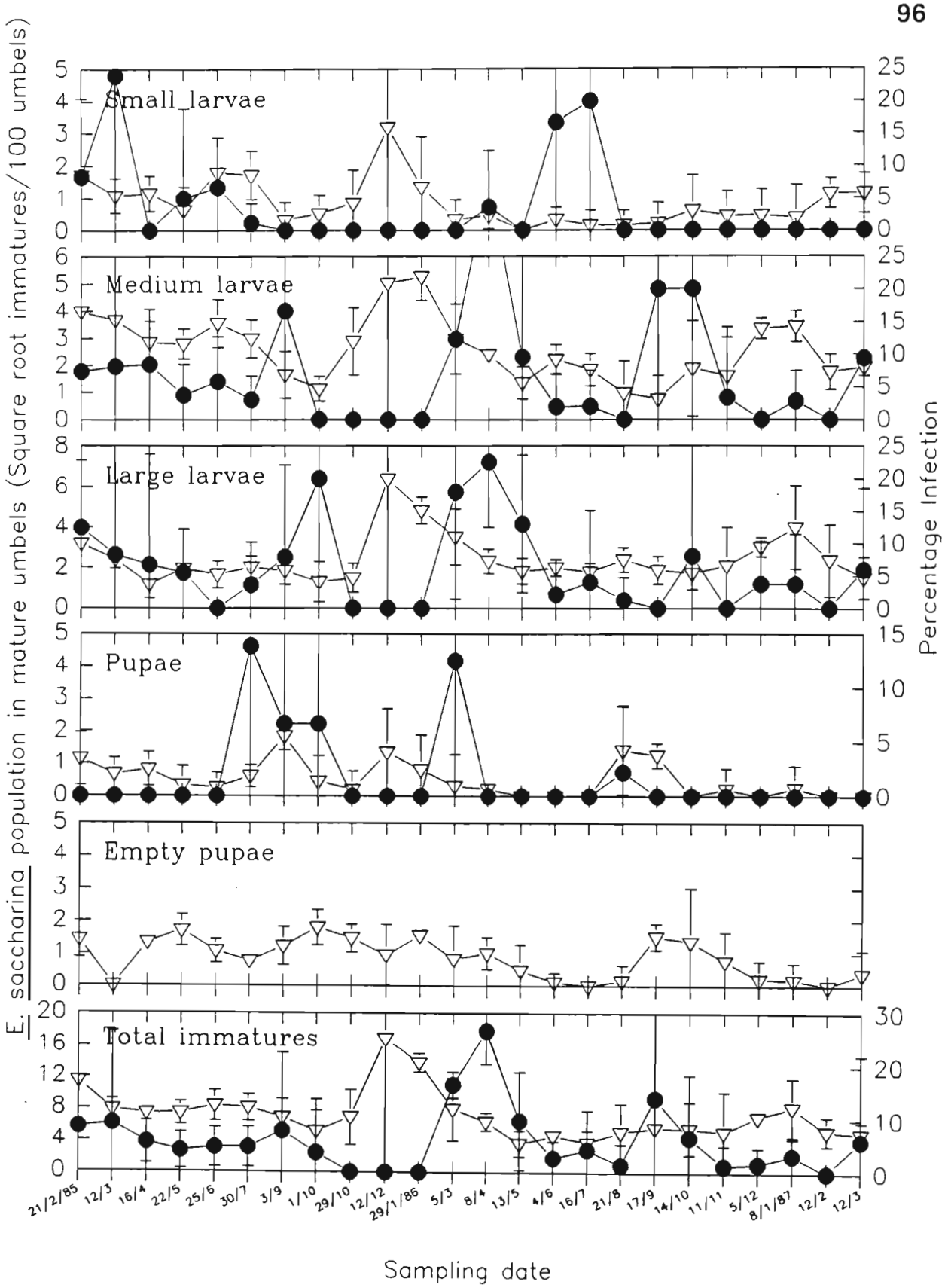


Figure 35: Impact of Beauveria bassiana on E. saccharina immature populations in mature C. papyrus umbels (▽——▽ E. saccharina immature population; ●——● B. bassiana parasitism; I = 95% confidence limits).

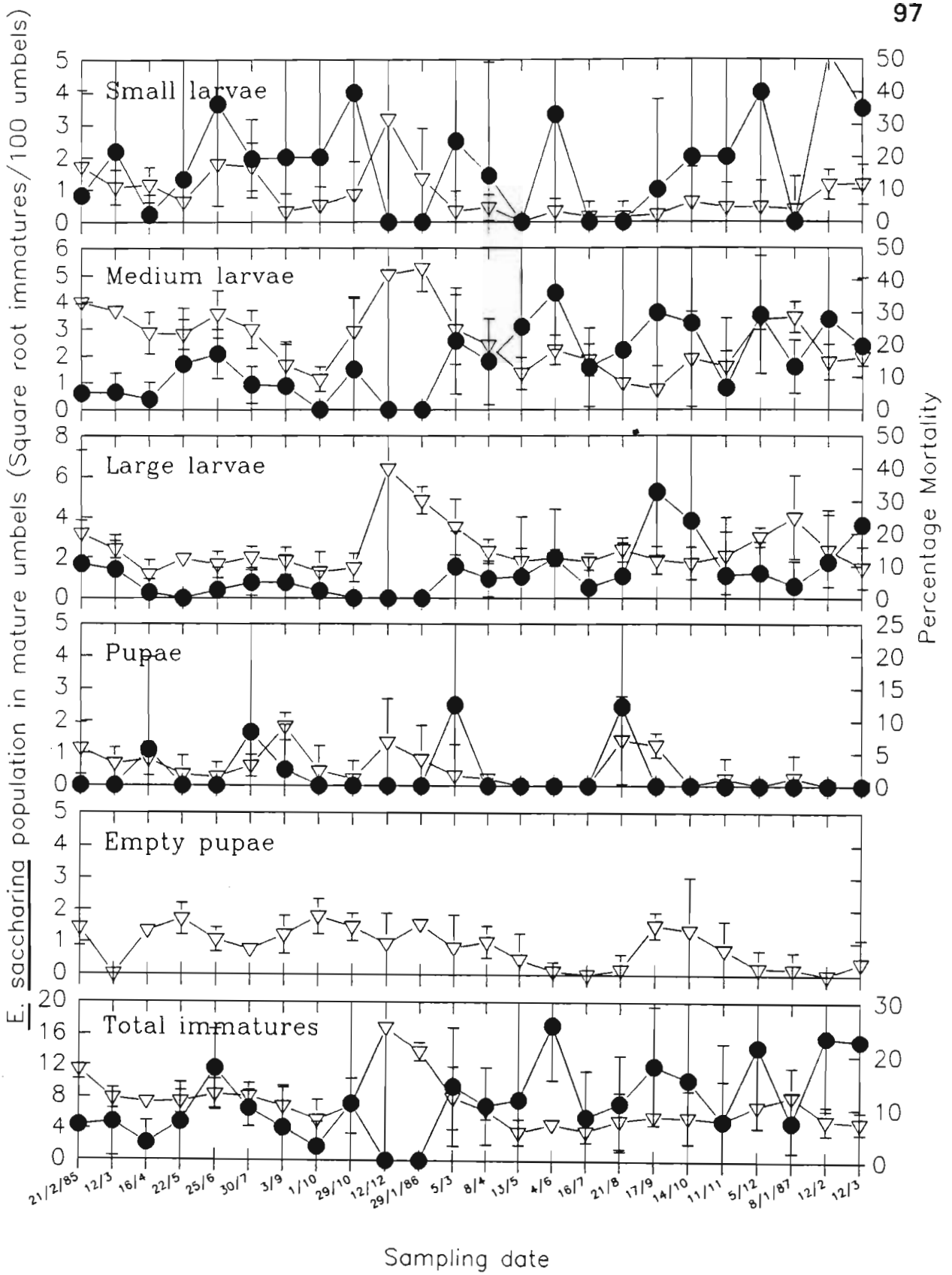


Figure 36: Impact of unknown mortality factors on E. saccharina immature populations in mature C. papyrus umbels (▽——▽ E. saccharina immature population; ●——● unknown mortality; I = 95% confidence limits).

March 1986 (0.5%) and July 1986 (1,5%) (Figure 37).

5.3.6 Natural enemy impact on E. saccharina populations in old C. papyrus umbels

The proportion of this umbel type in the total umbel standing crop was similar to that of young umbels (20%, Chapter 3). E. saccharina populations in these umbels were very low, and comprised mostly empty pupae (Chapter 4). However, small populations of all immature stages of E. saccharina were present, and mortality of these was recorded.

Beauveria bassiana was the most common mortality agent of immature stages, especially for the period March to June 1986 when infestations varied from 15 to 40%. It also occurred in September 1985 (10%) and September 1986 (20%) (Figure 38). Throughout the sampling period it occurred more commonly on medium larvae. In September and October 1985, 20% were infected. Infestations occurred again in March 1986 (30%) increased in April to >50% and then dropped to 20% in May and June 1986 (Figure 38). In September 1986, 20% were infected. Forty percent of large larvae were infected from April to June 1986 (Figure 38). Pupal Infestation by B. bassiana occurred in September 1985 (10%) and March 1986 (25%) (Figure 38). Small larvae were very uncommon. On only one occasion (July 1985) was B. bassiana recorded from them (20%, Figure 38).

Goniozus indicus was found in July 1985 (3%), March and April 1986 (10 to 20%) and February 1987 (23%) parasitising immature stages of E. saccharina (Figure 39). The most heavily affected immature stage was large larvae, which, in March 1986 had 50% parasitised. Parasitism dropped to 30% the next month. Ten percent of larvae were parasitised in June 1986, and then another high peak occurred in February 1987 (30%, Figure 39). A small proportion of medium larvae were parasitised in June 1985 (4%), and March 1986 (8%, Figure 39). No parasitism was recorded from small larvae nor pupae (Figure 39).

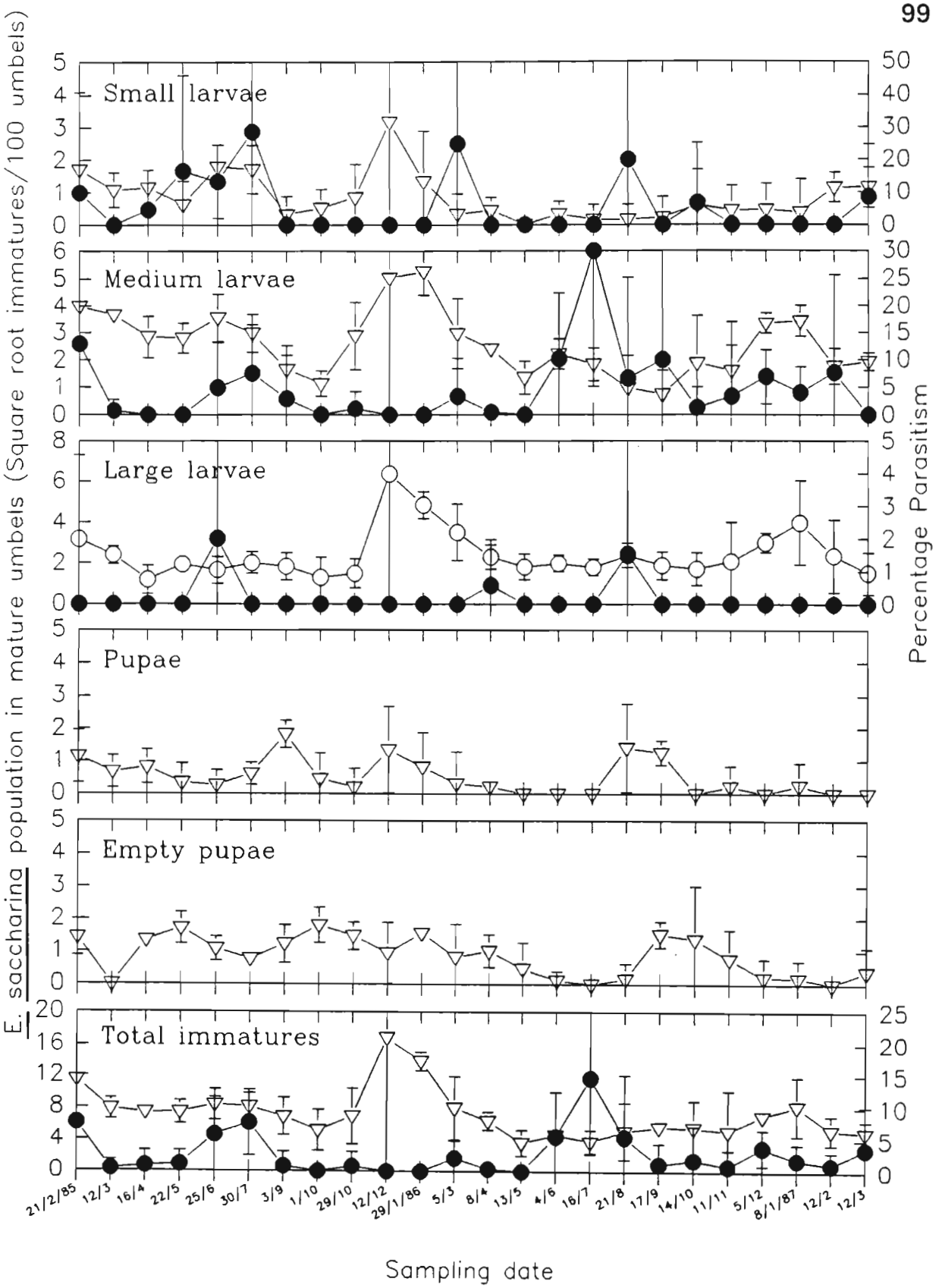


Figure 37: Impact of Orgilus bifasciatus on E. saccharina immature populations in mature C. papyrus umbels (▽——▽ E. saccharina immature population; ●——● O. bifasciatus parasitism; I = 95% confidence limits).

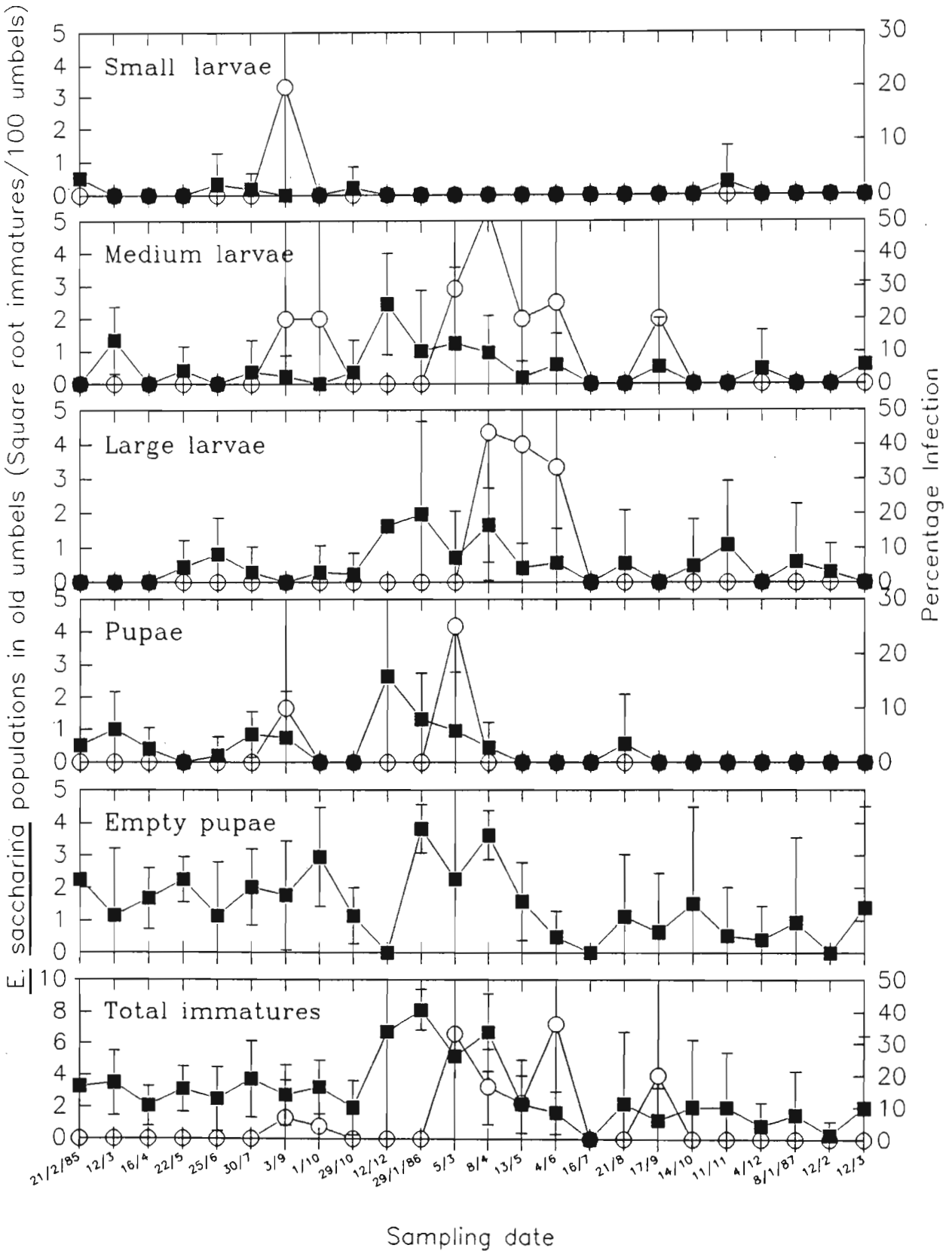


Figure 38: Impact of Beauveria bassiana on E. saccharina immature populations in old C. papyrus umbels (■——■ E. saccharina immature population; ○——○ B. bassiana parasitism; I = 95% confidence limits).

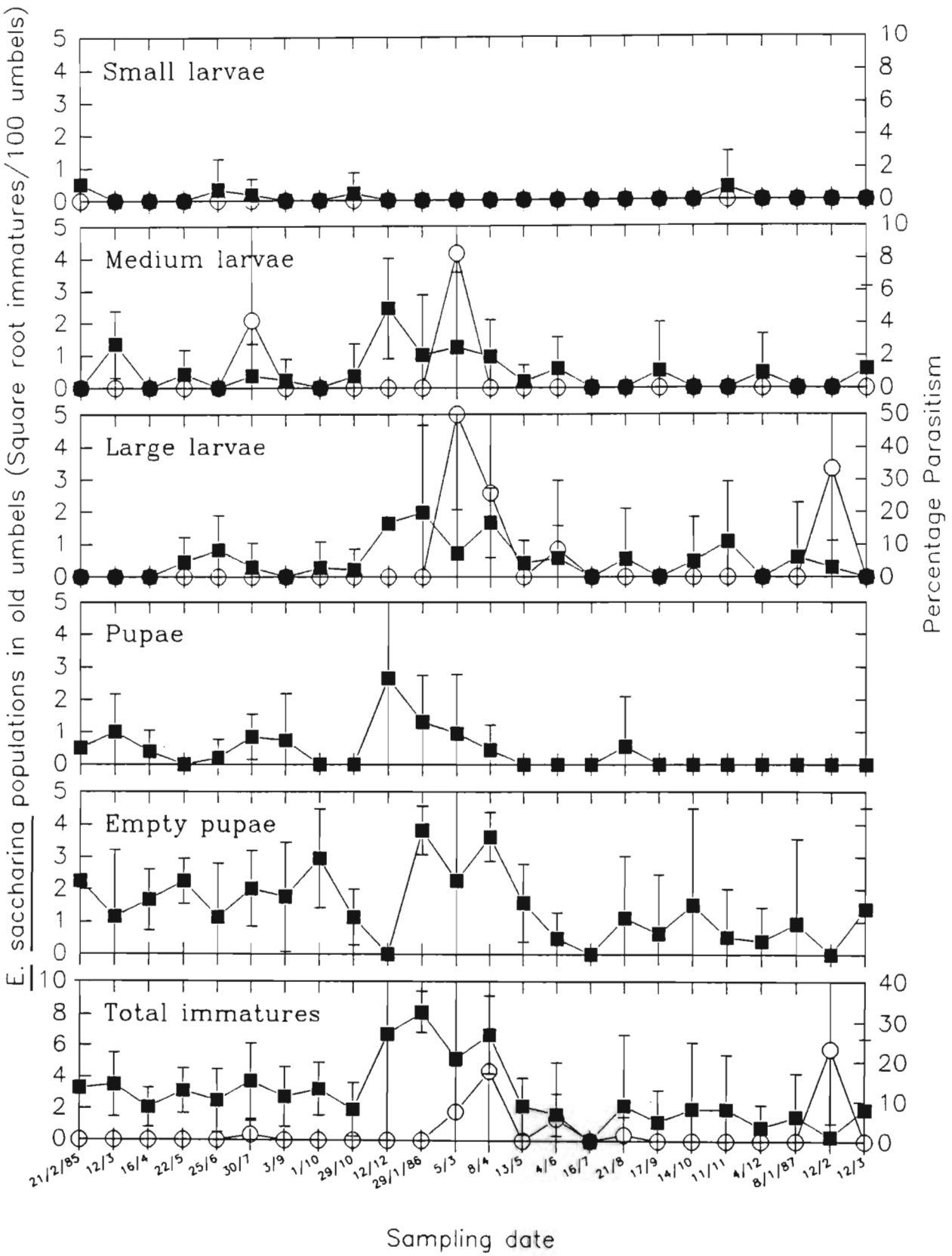


Figure 39: Impact of Goniozus indicus on E. saccharina immature populations in old C. papyrus umbels (■——■ E. saccharina immature population; ○——○ G. indicus parasitism; I = 95% confidence limits).

Because there were so few small and medium larvae, mortality due to unknown causes was lower in this umbel age class than in any others. Figure 40 shows that highest mortality of total immature stages occurred in November and December 1986 (18%). Levels below 10% were recorded in May and July 1985, March, April and August 1986 and February 1987. On three of four occasions when small larvae were found in this umbel class, 20% of them died of unknown causes (Figure 40). Less than 20% of medium larvae found in March, April and December 1986 died of unknown causes. Similar low levels of unknown mortality were recorded in the large larval category, but it was more evenly spread through the sampling period. In July 1985, 7% were found dead, 10 and 7% in March and April 1986 respectively, 20% in August and November 1986, and 5% in February 1987 (Figure 40). No mortalities were recorded from pupae collected from these umbels (Figure 40).

Despite low populations of small and medium larvae in this umbel type, O. bifasciatus was recovered from immature stages of E. saccharina. Fifty percent of the small larvae collected in February 1985 were parasitised, and in April 1986, less than 2% of medium and large larvae (Figure 41).

5.4 DISCUSSION

5.4.1 Parasitoid guilds in C. papyrus umbels

Despite speculation to the contrary (Carnegie, 1974), this study showed that there was a guild of parasitoids and other mortality factors acting on E. saccharina populations in just one of its natural host plants, C. papyrus. The term "guild" is used by ecologists to classify or group together those species in a given habitat which overlap significantly in their niche requirements (Miller and Ehler, 1990).

The two most common parasitoids, O. bifasciatus and G. indicus, although both parasitising E. saccharina, reduced their competition for this resource by

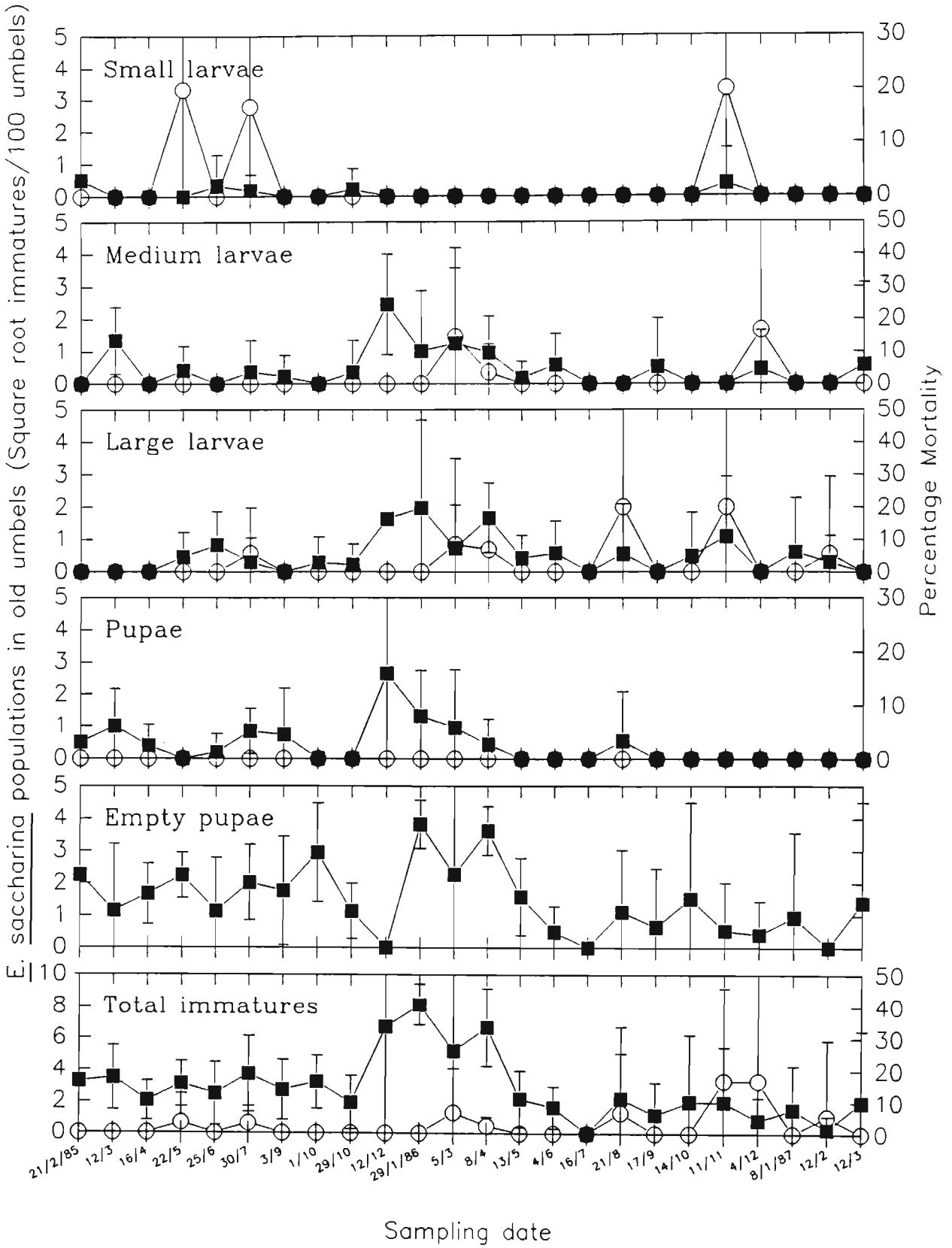


Figure 40: Impact of unknown mortality factors on E. saccharina immature populations in old C. papyrus umbels (■——■ E. saccharina immature population; ○——○ unknown mortality; I = 95% confidence limits).

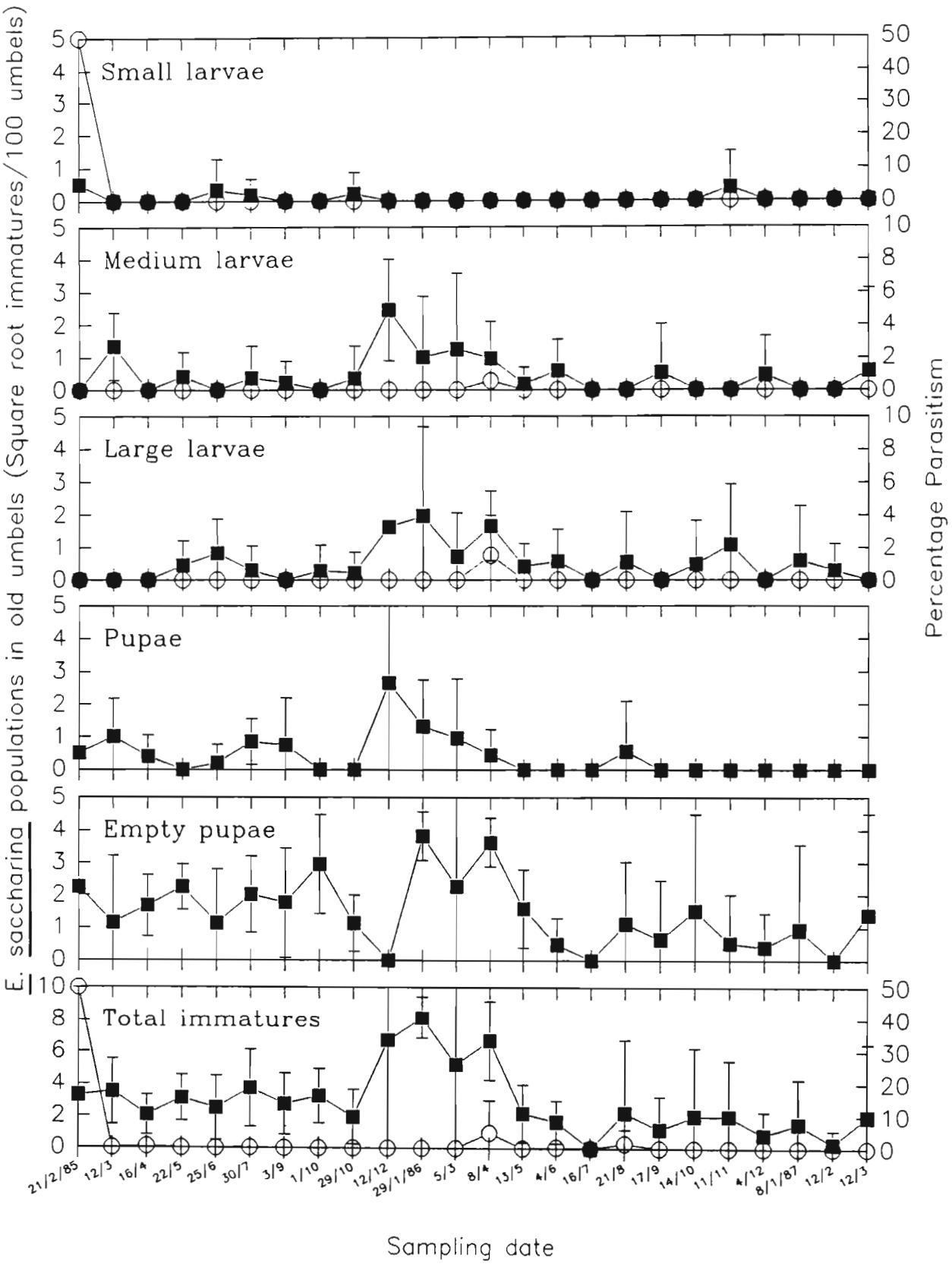


Figure 41: Impact of Orgilus bifasciatus on E. saccharina immature populations in old C. papyrus umbels (■——■ E. saccharina immature population; ○——○ unknown mortality; I = 95% confidence limits).

attacking different stages of host. O. bifasciatus prefers small and smaller medium larvae, while G. indicus attacks large and larger medium larvae. In addition, O. bifasciatus is generally more common during winter months, and G. indicus more common during summer and autumn months.

The "unknown mortality" factor comprised immature stages that were found dead in umbels, and those which died while in the screening process. High mortality of the smaller instars of E. saccharina has been reported, especially from sugarcane by Girling (1978) and Betbeder-Matibet (1981), although this has been mostly ascribed to the action of predators. However, strains of Bacillus thuringiensis De Barjac were the most common micro-organism isolated from larvae collected from natural hosts (Jacobs, 1989). Another mortality factor of especially small larvae was damage during collection. This could have dampened any seasonal effects of micro-organisms which may have been observed during the study, and contributed to this aspect having quite an impact on all the stages throughout the seasons sampled.

Beauveria bassiana, the other major component of the natural enemy guild, attacked any life stage of E. saccharina. As such it did compete for hosts with both O. bifasciatus and G. indicus. This competition was limited however, as B. bassiana was generally most evident in spring and autumn, especially when rainfall was high (Chapter 2).

The effectiveness of the three named biological control agents on E. saccharina immature populations in the total umbel sward has been illustrated by Conlong (1990). He showed that during most of the two year period, total parasitism maintained immature E. saccharina populations at around 8 to 14 per 100 umbels during winter months, and between 15 and 68 per 100 umbels during summer. The very high level of 68 per 100 umbels in the summer months of 1985 corresponded with exceptionally low parasitism over the same period. G. indicus and B. bassiana populations recovered within 2 months, and their combined interactions quickly depressed the E. saccharina population when it

threatened to increase. Thereafter it was maintained, with the help of O. bifasciatus, at a stable lower level for the remainder of the sampling period (Conlong, 1990). This follows the criteria set out by Waage and Hassell (1982) for a successful biological control programme - the parasitoids did initially reduce E. saccharina (pest) numbers significantly, with subsequent populations of both host and parasitoid persisting at lower levels in a stable equilibrium.

However, because of the spatial heterogeneity provided by C. papyrus (Chapter 3), it was important to determine its effect on pest - parasitoid interactions in this habitat, as spatial heterogeneity has emerged as a very important factor affecting population dynamics (Hassell, 1982).

5.4.2 Impact of umbel age and stand structure on parasitism of E. saccharina

A herbivorous insect's feeding niche can strongly influence its susceptibility to attack by parasitoids (Gross, 1991). In addition, when relationships between parasitism and host density per patch of habitat where the host occurs are analysed, it is necessary to account for both proportions of patches discovered, and within these, proportions of hosts parasitised (Hassell, 1982).

A stand of C. papyrus at any one time provides a diversity of environmental conditions, from rhizome level to the top of mature umbels (Chapter 3). Umbels themselves provide specific habitats for herbivorous insects as they grow from young to maturity in the canopy, and then their senescence and collapse to the rhizome layer (Chapter 3). The umbels thus form "patches" within the habitat provided by a stand of C. papyrus. In Chapter 4 it was shown that each of these "patches" or umbel types were exploited by E. saccharina, which bored into ray bases when small, and then into the meristematic apex of the culm, where the umbel is formed, as the larvae grew (Conlong, 1990).

The results presented in this chapter show that immature stages of E. saccharina are parasitised by a variety of parasitoids and are attacked and/or

affected by other natural enemies and mortality factors in every umbel type. Each "patch" available in this habitat thus has its own plant-host-natural enemy complex to consider, which together form an integral part of the tritrophic interaction in the whole C. papyrus habitat.

The E. saccharina population in young umbels, both with and without seeds, was less attacked by B. bassiana than the population in mature and old umbels. Young umbels were protected from the elements by a complete canopy of mature umbels, and also their morphology protected developing larvae. The infective stage of B. bassiana is spores, and has to get to immature stages of E. saccharina either by being transported to the borer in the apex of the culm by other insects, or by rainfall or heavy dew. In mature umbels this is more easily achieved, as these are exposed directly to rain and dew. The moisture can be channelled to the apex of the culm by the rays, which radiate out from this region. Spores can thus be more easily washed down the more openly structured rays to their tightly packed bases and the boring sites of immature E. saccharina. In contrast, young umbels do not have fully opened rays. It is therefore more difficult for rainfall to be channelled to the culm apex. In addition, this umbel age class is protected from direct effects of rainfall and heavy dew by the canopy of mature umbels.

The major impact of this entomopathogen was, however, on medium larvae found in mature umbels, which made up the bulk of the host plant (Chapter 3) and housed the bulk of the E. saccharina population (Chapter 4). Following the E. saccharina population increase in the 1985/86 summer period, when parasitism was very low, the percentage of this stage larva found infected with B. bassiana peaked two months after the peak of the larval period, at which stage the larval population had decreased significantly. Although the infestation over the same period by B. bassiana on large larvae was a little less, it was significant, and with G. indicus served to limit the growth of this stage of the E. saccharina population.

Because young umbels had developed into mature umbels at about the same time that E. saccharina larvae had developed into large instar larvae (Chapter 4), there were generally very few large larvae present in young umbels below the mature umbel canopy. G. indicus was thus not a common parasitoid in this area, as it normally parasitised larger larvae. However, the presence of some parasitism by G. indicus on the few large instars found indicates that it did search in this area for hosts. Its major impact however, was in mature umbels, where it had a major impact on large larval populations of E. saccharina. The magnitude of control exerted by this parasitoid has previously been described.

Young larvae were present in all umbel types, and O. bifasciatus was found parasitising these in all umbel age classes except young umbels with seeds. However, the E. saccharina population in this transient host was very small, and thus was not a major component of the total E. saccharina population. The more important impact of O. bifasciatus occurred on small and medium larvae in young umbels, especially during the winter months of 1986 when it exerted a regulating influence on the E. saccharina population in this umbel type. A similar pattern of parasitism of small and medium larvae in mature umbels was observed, emphasising the impact of O. bifasciatus on winter populations of small and medium E. saccharina larvae found in C. papyrus umbels. Its ability to parasitise E. saccharina in different umbel types, which occur in a number of different environmental conditions, points to a very good searching ability on its part.

However, no one natural enemy dominated populations of E. saccharina in any umbel type. A combination of parasitoids and other natural enemies found was most effective at regulating their hosts population. In C. papyrus, E. saccharina uses a number of niches as it grows (Conlong, 1990), and the major parasitoids, because of their different attack strategies, have been able to discover and use their hosts in these niches.

5.4.3 Attack strategies of natural enemies of E. saccharina in C. papyrus

Because of its telescopic ovipositor (Waladde, 1983) which can be extended to almost the length again of a female E. saccharina adult, the female can place her eggs within young C. papyrus spears, on developing bracts and rays, where they are relatively protected from predation. She can also do this at the base of mature umbels, where rays and bracts are closely packed and thus afford some protection from predation. When young larvae hatch, they bore into ray bases, where they stay until the ray can no longer support them (Conlong, 1990). At that time larvae are normally at the third instar stage (smaller medium larvae). They then bore into the culm apex, the meristematic region for bracts and rays, where they complete their development to pupae (Conlong, 1990). Once in their boring in the culm apex, they are relatively well protected from both predation and parasitism.

The possible mode of attack of B. bassiana on E. saccharina immature stages has been described in the preceding section. Spores of B. bassiana need only to attach to the cuticle of an insect to develop. This is why all immature stages of E. saccharina were infected. However, the silken cocoon of E. saccharina pupae protected them to some extent from B. bassiana.

O. bifasciatus is a small black braconid approximately 4 to 5 mm long. The female has a strengthened, visible ovipositor, also about 4 mm long. This is well suited to parasitising smaller E. saccharina larvae in ray bases, from which larvae parasitised by this parasitoid were collected. Its mode of parasitism is characterised as "drill and sting" (Smith et al., 1993). As such the parasitoid has to pierce plant material to parasitise its host. The thin epidermis of the ray base is thus ideal for O. bifasciatus to pierce and it is thus easy for the parasitoid to locate and parasitise small E. saccharina larvae. O. bifasciatus is a solitary parasitoid, and its offspring pupates adjacent to the larval cadaver in the boring of the ray base.

G. indicus, in contrast, attacks larger E. saccharina larvae. Females are between 4 and 5 mm long (Gordh, 1986), and ideally formed for their "ingress and sting" attack strategy (Smith et al., 1993), in that they are dorso-ventrally flattened, with their legs and wings small and held close to the body. This allows them to enter borings of large E. saccharina larvae in the apex of the culm to temporarily paralyse them for oviposition. She remains with the parasitised larvae as her brood develop externally. They pupate in the borer tunnel next to the larval cadaver. A mean of 8 offspring are produced and are female biased if the mother was mated. More information on this parasitoid's biology can be obtained from Conlong et al. (1988).

5.5 CONCLUSION

This study revealed that numerous parasitoids and other natural enemies occurred in only one of the natural host plants of E. saccharina. These had a marked effect on the regulation of E. saccharina populations in all different C. papyrus umbel types colonised by this borer. By exploiting different larval sizes and attack strategies, the parasitoids in particular minimised competition and maximised their combined effect on the E. saccharina population.

This type of study thus not only emphasises the importance of knowing the indigenous host of a pest species, but also the importance of investigating its life style in this host regularly over a number of seasons. Very important biological information is obtained on both the host and its natural enemies which can then be used in control strategies against the pest in agricultural situations.

REFERENCES

Betbeder-Matibet, M., 1981. Eldana saccharina Walker. Borer of the stalks of sugarcane in Africa. L'Agronomie Tropicale 36: 279 - 293.

Carnegie, A.J.M., 1974. A recrudescence of the borer Eldana saccharina Walker

(Lepidoptera: Pyralidae). Proceedings of the South African Sugar Technologists Association 48: 107 - 110.

Conlong, D.E., 1990. A study of pest-parasitoid relationships in natural habitats: an aid towards the biological control of Eldana saccharina (Lepidoptera: Pyralidae) in sugarcane. Proceedings of the South African Sugar Technologists Association 64: 111 - 115.

Conlong, D.E., 1994. A review and perspectives for the biological control of the African sugarcane stalkborer Eldana saccharina Walker (Lepidoptera: Pyralidae). Agriculture, Ecosystems and Environment 48: 9 - 17.

Conlong, D.E., Graham, D.Y. and Hastings, H., 1988. Notes on the natural host surveys and laboratory rearing of Goniozus natalensis Gordh (Hymenoptera: Bethylidae), a parasitoid of Eldana saccharina Walker (Lepidoptera: Pyralidae) larvae from Cyperus papyrus L. in southern Africa. Journal of the entomological Society of southern Africa 51: 115 - 127.

Girling, D.J., 1978. The distribution and biology of Eldana saccharina Walker (Lepidoptera:Pyralidae) and its relationship to other stemborers in Uganda. Bulletin of entomological Research 68: 471 - 488.

Gordh, G., 1986. A new species of Goniozus Foerster 1851 from southern Africa parasitising sugar cane borer, Eldana saccharina Walker, and taxonomic notes on species of the genus in Africa (Hymenoptera: Bethylidae; Lepidoptera: Pyralidae). Journal of the entomological Society of southern Africa 49: 257 - 265.

Gross, P., 1991. Influence of target pest feeding niche on success rates in classical biological control. Environmental Entomology 20: 1217 - 1227.

Hassell, M.P., 1982. Patterns of parasitism by insect parasitoids in patchy

environments. Ecological Entomology 7: 365 - 377.

Hassell, M.P. and Waage, J.K., 1984. Host-parasitoid population interactions. Annual Review of Entomology 29: 89 - 114.

Jacobs, S.J., 1989. Micro-organisms as potential biological control agents of Eldana saccharina Walker (Lepidoptera: Pyralidae). Proceedings of the South African Sugar Technologists Association 63: 182 - 186.

Miller, J.C. and Ehler, L.E., 1990. The concept of parasitoid guild and its relevance to biological control. In Mackauer, M., Ehler, L.E. and Roland, J. (Eds). Critical Issues in Biological Control. Intercept Limited, Andover, Hants, UK.

Mohyuddin, A.I. and Greathead, D.J., 1970. An annotated list of the parasites of graminaceous stem borers in East Africa, with a discussion of their potential in biological control. Entomophaga 15: 241 - 274.

Parker, R.E., 1973. Introductory Statistics for Biology. Institute of Biology, Studies in Biology no. 43. Edward Arnold, London.

Polaszek, A. and Krombein, K.V., 1994. The genera of Bethylinae (Hymenoptera: Chrysidoidea). Journal of Hymenoptera Research 3: in press.

Smith, J.W. Jr., Weidenmann, R.N. and W.A. Overholt, 1993. Parasites of Lepidopteran Stemborers of Tropical Gramineous Plants. ICIPE Science Press, Nairobi, Kenya.

Waage, J.K. and Hassell, M.P., 1982. Parasitoids as biological control agents, a fundamental approach. Parasitology 84: 241 - 268.

Waiyaki. J.N., 1974. The ecology of Eldana saccharina Walker, and associated loss in cane yield at Arusha-Chini, Moshi, Tanzania. Proceedings of the

International Society of Sugar Cane Technologists 15: 457 - 462.

Waladde, S.M., 1983. Chemoreception of adult stem-borers: Tarsal and ovipositor sensilla on Chilo partellus and Eldana saccharina. Insect Science and Application 4: 159 - 165.

CHAPTER 6

IMPLICATIONS OF THE STUDY FOR BIOLOGICAL CONTROL OF ELDANA SACCHARINA IN SUGARCANE

6.1 INTRODUCTION

Biological control of Eldana saccharina, although considered one of the better control options in sugarcane and other graminaceous crops (Mohyuddin and Greathead, 1970) in Africa, has been difficult to implement. In addition to the very cryptic nature of E. saccharina in these crops (Dick, 1945; Carnegie, 1974; Betbeder-Matibet, 1981; Cochereau, 1982), which protects it from a number of more conventional control measures such as pesticide applications, there are a number of other factors complicating the establishment of biological control agents.

- It is indigenous to Africa (Conlong, 1994), where it occurs in numerous wetland sedges and indigenous grasses (Girling, 1972; Atkinson, 1980). Classical biological control strategies therefore cannot be implemented.

- Even though it was described from sugarcane in Sierra Leone over 100 years ago (Walker, 1865), it is regarded as a recent invader of sugarcane in especially southern Africa. This is because it first reached pest status for a limited period from 1939, and since 1970 has been of major concern to the South African sugar industry (Carnegie, 1974). It is thus unlikely that indigenous natural enemies have had time to colonise this "new" habitat.

- Previous workers have found very few natural enemies, especially parasitoids, in these crops. The impression has thus been created that E. saccharina has very few parasitoids, and thus research into this aspect may be wasted. Conlong (1994) however pointed out that if successful

natural enemies were present in the crops investigated, this borer would not be a pest. In addition, no work had been done to investigate the natural enemy complex of E. saccharina in its natural host plants. Studies of this nature could thus provide some pointers to its control in the crop plants.

This Chapter discusses these concepts viz. pest-host plant association, host plant shift, indigenous pest control and biological control approach in the light of results presented in the previous chapters.

6.2 HOST PLANT ASSOCIATION

In 1848 George Morewood planted the first sugarcane on the Compensation Flats, north of Durban. During the 1880's, it was reported that the Uba variety of sugarcane was little damaged by white ants or the borer (Osborn, 1964). The identity of "the borer" was, however, unknown. In 1894 locust plagues appeared and devastated many cane fields around Durban. This was the first report of identified insect damage in southern African sugarcane. By 1913 settlers had reached the Umfolosi river and the mill started crushing in 1916 (Osborn, 1964).

Eldana saccharina was described from sugarcane in Sierra Leone, West Africa in 1865 (Walker, 1865). It was first reported from sugarcane on the Umfolosi Flats of Natal in 1939 (Naude, 1940), where it attacked 20 month old P.O.J. 2725 (Dick, 1945). This variety of sugarcane was known to be relatively soft (Carnegie, 1974). The older cane which was attacked by E. saccharina aged because of a quota restriction being imposed on it, which prevented it from being sent to the mill at the correct age (Naude, 1940). Subsequent knowledge has shown that older sugarcane is particularly vulnerable to E. saccharina (Carnegie, 1981).

Initially it was thought that E. saccharina was a recent introduction into southern

Africa (Dick, 1945), but records from indigenous plants from various west and east African countries, and in Natal, soon revealed that it was an insect indigenous to Africa (Dick, 1945; Carnegie, 1974; Atkinson, 1980).

It is thus apparent that in South Africa, E. saccharina is a fairly recent invader of sugarcane, being recorded as a localised pest on the Umfolosi Flats for the first time in 1939, 26 years after sugarcane was first planted on the Umfolosi Flats, and 91 years after this crop was first grown commercially in Natal. By 1954 it had disappeared, with a number of reasons being given (Carnegie, 1974). The current infestation of southern African sugarcane began in 1970. Its spread through southern African sugarcane is summarised by Carnegie (1974) and Atkinson et al. (1981).

6.3 HOST PLANT SHIFT

It is well known that sugarcane was planted in wetland areas to take advantage of the better soils. As a result, large portions of wetlands were increasingly drained and indigenous sedge areas were replaced by stands of sugarcane (Atkinson and Nuss, 1989). This practice placed sugarcane in touch with E. saccharina in its natural habitat, and exposed it directly to infestation by E. saccharina, particularly as the area of natural host plants of E. saccharina was decreasing.

An analysis of oviposition behaviour and its range of natural host plants provides further evidence of how E. saccharina could have shifted to sugarcane and other graminaceous crops. Generally there is a natural variation in individual lepidopteran female oviposition preferences, which allows them to oviposit on plants other than their known host plants (Thompson and Pellmyr, 1991). The lists of host plants of E. saccharina provided by Girling (1972) and Atkinson (1980) as well as the more recently found Prionium serratum (L.f.) Drege and Juncus exsertus Buchen. (Conlong, unpublished results) indicate that it attacks and can survive on three families of host plant: Cyperaceae, Graminae and

Juncaceae. Its ability to colonise this wide host plant range is helped by the oviposition behaviour of the female, which lays 400 to 500 eggs in batches of 1 to 20 eggs in well concealed positions in sugarcane (Carnegie, 1974), maize (Cochereau, 1981) and C. papyrus (Conlong, 1990). The female has a retractile, prehensile ovipositor, which can extend to the length of the female's body. Sensillae at the end of the ovipositor need to be in contact with three surfaces before oviposition will take place (Waladde, 1983). Eggs are thus laid in concealed positions which protect them from predation and parasitism. This behaviour allows the female to lay eggs on a variety of host plants which offer suitable oviposition sites. It can thus colonise new host plants very easily if its larvae accept the plant as a food source. The copious trash produced by mature sugarcane in particular provides many ideal oviposition sites. This trash is produced below the canopy level, in a similar environment to the young C. papyrus umbels, which are heavily exploited by small E. saccharina larvae (Chapter 4). In addition, there are sucrose sensillae in the front tarsi of E. saccharina (Waladde, 1983), and the lower portion of sugarcane stalks are where sucrose is stored. This is thus an additional stimulus to attract ovipositing females to the base of sugarcane. Changes in nitrogen levels are often accompanied by changes in other chemical constituents such as sugars (Thompson and Pellmyr, 1991). In Chapter 3 it was shown that E. saccharina prefers high nutrient areas of its natural host plants. It is not known if these are associated with areas of high sucrose. This does, however, provide a hypothesis of how E. saccharina managed to colonise sugarcane.

6.4 INDIGENOUS PEST CONTROL

The habitat provided by mature sugarcane is similar to that of C. papyrus in that the green leaves of sugarcane provide a closed canopy, below which light intensity is lower, and environmental conditions are changed. Mature umbels provide the same closed canopy. Jones and Muthuri (1985) and Breen and Stormanns (1989) have described the changed environmental conditions encountered below the C. papyrus canopy.

Differences are however greater. Generally the substratum below C. papyrus stands is water, while below sugarcane is soil. One would thus expect the microclimate below a sugarcane canopy to have lower relative humidity. In addition, growing umbels below the C. papyrus canopy provide spatial heterogeneity to the system, while below mature sugarcane there are no younger plants. Spatial heterogeneity is thus missing. In C. papyrus stands, this spatial heterogeneity exists throughout the year (Chapter 3), whereas in sugarcane, which is cut annually, there are very large areas which have plants of the same age growing at any one time. Since, in sugarcane, E. saccharina is a stalk borer, infestations generally begin only when the plant has some stalk on it (approximately 4 months old). In contrast, C. papyrus umbels are continually infested by E. saccharina (Chapter 4).

It is thus apparent that while similarities in terms of canopy cover and thus light intensity, and certain other environmental parameters between sugarcane and C. papyrus exist, which E. saccharina has recognised and exploited, the different spatial structure in particular may be a barrier yet to be overcome by indigenous parasitoids of E. saccharina. However, the complexity of the external sugarcane environment is not the only complication faced by indigenous natural enemies of E. saccharina. The very different boring behaviour shown by E. saccharina in the two host plants further complicates the task of natural enemies attempting to make the transition between C. papyrus, as the following sections will show.

6.4.1 Differences/similarities in behaviour between indigenous and crop hosts

The extensive boring pattern of E. saccharina larvae in sugarcane (as shown by Carnegie, 1974), which causes a great deal of crop loss, contrasts sharply with the small amount of boring found in C. papyrus umbels caused by the same sized larvae (Conlong, 1990). This indicates that the larva has to eat much more sugarcane to get the same amount of nutrients to complete its growth.

Sugarcane, under normal well irrigated conditions contains about 0.25% nitrogen (N) per dry mass, and under stressed conditions up to about 0.5% N (Atkinson and Nuss, 1989). The boring area of E. saccharina in C. papyrus umbels in contrast contains, under normal unstressed conditions an average 1,5% N, and under stressed conditions up to 2.4% N (Chapter 4). The N contents are thus greatly higher in the indigenous host in comparison to crop host, and corresponding lengths of boring are similarly different.

The longer borings which result in sugarcane are cleaned to some extent of frass by E. saccharina larva through holes chewed by the borer in the rind of sugarcane. There are thus a number of "holes" in the rind of an infested sugarcane stalk, and the chances of finding a larva close to one of them is remote because of the extensive area of tunnelling in the stalk. Contrastingly, in C. papyrus umbels, E. saccharina larvae only enlarge their borings to fit their increasing size, and as such are close to the "entrance" of their boring at all times, exuding frass through only this hole, in which they also pupate.

In addition, young larvae of E. saccharina are found in ray bases of umbels, where they feed until the bases are too small to contain them (Chapter 4). They are thus restricted in another small area of high nutrient value. In sugarcane, the young larvae scavenge on the stalk rind behind the leaf sheaths for up to two weeks before entering the stalk, and are thus more widely distributed on the stalk when compared to C. papyrus.

6.4.2 The use of parasitoids from indigenous hosts

In Chapter 5 it was shown that there was an effective parasitoid and pathogen guild (=compound guild; Miller and Ehler, 1990) attacking E. saccharina. It is considered that the concept of guilds may be useful in biological control, because often the choice of a species or combination of species for introduction against a pest is a major problem (Miller and Ehler, 1990). These authors suggest that where parasitoids associated with the target pest can be assigned

to component guilds, it may be worthwhile to base introduction strategies on this classification.

The parasitoid guild attacking larval stages of E. saccharina in C. papyrus is highly specialised, and has evolved with its host over many years. Its structure in C. papyrus is probably controlled by interspecific competition, as Orgilus bifasciatus attacks smaller larvae, and Goniozus indicus larger larvae (Chapter 5). The very rare Venturia sp., Iphiaulax sp. and Bassus sublevis, also collected from smaller larvae, may have been outcompeted by O. bifasciatus, or their searching behaviour was not suited to the C. papyrus habitat. Although not collected at this study site, the tachinid Schembria eldana Barraclough, was sometimes a common parasitoid of E. saccharina in C. papyrus umbels, being collected from larger larvae in local stands of this host plant (Conlong, 1994), and was recently found from E. saccharina larvae attacking C. papyrus at Lake Naivasha, Kenya (Conlong, unpublished results).

Miller and Ehler (1990) reviewing work of Force (1970, 1972, 1974), illustrated how an insignificant indigenous parasitoid in a stable habitat (parasitoid guilds attacking an indigenous gall midge) suddenly became very important when habitat stability was disrupted by clearing of the host plant. This species quickly colonised the new infestation of gall midge as the host plant grew again, but resumed its minor role once plants had established and other parasitoids of the guild became re-established. These findings led to the following characteristics being judged important when considering which parasitoids in a guild established in a stable habitat (such as C. papyrus) should be introduced into a disturbed agroecosystem environment (such as sugarcane):

1. It should be least dominant numerically in undisturbed habitats;
2. must be found consistently over a wide ecological or geographical range;
3. and be relatively more abundant in disturbed or newly available habitats.

In another study, Miller (1980), found the converse of what was found in this study, i.e., in a non disturbed habitat he could not recover any parasitoids from

the host insect, but in a highly disturbed environment (alfalfa grown for hay) there was a component guild of three indigenous species of parasitoid consistently exploiting the indigenous host larvae. In this case habitat instability was the primary factor contributing to guild structure.

Miller and Ehler (1990) thus show that habitat disturbance can have a profound influence on structure of a parasitoid guild, and in the context of biological control, consideration should be given as to how to construct a parasitoid guild consistent with ecological features of the target habitat.

Ecological features which may affect parasitoid performance in sugarcane have been described in preceding sections. Of additional importance to the ideas of Miller and Ehler (1990), is a knowledge of parasitoid foraging ability and oviposition behaviour once the habitat and host are encountered. These characters have been used by Smith et al. (1993) in defining and assigning parasites of lepidopteran stalkborers of tropical gramineous plants to guilds. Those found attacking E. saccharina in C. papyrus fall into some of their guilds quite clearly.

O. bifasciatus, the most common parasitoid of small larvae which tunnel in ray bases of umbels, falls into the "Drill and sting" guild. Smith et al. (1993) suggest that a parasitoid in this guild would be most successful parasitising hosts in plants with stems thin enough for drilling through, or where the host tunnel is sufficiently near the stem surface for the parasite ovipositor to reach and successfully parasitise any borers therein. The adaptation employed by parasitoids in this guild is thus to have a strong ovipositor that can drill and penetrate the plant stem (Smith et al., 1993). O. bifasciatus has these characters, and attacks E. saccharina in very thin stemmed rays of C. papyrus umbels. The conditions needed by this parasitoid to be successful in sugarcane are, however, not present. Small larvae are protected by numerous layers of dead leaf sheath material, the thickness of which places them out the reach of the O. bifasciatus ovipositor. The usefulness of this parasitoid in the sugarcane

environment would thus be minimal in attempts to establish a parasitoid guild.

Goniozus indicus, the most common parasitoid of large larvae in C. papyrus umbels, is a parasitoid belonging to the "ingress and sting" guild. Species belonging to this guild are small enough to gain ingress into the stalkborer tunnels and attack the host feeding in it (Smith et al., 1993). Despite the greater tunnel lengths in sugarcane, G. indicus was successful at finding its host and became established in standing sugarcane at a number of sites in Natal (Conlong, 1994). However, its biology which includes maternal care of her offspring, resulting in only one larva being parasitised by one female G. indicus, in addition to the production of only 8 female offspring per parasitised larva (Conlong et al., 1988), limited movement of the parasitoid from its site of establishment. Also, current management strategies of sugarcane during the drought period when releases took place did not enhance movement from parasitoid establishment sites. This was because sugarcane was cut younger, and very large areas were cut. Strip cropping, for instance, was impossible to implement because of drought severity and the deleterious effect of E. saccharina on more mature but droughted sugarcane.

However, more recent work in an undisturbed wetland area in Mkuze Game Reserve revealed that G. indicus attacked E. saccharina in umbels of Cyperus dives. These umbels are transient though and only occur during spring and summer. In an attempt to discover where this parasitoid disappeared to when umbels were absent, investigations revealed that it was a common parasitoid of the pyralid stalkborer Chilo partellus Swinhoe in an indigenous grass Sorghum arundinaceum in the same wetland habitat. This association is very common in Kenya (W.A. Overholt, 1994, pers. comm.). The broadening of the host habitat and host insect range of G. indicus has thus created further opportunities of sugarcane habitat manipulation in an effort to increase foraging range and establishment of this parasitoid.

The impact of G. indicus on E. saccharina in C. papyrus shown in Chapter 5, the

limited success in establishment of G. indicus on E. saccharina in sugarcane, and the recent discovery of G. indicus commonly attacking E. saccharina in C. dives, and C. partellus in S. arundinaceum comply with the last two criteria of Miller and Ehler (1990) as a good candidate from an established guild of parasitoids, to attempt to establish in a new disturbed habitat to form a new guild of parasitoids more suited to that habitat.

An uncommon parasitoid attacking small to medium E. saccharina larvae in C. papyrus, Bassus sublevis, complies with all three of Miller and Ehlers (1990) criteria. It is uncommon in C. papyrus, but more common on the same size E. saccharina larvae in the less stable habitat of C. dives umbels throughout Natal, and has also been collected from the same host in the rhizomes of Cyperus fastigiatus which are subject to frequent flooding in their wetland habitat (Conlong, 1994). During recent years it is also being found more frequently from E. saccharina in sugarcane. B. sublevis falls into the "probe and sting" guild of Smith et al. (1993), and exhibits all the attributes characteristic of species in this guild. It attacks early instar larvae by actively probing frass in leaf sheaths, or bracts in the Cyperaceae, for hosts. Its ovipositor is also longer than its body, allowing it to penetrate deeper into host plants to locate its insect host.

Not as much is known about the ichneumonid Venturia sp., nor the braconid Iphiaulax sp. Both have short stout ovipositors which indicate that they may belong to the "drill and sting" guild (Smith et al., 1993). The former has, however, been laboratory reared according to the methods advocated for "probe and sting" parasitoids by Smith et al. (1993). The latter has not been reared successfully, but, like Venturia sp., has been collected from smaller E. saccharina larvae attacking umbels of C. dives. They have also, on rare occasions, been collected from sugarcane. They show promising signs of being suitable for possible augmentation in sugarcane fields, but more investigation, in possibly other host plants is still needed.

Schembria eldana has so far only been found from E. saccharina in C. papyrus

but in widely spread localities, from Tongaat near Durban, northwards to Kosi Bay (both in Natal) and at Lake Naivasha in Kenya. Females of this tachinid lay eggs in the frass at the entrance of the boring of E. saccharina in C. papyrus umbels. These eggs have to be ingested by the larva for it to become parasitised. This species therefore belongs to the "bait and wait" guild (Smith et al., 1993). In C. papyrus umbels this is more easily accomplished, as E. saccharina larvae are in very short tunnels and in more contact with their own frass and thus eggs of S. eldana. However, in southern African sugarcane this mode of parasitism has very limited application against E. saccharina, because of its extensive tunnelling in the plant. It should not be discounted though, as in the New World, the tachinid parasitoid Palpozenillia palpalis (Aldr.) has been collected from stalkborers in sugarcane (Box, 1952). It is doubtful, however, if the boring habits of stalkborer species attacked by P. palpalis are the same as that of E. saccharina.

6.5 BIOLOGICAL CONTROL IN SUGARCANE: WORTHWHILE OR NOT?

Classical biological control revolves around the re-establishment of a naturally evolved natural enemy with its host, in the same habitat (or crop) but in a different area or country (Greathead, 1986). He expands the definition to include instances where the environment changed in such a way to exclude natural enemy regulation. In this instance, control is re-achieved by seeking natural enemies capable of effective control in the changed environment from elsewhere in the range of the pest or of related species. It is this latter expansion which Conlong (1994) has advocated as a workable control measure for E. saccharina in sugarcane.

This chapter shows that the association between E. saccharina and sugarcane in southern Africa has been relatively short. In other sugarcane growing areas, where there has been longer associations between sugarcane and its stalkborers, parasitoids are more abundant (Carnegie and Conlong, 1995). The lack of parasitoids in the former is thus not surprising. This study has shown

that parasitoids of E. saccharina do occur in at least one of its indigenous host plants (C. papyrus) and do have some measure of control on stalkborer populations. However, there are numerous more indigenous host plants to investigate.

In addition, because of the paucity of research on E. saccharina in its indigenous host plants, it was not known what natural enemies occurred in these environments. Three new species of parasitoids have so far been described from this study: Schembria eldana (Barraclough, 1991), Bassus sublevis (A. Polaszek, 1994, pers. comm.) and Goniozus natalensis (Gordh, 1986), later synonymised with Goniozus indicus (Polaszek and Krombein, 1994). Venturia sp. and Iphiaulax sp. cannot be described past the generic level, and may thus also be new species. The only known described species collected was O. bifasciatus.

The more intensive study on C. dives which was completed in March 1994 has revealed the first indigenous pupal parasitoid of E. saccharina found in southern Africa, as well as the same parasitoid complex found in C. papyrus (Conlong, unpublished results). Studies of this type are essential therefore to increased knowledge of parasitoid species range, their distribution and natural host plants, as well as kinds of host larvae accepted.

The more scientific analysis of pest/parasitoid/indigenous host plant interaction provides an invaluable database on which informed decisions on parasitoid introduction can be based. It also provides baseline information from which hypotheses about control strategies against indigenous pests can be tested. For example, the hypotheses of Force (1974) and Miller and Ehler (1990) about establishment of guilds of parasitoids more suited to unstable habitats, from those occurring in more stable indigenous habitats can be tested in a system which does not have parasitoids in it (E. saccharina/sugarcane). In addition, the knowledge gained from rearing the indigenous parasitoids found (e.g. Conlong et al., 1984; Carnegie et al., 1985; Conlong et al., 1988; Conlong and Graham, 1988) provides invaluable biological information on mode of parasitism, life cycle

lengths, searching behaviour etc. This information is a very useful adjunct to any biological control programme.

In terms of scientific challenge and potential for success therefore, a biological control programme along the lines of this study should be pursued. This study has just provided the first useful information on E. saccharina/parasitoid/C. papyrus interactions. It will be a pity if this programme, which has been going for a comparatively short time (14 years), especially on a new pest/host plant association, should be cut short. In addition, as Greathead (1986) points out, there has been a worldwide decrease in the rate of establishment of natural enemies and biological control success rates with time since 1888, and that easy and good biocontrol targets are getting fewer as time goes on. However, if the above type of ecological and behavioural knowledge can be obtained from all natural host plants of E. saccharina, the database available for assessment of potential parasitoids would be invaluable.

Using success rates of previous biological control programmes as an evaluation tool for the present programme, of which this study is part, however, should be done with caution. Especially in commodity based organisations, biological principles and human "foibles" have become confounded in the results of biological control programmes, to the extent that analyses of results which have been attempted are of limited value as guidelines for future action or in testing theory (Greathead, 1986). Beirne (1980) analysed the effect of administrative and political factors on the outcome of biological control programmes, and pointed out that these have been a major obstacle to success. This shortcoming by administrators of the present project would be disastrous, especially as there are no other short-term control measures available.

In contrast, DeBach (1964) concluded that success of biological control programmes was achieved in proportion to effort applied. Additionally, Greathead (1986) stated that success rate can be improved by a better and more scientific choice of targets (and agents) aided by ecological theory. Both

these points are covered by the present project and should contribute to its success.

REFERENCES

Atkinson, P.R., 1980. On the biology, distribution and natural host plants of Eldana saccharina Walker (Lepidoptera: Pyralidae). Journal of the entomological Society of southern Africa 43: 171 -194.

Atkinson, P.R. and Nuss, K.J., 1989. Associations between host-plant nitrogen and infestations of the sugarcane borer, Eldana saccharina Walker (Lepidoptera: Pyralidae). Bulletin of entomological Research 79: 489 - 506.

Atkinson, P.R., Carnegie, A.J.M. and Smaill, R.J., 1981. A history of the outbreaks of Eldana saccharina Walker in Natal. Proceedings of the South African Sugar Technologists Association 55: 111 - 115.

Barraclough, D.A., 1991. A new species of Tachinidae (Diptera) parasitic on the sugarcane borer Eldana saccharina (Lepidoptera: Pyralidae), in Natal, South Africa. Bulletin of entomological Research 81: 133 - 136.

Beirne, B.P., 1980. Biological control: benefits and opportunities. In Perspectives in World Agriculture. Commonwealth Agricultural Bureaux, Farnam Royal, England.

Betbeder-Matibet, M., 1981. Eldana saccharina Walker. Borer of the stalks of sugarcane in Africa. L'Agronomie Tropicale 36: 279 - 293.

Box, H.E., 1952. Palpozenillia palpalis (Aldr.), a tachinid parasite of sugarcane moth borers (Castnia and Diatraea). Proceedings of the Hawaiian Entomological Society 14: 485 - 490.

Breen, C.M. and Stormanns, C-H., 1989. Observations on the growth and productivity of Cyperus papyrus L. in a sub-tropical swamp. Thirty-fourth Congress of the International Association for Theoretical and Applied Limnology, Munich, 13-19 August, 1989. Unpublished presentation of the Institute of Natural Resources, University of Natal, Pietermaritzburg.

Carnegie, A.J.M., 1974. A recrudescence of the borer Eldana saccharina Walker (Lepidoptera: Pyralidae). Proceedings of the South African Sugar Technologists Association 48: 107 - 110.

Carnegie, A.J.M., 1981. Combating Eldana saccharina Walker: a progress report. Proceedings of the South African Sugar Technologists Association 55: 116 - 119.

Carnegie, A.J.M. and Conlong, D.E., 1995. Biology, Pest Status and Control Measure Relationships of Sugar Cane Pest Insects. Proceedings of the Second ISSCT Entomology Workshop. SASA Experiment Station, Mount Edgecombe, South Africa. (In Press).

Carnegie, A.J.M., Conlong, D.E. and Graham, D.Y., 1985. Recent introductions of parasitoids against Eldana saccharina Walker (Lepidoptera: Pyralidae). Proceedings of the South African Sugar Technologists Association 59: 160 - 163.

Cochereau, P., 1982. Observations on the borer Eldana saccharina Walker (Lepidoptera: Pyralidae) in maize and sugarcane in Ivory Coast. Proceedings of the South African Sugar Technologists Association 56: 82 - 84.

Conlong, D.E., 1990. A study of pest-parasitoid relationships in natural habitats: an aid towards the biological control of Eldana saccharina (Lepidoptera:Pyralidae) in sugarcane. Proceedings of the South African Sugar Technologists Association 64: 111 - 115.

Conlong, D.E., 1994. A review and perspectives for the biological control of the African sugarcane stalkborer Eldana saccharina Walker (Lepidoptera: Pyralidae). Agriculture, Ecosystems and Environment 48: 9 - 17.

Conlong, D.E. and Graham, D.Y., 1988. A comparison of the life histories of Goniozus natalensis Gordh and Parasierola sp. (Hymenoptera: Pyralidae). Journal of the entomological Society of southern Africa 51: 143 - 144.

Conlong, D.E., Graham, D.Y. and Hastings, H., 1988. Notes on the natural host surveys and laboratory rearing of Goniozus natalensis Gordh (Hymenoptera; Bethylidae), a parasitoid of Eldana saccharina Walker (Lepidoptera: Pyralidae) larvae from Cyperus papyrus L. in southern Africa. Journal of the entomological Society of southern Africa 51:115 - 127.

Conlong, D.E., Graham, D.Y., Hastings, H. and Leslie, G.W., 1984. Rearing parasitoids and their hosts for the biological control of Eldana saccharina Walker. Proceedings of the South African Sugar Technologists Association 58: 159 - 164.

De Bach, P., 1964. Biological Control of Insect Pests and Weeds. Chapman and Hall, London.

Dick, J., 1945. Some data on the biology of the sugarcane borer (Eldana saccharina Wlk.) Proceedings of the South African Sugar Technologists Association 7: 377 - 394.

Force, D.C., 1970. Competition among four hymenopterous parasites of an endemic insect host. Annals of the Entomological Society of America 63: 1675 - 1688.

Force, D.C., 1972. r- and K-strategists in endemic host-parasitoid communities.

Bulletin of the Entomological Society of America 18: 135 -137.

Force, D.C., 1974. Ecology of insect host-parasitoid communities. Science 184: 624 - 632.

Girling, D.J., 1972. Eldana saccharina Wlk. (Lepidoptera: Pyralidae), a pest of sugarcane in East Africa. Proceedings of the International Society of Sugar Cane Technologists 14: 429 - 434.

Gordh, G., 1986. A new species of Goniozus Foerster 1851 from southern Africa parasitising sugar cane borer, Eldana saccharina Walker, and taxonomic notes on species of the genus in Africa (Hymenoptera: Bethylidae; Lepidoptera: Pyralidae). Journal of the entomological Society of southern Africa 49: 257 - 265.

Greathead, D.J., 1986. Parasitoids in classical biological control. In Waage, J.K. and Greathead, D.J. (Eds). Insect Parasitoids. Academic Press Inc., London.

Jones, M.B. and Muthuri, F.M., 1985. The canopy structure and microclimate of papyrus (Cyperus papyrus) swamps. Journal of Ecology 73: 481 - 491.

Miller, J.C., 1980. Niche relationships among parasitic insects occurring in a temporary habitat. Ecology 61: 270 - 275.

Miller, J.C. and Ehler, L.E., 1990. The concept of parasitoid guild and its relevance to biological control. In Mackauer, M., Ehler, L.E. and Roland, J. (Eds.). Critical Issues in Biological Control. Intercept, Andover, Hants.

Mohyuddin, A.I. and Greathead, D.J., 1970. An annotated list of the parasites of graminaceous stem borers in East Africa, with a discussion of their potential in biological control. Entomophaga 15: 241 - 274.

Naude, T.J., 1940. Work on the control of insect pests. Annual Report of the Division of Entomology pg 516. In Farming in South Africa, December 1940 edition.

Osborne, R.F., 1964. Valiant Harvest. The Founding of the South African Sugar Industry 1848-1926. South African Sugar Association, Durban.

Polaszek, A. and Krombein, K.V., 1994. The genera of Bethylinae (Hymenoptera: Chrysidoidea). Journal of Hymenoptera Research 3: In press.

Smith, J.W. Jr., Weidenmann, R.N. and Overholt, W.A., 1993. Parasites of Lepidopteran Stemborers of Tropical Gramineous Plants. ICIPE Science Press, Nairobi, Kenya.

Thompson, J.N. and Pellmyr, O., 1991. Evolution of oviposition behaviour and host preference in Lepidoptera. Annual Review of Entomology 36: 65 - 89.

Waladde, S.M., 1983. Chemoreception of adult stem-borers: Tarsal and ovipositor sensilla on Chilo partellus and Eldana saccharina. Insect Science and its Application 4: 159 - 165.

Walker, P., 1865. List of specimens of lepidopterous insects in the collection of the British Museum. British Museum (Natural History) Part 32. Suppl. Part 2: 632 - 633.

PERSONAL COMMUNICATIONS

Dr A.J.M. Carnegie, South African Sugar Association Experiment Station, Private Bag X02, Mount Edgecombe, Kwazulu-Natal, 4300. South Africa.

Durban Meteorological Office, Louis Botha Airport, Durban, Kwazulu-Natal. South Africa.

Dr W.A. Overholt, International Centre for Insect Physiology and Ecology, P.O. Box 30772, Nairobi, Kenya.

Dr A. Polaszek, CAB International Institute of Entomology, 56 Queens Gate, London, SW7 5JR, UK.

Dr Sayed Abd Elurahab Morad, Crop Pest Research Division, Agriculture Research Centre, Plant Protection Institute, Dokki, Giza, Egypt.

Mr M. Way, South African Sugar Association Experiment Station, Private Bag X02, Mount Edgecombe, Kwazulu-Natal, 4300. South Africa.