Geographic distribution and host plant ranges of East African noctuid stem borers

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* DGIS funded Stem borer Biological Control NETwork for ESA (SBCNET)

Abstract. Surveys were carried out in Kenya, Tanzania, Uganda and Zanzibar to establish geographic distribution in the main vegetation mosaics and ecological (host plant range, feeding behaviour) characteristics of the East African noctuid stem borers. 49 wild plant species belonging to Poaceae, Cyperaceae and Typhaceae were found to harbour stem borers in the six vegetation mosaics surveyed. A total of 36 noctuid species belonging to nine genera were identified from 14,318 larvae collected, out of which 17 were new to science. The species diversity varied among vegetation mosaics and host plants. Most borer species appeared to be specialised feeders with 24 species being monophagous. Species belonging to the same types (named as the *Busseola* Thurau 1904 and the *Sesamia* Guenée 1852 types) or genus harboured common ecological characteristics such as pigmentation and feeding site. The *Sciomesa* Tams and Bowden 1953 genus was an exception as it had a mixture of these characters.

Résumé. Distribution géographique et spectre d'hôtes des foreurs de graminées d'Afrique de l'Est. Des enquêtes ont été conduites au Kenya, en Tanzanie, en Ouganda et à Zanzibar afin de connaître les caractéristiques écologiques des noctuelles foreuses africaines tels que le spectre d'hôtes, le mode de nutrition et les principales caractéristiques de développement. 49 espèces de plantes appartenant aux familles des Poaceae, Cyperaceae et Typhaceae ont été trouvées infestées par des foreurs dans les six phytochories rencontrées. Sur un total de 14318 chenilles récoltées, nous avons identifié 36 espèces de noctuelles appartenant à neuf genres. 17 espèces nouvelles ont été trouvées. La diversité spécifique varie d'une phytochorie à l'autre et d'une plante hôte à l'autre. La plupart des espèces de foreurs ont été trouvées dans les zones humides des phytochories et présentent un comportement alimentaire spécialisé : 24 espèces sont monophages, et la plupart des huit espèces oligophages montrent une préférence marquée pour une ou deux plantes.

Keywords: Stem borer, Poaceae, feeding behaviour, vegetation mosaic, Africa.

During the last 50 years, several surveys have been carried out in Kenya, Uganda and Tanzania to identify wild host plants of noctuid stem borers (Noctuidae) (Ingram 1958; Nye 1960; Seshu Reddy 1989; Randriamananoro 1996; Polaszek & Khan 1998). Ten noctuid species (two *Busseola* Thurau 1904, seven *Sesamia* Guenée1852, one *Poeonoma* Tams and Bowden 1953) were recovered from 34 wild host plants. It is expected that the list of host plants of these 10 species is by far not exhaustive because the surveys were short, carried out in a limited area and mostly on crops (Ingram 1958; Nye 1960; Seshu Reddy 1989; Polaszek & Khan 1998). The most damaging species in eastern Africa, *Busseola fusca* (Fuller 1901) and the less important species *Sesamia calamistis* Hampson 1910 were recovered from 25 and 28 host plants, respectively, and it was suggested that these species were polyphagous (Polaszek & Khan 1998).

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Accepté le 4 mai 2006

Noctuid stem borers characteristically feed inside the stems of grasses (Poaceae), sedges (Cyperaceae) and bulrush (Typhaceae). They are a very diverse group and over half of the 190 known tropical species are from Africa (Holloway 1998). 32 were reported from East Africa, among them eight *Acrapex* Hampson 1894, two *Busseola*, two *Manga* Bowden 1956 , one *Poecopa* Bowden 1956, one *Poeonoma*, five *Sciomesa* Tams and Bowden 1953, and 13 *Sesamia* spp. However, only hosts of the 10 species mentioned in the previous paragraph are known. The remaining 22 species were obtained as adults from light traps. Their description was based on scanty materials (one to three specimens) and frequently only on one sex. (Fletcher 1961; Rougeot 1984). As a result, the boring behaviour could not be verified for some genera such as *Acrapex, Sciomesa* and *Speia* Tams and Bowden, 1953.

To understand how this highly specialised phytophagous moth group has evolved is not an academic luxury for evolutionists and entomologists. It might be predictive as groups of taxa descending from a common ancestor are more likely to share common biological features (i.e. rapid population increase, short generation time), host plants, behavioural characteristics and common natural enemies (Holloway 1998). Current studies on how phytophagous insect-plant associations evolved combine studies of systematics with ecological and biogeographical data (Johnson 1990; Wahlberg 2001; Kergoat *et al.* 2004). Therefore, detailed knowledge on geographic distribution in the main vegetation mosaics, ecology (host plant ranges, feeding site) and interactions with other stem borers (i.e. guild diversity of the exploited host plants)), should contribute to future investigations on noctuid stem borer-plant evolutionary history.

The present work is an attempt to address the above principles in the study through extensive surveys in wild habitats surrounding cereal fields in Uganda, Kenya, Tanzania and Zanzibar, and to appraise the natural distribution of noctuid stem borers and associated host plant species in East Africa. It also provides some basic information necessary for future studies on the evolution of this moth group.

Materials and Methods

Selection of localities and description of the vegetation mosaics

Surveys were conducted in the major cereal growing areas in Kenya between January 2003 and April 2005, Uganda in April 2004 and March 2005, Tanzania in June 2004 and February 2005 and in Zanzibar in May 2004. A total of 158 localities distributed in the six main vegetation mosaics (described and numbered by White 1983) encountered in East Africa were visited. The vegetation mosaics included the Guineo-Congolian mosaic [mosaic of lowland rain forest and secondary grassland (Mosaic no. 11)], the Zanzibar-Inhambane mosaic [East African coastal mosaic (No. 16)], the Afromontane mosaic [undifferentiated montane vegetation (No. 19)], the Zambezian woodland mosaic [drier Zambezian miombo woodland dominated by *Brachystegia* and *Julbernardia* (No. 26)], the Somalia-Masai mosaic [Somalia-Masaï *Acacia-Commiphora* deciduous bushland and thicket (No. 42)] and the East African mosaic [mosaic of East African evergreen bushland and secondary *Acacia* wooded grassland (No. 45)] (tab. 1, fig. 1). Localities within the mosaics were selected on the basis of accessibility and presence of potential host plants. Each locality was referenced with its geographic coordinates (latitude, longitude and altitude) using a GARMIN 12X portable Geographic Positioning System (GPS). The localities ranged between sea level to 2396 m above sea level (m.a.s.l.), 1°15' North and 08°32' South and, 29°43' and 39°32' East. The climatic conditions found in the mosaics were sourced from Africa AWhere-ACT Database (2002) and summarized in Table 1.

Collection and rearing of stem borer materials

In each locality, the plant habitats (i) in and around crops, (ii) in open patches along forest roads, (iii) on banks of streams or rivers and (iv) in swamps were checked for stem borer infestation. Because noctuid borer densities on wild hosts are exceedingly low (Nye 1960; Gounou & Schulthess 2004), a biased rather than a random sampling procedure was use to increase the chances of finding borers. In all habitats, plant species belonging to Poaceae, Cyperaceae and Typhaceae families were carefully inspected for stem borer infestation symptoms or damage [scarified leaves, dry leaves and shoots (dead hearts), frass, holes bored]. Number of visits per locality varied between one (some localities from Uganda, Tanzania and Zanzibar) and nine (some Kenyan localities), and time spent examining host plants in a locality varied from one to four hours with two or three people depending of the infestation levels. Infested plants were cut and dissected in the field. The kind and location of damage were recorded for all plants found infested. The species collected were then grouped into the *S. calamistis* type and the *B. fusca* type. In the *S. calamistis* type the neonates fed on the basal leaf sheaths for 2-3 days, after which they rapidly penetrated into the stem. In the *B. fusca* type, the first and second instar larvae fed on young leaves (whorl) of the main stem producing the typical "window" damage, or on the flower spikes (Ingram 1958, Nye 1960). The number of young larvae (1st, 2nd, 3rd instars), old larvae (4th, 5th and 6th instars), pupae and, the colour and adornment of the larvae were also recorded (WDS: white with dark thin stripes, B: buff, BLPB: buff with longitudinal wide pale bands, BP: pink, DG: dark grey, OPR: olive with purple rings). Recovered pupae were kept in plastic vials (15 x 7 cm) closed with perforated plastic lids until emergence. Recovered larvae were all reared until pupation on artificial diet (Onyango & Ochieng-Odero 1994) kept in glass vials (7.5 x 2.5 cm) closed with cotton wool or fresh maize stems (10 cm long) kept in plastic vials (16 x 10 cm) with perforated plastic lids. Pupae taken out of the medium/ maize stems were kept separately in plastic vials (16 x 10 cm) closed with perforated plastic lids until adult emergence.

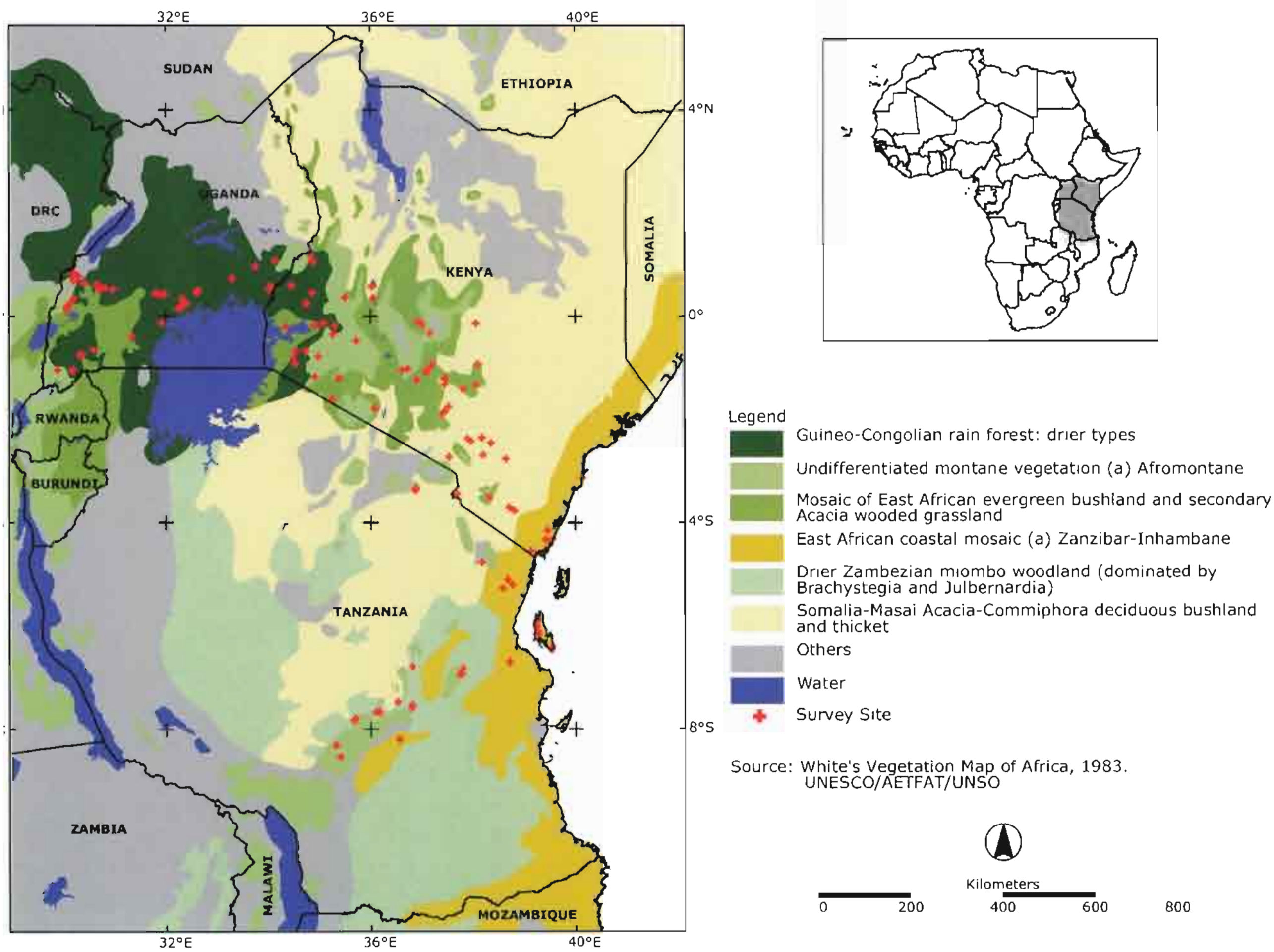

Figure 1
White's vegetation mosaic map of East Africa, 1983, Unesco/AETFAT/UNSO.

Table 1. Average climatic conditions of the different vegetation mosaics found in East Africa (from Africa AWhere-ACT database 2002).

Mosaic No	Rainfall (mm)	Moisture index	Min temp (°C)	Max temp (°C)	Altitude (m.a.s.l.)
11	961–1511 (1237)	0.64–1.05 (0.84)	12.05–17.04 (15.24)	26.10–29.40 (27.52)	699–2160
16	900–1330 (1102)	0.60–0.90 (0.77)	20.48–22.02 (21.22)	29.00–31.15 (30.31)	20–2130
19	669–1621 (1162)	0.46–1.26 (0.88)	06.46–18.42 (12.38)	18.89–29.28 (24.61)	851–2396
26	501–1337 (746)	0.33–1.00 (0.49)	11.90–20.19 (16.72)	22.46–32.95 (28.93)	479–1460
42	886–1304 (1081)	0.63–0.87 (0.74)	13.81–19.70 (17.32)	24.31–30.26 (27.50)	484–1754
45	597–1242 (940)	0.34–1.00 (0.63)	10.09–18.96 (14.44)	23.11–31.83 (27.23)	781–1956

Identification of moths and analysis of borer species diversity

Adult moths were identified to species level (Moyal, P.) and voucher specimens deposited in Museum National d'Histoire Naturelle (MNHN, Paris, France) and in ICIPE Museum (Nairobi, Kenya).

The identified borers were then grouped in their respective host plant and vegetation mosaic for analysis of species diversity. The data from each of the vegetation mosaics and from each host plants were then used to compute diversity indices described by Samways (1984) (tab. 2).

Species richness (S). This is based on presence, rather than relative abundance. This conceptually easy index is widely used both in ecology and biogeography.

Berger-Parker dominance index (d). This index uses the abundance of the dominant species relative to the abundance of all species together.

Fisher-Williams diversity index (α). This useful statistic is based on the log-series. It is particularly valuable if N>1000 because of its lack of sensitivity to the greatly fluctuating common species. It is a parametric index that describes the relationship between the number of species and the number of individuals in those species.

Rare species are defined as those recovered from only one locality.

Results

Vegetation mosaic

Results on noctuid stem borer species found in the 6 vegetation mosaics surveyed are summarized in Table 1. The total number of noctuid larvae collected ranged between 683 and 4094 in the dry and hot Zambezian woodland and cool afromontane mosaics, respectively. The highest species diversity (S = 22; α = 3.22) was recorded in the wet and hot Guineo-Congolian mosaic. Proportions of the dominant species varied between 0.26 in the Somalia-Masai mosaic and 0.81 [(Berger-Parker indices (d)] in the Zambezian mosaic. *Manga nubifera* Hampson 1910 was dominant in both Somalia-Masaï (d = 0.26) and East African bushland (d = 0.27) mosaics, while *Manga melanodonta* Hampson 1910 and *Busseola s.l. n. sp. 1* respectively dominated Guineo-Congolian (d = 0.33) and Afromontane (d = 0.30) mosaics. *Sesamia* n. sp. 5 dominated in Zanzibar-Inhambane (d = 0.51) and Zambezian miombo (d = 0.81) (tab. 1). Rare species were found in five vegetation mosaics, contributing 12 (33%) out of the total of 36 species collected (tab. 3). No rare species were found in the dry Zambezian woodland mosaic. The Afromontane mosaic alone harboured 42% of the rare species accounting for 28% of the total species recovered in this vegetation mosaic. In the other vegetation mosaics the proportion of rare species ranged between 6% (East African mosaic) and 37% (Zanzibar-Inhambane).

Host-plants

Noctuid stem borers were recovered from 49 plant species belonging to three families: Poaceae (35), Cyperaceae (13) and Typhaceae (1) (tab. 4). Out of the 14,318 larvae collected, 92.2% were from Poaceae, 3.4% from Cyperaceae and 4.4% from Typhaceae. 63.5% of the larvae belonging to 22 noctuid species of seven genera were collected from three species of Poaceae, namely *Pennisetum purpureum* Schumacher, *Panicum maximum* Jacquin and *Setaria megaphylla* (Steudel) Th. Durand & Schinz. Borer species richness within the host-plants varied between one (22 host plants) and 11 (*P. purpureum*) with α value varying between 0.14 (*Cynodon aethiopicus* Clayton & Harlan) and 1.59 (*Cyperus latifolius* Poiret).

Noctuid species

The 14,318 noctuid larvae/pupae collected belonged to 36 species, out of which one belonged to the genus *Acrapex*, three *Busseola*, three *Carelis* Bowden 1956, two *Manga*, one *Poeonoma*, nine *Sciomesa*, twelve *Sesamia*, one *Speia* and four species related to *Busseola*, temporarily named as *Busseola s.l.* (tab. 3). Seventeen out of the 36 species collected are new to

Table 2. Stem borer species diversity in respective vegetation mosaics.

Descriptive values			Statistics		
Veg. Mosaic associations (N localities)	Individual abundance	Species richness (S) (Endemic species: N/%)	α	Berger-Parker (d)	Dominant species
11 (43)	3046	22 (5/23)	3.22	0.33	*Manga melanodonta*
16 (16)	1595	8 (3/37)	1.10	0.51	*Sesamia* n. sp. 5
19 (20)	4094	18 (6/33)	2.45	0.30	*Busseola s.l.* n. sp.1
26 (9)	683	6 (0/0)	1.09	0.81	*Sesamia* n. sp. 5
42 (20)	3003	14 (1/7)	1.75	0.26	*Manga nubifera*
45 (20)	1897	16 (1/6)	2.58	0.27	*Manga nubifera*

Table 3. Noctuid stem borer species recorded from East Africa.
* : new borer species, Ns: Borer species number, IA: Individual Abundance (Y : Young larvae, O : Old larvae, P : Pupae) , NL: Number of Localities, WDS: white with dark thin stripes, B: buff , BLPB: buff with longitudinal wide pale bands, BP: pink, DG: dark grey, OPR: olive with purple rings, FL: young instars feed on leaves, BS: young instars bore straight into the stems.

Ns	Noctuid stem borer species	IA (Y/O/P)	NL	Host plants (see tab. 4)	Vegetation mosaics	Mature larvae colour	Feeding behaviour
	Acrapex						
1	*A. syscia* Fletcher	90 (8/82/0)	1	34	45	P	BS
	Busseola						
2	*B. fusca* Fuller	294 (104/185/5)	6	2, 26, 31, 33	11, 45	B	FL
3	*B. phaia* group	1241 (689/537/15)	31	4, 7, 10, 15, 17, 18, 19, 25, 26, 29, 32, 33	11, 19, 42,45	BLPB	FL
4	*Busseola n. sp. 1**	185 (45/137/3)	6	19, 27	11, 19, 26	BLPB	FL
	Busseola s.l.						
5	*Busseola s.l. n. sp. 1**	1197 (674/498/25)	3	31	11, 19	WDS	FL
6	*Busseola s.l. n. sp. 2**	91 (48/43/0)	1	31	19	OPR	FL
7	*Busseola s.l. n. sp. 3**	447 (69/335/33)	7	4, 10, 18, 23, 27, 28	11, 19, 45	WDS	FL
8	*Busseola s.l. n. sp. 4**	40 (5/34/1)	1	31	19	?	?
	Carelis						
9	*Carelis n. sp. 1**	39 (0/39/0)	1	39	19	P	BS
10	*Carelis n. sp. 2**	164 (15/149/0)	1	31	19	P	BS
11	*Carelis n. sp. 3**	17 (0/15/2)	1	48	11	P	BS
	Manga						
12	*M. melanodonta* Hampson	1440 (949/491/0)	8	17, 18, 19, 24, 31, 32, 33	11, 42, 45	DG	BS
13	*M. nubifera* Hampson	2043 (1463/580/0)	12	18, 19	11, 16, 26, 42, 45	DG	BS
	Poeonoma						
14	*P. serrata* Hampson	995 (928/64/3)	11	25, 26	11, 19	DG	FL
	Sciomesa						
15	*Sc. argocyma* Fletcher	11 (0/9/2)	1	38	19	P	BS
16	*Sc. mesophaea* Aurivillius	335 (24/302/9)	9	36, 37, 39, 41, 44, 49	11, 19, 42, 45	P	FL
17	*Sc. nyei* Fletcher	658 (538/119/1)	4	27	11, 19	WDS	BS
18	*Sc. piscator* Fletcher	1179 (184/995/0)	27	3, 7, 9, 10, 12, 13, 23, 25, 26, 27, 29, 30, 36, 41, 43, 46, 47, 48	11, 19, 26, 42, 45	P	BS
19	*Sc. venata* Fletcher	34 (2/32/0)	1	36	11	P	BS
20	*Sciomesa n. sp. 1**	58 (16/42/0)	2	31	19	WDS	BS
21	*Sciomesa n. sp. 2**	78 (47/31/0)	2	17	42, 45	P	FL
22	*Sciomesa n. sp. 3**	2 (0/2/0)	1	17	42	P	?
23	*Sciomesa n. sp. 4**	183 (128:55/0)	6	5	42, 45	WDS	BS
	Sesamia						
24	*S. calamistis* Hampson	354 (197/145/12)	24	6, 12, 18, 21, 22, 26, 29, 30, 33, 35, 36, 37, 40, 41, 42, 43, 44, 45, 46	11, 16, 19, 42, 45	P	BS
25	*S. jansei* Tams & Bowden	27 (0/25/2)	1	36	16	P	BS
26	*S. nonagrioides* Lefebvre	628 (183/445/0)	27	10, 11, 16, 20, 26, 29, 33, 36, 41, 42, 46, 49	11, 16, 19, 26, 42, 45	P	BS
27	*S. oriaula* Tams & Bowden	264 (102/156/6)	25	10, 18, 26, 29	11, 19, 45 ?	P	BS
28	*S. penniseti* Tams & Bowden	84 (17/66/1)	9	26	11	P	BS
29	*S. poephaga* Tams & Bowden	248 (194/54/0)	14	1, 8, 14, 18, 19, 26	11, 16, 26, 42, 45	P	BS
30	*Sesamia n. sp. 1**	52 (38/14/0)	2	7, 10, 18	11	P	BS
31	*Sesamia n. sp. 2**	80 (24/60/0)	1	36	11	P	BS
32	*Sesamia n. sp. 3**	415 (294/121/0)	9	9, 10	11, 42, 45	P	BS
33	*Sesamia n. sp. 4**	50 (16/34/0)	3	10	16	P	BS
34	*Sesamia n. sp. 5**	1215 (1017/186/12)	12	26	16, 26, 42, 45	P	BS
35	*Sesamia sp nr coniota*	4 (0/4/0)	1	18	16	P	BS
	Speia						
36	*Sp. vuteria* Stoll	53 (6/40/7)	7	49	11, 19, 45	P	FL

Table 4. Wild host plants of the different stem borer genus in East Africa.
N: reference number, Ac.: *Acrapex*, Bu.: *Busseola*, Ca.: *Carelis*, Busl: *Busseola sensu lato*, Ma.: *Manga*, Po.: *Poeonoma*, Sc.: *Sciomesa*, Se.: *Sesamia*, Sp.: *Speia*, I: individual abundance, S(M): species richness (Number of monophagous species), NG: Number of Genera, α = Fisher-Williams diversity index

Host plants		Number of stem borer species in each genera									Statistics on collected stem borers			
N°	Species name	Ac	Bu	Ca	Busl	Ma	Po	Sc	Se	Sp	I	S (M)	NG	α
	Poaceae													
1	*Andropogon amethystinus* Steud								1		3	1	1	0.53
2	*Arundo donax* L.		1								5	1	1	0.30
3	*Cenchrus ciliaris* L.							1			1	1	1	
4	*Cymbopogon nardus* (L.) Rendle		1		1						85	2	2	0.37
5	*Cynodon aethiopicus* Clayton & Harlan		1					1			183	1 (1)	1	0.14
6	*Cynodon dactylon* (L.) Pers.								1		13	1	1	0.25
7	*Cynodon nlemfuensis* Vanderyst		1					1	1		22	3	3	0.94
8	*Digitaria milanjiana* (Rendle) Stapf								1		29	1	1	0.20
9	*Echinochloa haploclada* (Stapf) Stapf							1			12	1	1	0.26
10	*Echinochloa pyramidalis* (Lam.) Hitchc. & Chase		1		1			1	4		653	7 (2)	4	1.10
11	*Eriochloa fatmensis* (Hochst. & Steud.)W.D. Clayton								2		251	2	1	0.30
12	*Eriochloa meyerana* (Nees) Pilg.							1	1		141	2	2	0.33
13	*Euclaena mexicana* Schrader							1			35	1	1	0.19
14	*Hyparrhenia papillides* (A. Rich.) Stapf		1								4	1	1	0.43
15	*Hyperthelia dissoluta* (Steud.) W.D. Clayton								1		3	1	1	0.53
16	*Miscanthus violaceus (*K. Schum.) Pilg.								2		10	2	1	0.75
17	*Panicum deustum* Thunb.		1			1		2			728	4 (2)	3	0.56
18	*Panicum maximum* Jacq.		1		1	2			3		3542	7 (3)	4	1.12
19	*Panicum merkeri* Mez		1						1		85	2	2	0.37
20	*Panicum poaeoides* Stapf								1		16	1	1	0.24
21	*Panicum porphyrhizos* Steud.								1		31	1	1	0.20
22	*Paspalidium geminatum* (Forssk.) Stapf								1		29	1	1	0.20
23	*Pennisetum hohenackeri* Steud.				1			1			178	2	2	0.32
24	*Pennisetum cladestinum* Chiov.					1		1			20	2	1	0.85
25	*Pennisetum macrourum* Trin.		1				1	1			75	3	3	0.38
26	*Pennisetum purpureum* Schumach.		3				1	1	6		3860	11 (3)	4	1.39
27	*Pennisetum trachyphyllum* Pilg.				1			2			808	3 (1)	2	0.40
28	*Pennisetum unisetum* (Nees) Benth.				1						30	1	1	0.20
29	*Phragmites mauritianus* Kunth.							1	3		48	4	2	1.26
30	*Rottboellia cochinchinensis* (Lour.) Clayton							1	1		7	2	2	0.94
31	*Setaria megaphylla* (Steud.) T. Duran & Schinz		1	1	3	1		1			1769	7 (5)	3	0.93
32	*Setaria plicatilis* (Hochst.)Engl.		1			1					186	2	2	0.31
33	*Sorghum arundinaceum* (Desv.) Stapf		2			1			2		241	5	3	0.89
34	*Sporobolus macranthelus* Chiov.	1	1								90	1 (1)	2	0.16
35	*Vossia cuspidata* (Roxb.) Griff.								1		24	1	1	0.21
	Cyperaceae													
36	*Cyperus articulatus* L.							1	3		166	4 (3)	2	1.01
37	*Cyperus atroviridis* C.B. Clarke							2	1		46	3	2	0.98
38	*Cyperus dereilema* Steud			1				1	1		16	3 (1)	2	0.64
39	*Cyperus dichroöstachyus* A. Rich.			1				1			49	2 (1)	2	0.42
40	*Cyperus distans* L.								1		6	1	1	0.34
41	*Cyperus dives* Del.							2	2		118	4	2	0.80
42	*Cyperus exaltatus* Retz.								2		15	2	1	0.62
43	*Cyperus involucratus* Rottb.							1	1		9	2	2	0.80
44	*Cyperus latifolius* Poir.							1	1		4	2	2	1.59
45	*Cyperus maculatus* Boeck.								1		8	1	1	0.30
46	*Cyperus rotundus* L.							1	2		29	3	2	0.84
47	*Schoenoplectus maritimus* (L.)K. Lye							1			3	1	1	0.53
48	*Scleria racemosa* Poir			1							14	1(1)	1	0.25
	Typhaceae													
49	*Typha domingensis* Pers.							1	1	1	618	3 (1)	3	0.41

science. Four species, *Sciomesa mesophaea* (Aurivillius) 1910, *S. piscator* Fletcher 1961, *S. calamistis* and *S. nonagrioides* (Lefebvre) 1827, were found on at least two host plant families and can therefore be considered to be polyphagous (cf Bernays & Chapman 1994). *S. nonagrioides* was found on all three host plant families. Seven species, including *B. fusca*, were oligophagous (feeding on a restricted number of plant species usually from one family or a subfamily (Bernays & Chapman 1994); and were found on two and seven host species within the same family. However, all seven species were more abundant on one or two host plants (i.e., about 85% of the specimens collected). A good example is *M. melanodonta*, of which 88.2 % were collected from *P. maximum* and 10 % from *S. plicatilis* (Hochstetter) Hackel, while the five other hosts together accounted for less than 2%. The host range status of the *B. phaia* Bowden 1956 group is not completed as identification is still in progress. The other 24 species are monophagous (feeding on a single species or genus of plants; Bernays & Chapman 1994).

The found stem borer larvae could be broadly divided into three types, based on colour and adornment: (a) *B. fusca* like species with dark ground colours sometimes adorned with longitudinal wide pale bands (*Busseola, Manga* and *Poeonoma*), (b) species with pale ground colours adorned with longitudinal thin dark stripes (*Busseola s.l.* and *Sciomesa* species related to *S. nyei* Fletcher 1961) and (c) *Sesamia* like species with pink ground colours (*Acrapex, Carelis, Sciomesa* not related to *S. nyei*, *Sesamia* and *Speia*), sometimes adorned with longitudinal wide pale bands [*S. mesophaea*, *S vuteria* (Stoll) 1783]. According to the feeding site, the *Sesamia, Acrapex* and *Carelis* species belong to the *Sesamia* feeding type while the *Busseola, Busseola s.l., Manga, Poeonoma* and *Speia* species belong to the *Busseola* feeding type. Both kinds of feeding behaviour were found in *Sciomesa* genera. A stem girdling behaviour was observed in *S. piscator*. Scarifying behaviour was facultative for both *S. mesophaea* and *S. vuteria* recovered from *Typha domingensis* Persoon.

Discussion

Vegetation mosaics

The results of the surveys indicated that noctuid stem borers are common in the six main vegetation mosaics of East Africa. However, borer species richness and abundance varies amongst the vegetation mosaics with the wet and hot guineo-congolian mosaic covering mainly the western area of East Africa (western Kenya and Uganda) being the richest. Similarly, Nye (1960) reported noctuid stem borer larvae mainly from the wetter parts of different vegetation mosaics. Nonetheless, in contrast to earlier surveys (Ingram 1958; Nye 1960; Seshu Reddy 1989), higher numbers of stem borer species were collected from non cultivated host plants. Each vegetation mosaic harboured dominant borer species accounting at least for 25% of the specimens collected per mosaic. We found rare species in the five vegetation mosaics. The strong influence exerted by rare species on the overall species assemblage has been underlined many times. However, their role and importance in structuring broad community patterns among regions is not well understood but they are thought to contribute significantly to diversity in the tropics (Price *et al.* 1995; Coddington *et al.* 1996; Novotny & Basset 2000). Not surprisingly the number of rare species was increasing with time and we can assume their contribution to the noctuid borer guild was underestimated in the course of this survey. As all the rare species found are monophagous, no doubt the proportion of specialist feeders was probably also underestimated.

Host plants

Stem borers were recovered from 48 plant species of which 32 have never been recorded as hosts of noctuids, thus increasing the number of known hosts to 66. Most of these hosts belonged to Poaceae family, corroborating earlier reports by Ingram (1958), Nye (1960), Seshu Reddy (1989), and Polaszek & Khan (1998). This study revealed important variation in species richness (*S*) and diversity index among the host plants. The species diversity reported on some grass species e.g. *Setaria megaphylla* was underestimated because at least three noctuid species collected from it could not be reared to adult stage as all collected larvae died. Data on resource availability suggest strongly that if plants species are extremely abundant and reliable, insects are able to specialize on them and often do so (Bernays & Chapman 1992). It is worth noting that *S. megaphylla* is one of the most common Poaceae species in mid (between 1000 and 1500 m) and high altitude forested areas (≥1500 m). It contained one of the highest borer species diversities (seven) with 71% monophagous species, all of them localised in one or two neighbouring localities usually at altitudes above 1500 m. The current high diversity and monophagy found on *S. megaphylla* could be attributed to major climatic changes of the Pleistocene that took place between 3.3 to 2.45 Million years ago (Wagner 2002; DeMenocal 1995). These major events are considered responsible for the preservation of altitudinal forested areas which worked as refuge zones comparable with an archipelago (White 1981). The role of these altitudinal forested areas on east Afromontane butterflies speciation and endemism has been well documented by De Jong and Congdon (1993).

Stem borers

The methodology adopted during this survey involved active searching for damage symptoms at irregular intervals in both time and space. Results therefore could not be used for rigorous comparison of stem borer diversity among the different vegetation mosaics, though the methodology allowed for rapid and efficient inventory of the noctuid stem borer guild in East Africa. Out of the 36 species collected, 17 are new to science. The number of known species of noctuids from East Africa is now 50 compare to 32 as reported earlier (Fletcher 1961; Laporte 1975). This study also provided numerous male and female specimens of species earlier described from very few specimens, sometimes from only one sex like *Acrapex syscia* Fletcher 1961, *Sciomesa nyei, Sciomesa venata* Fletcher 1961, *Sciomesa piscator* and *Sesamia oriaula* Tams & Bowden 1953. It is suggested that if the present study is extended to other poorly surveyed areas, the reported diversity of noctuid stem borers from East Africa would increase significantly. The current survey missed the montane biotopes above 2400m and could explain why only one *Acrapex* and 12 *Sesamia* species were recovered even though they are the most diverse noctuid stem borer genera in Africa (Fletcher 1961; Laporte 1975). Stem borer species collected could be categorised into monophagous, oligophagous and polyphagous groups. 63% of monophagous species were found in one vegetation mosaic only, while about 88 % of the oligophagous species were found in at least two vegetation mosaics. The four polyphagous species were present in at least five vegetation mosaics. Nonetheless, the distribution of many monophagous and oligophagous species could not be explained by the distribution of host plants. *Busseola s.l.* n. sp. 2 and *Busseola s.l.* n. sp. 4, that were only known from *S. megaphylla*, were collected from one locality though their host is widely distributed in Guineo-Congolian, afromontane and Zanzibar-Inhambane mosaics. *Sesamia* n. sp. 5 known only from *Pennisetum purpureum* was never recovered in the western part of the Rift Valley despite the wide distribution of the host plant in Kenya and Tanzania. Likewise, *Poeonoma serrata* Hampson 1910 which is widely distributed in Uganda and western Kenya and which was known from *P. purpureum* mainly was never found in the eastern part of the Rift Valley. The observed restricted distribution among stem borer species may be associated with major climatic changes experienced in East Africa since 3.3 Million years ago, oscillating between hot/humid and cooler/drier periods. These climatic changes coupled with the rise and expansion of the East Africa Rift Valley from 2.9 to 1.6 Million years ago (Zeitoun, 2000, Pitra *et al.*, 2002), were responsible for oscillations in savannah biotype expansion (Wagner 2002; DeMenocal 1995) and of a mosaic of refuge zones.

This study describes mature larval colouration and feeding behaviour of 29 species and six genera for the first time. In addition, it confirms two types of feeding behaviour reported in previous studies (Ingram 1958; Nye 1960). It was found that species belonging to one genus adopt a similar feeding behaviour with a notable exception within the *Sciomesa* genus. All the stem borer larvae with dark ground colours or with dark stripes belong to the *Busseola fusca* feeding type and all the stem borer larvae with pink ground colours belong the *Sesamia calamistis* type. It is not coincidental that larvae living outside the plants develop more pigmented and adorned skin than those ones living inside. When living outside, the larvae are more vulnerable to natural enemies and thus develop camouflage patterns like hiding colour and adornments. Reports indicate that herbivorous species frequently use stripes to escape predators (Caillois 1963; Ortolani 1999).

Conclusion

This paper provides for the first time basic information on noctuid species diversity and biogeography within the six main vegetation mosaics found in East Africa. Even though boring of monocot stems is a very specialized feeding behaviour among noctuids (Holloway, 1998), the major life history traits reported in this study show important behavioural plasticity between genera. Species belonging to the same genus harbour common ecological characteristics like colour of the larvae and feeding behaviour. The *Sciomesa* genus is an exception with a mixture of these characters and further investigations on its systematic and phylogenetic classification might show that it constitutes several genera.

Acknowledgments. The authors are grateful to Simon Mathengue, University of Nairobi, Botany department, for the identification of all the host plants.

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