

In Swaziland, conditions presumably become too cool for the insect along the western highlands of the country.

The areas where *E. saccharina* occurs in sugarcane are shown in Figure 1 and it is evident that the insect extends further south in the natural host than it does in sugarcane. This intrusion of the insect southwards along the Natal coast is presumably made possible by the warm Mocambique current, and Port Shepstone at present represents the extreme southern record of the insect.

Surveys for different natural hosts of *E. saccharina* have been conducted in Natal, the procedure being to demonstrate the presence of the insect in a known host at a given site before searching other plants in the vicinity. Plants in which mature larvae or pupae were found were regarded as true hosts, whereas those in which only small or medium sized larvae could be demonstrated, in different sites at several different times, were assumed as unlikely to be true hosts, particularly if they were small or slender plants. The results are listed in Table 1, together with natural or crop hosts recorded in the literature.

Previous host-records of *E. saccharina*, summarised by Girling¹³ have tended to stress the crop or graminaceous hosts,

but it is evident from Table 1 that the insect probably evolved in the Cyperaceae. Gramineaceous hosts seem to be either crops (that is, secondarily invaded), or grasses in which it is doubtful whether the insect could complete its life cycle. For example Nye²² recorded *Sorghum verticilliflorum* as a host, and although this was confirmed by rearing the insect, the host plant material was frequently renewed.

In Natal small or medium larvae of *E. saccharina* have occasionally been found in *S. verticilliflorum* adjacent to heavily infested cane, but damage to this grass suggestive of large larvae has never been seen. The insect has never been found in *Echinochloa pyramidalis* (Table 2) although this grass often grows abundantly among cyperaceous hosts. Isolated records from *E. stagnina* and *Paspalum urvillei* (Table 1) were undoubtedly due to chance incursions into these plants.

In northern Natal the insect has been recorded in ten species of true natural hosts, all Cyperaceae. From Richards Bay to the Umvoti River mouth only five true hosts have been recorded, while south to Port Shepstone, only the one host, *Cyperus immensus*, appears to be utilized. This species is a preferred host throughout the range of the insect in Natal and

TABLE 1

Natural and crop hosts of *E. saccharina*, recorded in the literature and in present surveys. (Where no authority is given, records are from present surveys)

Family, species and remarks on status as a host	Common name	Country and authority	Carbon fixation cycle
AMARANTHACEAE			
<i>Amaranthus dubius</i> Mart.—There was no oviposition on <i>A. spinosus</i> L. in current choice trials	Pigweed	Tanzania (24)	C ₄
EUPHORBIACEAE			
<i>Manihot utilissima</i> Pohl.—Girling ¹³ questions identification of insect. Although he reared <i>E. saccharina</i> on cassava, the shoots were apparently renewed	Cassava	Congo (17)	C ₃
CYPERACEAE			
<i>Cyperus papyrus</i> L.—A main host south to Richards Bay, Natal. Exposed rhizomes and inflorescences utilised	Papyrus	Uganda (15) Natal (1)	C ₄
<i>C. distans</i> L.f.	Sedge	Uganda (15)	C ₄
<i>C. immensus</i> C.B. Cl.—A main host south to Port Shepstone, Natal. Rhizome and inflorescence	Large sedge	Natal	C ₄
<i>C. prolifer</i> Lam.—Sporadic host south to Umvoti mouth. Small pupae in exposed rhizomes; but life-cycle probably not completed in aerial parts	Small papyrus	Natal	C ₄
<i>C. fastigiatus</i> Rottb.—Common host at pans; North Natal south to Sordwana Bay. Rhizomes only	Sedge	Natal	C ₄
<i>C. natalensis</i> Hochst.—Common host at lakes; North Natal south to Richards Bay. Rhizomes only	Sedge	Natal	C ₄
<i>C. sexangularis</i> Nees } Pupae recovered from rhizomes of both these related sedges; south to Umvoti	Sedge	Natal	C ₃ ?
<i>C. textilis</i> Thunb. } River.	Sedge	Natal	C ₃ ?
<i>C. rotundus</i> L. } Small sedges recorded as hosts once, near heavily infested cane. Unlikely that life-	Water grass	Natal	C ₄
<i>C. esculentus</i> L. } cycle completed. Rhizomes only	Water grass	Natal	C ₄
<i>C. latifolius</i> Poir.—Although similar to <i>C. immensus</i> small larvae only twice found in inflorescence, never in rhizome, despite coincidence of habitat	Large sedge	Natal	C ₄
<i>Mariscus riparius</i> Schrad.—Common but sporadically utilised south to Amatikulu R. Rhizome only	Sedge	Natal	C ₄
<i>Kyllinga elatior</i> Kunth—No pupae found, only small and medium larvae. Probably unable to complete life-cycle. Several records south to Umvoti mouth	Sedge	Natal	C ₄
<i>Pycreus polystachyus</i> Beauv.—Common host northern Natal. Rhizome only	Sedge	Natal	C ₄
<i>Fuirena umbellata</i> Rottb.—Only once recorded as host, north Natal. Pupae found. Rhizome only	Sedge	Natal	C ₃
<i>Cladium mariscus</i> (L.) Pohl.—Usually rooted in standing water. Only once recorded with small larvae in inflorescence. Unlikely to be true host	Large sedge	Natal	C ₃
GRAMINEAE			
<i>Eleusine coracana</i> Gaertn.	Millet	Nigeria (13)	C ₄
<i>Oryza sativa</i> L.—Record unsupported by adult specimens; unconfirmed by Harris's ¹³ own surveys	Rice	Nigeria (13)	C ₃
<i>Sorghum vulgare</i> Pers.	Sorghum	Several (12)	C ₄
<i>S. verticilliflorum</i> Steud.—Probably not a true host; pupae or large larvae never found in Natal. Nye artificially reared it renewing supply of host as necessary	Wild sorghum	Nye (20)	C ₄
<i>Pennisetum typhoides</i> Rich.	Bullrush millet	Uganda (12)	C ₄
<i>P. purpureum</i> Schumach	Napier fodder	Tanzania (24)	C ₄
<i>Zea mays</i> L.—Only once recorded in Natal despite many surveys of maize adjacent to cane or other hosts	Elephant grass		
<i>Rottboelia exaltata</i> L.	Maize	Many	C ₄
<i>Coix lachryma-jobi</i> L.—Not a true host. One record adjacent heavily infested <i>C. immensus</i>	Guinea fowl grass	Nigeria (13)	C ₄
<i>Paspalum urvillei</i> Steud. } Not true hosts. Recorded at same site, highly stressed from	Job's tears	Natal	C ₄
<i>Echinochloa stagnina</i> (Retz.) Beauv. } drought	Tall grasses	Natal	C ₄
<i>Saccharum</i> spp. hybrids	Cane	Many	C ₄

Table 2

Plants growing adjacent to natural hosts of *E. saccharina* which are fairly definitely not hosts of the insect, at least in Natal

Family	Species	Carbon fixation cycle
Cyperaceae	<i>Eleocharis plantaginea</i> R. Br.	?
	<i>E. limosa</i> Schult.	?
	<i>Scleria angusta</i> Nees	C ₃
	<i>Rhychospora corymbosa</i> (L.) Britt.	?
	<i>Scirpus maritimus</i> Poir.	?
Gramineae	<i>Echinochloa pyramidalis</i> (Lam.)	C ₄
	<i>Phragmites australis</i> (Car.) Trin. ex Steud.	C ₃
Typhaceae	<i>Typha latifolia</i> L.	C ₃
Juncaceae	<i>Juncus kraussii</i> Hochst.	C ₃

Swaziland. *Cyperus latifolius* is similar in appearance to *C. immensus*, often growing adjacent to it, but *E. saccharina* has never been found in it except on two occasions as small larvae feeding in the inflorescence.

Nearly all the recorded hosts of *E. saccharina* appear to be C₄ plants (Table 1). Plants were identified as C₃ or C₄ either from check-lists of C₄ plants (Downton¹², Smith and Epstein²⁵, Hattersley and Watson¹⁶) or, in the case of the Cyperaceae, from the Kranz or non-Kranz anatomy (Brown⁶) of the vascular bundles in leaves, bracts or culms. Only three of the true hosts of the insect appear to be C₃. Two of these *Cyperus sexangularis* and *C. textilis*, may be C₃ or C₄ because although there are chloroplast-containing cells inside and adjacent to the mestome sheath, these cells do not themselves form a continuous sheath. Of the remaining C₃ hosts, *Cladium mariscus* is probably not a true host, while the records from cassava and rice appear to be doubtful (Table 1). *Eldana dichromelus* (Wlk.) has, however, been recorded in rice in Ceylon (Jepson¹⁸).

Plants which are commonly associated with the known hosts, but which appear to be non-hosts, are listed in Table 2.

TABLE 3

Results of insectary choice-trials for oviposition preferences of *E. saccharina*; types of oviposition site

Site	Eggs		
	No.	%	No./batch
Curled edges of dead leaves or sheaths	1496	25,3	36,5
Between dead leaves or sheaths	1004	17,0	32,4
Rolled-up tips of dead leaves	581	9,8	32,3
Between dead sheaths and stems (cane only)	489	8,3	48,9
Under dead leaves on soil	394	6,7	39,4
Between dead leaves/green leaves	363	6,1	90,8
Along midribs of folded dead leaves	336	5,7	19,8
In soil cracks at base of plant	107	1,8	17,8
In dead grass leaves	96	1,6	48,0
Tips of live green leaves	80	1,4	40,0
Between green leaf sheaths	59	1,0	29,5
Between green leaves of grasses	57	1,0	14,3
Edges of green leaves of hosts	40	0,7	13,3
In mesophyll of dead-leaf cracks	38	0,6	12,7
Random sites (against drum edge, under drums, etc.)	777	13,1	55,5
TOTALS	5917	—	35,5

Oviposition

E. saccharina was tested for its egg-laying preferences between a natural host (*C. immensus*), a crop host (sugarcane) and a non-host (*C. latifolius*). The results of three insectary choice trials are given in Tables 3 and 4. Six of each type of plant, in drums, were used in the first trial, three

TABLE 4

Results of insectary choice — trials for oviposition preferences; host-plant preferences

Host	Trial 1		Trial 2		Trial 3		Totals	
	Eggs	Eggs/batch	Eggs	Eggs/batch	Eggs	Eggs/batch	Eggs	Eggs/batch
<i>Cyperus immensus</i>	1471	38,7	277	23,1	1160	31,4	2908	33,4
Sugarcane	539	41,5	248	24,8	748	31,2	1535	32,7
<i>C. latifolius</i>	474	52,7	188	23,5	35	17,5	697	36,7
Random sites (see Table 3)	586	58,6	135	67,2	56	28,0	777	55,5
<i>Amaranthus spinosus</i>	—	—	—	—	0	0	0	0

of each in the second and five in the third. A dicotyledon, *Amaranthus spinosus* L., was also included in the third trial, and a subsequent trial has confirmed that eggs are not laid on this plant. There are two points of interest in these tables. The first is the preference for dead material, green tissue rarely being used (Table 3). No eggs were found in the flowers of *C. immensus*, possibly for this reason. The second point is that although not the preferred host, sugarcane appears to have been actively chosen (Table 4), perhaps because it has abundant dead material around its base. For example the oviposition frequency in cane was twice that in the sporadically utilized host *C. latifolius*, and twice that in random, inappropriate sites (which would not occur in nature). These insectary results suggest that the invasion of cane has not been the result of random laying in an abnormal host, but that the crop may be actively selected by the insect.

Feeding Sites

Feeding sites in the Cyperaceae are nearly always in the rhizome. In papyrus, where the rhizome is usually submerged, the common feeding site is in the inflorescence; but when rhizomes are exposed by falling water levels, they become favoured feeding sites and high larval intensities may occur¹. In *C. immensus* the inflorescence is favoured during flowering (September to February) when up to 90% of the population is found in the inflorescence, particularly from October to December when peak population intensities occur in this host (present unpublished data). The young larvae presumably migrate to the inflorescence after hatching, because eggs are not apparently laid in the inflorescence. Young larvae are sometimes encountered feeding on the leaves of *C. immensus*, having dispersed from their hatching sites. Two Cyperaceae, *Cladium mariscus* and *Cyperus latifolius*, are attacked in the inflorescence only, while in *Kyllinga spp.* the insect feeds all over the plant (but large larvae have never been encountered).

Feeding sites in sugarcane are summarised in Table 5. The middle and base of mature tillers are primarily attacked. Within each segment, feeding usually starts around the node, which is the most common penetration site, and extends into the internode or throughout the segment(s). Beyond reflecting the penetration pattern, there was no evidence that feeding tended to concentrate around the node.

Cracking of cane undoubtedly aids penetration (Atkinson²) and the low proportion of penetrations through cracks (23%, Table 5) probably reflects the incidence of cracking in the field, rather than the exploitation of cracks by the insect. The internode is rarely penetrated unless cracked. Once cane has become severely damaged by borings there is evidence in the field that succeeding generations often penetrate through old borings.

The length of cane damaged by individual larvae is very

TABLE 5
Penetration and feeding patterns of *E. saccharina* in mature sugarcane. Results are from 144 sticks dissected

	Height above ground			Penetration site				Feeding site				
	Top	Mid	Base	Node	Near Node	Crack	Inter-node*	Around node	Inter-node	Both node and internode	Through-out segment	Surface only
No.	16	61	55	79	16	32	13	53	23	25	36	3
%	12,1	46,2	41,7	56,4	11,4	22,9	9,3	37,9	16,4	17,9	25,7	2,1
		87,9		67,9						43,6		

* Penetration independently of cracks.

TABLE 6
Frequencies of indicated lengths of feeding damage caused by individual larvae in sugarcane

	Length of damage in cm										
	1	2	3	4	5	6	7	8	9	10	>10
Feeding by larvae of all ages*	15	21	15	9	4	8	12	4	3	1	6
Feeding to produce mature individuals**		2	1	2	1	1	3	2			

* One individual certainly involved, or probably involved judging by boring, in each case.

** One large larva, or live or emerged pupa, found in each case.

variable but from 2-8 cm of feeding is required to produce a mature individual (Table 6).

Percentages of nitrogen in spot-samples of three host plants are given in Table 7. The nitrogen in the unsubmerged rhizome of papyrus is remarkably high, and this suggests why this feeding site is so favoured by the insect. Papyrus inflorescences are also relatively nutritious; but the inflorescences of *C. immensus*, sampled in February, were senescing and may not reflect the nitrogen levels of this feeding site at its most favourable. Sugarcane stalk is apparently not a particularly nutritious material compared to others utilised by the insect, especially unsubmerged papyrus rhizome; and available figures show only a small difference between cane and the most common wild host, *C. immensus*.

The activity of gut-symbiotic nitrogen-fixing bacteria could not be demonstrated in field-collected larvae, nor in dissected guts (B.S. Purchase, pers. comm.). The acetylene-reduction technique (Dilworth¹¹, Schöllhorn and Burris²³, Burris⁷) was used for these tests. Although the results may not be conclusive, the suggestion is that the insect is dependent upon ingested protein and amino acid. The quantities of frass characteristic of the insect support this conclusion; evidently large volumes of plant material must be processed to extract sufficient protein.

Discussion and Conclusions

The coast between Richards Bay and the Umvoti River mouth represents a region of marked ecological change. The Mocambique coastal plain, which extends into northern Natal with its associated lakes and marshes, comes to an end at the Umlalazi River mouth (Mtunzini). Papyrus extends no further south than this point and Vogel *et al.*²⁸, have shown that here the frequency of C₄ grass species falls from 100% to between 75% and 95%. Within this region the number of host plants species utilised by *E. saccharina* falls from at least ten, to five (excluding cane), while south of the Umvoti it falls to one. It is within this region of ecological change that sugarcane has been (on average) more heavily infested than elsewhere in the Natal cane belt. Just south of this region cane is (at present) hardly infested at all.

TABLE 7
Percentage nitrogen in spot-samples of three hosts of *E. saccharina* (samples split for analysis)

Host	Part of host	Nitrogen (N) %
<i>Cyperus papyrus</i>	Submerged rhizomes	{ 0,46 0,45
	Unsubmerged rhizomes	{ 1,29 1,12
" "	Inflorescences	{ 0,55 0,53
	Mature stalks	{ 0,39 0,42
<i>Cyperus immensus</i>	Lower 15 cm of plants with rhizomes	{ 0,41 0,49
	Senescing inflorescences	{ 0,38 0,41

Each host-plant species characteristically extends further south than the utilisation of that host by *E. saccharina*. For example *Cyperus prolifer*, *C. sexangularis*, *C. fastigiatus*, *Kyllinga spp.* and *Pycurus polystachyus* all occur south of Umvoti mouth, but are not apparently attacked. *C. immensus* extends into the Transkei but the insect has been recorded only as far south as Port Shepstone. While sugarcane extends to Port Edward, the most southerly record of the insect in cane is a single larva from Illovo mill. Similar distribution patterns occur moving inland. For some reason the various host species become free from attack as conditions become cooler. The heavy infestations of sugarcane in the Empangeni and Amatikulu areas appear to be associated with a decreased availability of natural hosts, resulting from their decreasing southerly abundance, and from their apparent increasing unsuitability.

In general C₄ plants have lower nitrogen levels, weight for weight, than do C₃ plants (Lyttleton²⁰, Brown⁵) primarily because of less RuDP carboxylase in their carbon fixation pathways. This fact led Caswell *et al.*⁹, to suggest that there may be less use of C₄ than of C₃ species by insect herbivores, as a result of passive avoidance of C₄ plants. But Boutton *et al.*⁴ found no significant differences in utilization between

C₃ and C₄ grasses. It seems more likely that phytophagous insect species will have evolved in conjunction with each group and this is exemplified by *E. saccharina* which is virtually dependent upon C₄ species. Evidently the insect is adapted to the relatively low nitrogen levels in its host plants.

In *C. immensus* during spring the insect population moves to the inflorescences, presumably by the upward dispersal of young larvae from their hatching sites at the bases of the plants because eggs are not laid in the inflorescences. In papyrus on the other hand, the larvae remain in the rhizome when this is exposed. McNeill and Southwood²¹ have emphasised that with other insects such changes of feeding sites are often associated with the exploitation of higher nitrogen levels. However if, as seems likely, *E. saccharina* moves to the inflorescences for this reason in its natural host *C. immensus*, it does not do so in sugarcane. Both Clements¹⁰ and Bishop³ have shown that nitrogen levels in the growing tip and in the zone of elongation of cane, are much higher (c 1.2-3.5%) than in the mature stalk (c 0.2-0.6%) yet the insect persists in feeding in the stalk. Possibly the morphology of cane, which is not a natural host, is inappropriate for the migrating behaviour of young larvae. For example in cane there is no smooth culm leading upwards as there is in papyrus or flowering *C. immensus*. Alternatively, it may be that secondary feeding attractants (Harbourne¹⁴) to which the young larvae respond are inappropriate in cane, and are not associated with high levels of nitrogen. For example in many lepidopterous larvae sucrose has been implicated as a feeding attractant (Schoonhoven²⁴), which in cane is concentrated in the stem where nitrogen levels are low.

The evidence offered here suggests that *E. saccharina* is attracted to oviposit in sugarcane because of the abundant dead-leaf material about the base of the plant. This conclusion is consistent with the observation that population intensities usually remain low in young green cane, but rise in older cane where dead-leaf material accumulates.

Acknowledgements

I should like to thank Prof. K. Gordon-Gray (Dept. Botany University of Natal, Pietermaritzburg) for identifying the Cyperaceae, and for advice on the recognition of Kranz anatomy; Dr. R. E. Schulze (Dept. Agriculture, University of Natal, Pietermaritzburg) for providing temperature isotherms for Natal; and Dr. B. S. Purchase (University of Rhodesia, Salisbury, Rhodesia) for conducting the acetylene-reduction tests.

REFERENCES

1. Atkinson, P. R. (1978a). Land management and the creation of habitat for *Eldana saccharina* Walker (Lepidoptera: Pyralidae) SASTA Proc 52, 137-138.
2. Atkinson, P. R. (1978b). Mass rearing and artificial infestation methods for *Eldana saccharina* Walker (Lepidoptera: Pyralidae). SASTA Proc 52, 143-145.

3. Bishop, R. T. (1965). Improved tissue diagnostic techniques for sugar cane. Unpublished MSc thesis, University of Natal, South Africa.
4. Boutton, T. W., Cameron, G. N. and Smith, B. N. Insect herbivory on C₃ and C₄ grass (in press).
5. Brown, R. H. (1978). A difference in N use efficiency in C₃ and C₄ plants and its implications in adaptation and evolution. Crop Sci 18, 93-98.
6. Brown, W. V. (1975). Variations in anatomy, associations and origins of Kranz tissue. Am J Bot 62, 395-402.
7. Burris, R. H. (1975). The acetylene-reduction technique. In, Stewart W. D. P. (Ed.) Nitrogen fixation by free-living microorganisms. Cambridge University Press. pp 249-257.
8. Carnegie, A. J. M. (1974). A recrudescence of the borer *Eldana saccharina* Walker (Lepidoptera: Pyralidae). SASTA Proc 48, 107-110.
9. Caswell, H., Reed, F., Stephenson, S. and Werner P. A. (1973). Photosynthetic pathways and selective herbivory: a hypothesis. Am Nat 107, 465-480.
10. Clements, H. R. (1940). Integration of climatic and physiological factors with reference to the production of sugarcane. Hawaii Plrs' Rec 44, 201-233.
11. Dilworth, M. J. (1966). Acetylene reduction by nitrogen-fixing preparations from *Clostridium pasteurianum*. Biochim biophys Acta 127, 285-294.
12. Downton, W. J. S. (1971). Check list of C₄ species. In, Hatch M. D., Osmond, C. B. and Stättyer, R. O. (Eds.) Photosynthesis and photorespiration. Wiley Interscience, N.Y. pp 554-558.
13. Girling, D. J. (1972). *Eldana saccharina* Wlk. (Lepidoptera: Pyralidae), a pest of sugarcane in East Africa. ISSCT Proc 14, 429-439.
14. Harbourne, J. B. (1977). Introduction to ecological biochemistry. Academic Press, London. 243 pp.
15. Harris, K. M. (1962). Lepidopterous stem borers in Nigeria. Bull ent Res 53, 139-171.
16. Hattersley, P. W. and Watson, L. (1976). C₄ grasses: an anatomical criterion for distinguishing between NADP-malic enzyme species and PCK or NAD-malic enzyme species. Aust J. Bot 24, 297-308.
17. Ingram, W. R. (1958). The lepidopterous stalk borers associated with Gramineae in Uganda. Bull ent Res 49, 367-383.
18. Jepson, W. F. (1954). A critical review of the world literature on the lepidopterous stalk borers of graminaceous crops. Commonw Agric Bureau Publication. 127 pp.
19. Lefevre, W. F. (1944). Note sur quelques insectes parasites de *Manihot utilisissima* Pohl. dans la region de Kasenyi (Lac Albert). Bull agric Congo belge 35, 191-200.
20. Lyttleton, J. W. (1973). Proteins and amino acids. In Butler, G. and Bailey, R. (Eds.) Chemistry and biochemistry of herbage, Vol 1. Academic Press, N Y pp 63-103.
21. McNeill, S. and Southwood, T. R. E. The rôle of nitrogen in the development of insect/plant relationships (in press).
22. Nye, I. W. B. (1960). The insects of graminaceous crops in East Africa. Colon Res Stud. No. 31, 48 pp.
23. Schollhorn, R. and Burris R. H. (1967). Acetylene as a competitive inhibitor of N₂ fixation. Proc natn Acad Sci USA 58, 213-216.
24. Schoonhoven, L. M. (1973). Plant-recognition by lepidopterous larvae. In Insect/plant relationships. van Emden, H. F. (Ed.) Blackwell, London, pp 87-99.
25. Smith, B. N. and Epstein, S. (1971). Two categories of ¹³C/¹²C ratios for higher plants. Plant Physiol 47, 380-384.
26. Vogel, J. C. Fuls, A. and Ellis, R. P. (1978). The geographical distribution of Kranz grasses in South Africa. S Afr J Sci 74, 209-215.
27. Waiyaki, J. N. (1968). The biology and control of the principal lepidopterous borers associated with sugarcane at the Tanganyika Planting Company, Arusha-Chini TPRI Misc Rep No. 653.