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BIONOMICS OF SMICRONYX GUINEANUS VOSS AND SM. UMBRINUS HUSTACHE (COLEOPTERA: CURCULIONIDAE), POTENTIAL BIOCONTROL AGENTS OF STRIGA HERMONTHICA (DEL.) BENTH. (SCROPHULARIACEAE) IN BURKINA FASO (WEST AFRICA)

by

Doulaye Traoré

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy (Ph.D.)

Department of Natural Resource Sciences McGill University Montréal, Québec Canada

January 1995

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SHORT TITLE

Bionomics of Smicronyx spp. on Striga hermonthica

Doulaye Traoré

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ABSTRACT

Ph.D.

Doulaye Traoré

Entomology

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A three-year (1991-1993) investigation was done in the field and laboratory to study the bionomics of Smicronyx guineanus Voss and Sm. umbrinus Hustache and the spatial distribution of Striga hermonthica (Del.) Benth. Studies on the life history of the weevils were undertaken. Seasonal activity and habits were established by monitoring life stages in the field. A behavioral Time Budget of Smicronyx adults was established in semi-field conditions. Dispersion patterns and the optimum sample size for Smicronyx and Striga were determined. Smicronyx adults as well as Striga plants were aggregated in the field. Smicronyx larvae were located in the upper stratum of the witchweed (93.2%) where they make galls and destroy large number of seeds. The effect of precipitation on emergence of Smicronyx adults was investigated in the insectary. The optimum rainfall required for Smicronyx adult emergence ranged from 30 to 40 mm. Good synchrony and positive association of Sm. guineanus and Sm. umbrinus with S. hermonthica were observed. There are good prospects for augmentation and/or conservation of Smicronyx populations as part of an integrated control strategy of S. hermonthica.

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Doctorat

Doulaye Traoré

Entomologie

Bionomie de Smicronyx guineanus Voss And S. umbrinus Hustache, agents potentiels de lutte biologique contre le Striga hermonthica (Del.) Benth. (Scrophulariaceae)

au Burkina Faso (Afrique de l'Ouest)

Trois années d'investigations (1991-1993) ont été menées au champ et au laboratoire pour étudier la bionomie de Smicronyx guineanus Voss et Sm. umbrinus Hustache et la distribution spatiale de Striga hermonthica (Del.) Benth. Des études sur le cycle biologique des charançons ont été faites. Les activités saisonnières et les habitudes ont été établies par le monitoring des stades biologiques des charançons dans leur habitat naturel. Un budget-temps du comportement de l'insecte a été déterminé en conditions semi-naturelles. La distribution spatiale et la taille optimum d'échantillon pour Smicronyx et Striga ont été évaluées. Une distribution groupée a été observée aussi bien pour les adultes de Smicronyx que pour les plantes de Striga au champ. Les larves du charançon étaient localisées dans le tiers supérieur où ils induisent des galles et dévorent une grande quantité de graines des capsules de Striga. L'effet des précipitations a été étudiée, indiquant que la hauteur optimum de pluie requise pour l'émergence des adultes de *Smicronyx* se situe entre 30 et 40 mm. Un bon synchronisme et une association positive entre *Sm. guineanus* et *Sm. umbrinus* avec *S. hermonthica* ont été observées. Il y a de bonnes perspectives d'augmentation et/ou de conservation des populations de *Smicronyx* dans le cadre d'une stratégie de lutte intégrée contre *S. hermonthica*.

Suggested short title: Bionomics of Smicronyx spp. on Striga hermonthica

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Doulaye Traoré

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DEDICATION

то

My spouse, Ramata Touré,

my son, Tho Salim Rachid Traoré.

RCKNOWLEDGMENTS

This research is part of a Plant Protection Project funded by the Canadian International Agency (CIDA 960325) managed by Agriculture Canada Research Station at Saint-Jeansur-Richelieu, Quebec, Canada.

I am grateful to the People of Burkina Faso, my home country, for awarding me a post graduate scholarship for this achievement.

I wish to express my great gratitude and love to my wife, Ramata Touré and my son, Tho Salim Rachid Traoré, to whom I dedicate this work. Without their support, understanding and love, this achievement could not have been completed.

Project Supervision

I would like to express my deep gratitude to my supervisors, Dr. Robin K. Stewart for his guidance, support and kindness, and Dr. Charles Vincent, for his suggestions, active participation in field work and his understanding. I am indebted to him for the preparation of the research project and by diligently putting so much effort to review the manuscripts and the thesis.

Staff Members

I would like to thank Pierre Langlois for assistance on purchasing some equipment necessary for my research in Burkina Faso. Special thanks to Marie J. Kubecki and Diane King for their excellent guidance on administrative policies and hospitality. I also wish to thank the members of the department of Natural Resource Sciences and the Graduate Students in Entomology for their nice collaboration.

External Scientists

I am particularly indebted to Dr. Donald M. Anderson, Systematic Entomology Laboratory, USDA, Washington, D. C., USA, for identifying Smicronyx umbrinus Hustache adults and the larvae of Sm. umbrinus and Sm. guineanus and for critically reading the manuscripts. Thanks are also extended to Dr. Michael Cox, International Institute of Entomology "C.A.B. International", London, UK, for confirming the identity of Sm. guineanus Voss adults. Dr. Elizabeth P. Roberts of Brooklandville, Maryland, USA drew the front legs and genitalia of Smicronyx adults.

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Gabiliga Thiombiano, Salia Ouattara and Diada Coulidiati for their help in collecting data.

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Dr. Seydou Traoré, for convincing me to pursue a graduate research.

The personnel of the Plant Protection in Kamboinsé, Burkina Faso, for the facilities.

2. Canada

I would like to express my gratitude to the personnel of Saint-Jean-sur-Richelieu Research Station and in particular to its Director, Dr. Denis Demars and Jacques Daneau for their assistance.

Last but not least, my special thanks to Gilbert Benharrosh, senior administrator of the project in Burkina Faso, for his support throughout the course of this project.

CLAIMS TO ORIGINALITY

The following findings from the present study, in the author's opinion, provide original knowledge on Smicronyx guineanus and Sm. umbrinus on Striga hermonthica.

1. The life history of Sm. guineanus and Sm. umbrinus has been determined for the first time.

2. External and internal morphological characters used to separate *Sm. guineanus* from *Sm. umbrinus* have been identified for the first time in Africa.

3. Periods of peak adult abundance are reported for the first time as mid-September.

4. This is the first study on determining the behavioral time budget of *Sm. guineznus* in semi-field conditions.

5. The best periods of day to sample Sm. guineanus in the field are reported for the first time as from 7:00 to 11:00 AM or from 4:00 to 6:00 PM.

6. Iwao's patchiness regression for determination of the dispersion patterns of *Smicronyx* adults on *Striga* have been used for the first time and shown to be valid.

7. An optimum sample size for population density estimates of Sm. guineanus and Sm. umbrinus on S. hermonthica has been developed.

8. A chart was designed which could be useful for determining the level of precision attainable at various densities of *Smicronyx* adults for any sampling and monitoring program.

9. Smicronyx larvae were found in the upper stratum of the Striga plants where they make galls and destroy large number of seeds.

10. Taylor's power law for determination of dispersion patterns of *S. hermonthica* have been used for the first time and shown to be valid.

11. An optimum sample size for population density estimates of S. hermonthica has been developed.

12. First demonstration of the effect of precipitation on the emergence of *Sm. guineanus* and *Sm. umbrinus* adults, indicating that the optimum rainfall required range from 30 to 40 mm.

13. First demonstration that Sm. guineanus and Sm. umbrinus pupae could have less than a three year life expectancy.

14. A soil vertical distribution of Sm. guineanus and Sm. umbrinus pupae has been established for the first time.

15. First demonstration that Sm. guineanus and Sm. umbrinus pupae enter into diapause not into quiescence.

16. First demonstration of a positive association and a good synchrony of the active stages of the life-cycle of Sm. guineanus and Sm. umbrinus with the period of occurrence of the Striga plants.

17. First assessment of the percentage of Striga plants bearing galls caused by Sm. guineanus and Sm. umbrinus in West Africa.

18. First record of Sm. guineanus outnumbering Sm. umbrinus onS. hermonthica in West Africa.

19. Overall, this is the first investigation on the potential of Sm. guineanus and Sm. umbrinus as biocontrol agents of S. hermonthica in the world.

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INTRODUCTION

Since the identification of Striga hermonthica (Del.) Benth. (Scrophulariaceae) on sorghum in Southern Africa in the early nineteen hundreds (Burrt-Davy, 1904 and Timson, 1931) researchers have worked on the problem throughout Africa. First noticed in Rhodesia, S. hermonthica was not then considered much of a problem: "since it produces few seed capsules, as compared with S. lutea, it should not be too difficult to eradicate" (Anon, 1936). Actually S. hermonthica is the most serious pest to food production in West Africa. It causes serious production losses in the host crops and the ruin and abandonment of precious farm lands.

Control practices for *Striga* have been known for 50-60 years (Doggett, 1991). Unfortunately, peasant farmers cannot or will not use most of them because they are feasible in the context of large-scale farms or research stations. The gross values of their crops is usually too low to justify the use of higher technological inputs such as artificial germination stimulants, herbicides, and solarization, even if the logistical problem of delivery of the input were solved.

It is now well recognized that no single method of Striga control can solve the problem in subsistence agriculture in practice in developing countries (Parker and Riches, 1993). Integrated Pest Management (IPM), defined in a practical

context as "The farmer's best mix of control tactics in comparison with yields, profits and safety of alternatives" (Iles and Sweetmore, 1991), is the ideal approach to control S. hermonthica. Biological control should be a part of an integrated control strategy by augmentation and/or conservation of natural enemies of Striga. This requires an adequate understanding of the biology and ecology of these species, together with knowledge about other factors in the ecosystem to fit the procedures in compatible manner in the crops where Striga occurs. Conservation and/or augmentation of Striga natural enemies, has never been tried, though it has been repeatedly recommended during international Striga symposia. Base-line research to determine the interrelationships among and potential utility of any of the biotic factors as potential biological control agents of Striga has never been done.

The hypothesis examined here was that the weevils Sm. guineanus Voss and Sm. umbrinus have potential to control S. hermonthica in West Africa. The present work, based on a three-year (1991-1993) field and laboratory investigation, was done to study the bionomics of the weevils and the spatial distribution of Striga. The six chapters presented here deal with (in order of appearance) life history of Smicronyx; behavioral time budget; dispersion patterns of adults and vertical distribution of larvae; dispersion patterns and

optimum sample size for *S. hermonthica;* effect of precipitation on emergence of *Smicronyx;* and association and synchrony of *Smicronyx* with *Striga*.

The present thesis format, accepted by the Faculty of Graduate Studies and Research and the Department of Natural Resource Sciences, Macdonald Campus of McGill University, requires a full citation of a section B, 2 (Manuscripts and Authorship), of the Guidelines Concerning Thesis Preparation of the Faculty of Graduate Studies and Research. "The candidate has the option, subject to the approval of their Department, of including as part of the thesis the text, or duplicated published text, of an original paper or papers.

Manuscript-style theses must still conform to all other requirements explained in the Guidelines Concerning Thesis Preparation.

Additional material (procedural and design data as well as descriptions of equipment) must be provided in sufficient detail (e.g. in appendices) to allow clear and precise judgment to be made of the important and originality of the research report.

The thesis should be more than a mere collection of manuscripts published or to be published. <u>It must include a general abstract</u>, a full introduction and literature review and a final overall conclusion. Connecting texts which provide

logical bridges between different manuscripts are usually desirable in the interest of cohesion.

It is acceptable for theses to include, as chapters, authentic copies of papers already published, provided these are duplicated clearly and bound as an integral part of the thesis. <u>In such instances connecting texts are mandatory</u> and supplementary explanatory material is always necessary.

- Photographs or other materials which do not duplicate well must be included in their original form.

While the inclusion of manuscripts co-authored by the candidate and others is acceptable, <u>the candidate is required</u> to make an explicit statement in the thesis of who contributed to such work and to what extent, and supervisors must attest to the accuracy of the claims at the Ph.D. Oral Defense. Since the task of the Examiners is made more difficult in these cases, it is in the candidate's interest to make the responsibilities of authors perfectly clear".

I followed the rules of scientific writing given in the CBE Style Manual (1983) and the MLA Handbook for Writers of Research Papers (Gibaldi and Achtert, 1988). I wrote each chapter to be presented to a specific scientific journal according to the requirements of that journal. The second chapter, (Life History Of Smicronyx guineanus Voss And Sm. umbrinus Hustache (Coleoptera: Curculionidae) On Striga

hermonthica (Del.) Benth. (Scrophulariaceae) has been submitted to Entomophaga (France) in January 1995. Chapter 3 (Behavioral Time Budget Of Smicronyx guineanus Voss (Coleoptera: Curculionidae) On Striga hermonthica (Del.) Benth. (Scrophulariaceae) In Semi-field Conditions) has been submitted to the Journal of Insect of Behavior (U.S.A.) in January 1995. Chapter 4 (Dispersion Patterns Of Adults And Vertical Distribution Of Larvae Of Smicronyx guineanus Voss And Sm. umbrinus Hustache (Coleoptera: Curculionidae) On Striga hermonthica (Del.) Benth (Scrophulariaceae) has been submitted to Insect Science and Its Application (Kenya) in September 1994. Chapter 5 (Dispersion Patterns And Optimum Sample Size For Striga hermonthica (Del.) Benth. (Scrophulariaceae) In Farmers' Fields) has been submitted to Weed Research (U. K.) in September 1994. Chapter 6 (Effect Of Precipitation On Emergence Of Smicronyx guineanus Voss And Sm. umbrinus Hustache (Coleoptera: Curculionidae) Adults And Soil Vertical Distribution Of Pupae) has been submitted to Tropical Pest Management (U. K.) in January 1995. Chapter 7 (Association And Synchrony Of Smicronyx guineanus Voss, Sm. umbrinus Hustache (Coleoptera: Curculionidae) And Striga hermonthica (Del.) Benth. (Scrophulariaceae) has been submitted to Biological Control (U.S.A.) in January 1995. All chapters were reviewed by my supervisors, Dr. R. K. Stewart and Dr. C. Vincent, and by the editorial committee of Agriculture and Agri-Food Canada Horticultural Research and Development Centre at Saint-Jean-sur-Richelieu. Some chapters were commented on by other scientists upon request. All papers were co-authored by my supervisors.

I used SuperANOVA (version 1.1 for the Macintosh Computer, (Abacus Concepts Inc., 1989), and StatView (Version 4.0, the ultimate integrated data analyses and presentation system for Macintosh, (Abacus Concepts Inc. 1992).

References are also at the end of the thesis.

Voucher specimens of Sm. guineanus and Sm. umbrinus were deposited at the Systematic Entomology Laboratory, USDA, National Museum of Natural History, Washington, D.C., USA, the International Institute of Entomology (C.A.B. International), London, UK, the Biosystematics Research Center (Agriculture Canada), Ottawa, Canada, the Lyman Museum, Macdonald Campus of McGill University, Sainte-Anne-de-Bellevue, Québec, Canada and in the Plant Protection Laboratory, Kamboinsé, Burkina Faso. The existence of voucher specimens was mentioned in each chapter whenever appropriate.

This study constitutes the first practical investigation on the bionomics of Sm. guineanus and Sm. umbrinus to better evaluate their potential as biocontrol agents of S. hermonthica in Africa.

CHAPTER 1

LITERATURE REVIEW

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1.1. SMICRONYX SPECIES

The nomenclatoral history of the genus Smicronyx began in 1836 when Schoenherr proposed the name Micronyx for a group of seven species and named Micronyx reichi Gyllenhal as the type of the genus (Anderson, 1962). Two of the included species had been described in Curculio, and one had been described in Elleschus. The rest of the species, including reichi, had not been previously described. Because the name Micronyx had already been published by Boisduval (in D'Urville, 1835) as a name for a genus of scarabaeid beetles, Schoenherr replaced his Micronyx with the name Smicronyx in 1843. Smicronyx reichi then became ipso facto the type of the genus.

The first synthesis of the North American Smicronyx was published by LeConte in 1876. Champion (1902) described six species from Central America and Mexico. European workers have erected two subgenera, which include a few Old World species. In 1896 Desbrochers des Loges erected the subgenus *Chalybodontus*, which included a few species occurring in southern Europe and North Africa. Hustache (1935) erected the subgenus Afrosmicronyx for a single species found in the French Sudan of Africa. Keys for identification of Sm. guineanus and Sm. umbrinus have not been yet published but are in progress for publication by Dr. Donald M. Anderson of the Systematic Entomology Laboratory, USDA, Washington, D. C., USA and Dr. Michael Cox of the International Institute of Entomology, C.A.B. International, London, UK (Appendix 1). The species described in Africa so far are as follows (D. M. Anderson and H. Perrin¹, personal communications):

Subgenus Smicronyx Schoenherr, 1843;

- 1) albofasciatus Chevrolat, 1879, Mauritania;
- 2) angusticollis Fairmaire, 1875, Algeria;
- 3) angustus Fairmaire, 1875, Tunisia;
- 4) bisignatus Hoffmann, 1968, Cameroon;
- 5) fallax Gyllenhal, 1836, "Kaffernland" (South-Eastern Africa);
- 6) gossypii Marshall, 1942, Sudan;
- 7) guineanus Voss, 1956, Guinea, Sudan (the type came from Bamako, Mali);
- 8) kiboanus Voss, 1971, Tanzania;
- 9) kiesenwetteri Tournier, 1874, Morocco, Algeria;
- 10) lallemanti Faust, Tunisia;
- 11) maerens Marshall, 1940, Kenya;
- 12) sopubiae Marshall, 1940;
- 13) remaudierei Hoffmann, 1954, Sudan;
- 14) brevirostris, Chad or Cameroon;

¹ Museum of Natural History, Paris, France.

Subgenus Afrosmicronyx Hustache 1935;

- 15) clavofulva Hoffmann, 1962, Tunisia;
- 16) giganteus Hustache, 1935, Sudan (very large);
- 17) umbrinus Hustache, 1947, Senegal.
- 18) quadritubulatus (cited by Parker and Riches, 1993).

The literature on African *Smicronyx* is scarce. A detailed consideration of the proper position of the genus *Smicronyx* in a natural classification of the family Curculionidae is beyond the scope of this review, but a brief consideration of its present position is presented hereafter.

1.1.1. TAXONOMY

The latest taxonomic paper on the revision of the genus *Smicronyx* is that of Anderson (1962). Based on this work and personal communications (D. M. Anderson and H. Perrin), the taxonomic position of *Sm. guineanus* and *Sm. umbrinus* is as follows:

Order: Coleoptera Suborder: Polyphaga Superfamily: Curculionioidea Family: Curculionidae Subfamily: Erirhininae Tribe: Smicronychini Subtribe: Smicronychi

Genus: Smicronyx Subgenus: Smicronyx Species: guineanus Subgenus: Afrosmicronyx Species: umbrinus

The adults of Sm. guineanus and Sm. umbrinus can be separated from the other Smicronyx spp. by external morphological characters which include the body shape, size and color; form of head and prothorax, thickness of rostrum, insertion of antennae; size and number of spurs on fore femora and tibia; structure of male and female genitalia (Anderson and Cox^2 , personal communications).

1.1.2. MORPHOLOGICAL AND ANATOMICAL CHARACTERS

1.1.2.1. Smicronyx guineanus

This species was first described by Voss (1956). A redescription is in progress by Dr. Anderson and Dr. Cox. They kindly made available to me the following information. Adult *Sm. guineanus* body is elliptical, moderately stout, its mature surface color black. Vestiture abundant, squamulose, light brown variegated with pale gray and white dorsally, pale gray ventrally. Rostrum moderately thick, slightly longer than head and prothorax, moderately curved, gradually tapered from base to apex; coarsely punctate behind antennal insertions;

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smoother, with two faint dorsal grooves anteriorly (not visible near apex in females); vestiture of light brown to gray setiform scales recumbent, except for two basal tufts. Basal groove separating rostrum from head shallow, distinct. Head convex, reticulate, glabrous, except for dorsal patch of appressed scales behind rostrum. Antennae inserted near middle of rostrum (females) or before the middle (males). First funicular segment stout, subequal in length to second and third segments; remaining segments no longer than wide; setiform scales pale gray, much longer on 7th segment. Club spindle-shaped, as long as last four funicular segments together. Prothorax slightly wider than long, strongly rounded at sides, broadest slightly behind middle, distinctly narrowed and slightly constricted behind apex; pronotum shining, strongly and closely punctate, finely punctulate between punctures; covered with mixture of flat, broadly oval scales and slightly arched, decumbent setiform scales, light brown, with white along midline and at sides. Elytra moderately convex, subparallel for approximately 2/3 of their length, converging to a narrowly rounded apex, and slightly over 1 1/2 times width (across humeri) in length. Declivital callosities distinct, not prominent. Striae narrow, sharply defined. Elytral intervals flat, surface shining, slightly wrinkled, sparsely punctuate, each covered with 2-3 rows of broadly ovate flat scales and a single row of arched, flattened setiform scales, ranging from medium brown to nearly white,

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pale scales forming an oblique patch extending posteriorly from humeri and also scattered patches among the darker scales. Scutellum small, almost concealed by vestiture. Underside of body sparsely covered with ovate, pale grayish scales. Femora clavate, black to reddish black, armed with a small ventral tooth (largest on profemora), and clothed with a mixture of pale gray elliptical and arched setiform scales. Tibiae straight, dark reddish brown, sparsely covered with pale gray setiform scales; pro- and midtibiae armed on inner margin with a row of 4-5 dark, stiff setae; mucros slightly curved. Tarsi dark reddish brown, 3rd tarsomere distinctly broadest, bilobed; 5th tarsomere exceeding 3rd by about 1/2 its length. Claws connate in basal 1/3, slightly divergent.

Males can be distinguished from females by their rostrum, which is slightly stouter and more coarsely punctate in the apical 1/3 than is the rostrum of females, which is distinctly smoother and more polished in that area.

Male genitalia: As illustrated in Figs. 1 and 2. Note the distinctive shape of the median lobe (penis), which is constricted behind the apex, and is rather elongate.

Female genitalia: As illustrated in Fig. 3 Note that neither the ovipositor nor the spiculum ventrale (apodeme) are very elongate, and that the ovipositor lacks pigmented internal support rods.

1.1.2.2. Smicronyx umbrinus

This species was first described by Hustache (1940). A redescription is in progress by Dr. Anderson and Dr. Cox. They kindly made available to the material for its me identification. The body of Sm. umbrinus is elliptical, moderately stout. Mature surface color black to reddish black. Vestiture dense, squamulose, brown, variegated with grayish dorsally, ashy gray ventrally. Rostrum moderately thick, slightly longer than head and prothorax, distinctly but not strongly curved, moderately tapered toward apex; coarsely punctate in posterior third; anteriorly smoother, more sparsely punctate and bearing three dorsal carinae, of which the median is divided above antennal insertions; a vestiture of narrow, elongate brownish scales denser behind antennal insertions and recumbent, except for erect tufts at basal corners of rostrum. Basal groove separating rostrum from the head shallow but distinct. Head convex, finely reticulate, glabrous, except for a patch of brownish, closely appressed scales behind base of rostrum. Antennae inserted near middle of rostrum (females) or before the middle (males); first funicular segment slightly longer than 2nd and 3rd segments together; remaining four segments slightly longer than wide; club spindle-shaped, shorter than combined length of last four funicular segments. Scales of funicle elongate, gray, progressively longer from base to club. Prothorax widest

slightly behind middle and slightly wider than long, moderately rounded at sides, distinctly narrowed and slightly constricted behind apex; pronotum shining, surface between punctures sparsely punctulate; closely covered by a mixture of flat, broadly ovate, scales, and arched setiform scales, the latter brownish or white; broad scales lighter grayish brown midline and at sides. Elytra moderately convex, subparallel for slightly more than 1/2 their length, rounded to an obtuse apex and slightly constricted behind declivital callosities; broadest near middle, slightly over 1 1/2 times width in length. Striae narrow, sharply defined; intervals flat, their surfaces slightly wrinkled and sparsely punctulate, closely covered with 2-3 rows of broadly rounded, imbricated scales and a single row of flattened, slightly arched setiform scales. Humeral areas marked with an oblique patch of pale brownish scales; other areas variegated with smaller patches of paler scales among darker, more grayish scales. Scutellum very small, squamose. Underside sparsely covered with flat, grayish, ovate scales. Femora clavate, armed with a single ventral tooth (largest on profemora), and covered with grayish white mixture of elliptical scales and slightly arched setiform scales. Tibiae straight, shallowly bisinuate on inner margin, covered with decumbent, grayish white setiform scales. Fore and midtibiae armed with an acute (females) or obtuse (males) tooth in basal 1/3 (opposing femoral tooth), and a row of 6-9 stiff, dark setae between tooth and apex. Tibial mucros

slightly curved. Tarsi with 3rd tarsomere broadly bilobed; terminal (5th) tarsomere exceeding 3rd by slightly more than 1/2 its length. Claws connate in basal 1/3, slightly divergent.

Males can be distinguished from females by their slightly shorter, stouter rostrum, which is more coarsely sculptured before antennal insertions than in females, by their less sharply pointed tibial teeth, and by their more deeply concave terminal abdominal ventrite.

Male genitalia: as illustrated in Figs. 1 and 2. Note that the median lobe (penis) is short, with a strongly deflexed apical margin.

Female genitalia: as illustrated in Fig. 3. Note that the spiculum ventrale (apodeme) is long and slender, and that the ovipositor is also elongate, with a pair of pigmented internal struts supporting it.

Figure 1. Male genitalia, dorsal view, A) Sm. guineanus and B) Sm. umbrinus.

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Figure 2. Male genitalia, lateral view, A) Sm. guineanus and B) Sm. umbrinus.

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Figure 3. Female genitalia, ventral view, with spermatheca, detached, shown in lateral view, A) *Sm. guineanus* and B) *Sm. umbrinus*.



1.1.3. BIOLOGY AND ECOLOGY

1.1.3.1. Life history

The life history is only partially known for any of the gall-forming species of *Smicronyx* but the following description of *Sm. albovariegatus*, a parasite of *S. hermonthica* in India, and some East African species of *Smicronyx* given by Greathead and Milner (1971) and Bashir (1987) is probably broadly correct for those species of arid environments.

The adult weevils live in the soil, which they leave to feed on Striga plants. The female oviposits into the stem or developing fruit. The eggs of Sm. albovariegatus are laid in the superficial tissues of the plant and lie embedded below the surface (Sankaran and Rao, 1966). In Uganda eggs of Smicronyx spp. have been found inside the lumen of young seed pods of S. hermonthica. On hatching, the larvae excavate a small cavity in the surrounding plant tissues, which swell up and produce galls which enlarge as the larvae feed inside them. The larvae depend, to a great extent, on the replacement growth of the seed pod, and young larvae in small galls removed from the plant die very soon in the laboratory. There are usually one or two larvae per gall which emerge when fully grown, burrow into the soil and pupate in small earthen cells. Pupation time varies with species but it is 6-10 months in Sm. albovariegatus. The adults of the East African species emerge after six to ten months. Williams and Caswell (1959) obtained emergence of a *Smicronyx* sp. after four to six weeks. Several species from East Africa have a single generation per year which corresponds to the life cycle of *S. hermonthica*, as does *Sm. albovariegatus* in India.

1.1.3.2. Natural enemies

Murthy (1960) stated that he collected no natural enemies of Sm. albovariegatus. However, Sankaran and Rao (1966) recorded Bracon sp. (Braconidae), Charitopodinus swezeyi (Cwdf.) (Eupelmidae), Eupelmus sp. (Eupelmidae), Anisopteromalus calandrae (How.) (Pteromalidae) and Habrocytus sp. (Pteromalidae).

Ademon sp. prob. new (Braconidae) emerged along with Bracon sp. from stem-galls of Smicronyx on S. lutea. As Ademon is known to parasitize only Diptera, this species had probably attacked a cecidomyid fly in the gall. Rhaconotus sp. and Eurytoma sp. were also reared from Smicronyx galls. Thompson (1953) has listed Rhaconotus sudanensis Wlkn. as a parasite of the cotton stemborer Sphenoptera gossypii Cotes (Buprestidae) in the Sudan. It is not certain whether Eurytoma is a primary or secondary parasite of Smicronyx. Sweetman (1958) remarks that Eurytomids that attack galls and stem-infesting hosts frequently are phytophagous in their later stages of

development and that they are largely external parasites. Polynema sp. (Mymaridae) and Aprostocetus sp. (Eulophidae) emerged from a gall on Striga sp. (Sankaran and Rao, 1966).

A small, solitary pteromalid parasite, Spintherus sp., was reared commonly from seed-pod galls and a Bracon sp. was reared from Smicronyx galls in Uganda (Greathead and Milner, 1971). Accurate assessment of parasitism is difficult since individual plants have galls at all stages of development and mortality of unparasitized weevils is very high in the laboratory (Greathead and Milner, 1971). Bashir (1987) found Pteromalus semothus Walker to be the main parasite attacking the larvae of Sm. umbrinus in the galls.

1.1.3.3. Alternate hosts

Williams and Caswell (1959) have studied a Smicronyx sp. attacking Striga in Nigeria which had a common alternative host in Sopubia ramosa. This is the only secondary host of Smicronyx spp. reported so far.

1.1.4. PROSPECTS OF SMICRONYX FOR BIOCONTROL OF PARASITIC WEEDS WITH SPECIAL REFERENCE TO STRIGA

Several attempts have been made to use gall-forming weevils of the genus *Smicronyx* as biocontrol agents of parasitic weeds. *Sm. jungermanniae* Reich. and *Sm. tartiricus* Faust have been used for biocontrol of *Cuscuta campestris*

Yuncker in Russia and Kazakhstan (Horvath, 1983; Anonymous, 1987). Smicronyx roridus Mshl. and Sm. rufovittatus Anderson from Pakistan were released on Cuscuta spp. in Barbados in 1967 and 1971 but failed to establish (Julien, 1992). These Smicronyx species are non-specific as to the parts of the host that they gall, although some species favor stems, which causes stunting of the host and may prevent flowering. However, Khan and Zafar (1981) pointed out that Smicronyx spp. associated with thin-vined Cuscuta did not attack thick-vined species and vice-versa. This factor should be considered when any of these weevils is used as biocontrol agent. This specificity in host type may also be responsible for the failure of Sm. roridus and Sm. rufovittatus to become established against C. indecara and C. americana in Barbados (Khan and Zafar, 1981).

The genus of greatest interest for biological control is Smicronyx, of which several species are thought to be highly specific to Striga (Parker and Riches, 1993). Species of Smicronyx on Striga are usually host specific and the timing of the life cycle and the number of generations per year depend on the life cycle of the host plant (Smith et al., 1993). Only one attempt of classical biological control has been made so far with Smicronyx against Striga. Sm. albovariegatus Faust from India was released on S. hermonthica in Ethiopia at Humera on the Setit River close to the Sudanese border (Greathead, 1984). Surveys to document the establishment of these species were not made due to political problems in that area. In 1978 a further importation of *Sm. albovariegatus* and releases were made at the Kobbo in Welo Province (Sudan). Recoveries were made in September 1979. The second release was thought to have resulted in establishment, but in 1988 there was no trace. It is now thought that there was confusion with the indigenous, unnamed *Smicronyx* species (Parker and Riches, 1993).

The maximum number of galls so far induced by Sm. albovariegatus on a single plant of S. lutea (Sankaran and Rao, 1966) was 34 (26 stem-galls and eight fruit-galls). In one lot of 280 infested S. lutea plants examined only 25% had fruit-galls, numbering from one to eight. In 1963 about 80 to 85% of the Striga plants in some sorghum fields in Ranebennur (India) were infested by Sm. albovariegatus, as evidenced by the presence of galls. Murthy (1959) stated that the presence of root-galls weakens the Striga plant and as the weevil grub destroys the seed-capsules the weevil may possibly exercise some degree of natural control on the witchweed. Khan and Murthy (1955) and later Murthy (1959, 1960) have described the galls produced by Sm. albovariegatus.

The effects of gall-formation on S. lutea plants were investigated by Sankaran and Rao (1966) by comparing infested and healthy Striga plants growing under similar conditions in the same fields. The height of the plants and the number of

primary branches and fruit-pods produced by them were recorded and compared. The results of this study have shown that the galls do not invariably bring about any appreciable reduction in the vigor and fertility of the plants. In about 400 infested and healthy plants examined, there was considerable variation in the number of pods produced and the absence or reduced number of fruit-pods had no significant correlation with the presence of galls. For instance, a S. lutea plant without galls and measuring ca. 33 cm high bore four primary branches and produced only eight fruit-pods whereas another of the same height in the same field had eight primary branches and produced 37 fruit-pods even though it was severely infested by S. albovariegatus and showed one root-gall, 26 stem-galls and one fruit-gall. In two infested plants of the same height (ca. 22 cm) from one field in a different area, one with six galls (one root-gall and five stem-galls) had only 15 fruit-pods while the other with five galls (one rootgall and four stem-galls) had produced 61 fruit-pods. In all these cases, only fruit-pods which contained ripe seeds or which were nearing maturity were taken into account. In other words, if the plants had not been uprooted from the soil, not only would these seed-pods have matured and dehisced in the normal manner but some more would also have developed and matured. Studying a Smicronyx sp. attacking Striga in Nigeria, Williams and Caswell (1959) concluded that this species appears to attack only the fruits.

In the Sudan, surveys have so far revealed the presence of three insect species causing damage to *Striga* of which *Sm*. *umbrinus* had some local potential use against *Striga* (Bashir and Musselman, 1984). Inspection of the inflorescence of the sampled plants indicated that 52.3 ± 30.9 % of the capsules were attacked and transformed into galls. Invariably, all the inspected capsule galls contained no seed, which suggested complete failure of seed set.

The incidence of Smicronyx spp. in East Africa is variable (Greathead and Milner, 1971). In northern Uganda galls were found on S. hermonthica at seven out of 12 localities, and on S. asiatica at five out of 14 localities. Root galls were seen on S. asiatica at three out of five localities in southeast Tanzania, and at two out of three localities in western Tanzania.

Estimations of numbers of plants infested by Smicronyx spp. were made in eastern Uganda in July 1965, when samples of mature S. hermonthica were taken over a single large area (Greathead and Milner, 1971). It varied from 10 to 100%, and dissections of random samples of 10 plants from each of 12 localities gave an average of 62.5% infestation for localities where Smicronyx spp. occurred. All localities pooled (n = 23), the mean infestation level was 32.6%. In southeast Tanzania counts of 400 plants of S. asiatica were made and numbers of galled plants varied between 1.25 and 90% in infested areas. Infestation levels of individual plants is also extremely variable. For example, of 20 *S. hermonthica* plants dissected at each of two localities near Arua (northern Uganda) ranges of 2-11 and 2-16 galled pods per plant were obtained. The number of seed pods galled per plant seems to depend on the age and size of the plant, as large vigorous plants appear to be more heavily galled.

Seed-pod galling by Smicronyx spp. appears to have little effect on plant growth and as single seed-pod may produce several hundred seeds. Even if many of the seed pods would be infested, those remaining would produce large numbers of seeds. The root galling species on S. asiatica does not appear to affect the vigor of the plants (Greathead and Milner, 1971).

There are at least six species of *Smicronyx* associated with *Striga* spp. in Africa (Bashir and Musselman, 1984). They are of particular interest as biological control agents, as they are likely to be host specific and some species are specialist fruit gallers. Observations on *Striga* spp. infestations in the Sahel region of western Africa in 1977 suggest that insect damage may be of greater significance than was observed in East Africa. Up to 80% destruction of fruits of *S. hermonthica* by weevils larvae was observed (C. Parker, personal communication).

It is now well recognized that no single method will effectively control *Striga* spp. (Anonymous, 1978; Lagoke et al., 1991; Parker and Riches, 1993). In the United States, where considerable resources are available, methods including quarantine, soil fumigation, germination stimulant (ethylene), cultural practices and herbicides have been developed which have gone a long way to eradicate *S. asiatica* from the soils. However, most of these methods are too expensive for farmers of developing countries. The American witchweed eradication program has been successful in preventing the long distance spread of the parasitic weed. From 1957 to 1983, witchweed had been eliminated from nearly 50% of the originally infested areas (170,000 ha). An additional 25% of this area was believed to be free of witchweed, but had not met the criteria for release from quarantine (Sand, 1987).

Developing countries need an integrated program involving economically feasible methods. The program should be based on resistant crop varieties (supplied by government research organizations), that could be used in rotation with trap crops. These could be alternative food crops, or cash crops where the necessary marketing system exists. Even without fertilizer and herbicide input, these measures should reduce infestation levels and allow natural enemies to be more effective than at present. Synthetic germination stimulants, if they can be produced cheaply enough, offer a further safe possibility for reducing *Striga* infestations in the future (Anonymous, 1978).

In devising an integrated *Striga* control program, further work is needed on the taxonomy and biology of *Smicronyx* species. Although any of these insects are likely to achieve a high degree of control on their own, their contribution to an integrated package could be significant (Parker and Riches, 1993).

The selection and integration of control measures must depend on many factors, including the combination and predominance of the different cereal crops, opportunities for fallowing and rotational cropping, the economic status of the farm, labor a ailability, access to fertilizer and pesticide supplies. Decisions on the optimum package of control measures is likely to be helped in due course by the development of mathematical modeling techniques. Three models have been published so far, by Kunisch et al. (1991), Cardwell et al. (1991) and Smith et al. (1993). In each case, Striga seed production and of the seed bank size in the soil are of paramount importance. The models help to show how complete any control system must be to achieve a steady decline in the infestation. The model devised by Cardwell et al. (1991) attempts to assess the likelihood of adoption of different control measures in different farming systems, according to socio-economic criteria. More data are needed before these models will be of predictive value, but they meanwhile serve a valuable purpose in pinpointing gaps in our knowledge and the need for specific research information.

Smith et al. (1993) investigated the potential of Sm. umbrinus based on the population model of S. hermonthica in Mali. The method showed that Sm. umbrinus, used as the sole control agent, would have to destroy 95% of S. hermonthica seeds each year to reduce the emerged plant density by 50%. Such a high rate of seed destruction would be necessary because S. hermonthica seed bank does not limit the parasite density in most situations. The effectiveness of Sm. umbrinus in conjunction with crop rotation, trap cropping or weeding was judged by the proportion of seeds that Sm. umbrinus needs to destroy when acting together with these control methods to reduce the equilibrium level, attained in their absence, by 50%. When trap crops are grown in years between the host crop, a slightly lower level of Sm. umbrinus action is required than for crop rotation.

A 4-year crop rotation cycle reduces the equilibrium density of emerged S. hermonthica to 61% of that with no control. Sm. umbrinus needs to destroy 22% of seeds each year to decrease this to 50%. For a five year crop rotation, this method alone reduces the equilibrium density of emerged S. hermonthica by more than 50% without additional control by Sm. umbrinus. For crop rotation cycle of six or more years and

five or more years for trap cropping, *S. hermonthica* eventually becomes eradicated without any intervention by *Sm. umbrinus*. When *Sm. umbrinus* is used in conjunction with weeding it does not become effective until the seed bank is limiting at very high levels of weeding (Smith *et al.*, 1993).

To better understand the problem of *Striga* in Africa some knowledge of the economic importance and geographical distribution of the main species is necessary. Details on the biology, ecology and control of *Striga* is beyond the scope of this review. The best reviews on the subject are Ayensu *et al.* (1984), Musselman (1987), Kim (1991) and Parker and Riches (1993).

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1.2. STRIGA SPECIES

1.2.1. ECONOMIC IMPORTANCE

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The problem of parasitism by *Striga* spp. and other members of the Scrophulariaceae in crop production differs from that caused by other weed species because of the close biological association with their host plants. *Striga* represents at this time the largest biological constraint for the food production in Africa (Sauerborn, 1991).

Striga hermonthica and most other Striga species are obligate parasites, capable of only limited seedling growth before the resources are exhausted. Striga species have evolved a germination requirement that is only satisfied by a stimulant substance exuded by the roots of a potential host.

Three species cause the greatest damage. Striga hermonthica and S. asiatica are mainly found on grains, such as sorghum, corn, pearl millet, rice and others, while S. gesmerioides parasitizes specially legumes, such as cowpeas, peanuts. The occurrence of economically important Striga species is reported from 59 countries from West and East Africa as well as Asia (Sauerborn, 1991). Striga is distributed in more than 40% of the arable land south of the Sahara (Mboob, 1989). Information on the infestation and loss situation is available from six West African countries (Sauerborn, 1991). According to this information, a mean of 48% of the grain fields are infested with *Striga*. The yield loss sums up to an average of 24%, the loss of total grain production amounts to 12%. From those average values the *Striga* infested area of Africa was estimated at 21 million ha. Yield losses caused by the infestation amounts to about 4.1 million t of grain. Overall, the grain production in Africa is endangered over an area of ca. 44 million ha, since those are situated in the distribution zone of *Striga*. This equals about 3.2% of the arable land of the world. The loss of revenues from corn, pearl millet and sorghum due to the parasite infection could total 2.9 billion \$US (Sauerborn, 1991). Mboob (1986) estimated the overall loss revenues in Africa to 7 billion \$US due to *Striga*.

Striga hermonthica is the most important Striga species in Kenya (Kiriro, 1991). It devastates sorghum and millet crops grown in Benin, Burkina Faso, Cameroon, Chad, Côte d'Ivoire, Ethiopia, the Gambia, Ghana, Guinea, Mali, Niger, Nigeria, Senegal, Sudan, and Togo. The expansion of maize cultivation in West Africa, seen as the real start of Africa's Green Revolution, is also threatened (Stewart, 1990). Smaller but nevertheless serious crop losses also occur in parts of Botswana, Mauritania, Mozambique, Swaziland, Tanzania, Zimbabwe and Uganda.

1.2.2. GEOGRAPHICAL DISTRIBUTION OF THE MAIN STRIGA SPECIES

The distribution of S. hermonthica, S. asiatica and S. gesnerioides is well known although collection has been limited to certain areas within their ranges, including the southern part of the Arabian Peninsula and the sorghum-growing parts of semi-arid Asia (India, Pakistan, China, Japan, Indonesia, Thailand and Burma). Striga hermonthica is mainly distributed throughout semi-arid areas of northern tropical Africa, but extending just into southwest Arabia and southern tropical Africa, including Angola and Namibia; also Madagascar Fig. 4). Occurrence is less widespread than the related S. asiatica in southern tropical Africa for reasons not fully understood. Musselman and Hepper (1986) believe the species originates from Sudan/northeast Africa on the basis of its commoner occurrence there on wild grass hosts. It is then surprising that its development and spread in Ethiopia has mainly occurred in the past 100 years, but this could be due to the relatively recent intensification of agriculture in the country. Striga hermonthica occurs on the wild host Setaria incrassata in western Ethiopia, but whether this is the origin of the infestations on cereal crops in that area, or the result of them is not certain (Parker and Riches, 1993).

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Figure 4. General distribution of Striga hermonthica (A), S. gesnerioides (B) and S. asiatica (C).

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General distribution of Striga hermonthica



General distribution of Striga gesnerioides



General distribution of Striga asiatica

Source: Musselma let al., 1991

CONNECTING STATEMENT

Literature on insects that attack Striga has been reviewed by Bashir (1987). Much is still to be learned about ecological requirements, damage capability and host specificity among the most promising gall-forming weevils, Smicronyx spp. (Akobundu, 1991). It is now well recognized that no single method of control can solve the problem (Parker and Riches, 1993). The natural enemies of Striga spp. have received more attention in recent years because of the successes achieved in the biological control of many other weeds. Although classical biological control is very attractive in that it promises permanent suppression of pests over a large area with no further input once control agents have been established, it is not always feasible. An alternative approach is augmentation of natural enemies populations. In the Tropics there remains a huge potential for biological control by enhancing the action of native natural enemies in integrated pest management. This will probably be the most promising research area for the future (Greathead, 1991). To do so, basic study on biology of biocontrol agents is needed. Life history study of Smicronyx spp. is a key factor for success in implementing any one of the techniques of biological control as part of an integrated Striga control strategy. Chapter 2 deals with the life cycle and population dynamics of Sm. guineanus and Sm. umbrinus for understanding more about their biology.

CHAPTER 2

LIFE HISTORY OF SMICRONYX GUINEANUS VOSS AND SM. UMBRINUS HUSTACHE (COLEOPTERA : CURCULIONIDAE) ON STRIGA HERMONTHICA (DEL.) BENTH. (SCROPHULARIACEAE)

Submitted to Entomophaga in January 1995.

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2.1. ABSTRACT

The life history of Sm. guineanus and Sm. umbrinus, weevils attacking S. hermonthica, was studied in Burkina Faso, West Africa. Field experiments were conducted in 1992 and 1993 at Kaya, in fields of sorghum (Sorghum bicolor (L.) Moench and pearl millet (Pennisetum americanum (L.) K. Schum. (syn. P. typhoides (Burm.) Stapf & Hubb.). The weevils are univoltine; the adults emerge in late August, mate and the larvae enter the ovary of Striga inflorescence with a subsequent formation of galls which prevent seed production. The main damage to Striga seed capsule is caused by the larvae of at least two Smicronyx species. The larvae drop to the soil and bury themselves to a depth of 1-15 cm, enter into dormancy and pupate. Most pupae are found in the upper 5-10 cm of the soil. The pupal period lasts from late October to late July. We found 75.6% of pupae against 24.4% of adults in dormancy. Smicronyx guineanus and umbrinus are candidates for biological control of S. Sm. hermonthica.

KEY-WORDS : Smicronyx guineanus, Sm. umbrinus, Striga hermonthica, Life history, biological control, Burkina Faso.

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2.2. INTRODUCTION

Thirty-three of the 35 known species of Striga, or witchweed, are known to occur in Africa (Raynal-Roques, 1991). Striga infestations can be highly damaging to crops, especially in dry areas and on poor soils. An average of 48% of the grain fields in 59 countries of Africa and Asia are infested with Striga, resulting in a mean yield loss of 24%. Striga hermonthica (Del.) Benth. (Scrophulariaceae) is the most widely distributed species in Africa and considered one of the greatest constraint to food production of this continent.

Possibilities for the integrated and biological control of Striga species have been reviewed by Girling et al. (1979) and Greathead (1984). Smicronyx spp. have been cited by several authors as potential biocontrol agents of S. hermonthica (Greathead & Milner, 1971; Bashir, 1987; Bashir & Musselman, 1984; Markham, 1985; Traoré et al., 1993, 1991; Smith et al., 1993; Perkins, 1981; Parker & Riches, 1993).

According to Greathead & Milner (1971), gall-forming weevils were first reported by Khan & Murthy (1955) in India attacking *Striga* spp. In Africa, Williams & Caswell (1959) first reported a *Smicronyx* sp. from *Striga* sp. in Nigeria. Galling of fruits of *S. hermonthica* by *Smicronyx* spp. in West Africa is often very heavy and seed production may be reduced by more than 80% (Parker & Riches, 1993).

So far only the life history of *Cuscuta* gall weevil *Sm.* roridus and *Sm. albovariegatus* associated with *S. asiatica, S.* angustifolia and *S. dersirlora* was published (Sankaran and Rao, 1966; Agrawal, 1983) as a model of a curculio-parasitic plant relationships. Since information on the life history of *Sm.* guineanus and *Sm. umbrinus* is lacking, we initiated this study of the life history of these weevils in Burkina Faso.

2.3. MATERIALS AND METHODS

The experiments were conducted from 2 August to 29 October 1992 and from 6 August to 4 November 1993 at Kaya (13°04'N, 1°40'W) in Burkina Faso, West Africa. Sampling was done at weekly intervals in a pearl millet (field A) and a sorghum field (field B) of 2.17 and 3.60 ha in 1992 and only in field A in 1993.

Striga and Smicronyx were monitored visually every day or every second day until their first appearance in the fields. As soon as the weevils emerged, samples were taken using a Univac portable suction sampler. Sampling was done by placing the 60 mm diameter suction cone on a Striga plant until it was about 5 cm above the ground. The cone was left in position for five seconds. Ten suctions constituted a sample unit to determine the population dynamics of the weevil on S. hermonthica.

Concurrently. 20 Striga plants were chosen at random in one field for a search for mating weevils. As soon as the first pair of mating weevils was observed, 30 S. hermonthica inflorescences were randomly sampled in the field and brought in ice containers to the laboratory at Ouagadougou. The flowers were then dissected under a binocular microscope and examined for the presence of weevil eggs.

The eggs, still inserted in the ovary, were kept in a Petri dish lined with Whatman filter paper in a growth chamber set at 32°C, 70-80% R.H. and 12 : 12 (L/D) photoperiod. They were moistened regularly with distilled water and observed under a binocular microscope every day from 13 September to 26 October 1992.

For observations of Smicronyx copulation, about 100 mg of S. hermonthica seeds collected in Kaya the previous year were sown with sorghum seeds (ca. 5 cm deep) in a 25 cm diameter and 26 cm deep pot filled with soil collected at Kaya and Kamboinsé. The pots were sown each year with ca. 10 seeds of sorghum (variety E 35-2). Twency pots were set up each week and watered every second day from April to November. When Striga plants were flowering, 10 pots were randomly selected. The pots were surrounded by a transparent plastic sheet that was taped to make a cage. The upper side of the cage was covered with a nylon screen (8 mesh/cm) to prevent escape of the weevils and yet to allow good ventilation. One female and one male were placed in every cage containing one or two plants of S. hermonthica.

The external characters used to separate Sm. guineanus from Sm. umbrinus are as follows (D. M. Anderson & M. Cox, pers. comm. 1991, 1993) :

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1) Sm. guineanus has a body shorter (ca. 2.50 cm) than Sm. umbrinus (ca. 3.45 cm); the former is black whereas the latter is black to reddish black. 2) The front tibia has no teeth on Sm. guineanus whereas there is a tooth, which may be obtuse, on the inner margin of the anterior tibia opposite the tooth on the femur and the femoral tooth is distinctly larger in Sm. umbrinus (Fig. 5). 3) The apical abdominal sternite has no distinct depression on Sm. guineanus but this depression is distinct on Sm. umbrinus. 4) When the antennae are folded up, the tip of the antennae is closer to the apex of the rostrum in Sm. guineanus whereas it is further from the apex of Sm. umbrinus rostrum.

The internal differences based on genitalia are as follows:

2.3.1. MALE GENITALIA

1) Sm. guineanus has a distinctive shape of the median lobe (penis) which is constricted behind the apex and is rather elongate whereas in Sm. umbrinus the median lobe of adeagus is short, with a strongly deflected apical margin and a broadly rounded apex (Fig. 1).

2) Tegmen smaller with apices of epimeres distant from apex of median lobe in *Sm. guineanus* (Fig. 1 and 2). Tegmen larger with apices of epimeres closer to apex of median lobe in *Sm. umbrinus* (Fig. 1 and 2). The epimeres of *Sm. guineanus* are

farther from the apex of the median lobe because the median lobe is longer than in *Sm. umbrinus*, not because they are shorter.

2.3.2. FEMALE GENITALIA

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Smicronyx guineanus ovipositor and the spiculum ventral (apodeme) are not elongate and the ovipositor lacks pigmented internal support rods (Fig. 3A). The spiculum ventrale of Sm. umbrinus is long and slender and the ovipositor is also elongate, with a pair of pigmented internal struts supporting it (Fig. 3B).

Sexing was done on the basis of the following characters. 1) Male usually slightly smaller, with the rostrum shorter and stouter. The insertion of the scape (basal antenna segment) is more distal on the rostrum. Rostrum dorsally with scales anterior to antenna insertions; dull in the apical half and micro sculptured. Eyes are contiguous ventrally. 2) Female usually larger, with the rostrum relatively longer and more slender. The insertion of the scape is medial on the rostrum which is without scales anterior to antenna insertions. In the apical half, the rostrum is shiny, not micro sculptured.

Every week, visual observations made done to find galls in the fields after the first eggs were recorded. Then the appearance time of the first exit holes of the last larval instar of *Smicronyx* was recorded.
Twenty wooden containers (2 X 1 m and 0,30 m deep), full of soil collected from fields at Kaya were transferred to the laboratory and kept at ambient temperature. *Striga* plants bearing galls were collected and allowed to dry on containers. More than six months later, the soil was sieved to collect *Smicronyx* pupae and adults.

Although several Smicronyx species have been observed on Striga spp. (Greathead & Milner, 1971) the taxonomy of Smicronyx in Africa is very confused. Specimens of Smicronyx adults collected in 1992 and 1993 were sent to Dr. Donald M. Anderson (Systematic Entomology Laboratory, USDA, National Museum of Natural History, Washington, D.C., USA). Others specimens were forwarded to Dr. Michael Cox (International Institute of Entomology, C.A.B. International, London, UK.) for identification. Voucher specimens of Sm. guineanus and Sm. umbrinus were deposited at the Systematic Entomology Laboratory, USDA, National Museum of Natural History, Washington, D.C., USA, the International Institute of Entomology (C.A.B. International), London, UK, the Lyman Museum, Macdonald Campus of McGill University, Sainte-Anne-de-Bellevue, Québec, Canada and the Biosystematics Research Center (Agriculture Canada), Ottawa.

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2.4. RESULTS AND DISCUSSION

Weevil adults collected for identification (n = 896) were composed of 94.3% of *Sm. guineanus* and 5.3% of *Sm. umbrinus* in areas sampled in Burkina Faso.

2.4.1. ADULT POPULATION DENSITY

Smicronyx adults emerged in late August (Fig. 6A) or in early September (Fig. 6B). The peak of adult emergence was observed in fields A and B during the first fortnight of September 1992 whereas it was recorded in field A late in September 1993. This delay is probably due to the late onset of the rainy season in 1993. Adults were sampled until late October (Fig. 6A and 6B). We observed one generation a year. Our results are similar to those of Sankaran & Rao (1966) who worked on Sm. albovariegatus attacking S. lutea, S. angustifolia and S. densiflora in India.

As soon as they emerged, Smicronyx adults start mating on green Striga plants before the flowering stage. The peak of copulatory activity was observed one week after the first record of Smicronyx adult mating pairs (Figs. 6C and 6D). Courtship behavior for Smicronyx spp. is nonexistent (Piper & Mulford, 1980). A male approached a female, either from the front or the rear and immediately attempted copulation. When the approach was made from the front, the male quickly reversed

his position atop the female and aligned his body with hers so that both faced in the same direction. The male's front tarsi clasped the female humeri, his middle tarsi gripped her metasternum and his hind tarsi were pressed against the female's abdominal sternite. The time of copulation varied from 15 to 60 min. but in two occasions, it lasted 10 h (20.00-06.00 h). During copulation, the male merely rode the female's dorsum while she was moving around and feeding. Mating occurred most frequently at sunset on the inflorescence of *S. hermonthica*.

2.4.2. EGGS

They were recorded in field A from 13 to 24 October 1992 (Fig. 7) indicating that females lay eggs within a week after mating and fertilization. In growth chamber, the incubation period lasted from 4 to 8 days. Agrawal (1983) observed eggs of *Sm. roridus* Mshl. on *Cuscuta* incubating for 6 to 8 days in India. Many punctures made by the female with its rostrum were observed in the *Striga* corolla tube in attempts to find the right substrate for laying her eggs. A small circular hole was gnawed through the calyx and the ovary wall. Through this opening an egg was deposited into the young, fleshy ovary. Eggs were located frequently in the proximal end of the ovary. Only one egg was deposited in a single ovary, surrounded by many embryos/seeds of *Striga*. The egg of *Smicronyx* ranged from 0.216 to 0.576 mm in length, from 0.126 to 0.396 mm in width. Agrawal (1983) found *Sm. roridus* eggs white, ovoid and measuring 0.43 mm long and 0.31 mm wide. The Sm. guineanus and Sm. umbrinus newly laid egg was bell-shaped with a tapered end and was creamy white. It had an outer shiny, smooth, thin and transparent shell or chorion which allowed sight of a light brownish mass in the egg center. As the egg matured, it became opaque, then turned brown in the lengthwise center with a prominent dark spot on one end which is the head capsule of the larva.

2.4.3. LARVAE

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The full grown larva of *Sm. umbrinus* is about 4 mm and that of *Sm. guineanus* is ca. 3 mm long. The former has a longer, more darkly pigmented, less convex head capsule. Its mandibles are longer, darker in the apical 1/3 and have a small third tooth on the cutting edge. The first (basal) segment of the maxillary palpus is noticeably more robust and more rounded at the sides in *Sm. umbrinus*. Larvae of both types were found in galls and in mature (ungalled) seed capsules. Larvae usually occurred singly, but in some instances two were located in one gall. Most of the galls showed no development of seeds, as if the galling had totally suppressed the production of seeds and that the larvae in the seed capsules often destroyed large numbers of the seeds. The larvae were recorded from mid-September to early November (Fig. 7). They were soft bodied, legless, white and distinctly curved. They turned yellow to brownish as they matured. The head was weakly sclero'ized and provided with mouth parts for cutting and chewing.

Of the galls examined (n = 115) of a sample collected at Zorkoum (Kaya) in 1992, we found ca. 75% containing larvae.

2.4.4. PUPAE

Upon reaching maturity, the larva cut a circular hole through the gall wall and emerged. The larva dropped to the soil and buried itself to a depth of 1-15 cm. As soon as the last instar larva reached the appropriate depth in the soil, it formed an earthen cell by cementing soil particles around its body. The larva did not pupate until much later and entered into dormancy. Most pupae were located in the upper 5-10 cm of the soil. Pupation occurred from early October to late November according to the growing season. The duration of pupal period in nature lasted from October to late July (Fig. 6). The pupae were about the size of the larvae but more pigmented. While sorting the pupae from the soil containers more than six months later, we found 75.6% of pupae and 24.4% of adults of *Smicronyx* in dormancy (Traoré et al., 1995).

Although our results showed that Sm. guineanus adults are dominant in areas sampled (94.3%) it is unlikely that their searching and reproductive capacity is higher than those of Sm. umbrinus. Fifty-two percent of those galls contained larvae of

Sm. umbrinus and 48% of them held larvae of Sm. guineanus (n = 75). Our findings indicated that both species exploit their food resource with nearly equal numbers of larvae in the Striga seed capsules. This ratio could be accounted for the sample areas and the time of collections by the exit of large numbers of Sm. guineanus larvae for diapause before the Striga sample were collected. The S. hermonthica seed capsule was exploited by at least two Smicronyx species.

Smicronyx guineanus and Sm. umbrinus could be used in integrated control programs of S. hermonthica in Africa. It is believed that these weevils have good potential because larvae feed on Striga seed capsule. The assessment of the impact of Smicronyx larvae on the reduction of Striga seed is a prerequisite to any manipulation of the weevil populations. Unfortunately, no accurate method of counting the dust like seeds of Striga is yet available. However, histological studies of Striga ovaries might be helpful in addressing this issue (Paré, 1993).

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Figure 5. Femur and tibia of forelegs, lateral view, with scales partly removed to expose femoral and tibial teeth for A) Sm. guineanus (there is no tooth on the tibia) and B) Sm. umbrinus.



Figure 6. Smicronyx guineanus and Sm. umbrinus adult abundance in peasant fields, A) 1992 and B) 1993 and pairs mating period, C) 1992 and D) 1993 at Kaya, Burkina Faso.

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Figure 7. Life cycle of Sm. guineanus and Sm. umbrinus in relation with the presence or absence of S. hermonthica at Kaya, Burkina Faso.

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CONNECTING STATEMENT

The list of questions about the simple behavior of an insect could be extended greatly, but no matter how long the list, each question could be assigned to one of just two categories: "how questions" about the proximate causes of the behavior, or "why questions" about its ultimate causes (Mayr, 1961; Orians, 1962, Alcock, 1989). "How" questions ask how an individual manages to carry out an activity; they ask how mechanisms within an animal operate to make its behavioral responses possible. "Why" questions ask why the animal has evolved the proximate mechanisms that enable it to do certain things. Biologists use a particular hypothesis to produce a prediction, which they then test in some way. If the prediction does not match reality, then the hypothesis can be rejected as false. As John Hartung (1982) says, "in science you are wrong until you prove you might not be". In Chapter 3 we tested the prediction that Sm. guineanus adults spend more time on the reproductive organs of Striga plant and that their activities are performed at a specific time a day. Addressing these issues will permit better use of Sm. guineanus in an integrated Striga control program and will determine the best time of day for sampling the weevils. Understanding the mechanism underlying behavior requires first understanding the behavior itself. As part of the studies on the bionomics of Smicronyx guineanus, its behavior was measured and related to its ecological conditions in which the weevil lives.

CHAPTER 3

BEHAVIORAL TIME BUDGET OF SMICRONYX GUINEANUS VOSS (COLEOPTERA: CURCULIONIDAE) ADULTS ON STRIGA HERMONTHICA (DEL.) BENTH. (SCROPHULARIACEAE) IN SEMI-FIELD CONDITIONS

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3.1. ABSTRACT

The behavioral time budget of Sm. guineanus Voss was studied in semi-field conditions. Pairs of weevils were observed on a 24-h cycle starting from 0800 to the next day at 0600 and repeated for 21 days in cages containing S. hermonthica (Del.) Benth plants parasitizing sorghum. Each female and male was observed every two hours. Occurrences for the various behaviors exhibited by the weevil were recorded. In decreasing order, the weevils were observed to exhibit standing still, feeding, mating, walking, moving and foraging. In addition, the difference in time spent on the different parts of the host plant was highly significant (p = 0.0001, 10)couples/days, n = 21 days). These parts were classified in four groups. Group A: stem, leave and bud; group B: coroila; group C: calyx; group D: sorghum, petiole, soil, capsule, and cage. The weevil adults spent 46.8% of their time on the Striga inflorescence (bud, corolla and calyx). Striga plants were stratified with respect to distance from the base and categories were designated as upper, central and lower parts. Smicronyx adults spent 85.2% of their time in the upper stratum, 9.8% in the central stratum and 5% of their occurrences were in the lower third of the Striga shoot. They were more active in daytime, suggesting that the best period of day to sample these weevils in the field is from 0700 to 1100 or from 1600 to 1800.

3.2. INTRODUCTION

Witchweeds are considered to be the single greatest constraint to food production in Africa at this time. A conservative estimate of crop losses due to *Striga* spp. in Africa is 40 percent of crop yield, representing an annual loss of cereals worth US \$7 billion (Mboob 1986).

Possibilities for the integrated and biological control of *Striga* species have been reviewed by Girling *et al.* (1979) and Greathead (1984). It is suggested that *Sm. guineanus* Voss (Curculionidae) may be useful as a biocontrol method where other controls reduce the seed bank to limiting levels, and may have a role in slowing the growth rate of new *S. hermonthica* infestations.

The weevils are univoltine, the adults emerge in late August and mate. The eggs are deposited in the proximal end of the ovary of the Striga flower. The larvae develop in the ovary of the Striga inflorescence with a subsequent formation of galls which prevent seed production. The main damage to the Striga seed capsule is caused by the larvae. Galling of fruits of S. hermonthica by Smicronyx spp. in West Africa is often very heavy, and seed production of the weed may be reduced by 80% or more (Parker and Riches, 1993). There is a good synchrony between the presence of Sm. guineanus adults with the occurrence of S. hermonthica (Traoré, 1995). Although Smicronyx species have been cited as potential candidates for biological control of Striga (Greathead and Milner, 1971; Girling et al., 1979; Bashir and Musselman, 1984; Greathead, 1984; Bashir, 1987; Parker and Riches, 1993), no study on the activity and behavior of Sm. guineanus has been yet published. Consequently, a series of experiments was undertaken in 1992 and 1993 on the daily behavior of the weevil within cages simulating field conditions.

Our objective was to address questions concerning the proximate causes (= how, Sensu, Alcock, 1989) of Smicronyx behavior in semi-field conditions. Addressing these questions will allow better use of Sm. guineanus in an integrated Striga control program and should be useful information to implement a sampling program.

3.3. MATERIALS AND METHODS

The experiments were conducted from 27 October to 29 December 1992 and from 3 October to 16 December 1993 at Kaya (13°04'N, 1°40'W) and Ouagadougou (12°55', 1°30'W) in Burkina Faso, West Africa.

About 100 mg of S. hermonthica seeds collected in Kaya the previous year were sown with sorghum seeds (ca. 5 cm deep) in a 25 cm diameter and 26 cm deep pot filled with soil collected at Kaya and Kamboinsé. The pots were sown each year with ca. ten seeds of sorghum, variety E 35-1. Twenty pots were set up every week and watered every second day from April to November. When Striga plants were flowering, 10 pots were randomly selected. The pots were surrounded by a transparent plastic sheet, taped to form a cylindrical cage. The upper side of the cage was covered and taped with a nylon screen (8 mesh/cm) to prevent escape of the weevil pairs and to allow g_{c} od ventilation inside. One female and one male were placed in each cage containing one or two plants of S. hermonthica.

A Univac portable suction sampler (Burkard Company Ltd., Woodcock Hill Industrial Estate, Rickmansworth Hertfordshire WD3 1PJ, England) was used to collect *Smicronyx* adults at Kaya. Collection was done by lowering the 60 mm diameter suction cone onto a *Striga* plant at ca. 5 cm above the ground. Adult weevils were transferred to Ouagadougou and sorted out to species, then

to sex. Smicronyx guineanus was separated from Sm. umbrinus Hustache, which also was present in those fields. The external characters used to differentiate Sm. guineanus from Sm. umbrinus adults are as follows (D. M. Anderson and M. Cox, personal communication):

1) Smicronyx guineanus has a body shorter (ca. 2.50 cm) than Sm. umbrinus (ca. 3.45 cm); the former is black whereas the latter is black to reddish black.

2) The front tibia has no teeth on *Sm. guineanus* whereas there is a tooth, which may be obtuse, on the inner margin of the anterior tibia opposite the tooth on the femur and the femoral tooth is distinctly larger in *Sm. umbrinus* as depicted in Fig. 5.

3) The apical abdominal sternite has no distinct depression on *Sm. guineanus* but this depression is distinct on *Sm. umbrinus*.

4) When the antennae are folded up, the tip of the antennae is closer to the apex of the rostrum in *Sm. guineanus* whereas it is further from the apex of *Sm. umbrinus* rostrum.

Sexing was done on the basis of the following characters:

1) Male usually smaller, with the rostrum shorter and stouter. The insertion of the scape (basal antenna segment) is more distal on the rostrum. Rostrum dorsally with scales anterior to antenna insertions; it is dull in the apical half and micro sculptured. The eyes are contiguous ventrally.

2) Female usually larger, with the rostrum relatively longer and more slender. The insertion of the scape is medial on the rostrum which is without scales anterior to antenna insertions. In apical half, the rostrum is shiny, not micro sculptured. The eyes are very narrowly separated ventrally.

A day before the experiments, females and males were marked on the dorsal surface of elytra with fluorescent dye. The females were colored with yellow spots (Wax 17, Saturn Yellow Dispersion) and the males with red spots (Wax 13, Rocket Red Dispersion) of Day-Glo dyes (Day-Glo Color Corp., Cleveland, Ohio). The evening before the day of observation, a vial containing one male and one female was placed at the base of the *Striga* plant in the cage. Every individual was used once for the experiment. In preliminary laboratory tests, the dye had no effects on behavior or mortality. The cages were kept at ambient temperature on a table placed outdoors.

The observations were done every second hour on a 24 h cycle basis starting from 0800 to the next day at 0600. Twentyone cycles (= days) were done. At night, a battery operated black-ray UV lamp (Lamp 366 NM, ML-49, UVP inc., San Gabriel, California, USA) was used to locate the weevils.

A one-zero scheme was used (Martin and Bateson, 1989), meaning that one individual was observed for a time period and all categories of its behavior were recorded. The recording

session (10 min. for 20 individuals) was divided into 30 sec. intervals, i.e. the sampling unit. The observer recorded whether or not the behavior patterns occurred during the preceding sampling interval. A small electronic timer was used that beeped through an earphone to indicate termination of a sample unit (30 sec.). Observations were made on every individual of the weevil pairs, every second hour (e.g. 0600, 0800, 1000 etc.).

The behaviors were recorded on paper and on an audio tape recorder as a backup. Audio recordings of behaviors were transcribed in the laboratory whenever the data could not be properly recorded on paper because of darkness. Adapted from Chouinard *et al.* (1992), Johansson (1993), Kaas *et al.* (1993), Wiskerke and Vet (1994), the following behavioral categories were established:

Standing still: Standing still on substrate.

Walking: Displacement without antennal drumming

on substrate.

Foraging: Walking with antennal drumming on substrate for search of food.

Moving: No displacement, slow movement around without antennal drumming

on substrate.

Feeding: Motionless with the rostrum deep inside the plant.

Mating: Male riding the dorsum of the female.

Preening: Standing on substrate while cleaning mouth parts, rostrum or antennae with forelegs.

The different parts of the substrate were recognized as:

Bud of Striga flower. Calyx of Striga flower. Corolla tube and lobes of Striga flower. Galled seed capsule of Striga plant. Leaves of Striga plant. Petiole of Striga leaf. Stem of Striga plant. Sorghum plant. Cage.

Soil.

Striga shoots were stratified with respect to distance from the base and categories were designated as upper, central and lower parts of the plant to record the position of the weevil.

3.3.1. STATISTICAL ANALYSIS

Each sampling unit was treated according to the frequency of occurrences. This was done irrespective of how often (or how long) a behavior occurred during that sampling unit. To examine the relative importance of the different behavior on each part of the substrate, a contingency table for each sampling unit, a total of 12 per day, was made up for 21 days using StatView (Version 4.0 for the Macintosh Computer, Abacus Concepts Inc., 1992). Percents of overall total frequency for categories of behavior and parts of substrate were computed thereafter.

Out of these contingency tables, analysis of variance (ANOVA) using SuperANOVA, (version 1.1 for the Macintosh Computer, Abacus Concepts Inc. 1989) and the Scheffe's mean separation procedure (p < 0.05) was performed on the different parts of substrate and the behavioral categories for the overall period of the study. Then ANOVA was performed for the categories of behavior on every part of substrate.

3.4. RESULTS AND DISCUSSION

There was a highly significant difference among the categories of behavior of the *Smicronyx* adults (p = 0.0001, 10 couples/days, n = 21 days). The weevils were standing still 58.8% of the total occurrences on *Striga*, feeding 20.4%, mating 7.9%, walking 4.7%, moving 4.3% and foraging 3.9% (Fig. 8). The time allowed to standing still, feeding and mating was significantly different from the other behavioral categories (Scheffe's test, $\alpha = 0.05$). While standing still and without performing any one of the above activities, weevils usually were preening. Preening was not quantified because this behavioral category was not obvious during the two preliminary tests.

In addition, differences between the time spent on the different parts of substrate were highly significant (p = 0.0001, 10 couples/days, n = 21 days). According to the Scheffe's test, these parts were classified in four groups. Group A: stem, leave and bud; group B: corolla; group C: calyx; group D: sorghum, petiole, soil, capsule, and cage (in decreasing order of time spent on them). *Smicronyx* adults were on stem 22.2%, leave 22.5%, bud 22,3%, corolla 14.3%, calyx 10.2%, sorghum 3.1%, petiole 2.6% and less than 1% of the total time observed on soil, capsule or cage (Fig. 9). The weevil adults spent 46.8% of their time on the *Striga* inflorescence

(bud, corolla and calyx). Smicronyx adults spent 85.2% of their time in the upper stratum, 9.8% in the central and 5% of their time in lower third of the Striga shoot (Fig. 10). There was a highly significant difference among the strata (ANOVA, p = 0.0001, 10 couples/days, n = 21 days).

Smicronyx adults were more active in daytime (Fig. 8). The proportion of time spent standing still peaked between 2000 to 0600. The weevils spent more time feeding (20.4%) and mating (8%) while standing still (58.8% of their behavior). We observed a male riding a female back all night long on three occasions. In this copulating posture, the female fed and sometimes moved around with the male on her dorsum. Smicronyx adults exhibited a higher percentage of time moving, walking and foraging from 0600 to 1800. The best period of day to sample these weevils in the field is from 0700 to 1100 or from 1600 to 1800. These period overlap with their activity and they are in the upper stratum of the plant. In peasant fields we observed them in the lower strata of Striga only when the sunshine is at maximum (from 1300 to 1400). Smicronyx adults were observed walking and even mating, but never feeding on sorghum plants in semi-field conditions.

Our findings indicated that *Smicronyx* adults spend most of their time on the upper stratum of *S. hermonthica*. Subsequently, they are more likely to feed, copulate and lay eggs on the reproductive organs of the witchweed. Even though

we could not define a category of behavior on the laying of eggs, other experiments showed that eggs are laid in the proximal end of the ovary through a hole made in the calyx wall by the female (Traoré, 1995). These results reflect an overall preference for *Striga* inflorescence since the majority of the larvae were inside galls of the upper stratum of the witchweed plant.

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Figure 8. Mean proportion (%) of Smicronyx occurrences of behaviors (10 couples/session, 12 sessions/day; n = 21 days). Grey zones represent scotophase.

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Figure 9. Mean proportion (%) of Smicronyx occurrences on various substrates (10 couples/session, 12 sessions/day; n = 21 days).


Figure 10. Mean proportion (%) of Smicronyx occurrences per Striga plant stratum.(10 couples/session, 12 sessions/day; n = 21 days). Grey zones represent scotophase.

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CONNECTING STATEMENT

The description of distribution pattern of insects in space has been termed as spatial pattern or spatial distribution (Harcourt, 1965) or dispersion (Southwood, 1978). The spatial distribution of the insect in the field must be determined in order to decide on an optimum sample size for estimate of population density (Sevacherian and Stern, 1972; Karandinos, 1976). As part of the studies on the bionomics of Smicronyx guineanus and Sm. umbrinus, a sampling program was carried out as described in Chapter 4 to investigate the spatial distribution of the weevils and determine the number of samples required to estimate the density of Smicronyx guineanus and Sm. umbrinus adults, with a given level of accuracy. This measure of precision is meaningful in ecological research because a fixed level of (D) = $(S\overline{\chi}/\overline{\chi})$, where $S\overline{\chi}$ is the standard error of the mean for a series of population estimates guarantees a stable magnitude of the error variance when estimate are transformed to logarithms (Kuno, 1969). Iwao's patchiness regression for determination of the dispersion patterns of Smicronyx adults on Striga have been used for the first time and shown to be valid. Another hypothesis investigated in Chapter 4 was whether the larvae were located in the upper stratum, bearing the reproductive organs of the Striga plants. The vertical distribution of the larvae on the host was determined to assess the potential of the larvae in making galls of the seed capsules of the witchweed.

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CHAPTER 4

DISPERSION PATTERNS OF ADULTS AND VERTICAL DISTRIBUTION OF LARVAE OF SMICRONYX GUINEANUS VOSS AND SM. UMBRINUS HUSTACHE (COLEOPTERA: CURCULIONIDAE) ON STRIGA HERMONTHICA (DEL.) BENTH (SCROPHULARIACEAE)

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4.1. ABSTRACT

Adult populations of Sm. guineanus Voss and Sm. umbrinus Hustache were sampled on S. hermonthica (Del.) Benth in Burkina Faso. Samples were taken at four localities in 1991 and one in 1992 and 1993 using a Univac portable suction sampler, beginning at emergence time of the adult weevils to assess their dispersion patterns and the optimum sample size for Smicronyx. Sampling was done weekly by placing the 60 mm diameter suction cone on a Striga plant until it was about 5 cm above the ground. Smicronyx adults on S. hermonthica were aggregated. A sample size of 20 and 126 units provided a 25 and 10% precision level respectively at 6 Smicronyx adults per sampling unit. A chart was designed which could be useful for determining the level of precision attainable at various densities of Smicronyx adults for any sampling and monitoring program. Larval vertical distribution of Smicronyx was described. Striga plants were stratified with respect to distance from the base and categories were designated as upper, central and lower parts. Our results indicate that Smicronyx larvae are located in the upper stratum of the witchweed where they make galls and destroy large numbers of seeds.

4.2. INTRODUCTION

Parasitic weeds, such as *Striga* spp., threaten the lives of over 100 million people in Africa (Lagoke *et al.*, 1991). Two-thirds of the 73 million ha devoted to cereal crop production in Africa is seriously affected (Mboob, 1986). *Striga* represents at this time the largest biological constraint for the food production in Africa (Sauerborn, 1991). *S. hermonthica* (Del.) Benth. (Scrophulariaceae) is the most widely distributed witchweed species of Africa, mainly found on grains such as sorghum, corn, pearl millet, rice and others. A conservative estimate of crop losses due to *Striga* spp. in Africa is 40 percent of crop yield, representing an annual loss of cereals worth US \$7 billion (Mboob, 1986).

In Burkina Faso (West Africa), both farmers' and research fields are heavily infested with *Striga*, resulting in the abandonment of many farms. A survey conducted in eleven regional development areas showed that *Striga* infestations occurred throughout the country (Ouédraogo, 1986). *Striga* control requires the development and implementation of an integrated farming system, the major constraints being of socio-economic nature (Stewart, 1990). Recommended control practices such as hand pulling, crop rotation, fallowing, inter-cropping, nitrogen fertilization, chemical use and the use of tolerant varieties may be effective if properly integrated, but generally, concerted efforts have not been made to design economically feasible and effective control programs for peasant conditions (Ogborn, 1984).

Biocontrol should be one important component of an integrated management program for *Striga* (Musselman, 1983; Cardwell *et al.*, 1991). However, there is a lack of data concerning the potential of biocontrol agents for *Striga*. Although no study has yet been done on the bionomics of *Smicronyx* spp., these weevils have been cited by several authors as potential biocontrol agents of *S. hermonthica* (Khan and Murthy, 1955; Williams and Caswell, 1959; Girling *et al.*, 1979; Greathead and Milner, 1971; Bashir, 1987; Bashir and Musselman, 1984; Greathead, 1984; Markham, 1985; Traoré *et al.*, 1990, 1991; Smith *et al.*, 1993).

According to Greathead and Milner (1971), gall-forming weevils were first reported attacking *Striga* spp. by Khan and Murthy (1955) who found *Sm. albovariegatus* Faust. associated with *S. asiatica*, *S. angustifolia*, and *S. densiflora* in India. In Africa Williams and Caswell (1959) first reported a *Smicronyx* sp. from *Striga* sp. in Nigeria. Eggs of *Sm. guineanus* have been found in the ovary of *S. hermonthica* flowers (Traoré, 1995). On hatching, the larvae excavate a small cavity in the surrounding tissues of young seed pods, which swell up and produce galls which enlarge as the larvae feed inside them. One or two larvae are found in a single seed pod; when fully grown they emerge from the galls, burrow into the soil and pupate in small earthen cells.

The larvae destroy large numbers of ovules in the seed capsule (Paré, 1993). A galled capsule does not produce seed and thus *Sm. guineanus* and *Sm. umbrinus* could be effective biocontrol agents by reducing seed production and therefore depleting the *S. hermonthica* seed bank. Galling of *S. hermonthica* fruit by *Smicronyx* in West Africa is often heavy, and Seed production of the weed may be reduced by 80% or more (Parker and Riches, 1993).

A knowledge of the dispersion of a population, i.e. the description of its distribution pattern, is of considerable ecological significance (Southwood, 1978). For the development of a sampling program it is essential to have a knowledge of the distribution pattern (dispersion) of the insect in its habitat (Southwood, 1978). An effective sampling program for insects requires knowledge of the smallest numbers of samples that need to be taken for reliable population density estimates, as known as the optimum sample size (OSS) (Karandinos, 1976). No statistics on dispersion patterns of adults have been yet published for *Sm. guineanus* and *Sm. umbrinus*, nor on the vertical distribution of the larvae. The objectives of this study were (1) to evaluate spatial distribution patterns of *Smicronyx* adults, (2) to apply this information to determine the relationship between density and OSS at a 25% precision level, and (3) to describe the vertical distribution of *Smicronyx* larvae on *S. hermonthica*.

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4.3. MATERIALS AND METHODS

The experiments were conducted from 5 October to 30 November 1991 at Ouahigouya (13°31'N, 2°20'W), Kaya (13°04'N, 1°40'W), Douna (Banfora, 10°36'N, 4°45'W) and Djibasso in Burkina Faso, West Africa. Samples were taken from 26 August to 4 November 1992 and from 1 September to 4 November 1993 at Kaya. On 9 occasions in 1991, 13 in 1992 and 10 in 1993, sampling units were taken randomly from farmers' fields ranging in size from 2.17 to 3.60 ha. Sampling was done weekly in 1991, 1992 and 1993 and a total of 990 sample units were taken over the three years. The sampling efforts encompassed the period of *Smicronyx* activities throughout the season.

A Univac portable sampler (Burkard Company Ltd., Woodcock Hill Industrial Estate, Rickmansworth Hertfordshire WD3 1PJ, England) was used to sample *Smicronyx* spp. Sampling was done weekly by placing the 60 mm diameter suction cone on a *Striga* plant until it was about 5 cm above the ground. The cone was left in position 5 seconds of suction before being removed. Five suctions constituted a sample unit in 1991. Ten suctions constituted a sample unit in 1993. Adult weevils were sorted out and counted *in situ* or transferred to the laboratory as necessary.

4.3.1. REGRESSION ANALYSES

Dispersion patterns of *Smicronyx* adults on *Striga* were determined by using Iwao's patchiness regression (Iwao, 1968, 1977; Iwao and Kuno, 1971). Iwao's regression method quantifies the relationship between variance (s^2) and mean density (\bar{x}) by calculating the Lloyd's (1967) mean crowding index (\tilde{m}) for each data set, where $\tilde{m} = \bar{\chi} + [(s^2/\bar{\chi}) - 1]$. Mean crowding was regressed on $\bar{\chi}$ such that $\tilde{m} = \alpha + \beta \bar{\chi}$, and least-squares estimates of α and β were calculated using a linear regression procedure (SuperANOVA, version 1.1 for the Macintosh Computer, Abacus Concepts Inc., 1989).

A slope β <1 indicates a uniform dispersion, β = 1 indicates a random dispersion and β >1 indicates an aggregated dispersion. A t-test was performed to determine whether the slope was significantly different from 1.

The intercept α is a measure of the basic unit of aggregation where α is the number of individuals that make up a "group" (Iwao and Kuno, 1971). When $\alpha > 0$, the population exists as groups of individuals (i.e., colonies), whereas the individual is the primary unit of aggregation when $\alpha = 0$. There is a positive or negative association between individuals when α is >0 or <0 respectively.

Optimum sample size determination

Iwao (1977) gives an optimum sample size (OSS) equation that incorporates lpha and eta parameters obtained from a regression analysis. OSS = $(t^2/D^2)[((\alpha + 1)/m) + \beta - 1]$, where t is Student's t value at 5%, D is the desired precision level (set by the experimenter), m is the population mean, α is the index of basic contagion, and b is the density-contagiousness coefficient. The precision level is defined as the standard error of the mean as a proportion of the mean (Iwao, 1977). A precision level D of 0.10 (10%) has been cited as a desirable level for "intensive" ecological research and a D of 0.25 (25%) desirable for "extensive" management applications as (Southwood, 1978). Precision levels (D) of 0.10 (10%), 0.15 (15%) and 0.25 (25%) may satisfy requirements for different types of field studies or monitoring (Ekbom, 1985; Elliott and Kieckhefer, 1986; Ward et al., 1986). We calculated a range of D from 10 to 30% (by increment of 5) to provide a sampling tool for population density estimates of Smicronyx adults.

4.3.2. LARVAL VERTICAL DISTRIBUTION

Sampling was initiated when galls were observed on *Striga* plants. The sample size was 50 shoots randomly cut at ground level. They were brought to the laboratory in an ice container. Samples were stratified with respect to distance from the base and categories were designated as upper, central and lower parts of the plant. Galls of each stratum were dissected and

the number of larvae was recorded. On 17 occasions, 27 samples were collected and a total of 1,350 *Striga* galled plants were stratified and larvae removed from the galls.

Data were subjected to a square root transformation to stabilize error variance and were analyzed by analysis of variance (ANOVA) using SuperANOVA and the Scheffe's mean separation procedure of that software (p < 0.05). A contingency table was performed using StatView to determine the percentage of larvae in each stratum of the *Striga* galled plant.

Several species have been observed on Striga spp. in various parts of Africa (Greathead and Milner, 1971). However, the taxonomy of Smicronyx in Africa is very confused. Specimens of Smicronyx adults were collected in 1990, 1991 and 1992 and sent to Dr. Donald M. Anderson of the Systematic Entomology Laboratory, USDA National Museum of Natural History, Washington, D.C., USA. Some specimens were also forwarded to Dr. Michael Cox of the International Institute of Entomology (C.A.B. International), London, UK., for identification. Voucher specimens of Sm. guineanus and Sm. umbrinus were deposited at the Systematic Entomology Laboratory, USDA, National Museum of Natural History, Washington, D.C., USA, at Institute of Entomology the International (C.A.B. International), London, UK, at the Lyman Museum, Macdonald Campus of McGill University, Sainte-Anne-de-Bellevue, Québec, Canada and the Biosystematics Research Center (Agriculture Canada), Ottawa, Canada.

4.4. RESULTS AND DISCUSSION

4.4.1. REGRESSION ANALYSES

Adults were clumped, with b significantly >1 in Iwao's patchiness regression for 1991, 1992 and 1993 data. The index of basic contagion a was statistically not significant from 0, meaning that a single individual is the basic component of the distribution. Therefore, the results obtained over the three years of study were pooled. Table 1 and Fig. 11 show estimates of indices of dispersion and the coefficients of determination (r^2) ranged from 0.7 to 0.85. The observed variation of adult numbers indicates a highly clumped distribution of *Smicronyx* adults within the fields.

Smicronyx adults are poor flyers. The contagious distribution of Smicronyx adults can be accounted for by the presence of more green and/or flowering Striga plants in the vicinity of previously attacked Striga plants. Heterogeneity in the "quality" of food plants can lead to a clumped distribution which may be associated with the stabilization of the insect population (Monro, 1967; Osmond and Monro, 1981).

Although more research is needed on the bionomics of these weevils, our findings can be of interest in relation to the distribution pattern of *S. hermonthica* for future conservation and/or augmentation programs of *Smicronyx* adults. Before

implementing any biological control program, assessment of the effectiveness of the natural enemy should be done.

4.4.2. OPTIMUM SAMPLE SIZE DETERMINATION

When Smicronyx population averages ca. six per sampling unit, a sample size of 20 units provided a 25% precision level whereas 124 units provided a 10% precision level. The relationship between sample size and mean number of Smicronyx adults for precision levels ranging from 10 to 30% is shown in Fig. 12.

Fig. 12 is a tool to determine the level of precision according to the mean number of *Smicronyx* adults. Before undertaking a sampling program, a few preliminary samples should be taken to get appropriate density estimates. For instance, based on a mean number of 6 *Smicronyx* adults, the sample size is 14 for 30%, 20 for 25%, 32 for 20%, 56 for 15% and 127 for 10% precision level. A 10% precision would be difficult to achieve for most *Sm. guineanus* and *Sm. umbrinus* sampling program without collecting large numbers of samples. However, the 25 and 20% precision level probably could be achieved most of the time with a sample number of 20 and 32 respectively.

One attribute of OSS is that, at fixed precision levels D, required sample size decreases with increasing population density (Karandinos, 1976) / Another attribute of OSS is that, at a given density, required sample size increases as dispersion patterns become more aggregated (Karandinos, 1976).

4.4.3. LARVAL VERTICAL DISTRIBUTION

Our results indicated that *Smicronyx* larvae make 93.22% of galls in the upper stratum, 6.73% in the central and 0.05% in the lower stratum of the witchweed (Fig. 13). There was a statistically significant difference among the strata (p < 0.001, n = 1350) and all were significantly different at this level according to the mean separation procedure.

These results reflect an overall preference for Striga inflorescence by Smicronyx since the majority of the larvae were inside galls of the upper stratum of the witchweed. The main damage to Striga is caused by the larvae which destroy large numbers of seeds.

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Table 1. Statistics for Iwao's patchiness assessing dispersion patterns of Univac counts for *Smicronyx guineanus* and *Sm. umbrinus* in Burkina Faso.

Year	n•	Intercept			Slope	
		α	t	p**	β	t
1991	48	0.364	0.723	0.473	1.409	2.999
1992	61	-0.157	-0.288	0.774	1.258	4.639
1993	14	-0.882	-0.683	0.508	1.434	2.38
Pooled data	129	0.365	1.177	0.241	1.238	5.179

** Probability of type I error associated with t test of a (H₀: $\alpha = 0$, H₁: $\alpha \neq 0$). * Value of β significantly greater than 1.0 (p<0.05).

I value of β significantly greater than 1.0 (p<0.01).

Figure 11. Regression of mean crowding (\tilde{m}) on mean density $(\bar{\chi})$ of Smicronyx guineanus and Sm. umbrinus adults in 1991 (A), 1992 (B), 1993 (C) and pooled data (D).



Figure 12. Optimum sample size to provide precision levels (D) from 10 to 30% from 2 to 30 *Smicronyx* adults per Univac sampling unit.



Mean number of Smicronyx counts

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Figure 13. Proportion of *Smicronyx* larvae found in galls per *Striga* stratum.

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CONNECTING STATEMENT

In biological control theory, positive density-dependent reaction of a beneficial agent to the population size of its host has been considered a key element (May and Hassell, 1988). Basic research on the biology of a natural enemy or of the host or prey insect can be the key to success in any given project. To a large extent biological control is dependent on ecological research (DeBach, 1974). In Chapter 5 the dispersion patterns of S. hermonthica was determined. It is essential to know whether the dispersion patterns of Sm. quineanus and Sm. umbrinus match that of S. hermonthica since usually, a parasite follows the spatial distribution of its host. An understanding of dispersion is vital in the analysis of host-parasite relationships (Crofton, 1971; Hassell and May 1974; Anderson, 1974). Taylor's power law for determination of dispersion patterns of S. hermonthica have been used and provided a better fit to the data than did Iwao's patchiness regression according to the values of the coefficients of determination (r^2) .

CHAPTER 5

DISPERSION PATTERN AND OPTIMUM SAMPLE SIZE FOR STRIGA HERMONTHICA (DEL.) BENTH. (SCROPHULARIACEAE) IN FARMERS' FIELDS

Submitted to Weed Research in September 1994.

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Authors: Doulaye TRAORÉ, Charles VINCENT, and Robin K. STEWART.

5.1. ABSTRACT

Field experiments were conducted in 1992 and 1993 at Kaya in Burkina Faso, West Africa, in sorghum (Sorghum bicolor (L.) Moench) and pearl millet (Pennisetum americanum (L.) K. Schum. (syn. P. typhoides (Burm.) Stapf and Hubb.) fields. S. hermonthica plants were sampled every week using a sample unit of one square metre, starting two weeks after the emergence of first shoots, to assess the dispersion patterns and the optimum sample size. Plants of S. hermonthica were aggregated. Sample sizes of 20 and 120 sample units provided a 25 and 10% precision level respectively at a density of 33 Striga shoots per square metre. A chart was designed which could be useful for agronomists, extension officers and weed scientists for determining the level of precision attainable at various densities of Striga shoots for any sampling and monitoring program.

5.2. INTRODUCTION

The genus Striga, generally known as witchweeds, is currently thought to include 35 species (Raynal-Roques, 1991). At least 11 species are known to be economically important including S. hermonthica, S. asiatica, S. gesnerioides, S. densiflora, S. euphrasioides, S. aspera and S. forbesii (in decreasing importance). Thirty-three Striga species are known to occur in Africa (Raynal-Roques, 1991) and a new species has recently been described (Aweke, 1992). Striga asiatica (L.) Kuntze and S. hermonthica (Del.) Benth. attack maize (Zea mays L.), sorghum (Sorghum bicolor (L.) Moench, pearl millet (Pennisetum americanum (L.) Leeke), up-land rice (Oryza sativa L.), sugar cane (Saccharum officinarum L.) and fonio (Digitaria exilis Stapf.). Striga gesnerioides (Willd.) Vatke parasitizes cowpeas (Vigna unguiculata (L.) Walp.), tobacco (Nicotiana tabacum L.) and groundnuts (Arachis hypogaea L.) with economic reduction (Mbwaga, 1990; Hartman, 1991).

Socio-economic implications of *Striga* infestations are the migration of peasant families to *Striga*-free areas, shifting cultivation, farm abandonment or change of cropping pattern (Riches et al., 1986). *Striga hermonthica* has been is the direct cause of the depopulation of potentially useful agricultural land in Tanzania (Mbwaga, 1990), and is also an important cause of food shortages in some years (Doggett, 1965). Striga hermonthica is the most important weed species of the genus in Burkina Faso (Ouédraogo, 1986; Combari, 1987; Nikièma, 1992). Both farmers' and research fields are heavily infested with Striga, resulting in the abandonment of many farms (Ouédraogo, 1986). Yield losses due to Striga are estimated to be in the range of 20-35% in the Gambia (Carson, 1986), 10-91% in Nigeria (Parkinson, 1985), 30-90% in Togo (Lagoke et al., 1991), 15-20% in Cameroon (Lagoke et al., 1991), 25-100% in Mali (Konaté, 1986), 70-100% in Sudan (Hamdoun & Babiker, 1986) and 60-100% in Burkina Faso (Nikièma, 1992).

Control methods to reduce *Striga* infestation include heavy application of nitrogen fertilizer, use of trap crops and chemical stimulants to abort seed germination, hoeing and hand pulling, herbicide application and the use of resistant or tolerant crop varieties. All these, including the most widely practiced hoe weeding, have a serious limitation in reluctance of farmers to accept them, for both biological and socioeconomic reasons (Lagoke *et al.*, 1991).

The geographical distribution of *S. asiatica, S. gesnerioides* and *S. hermonthica* is well known. They have been found in Africa, Australia, Tropical Asia, India, North America, the Arabian Peninsula and parts of western China and Indonesia (Musselman *et al.*, 1991).
Spatial distribution is one of the most characteristic ecological properties of species. Knowledge of the dispersion patterns of *S. hermonthica* is desirable for extensive surveys or implementation of sound IPM programs. The design of a sound sampling program requires the knowledge of the underlying spatial distribution (Taylor, 1984). To achieve that, the assessment of the smallest numbers of samples that need to be taken for reliable density estimates is necessary, as also known as the optimum sample size (OSS) (Karandinos, 1976).

In spite of its economic importance, there are presently no published sampling programs that would allow an objective evaluation of *S. hermonthica* populations. We conducted our investigation in farmers' fields instead of research station plots to have a more typical picture of farming conditions. The objectives of this study were (1) to evaluate spatial distribution patterns of *S. hermonthica*, and (2) to use this information to determine the relationship between density and OSS for fixed precision levels to be used for reliable density estimates.

5.3. MATERIALS AND METHODS

The experiments were conducted from 4 September to 28 October 1992 and from 8 September to 4 November 1993 at Kaya (13°04'N, 1°40'W) in Burkina Faso, West Africa. Sampling was done at weekly intervals in two sorghum fields and one pearl millet field in 1992 and 1993.

The sampling unit was a 1 by 1 m quadrat (Oosting, 1956). In each field, ten quadrats were placed randomly by throwing a 1 m² metal frame, making a total of 10 m² in each field. The total number of *Striga* shoots per quadrat was counted visually. On eight occasions in 1992 and nine in 1993, 320 samples were taken randomly from three farmers' fields ranging in size from 2.17 to 3.60 ha.

5.3.1. STATISTICAL ANALYSIS

Dispersion patterns of *S. hermonthica* were described using Taylor's power law. Taylor's power law relates the variance S^2 to the mean \overline{X} by the formula $S^2 = a\overline{X}^b$ (Taylor, 1961, 1965, 1984; Taylor *et al.*, 1978). *a* is a sampling factor that depends on the size of the sampling unit and has no ecological significance. *b* represents an intrinsic property of the species that describe the degree of aggregation. The slope coefficient (*b*) = 1 indicates a random pattern, (*b*) < 1 regular and (*b*) > 1 aggregated patterns. A log-linear regression model, $\{\log_{10}(s^2) = \log_{10}(a) + (b)\log_{10}(\bar{\mathcal{I}})\}$ was used to calculate least-square estimates of *a* and *b* (StatView, version 4.0 for the Macintosh Computer, Abacus Concepts Inc., 1992). A t-test was performed to determine whether the slope was significantly different from 1.

5.3.2. OPTIMUM SAMPLE SIZE DETERMINATION

The number of sampling units necessary to estimate the mean with fixed precision level is calculated as (Elliott & Kieckhefer 1986, $Pe\overline{N}a$ & Duncan 1992):

$$n = \frac{a\overline{x}^{(b-2)}}{D^2}$$

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Where *n* is the sample size, *a* and *b* are coefficients obtained from Taylor's power law regression. The precision level was defined as $D = S\vec{I}/\vec{X}$, where $S\vec{x}$ is the standard error of \vec{X} . Precision levels (D) of 0.10 (10%), 0.15 (15%) and 0.25 (25%) are usually acceptable for intensive and extensive sampling, and may satisfy requirements for different types of field studies or monitoring (Southwood, 1978; Ekbom, 1985; Elliott & Kieckhefer, 1986; Ward *et al.*, 1986). We calculated a range of D from 10 to 30% (by increment of 5) to provide a sampling tool for future density estimates of *S. hermonthica*.

5.4. RESULTS AND DISCUSSION

5.4.1. REGRESSION ANALYSES

Data from both years were combined for the dispersion analyses after slope tests and the regression $\log_{10}(s^2) = 0.44$ + 1.47 $\log_{10}\overline{I}$ were obtained (Fig. 14). The slope was significantly (p < 0.05) greater than 1. The observed variation of combined shoot numbers of *S. hermonthica* indicates a clumped distribution within the fields.

It is likely that the bulk of dust like seeds of *S*. hermonthica are scattered in the vicinity of the stem mother. Also wind speed is very low within sorghum and millet fields. A contagious, rather than random, distribution can be expected for *S*. hermonthica because one plant of the witchweed is capable of producing thousands of seeds (Doggett, 1965). Therefore, habitat heterogeneity of scattered weedy areas is more likely to occur.

5.4.2. OPTIMUM SAMPLE SIZE DETERMINATION

We found a density of *Striga* shoots ranging from 6 to 108 per square metre. The relationship between sample size and mean number of *Striga* shoots is shown in Fig. 15. for precision levels ranging from 10 to 30%. To provide respectively a 25 and 10% precision level at a mean density of 33 specimens per square metre, a sample size of 20 and 120 quadrats is necessary. One attribute of OSS is that, at fixed precision levels D, sample size decreases with increasing population density (Karandinos, 1976). Another attribute of OSS is that, at a given density, required sample size increases as dispersion patterns become more aggregated (Karandinos, 1976).

Fig. 15 is a tool for agronomists, extension officers and weed scientists to determine the level of precision according to the mean number of *Striga* shoots. Before undertaking a sampling program, a few preliminary samples should be taken to get appropriate density estimates. For instance, based on an approximate density of 30 *Striga* shoots per square metre, the sample number required is 14 for a 30%, 20 for 25%, 31 for 20%, 56 for 15% and 126 for 10% precision level. A 10% precision would be difficult to achieve for most *Striga* sampling program without collecting large numbers of samples. However, the 25 and 20% precision level probably could be achieved most of the time with a sample number of 20 and 32 respectively.

The size of the sample unit has a considerable effect on the variance of the data obtained when the plants are not distributed at random (Kershaw, 1964). If there is a tendency for individuals to be grouped together, the measure of the variance of the data is at a maximum when the sample unit size is approximately equal to the mean area of the groups of individuals. Since it is usually impossible to pre-determine the scale of this pattern and since such patterns are often

repeated on larger scales, the size of sample unit has to be chosen quite arbitrarily. The most suitable sample unit on theoretical grounds being the smallest possible, based on the type of vegetation and the practicability of the enumeration of such sample unit. The square metre sample unit or larger proved to be satisfactory for *Striga* density estimates.

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Figure 15. Optimum sample size to provide precision levels from 10 to 30% for densities of 10 to 120 Striga shoots per square metre quadrat.

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CONNECTING STATEMENT

Among the characteristics that enable insects to have widespread ranges and occupy a multitude of habitats is their ability to anticipate adverse seasonal conditions in order to synchronize their life cycles to the seasonal character of the environment (Tauber et al., 1984). The ecological manifestations of these functions include dormancy, drought and various forms of migration. Dormancy is a general term that refers to a seasonally recurring period (phenophase) in the life cycle of a plant or animal during which growth, development and reproduction are suppressed. It includes either diapause or quiescence (or both) provided they occur on a regular seasonal basis (Huffaker, 1984). Reports of diapause occurring in tropical insects are rare (Nishida, 1955) though it is probably a common phenomenon in those tropical areas that have seasons during which suitable host plants are absent. Masaki (1980) reviewed summer diapause of the temperate zone which is much akin to dry season diapause of the tropical environment. He concluded that summer diapause is a common occurrence and has been reported to occur in over 180 insect species. Rainfall pattern is the most conspicious aspect of tropical seasons. Onset of the rains is frequently linked to diapause termination (Denlinger, 1986). An appreciation of diapause is essential for conservation and/or augmentation of Smicronyx populations. In Chapter 6, the effect of artificial wetting simulating rainfall was assessed.

CHAPTER 6

EFFECT OF PRECIPITATION ON EMERGENCE OF SMICRONYX GUINEANUS VOSS AND SM. UMBRINUS HUSTACHE (COLEOPTERA: CURCULIONIDAE) ADULTS AND SOIL VERTICAL DISTRIBUTION OF PUPAE

Submitted to Tropical Pest Management in January 1995. Authors: Doulaye TRAORÉ, Charles VINCENT, and Robin K. STEWART.

6.1. ABSTRACT

A three-year study was conducted to evaluate the effect of rainfall on pupae of Sm. guineanus Voss and Sm. umbrinus Hustache and their vertical distribution in the soil. Field collection of data was conducted in 1990, 1991 and 1993 in sorghum and millet fields infested by S. hermonthica at Kaya and Ouahigouya (Burkina Faso, West Africa). In 1993, experiments were conducted in an insectary with the use of simulated rainfall. Ten, 20, 30, 40, and 50 mm of rainfall were simulated and the effect on the pupal emergence mentioned. Each of the six levels of the factor "rainfall" was tested with pieces of Striga flower, stem and no Striga present. A highly significant difference was observed among rainfall heights, indicating that the optimum rainfall for Smicronyx adult emergence ranged from 30 to 40 mm. No interaction was found between rainfall and Striga. To assess the vertical distribution of Smicronyx pupae in soil, five field quadrats were collected at Kaya and Ouahigouya respectively in October 1991, 1992 and 1993. Four vertical layers, 0-5, 5-10, 10-15, and 15-20 cm, were extracted separately and 0-5 and 5-10 cm layers showed significantly higher percentages of Smicronyx pupae in 1991 (63.2%) and 1993 (58.9%).

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6.2. INTRODUCTION

Striga species are of economic importance in 59 countries (Sauerborn, 1991), mostly in West and East Africa as well as Asia. According to Mboob (1989) Striga is present in more than 40% of the arable land south of the Sahara, and information on the intensity and loss situation is available from six West African countries (Sauerborn, 1991). Overall, the grain production in Africa is endangered over an area of 44 million ha which is equal to about 3.2% of the arable land of the world. The loss of yield, caused by the infestation amounts to about 4.1 million t of grain. The loss of revenues from corn, pearl millet and sorghum due to the parasite infection could total 2.9 billion \$US (Sauerborn, 1991). Mboob (1986) estimated the overall loss of revenues due to Striga in Africa to be 7 billion \$US.

Smicronyx spp. offer the greatest potential for biocontrol of Striga (Parker and Riches, 1993). Species of Smicronyx on Striga are usually host specific and the timing of the life cycle and the number of generations per year depend on the life cycle of the host plant (Smith *et al.*, 1993). Only one attempt of classical biological control has been made so far against Striga. Sm. albovariegatus Faust from India was released on S. hermonthica in Ethiopia at Humera on the Setit River close to the Sudanese border (Greathead, 1984). The main damage to *Striga* seed capsule is caused by the larvae. Galling of fruits of *S. hermonthica* by *Smicronyx* spp. in West Africa is often very heavy, and seed production of the weed may be reduced by 80% or more (Parker and Riches, 1993). The larvae drop to the soil and bury themselves to a depth of 1-15 cm. They made earthen pupal cells but do not pupate until much later. The pupae enter into diapause from October to July (Traoré, 1995) until the emergence of *Striga* plants the following rainy season when the adults emerge in late August. The weevils are univoltine in Burkina Faso (Traoré, 1995).

Diapause is frequently viewed as a developmental strategy unique to insects of temperate zones. Winter in temperate zones presents a conspicuous obstacle, and a wealth of studies examine diapause as an adaptation to circumvent this inimical period. Masaki (1980) reviewed summer diapause of the temperate zone which is much akin to dry season diapause of the tropical environment. He concluded that summer diapause is a common occurrence and has been reported to occur in over 180 insect species. Diapause occurs during the immobile stages, egg and pupa, in 37% of the tropical species (Denlinger, 1986).

Although there are many definitions of diapause, Denlinger (1986) used the term "diapause" to refer to an arrest in development that occurs at a specific stage. Egg, larval, pupal, and adult diapause is well documented, but for most species diapause can be expressed in only one stage of the life cycle. Diapause is programmed in advance of the development arrest and thus differs from a simple quiescence that is an immediate response to adverse conditions. For some tropical species the information available is too limited to allow adequate distinction between diapause and quiescence, and Denlinger (1986) used the more general term of "dormancy" to include both possibilities. Tropical diapause frequently encompasses significant portions of both dry and rainy season though the terms aestivation (dry season diapause) and pluviation (wet season diapause) may falsely connote that the environmental requirement and the special physiological mechanism have been identified.

Limited experimentation has demonstrated roles of photoperiod, temperature, rainfall, nutrition, and airborne chemicals on diapause breaking (Denlinger, 1986), but, the environmental cues of tropical diapause have been identified for very few species. Although dry-season diapause is very common, there is little evidence to suggest that lack of rainfall or decrease in relative humidity provides cues responsible for diapause induction. Rainfall pattern is the most conspicuous aspect of tropical seasons. Onset of the rains, however, is frequently linked to diapause termination.

An appreciation of diapause is essential for an understanding of the temporal distribution of tropical insects and for developing effective strategies of insect management.

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This study was undertaken to find out whether the emergence of Sm. guineanus and Sm. umbrinus adults is triggered by rainfall alone or by a combination of rainfall and the presence of Striga and whether the weevils enter into diapause or simply are quiescent during their dormancy phase. Finally, we investigated the position of the weevil pupae in the soil for better understanding on the way to store them for biocontrol purposes.

6.3. MATERIALS AND METHODS

The experiments were done from October to December 1990, 1991 and 1993 at Ouagadougou (12°20'N, 1°40'W), Kaya (13°04'N, 1°40'W) and Ouahigouya (13°31'N, 2°20'W) in Burkina Faso, West Africa.

6.3.1. BREAKING OF DORMANCY

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Thirty wooder containers (2 X 1 X 0.30 m), filled with soil collected from fields at Kaya were transferred to the laboratory and kept at ambient temperature. In 1990 and 1991, S. hermonthica plants bearing fruit galls were collected and deposited in 10 containers in each year until they dried out. Approximately six months later, the soil was sieved to collect Smicronyx pupae in their earthen cells whenever there were not broken. The pupie collected were then kept in the laboratory, inside six 3.8 1 bottles, filled with 2 1 of soil and closed with a nylon screen (8 mesh/cm) to allow ventilation.

In an insectary, 1 l plastic bottle, cut off at its upper one quarter to obtain a wide mouth, was filled with soil up to one third of its capacity. The top was covered with fine muslin netting and 10 holes were made in the bottom. Ten pupae were buried at ca. 3 cm deep in each of 90 bottles. A small plastic container (25 ml) with a piece of cotton-wool was deposited onto the soil, inside each bottle and moistened to saturation

as necessary to obtain a relative humidity close to ambient (70-80% R.H.). In 1993, ten *Striga* fruit galls without larva exiting holes were deposited in each bottle. The larvae emerged from the galls and buried themselves in the soil.

Rainfall was simulated by using a watering-can held at ca. 50 cm above every bottle and an electronic rain-gauge (RAIN-O-MATIC[®], Bekhøi International Trading, Denmark). By trial and error, we determined that ca. 1 sec. of artificial rainfall from a watering-can at ca. 50 cm height corresponded to 1 mm of rainfall. The 10, 20, 30, 40 and 50 mm of rainfall were simulated by 10, 20, 30, 40, and 50 sec. of watering respectively. The simulations were done on 4 October for the 1990 and 1991 pupae and 23 November 1993 for the 1993 pupae. After the treatments, the bottles were checked every day until no emergence of adults was recorded for four consecutive weeks. Then, all *Smicronyx* pupae (living or dead) and adults were extracted from the soil manually and their number recorded. The extraction was done on 2 November for the 1990 and 1991 batches and on 27 December 1993.

A randomized block design was set up with a 6 X 3 (rainfall X Striga) factorial arrangement. Each of the six levels of the factor "rainfall" (including the control) was assigned a piece of Striga flower, stem and no Striga at all. Each block, consisting of 18 bottles, was replicated five times. A total of 900 Smicronyx pupae was used every year. The 1992 batch was not included in the analysis because of shortage of pupae. Contingency tables were made up for 1991 and 1993 and the percentage of *Smicronyx* emergence was recorded accordingly. Analysis of variance (ANOVA) using StatView (Version 4.0 for the Macintosh Computer, Abacus Concepts Inc., 1992) and the Scheffe's mean separation procedure (p < 0.05) were performed on the different levels of rainfall.

6.3.2. PUPAL VERTICAL DISTRIBUTION IN THE SOIL

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After harvest in October 1991, 1992 and 1993, one field was chosen at Kaya and Ouahigouya. In each field, five plots of 0.25 X 0.25 m section were dug to 0.20 m deep. Each plot was subdivided into four layers, 0-5, 5-10, 10-15, and 15-20 cm, which were extracted separately. All the samples were brought to Ouagadougou and sieved to collect and record the number of *Smicronyx* pupae and pupal cells.

Contingency tables were made up to determine the percentage of *Smicronyx* pupae at the four different soil layers. Analysis of variance using StatView (Version 4.0 for the Macintosh Computer, Abacus Concepts Inc., 1992) and the Scheffe's mean separation procedure (p < 0.05) were performed. The 1992 data were discarded due to the paucity of *Smicronyx* pupae collected.

6.4. RESULTS AND DISCUSSION

6.4.1. BREAKING OF DORMANCY

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Emergence of Smicronyx adults was observed 10 days after watering for 1991 and 1993 batches. There was no emergence from the 1990 pupae from 4 October to 2 November 1993, suggesting that the weevil pupae could have up to two year life expectancy. This could be valuable information for the storage of Smicronyx pupae for biocontrol purposes. Although the diapausing stage can be prolonged to more than one year, there is a limit beyond which a further normal development can be achieved. This period could range from 12 to 24 months. van Dinther (1961) obtained similar results with the white rice borer, Rupela albinella (Cr.), in Surinam. There was a highly significant difference among the rainfall heights (p < 0.001, n = 900) for the 1991 batch.

An optimum of 40 mm rainfall was required to allow *Smicronyx* adult emergence (35.29%; Fig. 16A). In 1993, there was a highly significant difference among the rainfall levels (p < 0.013, n = 900) and an optimum rainfall of 30 mm was required to allow 31.1% adult emergence (Fig. 16B). On 23 November 1993, 24.4% of the 1993 batch had emerged as *Smicronyx* adults after 30 mm of precipitation. Six hundred eight out of 900 pupae did not undergo further development suggesting that *Smicronyx* entered into diapause but not into quiescence.

In any type of life cycle, the dormant phase more or less overlaps with the warmer part of the year (Masaki, 1980). This is because diapause is induced by a physiclogical process while insects are growing (Andrewartha, 1952; Danilevsky, 1961; Lees, 1955). In most cases, diapause appears to have two phases (Beck, 1967): an initial phase in which considerable diapause development occurs, and a second phase that is somewhat static until the terminating stimulus occurs. Diapause often begins long before the advent of the dry season. Onset of the rains, however, is frequently linked to diapause termination (Denlinger, 1986). Our results are similar to those showing that rainfall or artificial wetting stimulates pupation in diapausing larvae (Squire, 1939; Kevan, 1944; van Dinther, 1961; Usua, 1970); Geering, 1953; Coutin and Harris, 1968; Bowden, 1976; Lamborn, 1938; Greathead, 1958; Hynes, 1947). Diapause in the pupae of ethmiid moths is broken in response to sporadic rainfall in desert situations (Powell, 1974). In sahelian zones, arrival of the rains acts as a "releaser" that triggers further development of the diapausing stage of Smicronyx, or acts as the terminating stimulus, resulting in adult emergence. This type of reaction, in which rainfall triggers the final phase of development, may be widespread and could account for the rapid increase in insect numbers that normally follows onset of the rainy season in tropical area.

No significant interaction was found between the different parts of *Striga* plant (flowers and stems) and rainfall for 1991 and 1993 batches (p = 0.964 and 0.488). Presence or absence of food is rarely a cue for diapause induction or termination (Denlinger, 1986).

6.4.2. PUPAL VERTICAL DISTRIBUTION

Our findings for 1991 and 1993 indicate a highly significant difference (p < 0.013, n = 80) among soil layers (Fig. 17). Accounting for 58.9% of *Smicronyx* pupae in soil in 1991, the 5-10 cm layer gave a significantly higher percentage, whereas the of 0-5 cm layer was significantly higher (63.2%) in 1993. In 1991, 30.5% of the pupae were located in the 10-20 cm layers compared to 5.3% in 1993.

The diapausing larvae and pupae of Smicronyx are the best stages to manipulate for conservation and/or augmentation for biological control of Striga. However, care must be taken in Smicronyx pupae storage in order to locate most of them in soil layer from 5 to 10 cm deep. This has to be done in natural conditions to be close to the temperature, relative humidity and darkness accounting for the maintenance and termination of diapause.

In conclusion: (1) Although the adult weevils emerged at all rainfall treatments except for the control, 10 and 20 mm of artificial rainfall were not significantly different from 0 mm. The amount of precipitation that allowed the maximum of *Smicronyx* adults emergence ranged from 30 to 40 mm. These treatments correspond with the required precipitation to start sowing sorghum and millet in Burkina Faso. This precipitation level, known as "useful precipitation", varies from 20 to 30 mm (Sivakumar and Gnoumou, 1987). At 50 mm of rainfall, there was not a higher emergence than 30 and 40 mm. (2) The breaking of dormancy caused by artificial rainfall is efficient for pupae which entered diapause between one and three years probably after they enter into diapause in soil. (3) The storage of *Smicronyx* pupae is best done in soil from 5 to 10 cm deep.

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Figure 16. Percentage of Smicronyx adult emergence following artificial rainfall on pupae collected in A) 1991 and B) 1993. Above columns, similar letters indicated no significant difference (Scheffe's test, $\alpha = 0.05$) among treatments.

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Figure 17. Soil vertical distribution of *Smicronyx* pupae in fields, in 1991 and 1993. Above columns, (S) stands for significant difference and (NS) indicates no significant difference (Scheffe's test, $\alpha = 0.05$) among treatments for same year.

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CONNECTING STATEMENT

Smicronyx spp. have the greatest interest for biological control for Striga (Parker and Riches, 1993). Only one attempt of classical biological control has been made so far against Striga. Sm. albovariegatus Faust from India was released on S. hermonthica in Ethiopia but did not established (Greathead, 1984). Augmentation and/or conservation of Sm. guineanus and Sm. umbrinus as part of an integrated control strategy of Striga, require an adequate understanding of the interaction of the weevils and the witchweed. Chapter 7 deals with some of the important information which include: the synchrony and association of Smicronyx and Striga which are essential in assessing the potential of the weevils as biological control agents of Striga. Galling percentage of S. hermonthica induced by Sm. guineanus and Sm. umbrinus was also determined and a search for alternate hosts was carried out.

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CHAPTER 7

ASSOCIATION AND SYNCHRONY OF SMICRONYX GUINEANUS VOSS, SM. UMBRINUS HUSTACHE (COLEOPTERA: CURCULIONIDAE) AND THE PARASITIC WEED STRIGA HERMONTHICA (DEL.) BENTH. (SCROPHULARIACEAE)

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7.1. ABSTRACT

Field experiments were conducted in 1992 and 1993 at Kaya, Burkina Faso, West Africa, in fields of sorghum (Sorghum bicolor (L.) Moench and pearl millet (Pennisetum americanum (L.) K. Schum, (syn. P. typhoides (Burm.) Stapf and Hubb.). S. hermonthica was sampled weekly using a square meter metal frame. The sample size for each field was ten quadrats making a total of 10 m^2 in each field. Concurrently, adult populations of Sm. guineanus Voss and Sm. umbrinus Hustache were sampled using a Univac portable suction sampler to assess the synchrony of Smicronyx with Striga. Sampling of adult weevils was done weekly by placing the 60 mm diameter suction cone on a Striga plant until it was about 5 cm above the ground. The cone was left in position for five seconds. Ten suctions constituted a sample unit. Chi-square tests for independence of the populations of Smicronyx and Striga indicate a good synchrony of the active stages of the life-cycle of the weevils with the period of occurrence of the witchweed.

A 0.5 by 0.5m metal frame was thrown ten times in each field and a Univac portable suction sampler was used to determine the degree of association between *Smicronyx* and *Striga*. There was a positive association between the weevil and the witchweed.

The percentage of *Striga* plants bearing galls caused by *Smicronyx* was determined on 39 occasions. The mean range galling percentage was 1-84% and we found galls in every field visited during this investigation (n = 50).

A search for alternate hosts was carried out by sampling weevil adults on weeds surrounding farmers' fields. No Smicronyx adult was caught on these weeds befc.e the emergence of volunteer Striga plants.

7.2. INTRODUCTION

Parasitic weeds threaten the lives of over 100 million people in Africa (Lagoke *et al.*, 1991) by land abandonment. Two-thirds of the 73 million hectares devoted to cereal crop production in Africa is seriously affected. The genus *Striga*, generally known as witchweeds, is currently thought to include 35 species (Raynal-Roques, 1991). Thirty-three *Striga* species are known to occur in Africa. *Striga hermonthica* (Del.) Benth. (Scrophulariaceae) is the most widely distributed witchweed species of Africa. A conservative estimate of crop losses due to *Striga* spp. in Africa is 40 percent of crop yield, representing an annual loss of cereals worth ranging from US \$ 2.9 to 7 billion (Mboob, 1986; Sauerborn, 1991).

The socio-economic implications of *Striga* include the migration of peasant families to *Striga*-free areas, shifting cultivation, farm abandonment or change of cropping pattern (Riches *et al.*, 1986). *Striga hermonthica* is the most important weed species of the genus in Burkina Faso (Ouédraogo, 1986; Combari, 1987; Nikièma, 1992). It is now well recognized that no single method of control can solve the problem (Ogborn, 1984; Stewart, 1990; Parker and Riches, 1993).

The natural enemies of *Striga* spp. have received more attention in recent years because of the successes achieved in the biological control of other weeds. Various insects which

feed on Striga have been described (Murthy and Rao, 1949; Uttaman. 1949; Agarwala and Maquvi, 1952; Khan and Murthy, 1955; Williams and Caswell, 1959; Murthy 1959; 1960; Davidson, 1963; Rao, 1965; Sankaran and Rao, 1966; Sankaran, 1970, 1973; Greathead and Milner, 1971; Rao and Sankaran, 1974; Boonnitee, 1981; Perkins, 1981). Although no study has yet been done on the bionomics of *Smicronyx* spp., they have been cited by several authors as potential biocontrol agents of *S. hermonthica* (Khan and Murthy, 1955; Williams and Caswell, 1959; Greathead and Milner, 1971; Girling et al., 1979; Perkins, 1981; Bashir and Musselman, 1984; Greathead, 1984; Markham, 1985; Bashir, 1987; Traoré et al., 1990; 1991; Smith et al., 1993; Parker and Riches, 1993). However, there is a lack of data concerning the potential of these weevils as biocontrol agents.

According to Greathead and Milner (1971), these gallforming weevils were first reported attacking *Striga* spp. by Khan and Murthy (1955) who found *Sm. albovariegatus* Faust. associated with *S. asiatica*, *S. angustifolia*, and *S. densiflora* in India. In Africa Williams and Caswell (1959) first reported a *Smicronyx* sp. from *Striga* sp. in Nigeria. *Smicronyx guineanus* eggs have been found in the ovary of *S. hermonthica* flowers in Burkina Faso (Traoré, 1995). On hatching, the larvae excavate a small cavity in the surrounding tissues of young seed pods, which swell up and produce galls enlarging as the larvae feed inside them. Fully developed larvae emerge from the galls, burrow into the soil and pupate ir small earthen cells. The larvae destroy large numbers of ovules in the seed capsule (Paré, 1993). Diapausing larvae remain in the soil during the dry season. A galled capsule does not produce seeds because of failure of seed set due to the transformation of the ovary into a gall by the feeding larva. Thus *Sm. guineanus* and *Sm. umbrinus* could be effective biocontrol agents, reducing seed set and therefore the *S. hermonthica* seed bank. Galling of fruits of *S. hermonthica* by *Smicronyx* spp. in West Africa is often very heavy, and seed production of the weed may be reduced by more than 80% (Parker and Riches, 1993).

The understanding of the association between Smicronyx and Striga is essential to assess their potential as biological control agents of the witchweed. No study has yet been done on the synchrony and association of Smicronyx and Striga. Galling percentage of S. hermonthica induced by Smicronyx has not been estimated in West Africa. Our investigations address these issues.

7.3. MATERIALS AND METHODS

Experiments were carried out from 4 September to 28 October 1992 and from 8 September to 4 November 1993 at Kaya (13°04'N, 1°40'W) in Burkina Faso, West Africa. Sampling was done at weekly intervals in one field of sorghum and one of pearl millet in 1992 and 1993. The fields sampled were pesticide free.

7.3.1. SYNCHRONY OF SMICRONYX ADULTS WITH STRIGA

A Univac portable suction sampler (Burkard Company Ltd., Woodcock Hill Industrial Estate, Rickmansworth Hertfordshire WD3 1PJ, England) was used to sample *Smicronyx* adults. Sampling was done by lowering the 60 mm diameter suction cone onto a *Striga* plant at ca. 5 cm above the ground. The cone was left in position for five seconds. Ten suctions constituted a sample unit. Adult weevils were counted *in situ* or in the laboratory.

The Striga sample unit was a 1 by 1 m quadrat (Oosting, 1956) and the sample size for each field was ten quadrats set up randomly by throwing a square meter metal frame, making a total of 10 m² in each field. On seven occasions in 1992 and nine in 1993, sampling units were taken randomly from farmers' fields ranging in size from 2.17 to 3.60 ha. Sampling was done weekly in 1992 and 1993 and a total of 260 sample units were taken over the two years.

Pot experiments were done in 1992 and 1993 in one field at Kaya. The pots were sown each year with about ten seeds of sorghum, variety E 35-1. Around 100 mg of *S. hermonthica* seeds collected in Kaya the previous year were sown with sorghum seeds (ca. 5 cm deep) in a 25 cm diameter and 26 cm deep pot filled with soil collected at Kaya and Kamboinsé. Twenty pots were set up each week and watered every second day from April to November. When *Striga* plants were flowering, 20 pots were placed in the farmer's fields and replaced as the *Striga* plants senesced and died out. The potted *Striga* plants were brought from Ouagadougou to Kaya (100 km away) on 3 July in 1992 and 22 July in 1993.

7.3.2. Association of Smicronyx with Striga

A 0.5 by 0.5 m metal frame was thrown at random ten times in each millet or sorghum field sampled. Using the Univac portable suction sampler as previously in each quadrat, the weevil adults were collected and counted. Concurrently, the number of *Striga* shoots were recorded. Samples were taken on 5 occasions in 1992 and 8 in 1993 to give a total of 190 quadrats over the two year interval.

7.3.3. PERCENTAGE OF S. HERMONTHICA BEARING GALLS CAUSED

Fifty Striga shoots were randomly collected in 1991, 1992 and 1993 in all fields, and the number of shoots bearing galls

caused by Smicronyx was recorded. On 24 occasions, 50 fields of millet and sorghum were surveyed and 250 Striga shoots were collected randomly. In 1992 and 1993, the gall populations were surveyed throughout the rainy season from September to November. This was done by recording the number of Striga with galls caused by Smicronyx in a 1 X 1 m quadrat in two fields.

7.3.4. ALTERNATE HOSTS OF SM. GUINEANUS AND SM. UMBRINUS

A Univac suction sampler was used to sample Smicronyx spp. on weeds surrounding three fields from 3 July to 14 October 1992 and two fields from 22 July to 4 November 1993. Adult weevils counted were in situ or in the laboratory. The main weed species surrounding these fields were collected and sent to the National Center of Scientific and Technological Research of Burkina Faso for identification.

7.3.5. IDENTIFICATION OF SM. GUINEANUS AND SM. UMBRINUS

Although several Smicronyx species have been observed on Striga spp. (Greathead and Milner, 1971) the taxonomy of Smicronyx in Africa is confused. Specimens of Smicronyx adults collected in 1991 and 1992 were sent to the Systematic Entomology Laboratory, USDA, National Museum of Natural History, Washington, D.C., USA. Other specimens were forwarded to the International Institute of Entomology (C.A.B. International), London, UK., for identification. Voucher specimens of *Sm. guineanus* and *Sm. umbrinus* were deposited at the Systematic Entomology Laboratory, USDA, National Museum of Natural History, Washington, D.C., USA, at the International Institute of Entomology (C.A.B. International), London, UK, at the Lyman Museum, Macdonald Campus of McGill University, Sainte-Anne-de-Bellevue, Québec, Canada and the Biosystematics Research Center (Agriculture Canada), Ottawa, Canada.

7.3.6. STATISTICAL ANALYSIS

Synchrony⁸ Chi-square tests for independence of populations were performed on data for each two consecutive weeks (e.g. weeks 1 and 2, weeks 2 and 3, weeks 3 and 4, etc.) over a period of eight weeks to assess the synchrony of *Smicronyx* and *Striga* based on the total counts of shoots and the flowering *Striga* plants. Data were combined to compute a χ^2 value for 1992 and 1993 (StatView, version 4.0 for the Macintosh Computer, Abacus Concepts Inc., 1992).

Association: The data were tabulated in a contingency form in which the observed numbers of quadrats, containing none, one or both species, were entered in the four cells of the table (Kershaw, 1964; Southwood, 1978). To assess *Smicronyx* and *Striga* association, χ^2 tests were performed for 1992, 1993, and combined data over the study period.

If there is no correlation between the presence of the species, the frequencies will tend to be evenly distributed in

the four cells and the difference, ad-bc, will be so small as to be non-significant. If the relation is associative the cells a and d will be inflated and b and c accordingly depleted, so that the difference will be positive; the reverse will be true if the relation is repulsive. The significance of the relation is tested by a contingency χ^2 test of the form:

$$\chi^{2} = \frac{n\left(\left|ad - bc\right| - \frac{n}{2}\right)^{2}}{(a+b)(c+d)(a+c)(b+d)}$$

with one degree of freedom (df = 1).

The degree of association or repulsion is given by the contingency coefficient (Debauche, 1962):

$$C_{AB} = \sqrt{\frac{\chi^2}{n + \chi^2}}$$

where C_{AB} = coefficient of association between A and B, n = total number of occurrences, and the χ^2 value is obtained as above. Only coefficients extracted from tables of the same kind can be compared because the coefficient is never equal to one but varies according to the kind of table used (Debauche, 1962). In a 2 X 2 table, the coefficient's upper limit is $\sqrt{\frac{1}{2}} = 0.707$.

7.4. RESULTS

Smicronyx umbrinus was identified by Dr. Anderson and the identity of Sm. guineanus was confirmed by Dr. Cox after comparison with types and paratypes from the Museums of Washington, D.C., London, Paris, Munich and Hamburg. Our collections were composed of 94.3% of Sm. guineanus and 5.3% of Sm. umbrinus adults.

Smicronyx and Striga populations were not independent from each other (Table 2 and Fig. 18). The pooled data of 1992 and 1993 gave $\chi^2 = 1238.49$ (df = 15, p < 0.0001) for flowering Striga plants and $\chi^2 = 768$ (df = 15, p < 0.0001) for total Striga shoots respectively. Fig. 19 shows the results of the pot experiments.

There was a positive association and the coefficient of association was 0.30, indicating a good correlation between the presence of weevil and the presence of witchweed (Table 3).

7.4.1. PERCENTAGE OF S. HERMONTHICA BEARING GALLS CAUSED BY SM. GUINEANUS AND SM. UMBRINUS

The mean galling percentage of 1991, 1992 and 1993 was 52%, 24.4% and 10.9% respectively. The range was 28-84% for 1991, 1-52% for 1992 and 5.5-27.2% for 1993. We found galls in every field visited in 1991, 1992 and 1993 (n = 50). The maximum percentage of plants with galls in one field surveyed

in 1992 and 1993 was 10.7 and 27.5% respectively. The peaks of plant galls were observed 4 weeks after the first galls were recorded in the field in 1992 and 5 weeks in 1993 (Fig. 20).

7.4.2. ALTERNATE HOSTS OF SM. GUINEANUS AND SM. UMBRINUS

No Smicronyx adult was caught on weeds surrounding the fields sampled, before the emergence of volunteer Striga plants. The main weed species were collected and identified (Table 4).

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7.5. DISCUSSION

Identification: Sm. umbrinus has been cited as the best insect candidate for biological control of Striga in Africa (Bashir and Musselman, 1984; Markham, 1985; Smith et al., 1993). It occurs in Burkina Faso (Greathead, 1984; Markham, 1985) and in Nigeria (Williams and Caswell, 1959). Sm. guineanus was described in 1956 by E. Voss and has been recorded on Striga in Ethiopia, the Gambia, Mali, Niger, Nigeria, Senegal, Sudan, Uganda and Tanzania (M. Cox, personal communication). Our findings indicate that Sm. guineanus is dominant (94.3%) in areas sampled in Burkina Faso.

Since the taxonomy of *Smicronyx* in Africa is confused (Greathead and Milner, 1971; Markham, 1985), effort must be put on the correct identification of specimens. The Indian species *Sm. albovariegatus* Faust. was released in Ethiopia and in the Sudan in 1974 and 1978 in an attempt to control *S. hermonthica* (Greathead, 1984). The second release was thought to have resulted in establishment, but in 1988 specimens were not recovered. It is now thought that there was confusion with the indigenous, unnamed *Smicronyx* species (Parker and Riches, 1993). Misidentifications underscore the need for accurate identification in successful biological control programs (Herren and Neuenschwander, 1991).

Synchrony: According to the χ^2 tests which were highly significant for 1992, 1993 and combined data, *Striga* and *Smicronyx* populations were found to be dependent. Our results indicate that the active stages of *Sm. guineanus* and *Sm. umbrinus* life-cycle synchronized very closely with the period of occurrence of *S. hermonthica* (Table 2; Fig. 18). Similarly Sankaran and Rao (1966) found that *Sm. albovariegatus* stages synchronized well with the emergence of *S. lutea*, *S. angustifolia* and *S. densiflora* in India. Flowering plants of *Striga* were more closely synchronized with *Smicronyx* adults presence than *Striga* plants without flowers in 1992 and 1993.

The pot experiments showed the emergence of Smicronyx adults 13 days in 1992 and 16 days in 1993 before the emergence of the first Striga plants in peasant fields (Fig. 19). The question arising from this observation is whether the weevil adults emerged two weeks before the appearance of Striga plants. No Smicronyx adults were found on surrounding weeds before the emergence of volunteer Striga plants around the fields. Alternate hosts of S. hermonthica in Nigeria include Pennisetum spp., Andropogon spp. Rottboelia cochinchinensis, Setaria palledifusca, Brachiaria spp., Digitaria spp. and Dactyloctemium aegyptum (Lagoke et al., 1986) but they did not divert the Smicronyx from finding Striga. Some of these plant species are common in Burkina Faso and many belong to the same families as the weeds that surrounded our peasant fields. Such

a finding capacity of *Striga* by *Smicronyx* may involve allelochemicals (kairomones or synomones) which are unknown so far.

Percentage of galls: Bashir and Musselman (1984) reported Sm. umbrinus from western Sudan on S. hermonthica and found that the larvae of the species caused only fruit galls; 42% of the plants contained galls and 52% of the capsules were transformed into galls. None of the galled capsules contained seeds, suggesting total failure of seed production in these fruits. Sm. guineanus is a fruit gall maker like Sm. umbrinus. We observed no stem galls caused by Sm. guineanus during this investigation on S. hermonthica in Burkina Faso. Levels of infestation of S. hermonthica by Sm. guineanus and Sm. umbrinus are variable depending on the growing season. Greathead and Milner (1971) also reported that in East Africa, the incidence of Smicronyx spp. and the level of infestation of Striga were erratic, varying from 10 to 100% with an average of 62.5%. The number of capsules galled per plants seems to depend on the age and size of the plant; large vigorous plants appear to be more heavily galled (Bashir, 1987). Year-to-year variability may be due to seasonal change, affecting directly the insects' activity, or, indirectly, by affecting their hosts (Dewar and Watt, 1992). Timing and abundance of rainfall in Burkina Faso is a key factor for emergence of both Smicronyx and Striga (D. Traoré, unpublished).

Our study demonstrates that there is a good synchrony and a positive association of Sm. guineanus and Sm. umbrinus with S. hermonthica. There are good prospects for augmentation and/or conservation of natural enemies as part of an integrated control strategy of Striga. This requires an adequate understanding of the biology and ecology of these species, together with knowledge about other factors in the ecosystem to fit the procedures in compatible manner in the crops where Striga occurs. In the tropics, a huge potential remains for enhancing the action of native natural enemies in integrated pest management. This will probably be the most promising research area for the future (Greathead, 1991). To do so, basic studies on the biology and bionomics of biocontrol agents are needed and this study contributes to this.

Even though our investigations indicate a possible recommendation for conservation and/or augmentation of *Smicronyx* populations, an assessment of weevil impact on witchweed is necessary. The effectiveness of *Smicronyx* will be known only by recording the number of *Striga* seeds the weevil is capable of destroying. Although no accurate method of counting the dust like seeds of *Striga* is yet available, embryological study of *Striga* might be helpful in addressing this issue. The paraffin method serial sections (15µm) and Heidenhain's iron alun-hematoxylin staining process (Paré, 1993) may be appropriate.

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Table 2. Chi-square analysis for synchrony of Smicronyx and Striga flowering plants and Striga total shoot counts,

A) 1992 and B) 1993.

A) 1992

Smi	cronyx/Striga flowering plants	Smicronyx/Striga shoots
Week combinatio	n χ ²	χ ²
1-2	10.1**	8.4**
2-3	6.4*	154.4**
3-4	24.8**	21.5**
4-5	31.2**	1.4 ^{NS}
5-6	8.6**	6.5*
6-7	50.7**	77.4**
7-8	52.1**	72.4**
8-9	0.3 ^{NS}	2.0 ^{NS}
Combined data	425.8**	521.7**

B) 1993

	Smicronyx/Striga flowering plants		nts Smicronyx/Striga shoots
Week combin	ation	χ²	χ ²
1-2		1.1 ^{NS}	1.2 ^{NS}
2-3		0.9 ^{NS}	50.3**
3-4		10.0**	76.9**
4-5		131.3**	110.8 ^{NS}
5-6		39.9**	41.1*
6-7		90.6**	94.3**
7-8		23.9**	9.1**
8-9		2.2 ^{NS}	1.9 ^{NS}
Combined da	ita	677.2**	399.4**
Probability df = 1 for	v of a gre week to v	eater χ^2 due to char week analysis	ace were:

df = 8 for combined data NS = NO significant difference (p \geq 0.05) * Significantly different (p < 0.05) ** Significantly different (p < 0.01).

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Table 3. Contingency table for association between Smicronyx and Striga, A) 1992 and B) 1993.

A) 1992

		Striga				
		Present	Absent	Total	χ2	C _{AB} †
	Present	70	l	71		
Smicron	yx					
	Absent	7	2	9		
	Total	77	3	80	9.59**	0.33
A) 1993						
	Present	86	0	86		
Smicron	yx					
	Absent	21	3	24		
•	Total	107	3		11.05**	0.30
Combined	<u>data (</u> 199)	2 and 1993)		· <u>1</u> 8.78**	0.30

Probability of a greater χ^2 (df = 1) due to chance were: ** Significantly different (p<0.01). † Coefficient of association (see Materials and Methods).

Table 4. Main weed species collected around two sorghum and

millet fields in 1992 and 1993, in Burkina Faso.

Genus/Species	Family	
Alysicarpus sp.	Fabaceae	
Andropogon gayanus (Kunth.)	Poaceae	
Aristida adocensionis (L.)	Poaceae	
Borreria sp.	Rubiaceae	
Buchnera hispida (BuchHam. ex D. Don)	Scrophulariaceae	
Cassia nigricans (Vahl)	Caesalpiniaceae	
Ceratotheca sesamoides (Endl.)	Pedaliaceae	
Chloris pilosa (Schumach.)	Poaceae	
Corchorus fascicularis (Lam.)	Tiliaceae	
Corchorus tridens (L.)	Tiliaceae	
Cymbopogon schaenanthus (L.) Spiengel	Poaceae	
Eragrostis ciliaris (L.) R.Br.	Poaceae	
Eragrostis tremula (Hoechst ex Stend)	Poaceae	
Hyptis spicigera (Lam.)	Lamiaceae	
Indigofera secundiflora (Poir.)	Fabaceae	
Ipomea coscinosperma (Hochat.ex choisy)	Convolvulaceae	
Ipomea eriocarpa (R.Br.)	Convolvulaceae	
Leucus martinicensis (R.Br.)	Lamiaceae	
Mitracarpus villosus (Sw.) DC.	Rubiaceae	
Monechma ciliatum (Jacq.) Hilne-Redh	Acanthaceae	
Oldenlandia corymbosa (L.)	Rubiaceae	
Pennisetum pedicellatum Trin.	Poaceae	
Schoenfeldia gracilis (Kunth.)	Poaceae	
Sida alba (L.)	Malvaceae	
Triumfeta bartiamia	Tiliaceae	
Waltheria americana (L.)	Sterculiaceae	





Figure 19. Smicronyx adult counts on Striga plants grown in pots (n = 20), at Kaya, Burkina Faso in 1992 (A) and 1993 (B); arrows indicate the first emerging Striga plants in the fields.



Figure 20. Percentage of *Striga* plants bearing galls induced by *Smicronyx* in a peasant field at Kaya, Burkina Faso in 1992 (A) and 1993 (B).


GENERAL DISCUSSION AND CONCLUSIONS

Striga is considered to be the single greatest threat to food production in Africa at this time. Constraints on Striga control research in Africa include shortage of professionally trained personnel, lack of infrastructure for applied research, inherently low yield of major host crops, inadequate knowledge of host-parasite ecological relationships and inadequate knowledge of the impact of cropping systems on Striga persistence (Akobundu, 1991).

Biological suppression of weeds is not new to agriculture, but for Africa it is a new and potentially very important development. In the case of natural suppression of S. hermonthica there seems to be a natural control with various biotic sources. Components of this natural control, Sm. guineanus and Sm. umbrinus have been identified (K. Cardwell, personal communication). Augmentation and/or conservation of Smicronyx spp. have never been tried, though they have been repeatedly recommended during international Striga symposia. At this time, only two papers (Greathead and Milner, 1971; Greathead, 1984) are the backbone of the possibilities of biological control of Striga. Due to the lack of studies on the natural enemies of Striga spp. and no systematic observations on their impact on populations of the host plants, these authors indicated the kinds of insects and pathogens which are likely to be encountered and speculated on ways that they may be exploited alone or as part of an integrated management program of *Striga*. No study has been done so far on the bionomics of *Sm. guineanus* and *Sm. umbrinus*. Considering the lack of research noted by several authors (Cardwell *et al.*, 1991; Riches and Parker, 1993; Smith *et al.*, 1993), this work was consequently initiated to address these issues.

Specific conclusions have been drawn in each chapter of this thesis. In considering the whole study, the main areas investigated form three components. 1) biology of the weevils, 2) spatial distribution of the weevils and the witchweed, and 3) the interaction of *Smicronyx* and *Striga*. They help in assessing the potential of *Sm. guineanus* and *Sm. umbrinus* as natural enemies of *S. hermonthica*.

The life history of Sm. guineanus and Sm. umbrinus was studied in the field and in the laboratory. Under natural field conditions the weevils were found to have one generation a year. The adults emerge in late August and emergence peak was observed in fields in mid-September. They mate and the larvae enter the ovary of Striga inflorescence with a subsequent formation of galls which prevent seed production. The main damage to Striga seed capsule is caused by the larvae. Upon reaching maturity, the larva cut a circular hole through the gall wall and emerged. The larva dropped to the soil and buried itself to a depth of 1-15 cm and pupated. Most pupae were deposited in the upper 5-10 cm of the soil. We observed a well adapted life history of the weevils with the aerial and subterranean stages of the witchweed. The biological meaning of the behavioral time budget of *Sm. guineanus* is as follows: *Smicronyx* adults are more active in daytime. Our results indicate that the weevil adults spent 46.8% of their time on the *Striga* inflorescence (bud, corolla and calyx). The results of observations with respect to the stratification of the plant showed that *Smicronyx* adults spent 85.2% of their time in the upper stratum, reflecting an overall preference for *Striga* inflorescence since the majority of the larvae were inside galls of the upper stratum of the witchweed plant. The weevils were more active in daytime, suggesting that the best period of day to sample these weevils in the field is from 0700 to 1100 or from 1600 to 1800.

Based on dispersion patterns a sampling program was designed to evaluate the number of samples required to estimate the density of Sm. guineanus and Sm. umbrinus adults with a given level of accuracy. An understanding of dispersion is vital in the analysis of host-parasite relationships. An aggregated distribution was observed for both Smicronyx adults and the Striga plants. The tendency for aggregation of Smicronyx adults counts was because of scattered Striga areas which are clumped. The contagious distribution of Smicronyx adults can be accounted for by more green and/or flowering Striga plants in the vicinity of previously attacked plants. Heterogeneity in the "quality" of food plants can lead to a clumped distribution which may be associated with the stabilization of the insect population (Birch 1971, Osmond and Monro 1981, Monro 1967).

A good synchrony and a positive association of Sm. guineanus and Sm. umbrinus with S. hermonthica were observed in this study, indicating that the active stages of the weevil life-cycle synchronized very closely with the period of occurrence of the witchweed. These findings are valuable for future conservation and/or augmentation programs of Smicronyx adults. Effective conservation of established natural enemies is absolutely essential if biological control is to work at all for Striga. The process involves manipulation of the environment to favor natural enemies. Augmentation of parasites or predators to increase their effectiveness involves their direct manipulation either by mass production and periodic colonization (DeBach and Hagen, 1964). The successful implementation of these techniques requires information on the bionomics of the natural enemy and the target.

In view of the present results, there is some hope for conservation or/and augmentation of *Smicronyx* populations in Africa as part of an integrated *Striga* control strategy. Biological control by repeated mass rearing and inundation with insects has been considered impractical due to the perceived

cost of the process (Bashir, 1987). Full scale rearing of natural enemies is a costly process and difficult to transfer to national programs. Nevertheless, natural enemy conservation methods could be developed so that the greatest cost would be the initial training and extension.

When flowering Striga plants are collected, as in recommended hand-weeding practice, there can be a large population of Smicronyx larvae emerging from the Striga plants as they dry. It should be worth considering how these larvae might be preserved rather than destroyed with the Striga plants, so that they are available for re-infesting Striga the following season. This can be done by plowing plots in the same or new fields and leave the galled witchweed plants and remove them as they dry to build up a bank of Smicronyx pupae which will undergo further development to emerge as adults the next growing season.

The integration of this technique to an overall Striga management program requires research to learn what the benefit of the practices in terms of Striga population reduction, and what are the constraints to implementation. A prerequisite to conservation or/and augmentation of Smicronyx in Africa is assessing the detrimental effect of the larvae on Striga seed production. The effectiveness of Smicronyx will be known only by recording the number of Striga seeds the weevils is capable of destroying. Although no accurate method of counting the dust like seeds of *Striga* is yet available, embryological study of *Striga* might be helpful in addressing this issue. The paraffin method serial sections $(15\mu m)$ and Heidenhain's iron alunhematoxylin staining process may be appropriate (Paré, 1993). Further work on life table study and key factor analysis could be necessary to complete the knowledge on *Sm. guineanus* and *Sm. umbrinus* biology.

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APPENDIX 1.

KEY TO ADULT SMICRONYCHINI ASSOCIATED WITH STRIGA HERMONTHICA IN BURKINA FASO

By D. M. Anderson and M. Cox

 Pro- and midtibiae armed with a small ventral tooth opposing femoral tooth (fig. 5B); profemoral tooth (fig. 5B) distinctly larger than in fig. 5A; antennal club

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APPENDIX 2.

MANUSCRIPTS BASED ON THIS THESIS

Papers submitted

- Traoré, D., Vincent C. and Stewart, R. K. Dispersion Patterns Of Adults And Vertical Distribution Of Larvae Of Smicronyx guineanus Voss And Sm. umbrinus Hustache (Coleoptera: Curculionidae) On Striga hermonthica (Del.) Benth (Scrophulariaceae). Insect Science and Its Application, September 1994.
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- Traoré, D., Vincent C. and Stewart, R. K. Life History Of *Smicronyx guineanus* Voss And *Sm. umbrinus* Hustache (Coleoptera: Curculionidae) On *Striga hermonthica* (Del.) Benth. (Scrophulariaceae). *Entomophaga*, January 1995.
- Traoré, D., Vincent C. and Stewart, R. K. Behavioral Time Budget Of Smicronyx guineanus Voss (Coleoptera: Curculionidae) On Striga hermonthica (Del.) Benth. (Scrophulariaceae) In Semi-field Conditions. Journal of Insect of Behavior, January 1995.

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