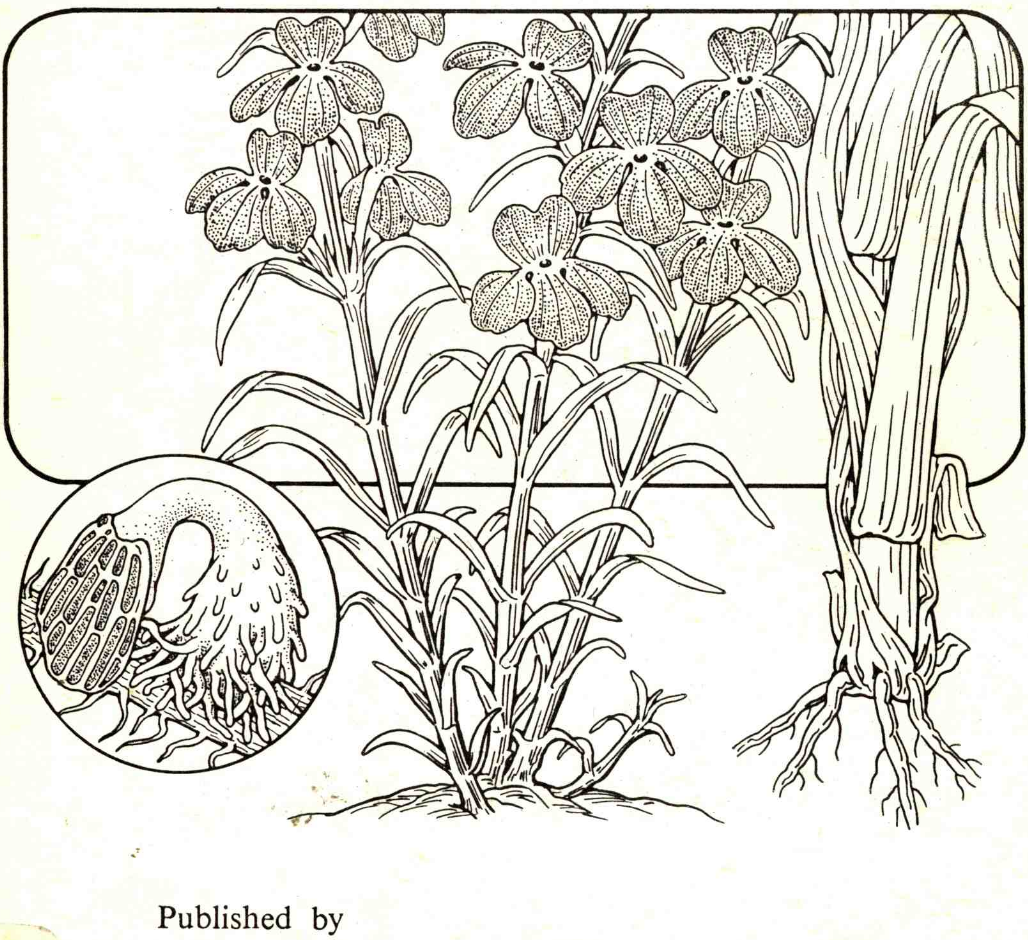
STRIGA

BIOLOGY AND CONTROL



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STRIGA

BIOLOGY AND CONTROL

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I

INTRODUCTION

INTRODUCTION

A. The Problem

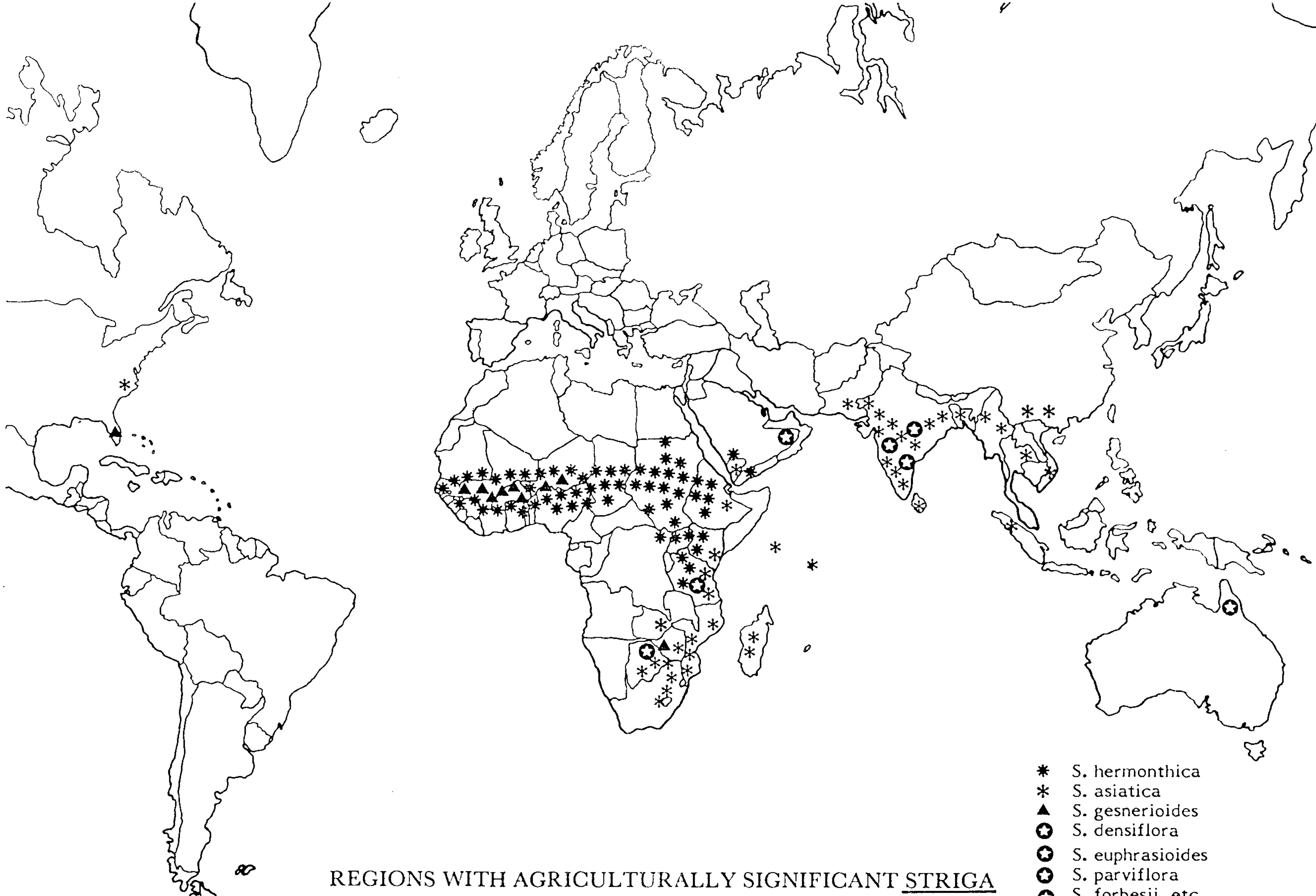
Striga spp. are obligate parasitic weeds which attach themselves to the roots of cereals and other plants, not only robbing them of nutrition but also causing various debilitating effects which have earned them their common name of "witchweeds". The two most important species (S. hermonthica and S. asiatica) parasitize cereal crops, particularly sorghum and millets, but also maize, upland rice and sugarcane. Another, (S. gesnerioides) attacks cowpeas. Striga produces numerous tiny seeds which remain viable in the soil for many years and do not germinate unless a sorghum, millet or maize root grows very near to them. Once established, it is therefore very hard to eradicate, and in some areas where infestation is heavy, there may be total crop failure in some years.

The following map shows countries most severely affected : Mali, Upper Volta, Niger, Nigeria, Cameroon, Chad, Sudan, Ethiopia and India. In regions of these countries where Striga is common, crop yields may regularly be reduced by 60% to 70%. Serious crop losses also occur widely in parts of the Gambia, Senegal, Mauritania, Togo, Ghana, Kenya, Tanzania, Uganda, Botswana, Swaziland and Mozambique and more locally elsewhere in Africa, Asia, Australia and the USA.

The problem caused by Striga is steadily increasing as population pressures result in more continuous cereal cultivation. Striga is favoured by low fertility and unreliable rainfall, and so affects the small-scale farmers who are least productive and least able to afford any inputs for its control. On some soils in India the yield of Striga-susceptible hybrids may decrease in a few years to the point where the farmer can no longer grow sorghum, and either attempts another crop such as pearl millet or has to abandon his land altogether. Infestation may therefore lead to the migration of whole villages and in regions where there is no fresh land to move to, famine can result or at least be aggravated, as currently in Ethiopia.

In the USA, Striga has been brought under control with the aid of herbicides, ethylene injection fumigation and the lavish application of fertilizer. Large farmers in Southern Africa combat the weed by crop rotation, use of nitrogen fertilizer, herbicides and weeding out. But rotation effects are slow to build up, fertilizer is expensive or not available to the small farmer, herbicides are often difficult to apply, and weeding out the parasite requires a prohibitive amount of labour once Striga is fully established. Control systems suitable for subsistence farmers with very limited resources have never been worked out.

The breeding of crop-resistant cultivars should offer the best solution for the small farmer, but they are not yet available on anything like an adequate scale. ICRISAT (International Crops Research Institute for the Semi-Arid Tropics) is actively developing resistant cultivars of acceptable yield and grain quality both



REGIONS WITH AGRICULTURALLY SIGNIFICANT STRIGA in India and in Africa, but the work is long term and the resistant varieties are difficult to identify and therefore to select. Moreover, resistant cultivars are dangerous to apply in isolation, since their resistance may break down. The most promising approach is an integrated one, using the breathing space provided by resistance to Striga in order to develop agronomic control measures which can be used in conjunction with it, any such methods being suitable for use by small farmers in their own fields. However, little progress is being made on the agronomic front to augment the breeding of resistant varieties in Africa, apart from some part-time activities in the Sudan national programme. The need for a greatly intensified Striga programme is urgent.

B. The Workshop

The Workshop on the Biology and Control of Striga was held at the Unesco Regional Office for Education in Dakar, Senegal, from 14-17 November 1983. This Workshop was organized by the African Biosciences Network (ABN) and the Inter-Union Commission on the Application of Science to Agriculture, Forestry and Aquaculture (CASAFA) of the International Council of Scientific Unions (ICSU), with the objectives of :

- examining the latest state of knowledge of the biology of the parasitic weed Striga;
- identifying gaps in this knowledge;
- proposing means of minimizing the damage caused by Striga to several important food crops in Africa and elsewhere; and
- proposing research strategies that will lead to effective and economically feasible control of Striga.

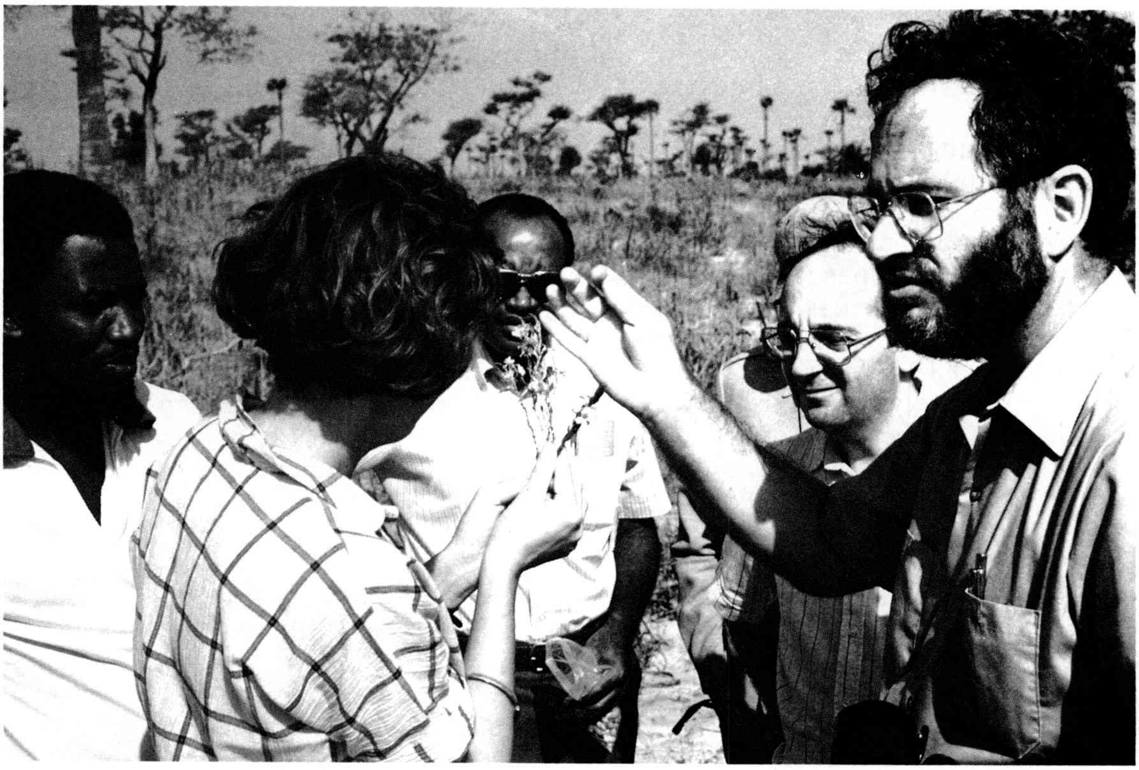
The Workshop marked the opening of the Office for the African Biosciences Network at the Unesco Regional Office in Dakar. The African Biosciences Network is the African regional arm of the International Biosciences Networks (IBN), which is a collaborative activity between Unesco and the ICSU. The IBN was set up in 1979 in order to assist biologists throughout the world to contribute more effectively to a rapid application of recent advances in biological knowledge for the benefit of mankind. At present, the IBN has active networks in Asia and Latin America, and the African Network, launched at a Symposium held in Ghana in 1981, has begun its full operations with the Striga Workshop. A network in the Arab region has recently been instituted.

CASAFA was established in 1978 in an effort to find ways to focus the wide range of scientific talent encompassed by the members of the ICSU family on the world's food situation. CASAFA's principal objectives are to direct the attention of scientists to agricultural problems; to collaborate with interested organisations; to act as a clearing house for suggestions for areas of research and to stimulate appropriate groups to undertake such research.

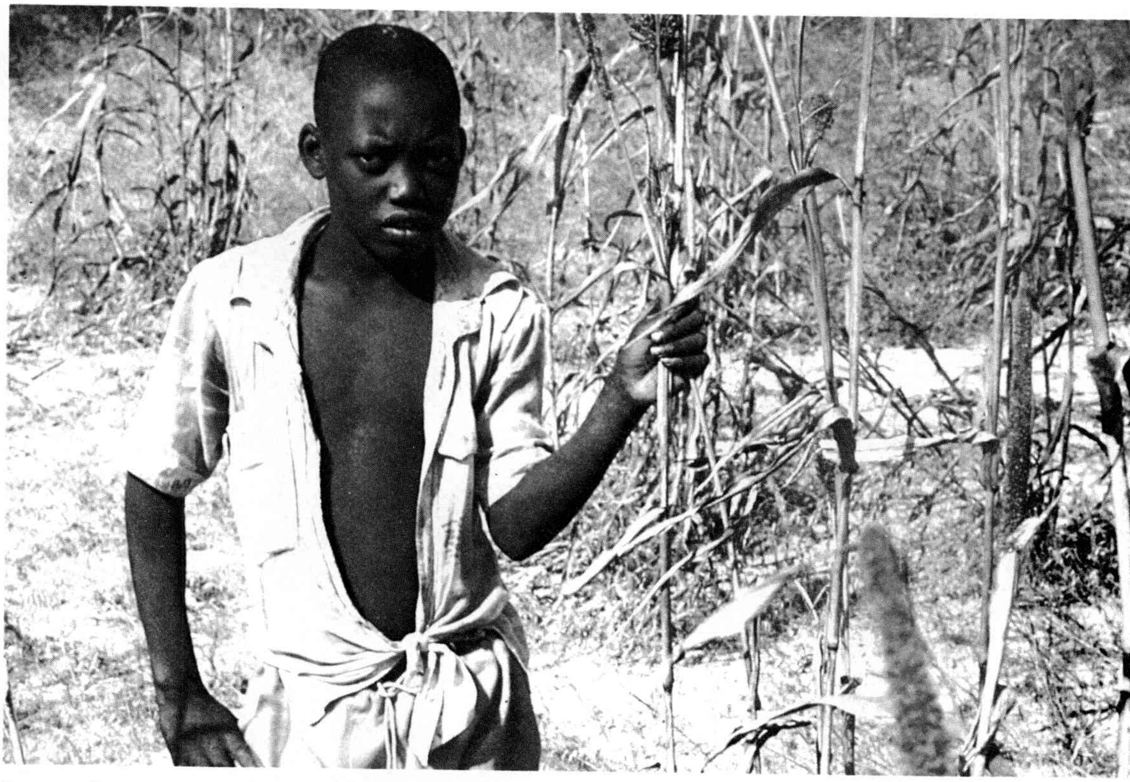
The organisation of the Workshop on the Biology and Control of Striga was made possible through generous contributions received from the International Development Research Centre (IDRC) of Canada, CASAFA, IBN, ICSU and Unesco.

The Workshop was formally opened by Dr. Balla Moussa Daffé, Minister of Scientific and Technological Research of the Republic of Senegal, Professor R.D. Keynes, Chairman of the International Biosciences Network, Professor E.S. Ayensu, Chairman of the African Biosciences Network and Vice-Chairman of CASAFA, and Dr. K.A. Tuffour, Unesco Regional Hydrologist for Africa, representing the Director General of Unesco. The full texts of these opening addresses are found in Chapter 3.

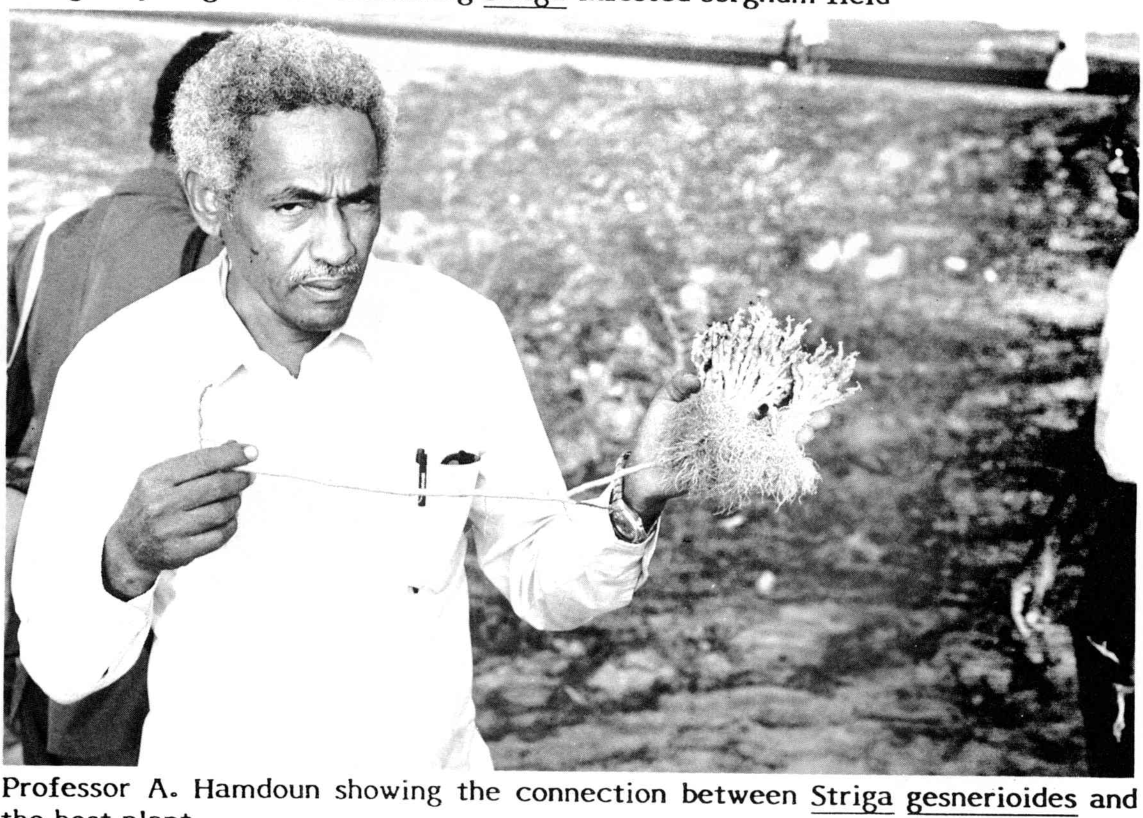
The Workshop was attended by 28 scientists from 11 countries, many of these being specialists in various approaches to the biology and control of Striga in different parts of the world. The participants listened to eleven prepared presentations and took part in active discussions after each of them. The principal papers, revised to take into account the deliberations at the meeting, are reproduced in full in Chapter 4 of this book. On the third day of the Workshop, participants were taken to visit some fields infested with Striga and then to the Agricultural Research Station at Bambey. The final day was devoted to the formulation of conclusions to the deliberations and to the proposal of concrete recommendations for further research.



Professor L.J. Musselman explaining to Workshop participants the differences between Striga hermonthica and Striga aspera



Senegal : young farmer examining Striga-infested sorghum field



Professor A. Hamdoun showing the connection between Striga gesnerioides and the host plant

II

WORKSHOP CONCLUSIONS AND RECOMMENDATIONS

WORKSHOP CONCLUSIONS AND RECOMMENDATIONS

A. CONCLUSIONS

The seriousness of the Striga problem was repeatedly reaffirmed in the course of the Workshop. In many areas it is becoming steadily more serious, as in Ethiopia and Botswana, while in India there is considerable alarm resulting from the acute susceptibility of many of the new high-yielding sorghum hybrids.

Available control measures were reviewed in detail. Most techniques are either impracticable for the majority of small farmers (e.g. crop rotation) or too expensive or unavailable (e.g. irrigation, high nitrogen fertilization, herbicides, germination stimulants). The most notable advance in control measures in recent years has been the development in the United States of America of ethylene as a stimulant to cause suicidal germination of Striga seeds.

In the approaches of greatest relevance to small-scale farming, there had been very little progress in biological control, although some useful leads and indications have been noted.

In the development of resistant varieties, there has been some notable progress as a result of ICRISAT's efforts in India, but progress in Africa against the more virulent S. hermonthica has been less rapid.

Basic and background research has recently made some significant advances in the understanding of the biology, physiology and biochemistry of Striga spp. (e.g. in floral biology and reproductive systems, in germination requirements, haustorial initiation and various aspects of nitrogen metabolism and host-parasite relations), but continued effort is required in the laboratory and most especially in the field to gain a better understanding of factors influencing germination and development of the parasite in relation both to the use of more resistant host varieties and to agronomic practices including 'trap crops'. Research on agronomic approaches has been negligible in recent years.

The range of research needs at different levels is summarised in the following table.

Table 1 : Table of Research Needs

Approach	Adaptive Research	Applied Research	Basic Research
Host resistance	Multilocational variety testing/ demonstration (sorghum only)	Selection and breeding for resistance (sorghum, millet and cowpea). Screening techniques	Resistance mechanisms. Genetics of resistance. Striga taxonomy/genetics
Agronomy (and fertilizers)	N-application (especially in maize). Irrigation. Crop substitution (e.g. millet for sorghum)	Field experimental techniques. Effects of crop density, water, mixed cropping, shading, mulch, etc. Dates of planting. Coriander and other "Striga-chasers". Agro-climatological monitoring in relation to Striga occurence	Physiology and biochemistry of N-metabolism in host and parasite. Host/parasite relations as influenced by nutrient, light, drought, etc.
Trap-cropping and artificial stimulants	(Use of ethylene to create clean plots and so estimate losses)	Testing trap crops for stimulant activity on different Striga types. Monitoring Striga seed behaviour in field soil. Ethylene, GR 24, ethephon, etc. application/equipment	Understanding synthesis and exudation of stimulant in host and trap crops. Factors influencing Striga seed conditioning and germination. New germination stimulants based on strigol, ethylene, etc.
Herbicide and other chemical approaches	2,4D application in sole crop cereals. Other herbicides for spot spraying	Systemic herbicides for translocated effect in cereals. Herbicides for selective control in cowpea. Phenolics for seed-hardening	Biochemical studies with potential for development of Striga-specific herbicides. Chemotropism. Haustorial initiation
Bio-control		Introduction of Eulocastra etc. from India to Africa	Biology and taxonomy of insects attacking Striga. Study of fungi, virus and bacteria (including rhizosphere organisms) on Striga

B. RECOMMENDATIONS

1. The serious actual and potential crop losses caused by Striga demand a greatly intensified research effort, and the development of more effective control measures, especially suitable for use by small-scale farmers. The Workshop recommends that immediate steps should be taken to establish a consortium of donor agencies to fund a Striga Programme for the support of research at all levels, covering both National Agricultural Research and Extension Projects and a strengthening of the work in progress on Striga at ICRISAT and IITA (International Institute for Tropical Agriculture).

2. In order to conduct a continuing survey of the economic losses caused by Striga in the affected areas of the world in conjunction with national authorities, coordinate the various parts of the research programme and to monitor its progress, an agronomist with appropriate experience should be appointed as Striga liaison officer.

3. The ICRISAT Striga Project in Africa should be greatly strengthened (see Annex I). Host plant resistance provides the best basis for effective control. Sorghum and millet possess different breeding systems and occupy adjacent but distinct agroclimatic zones, so there should be one Striga resistance breeder for each of these major cereal crops. Integrated control measures that combine resistant varieties with good agronomic practices and deliberate control measures are essential. Much research remains to be done on these topics and the project should be additionally manned by the inclusion of an agronomist and a crop physiologist.

4. The importance of damage from Striga to other tropical crops is noted, particularly to cowpea and maize, and the Workshop recommends that IITA should increase its research efforts on Striga in these two crops.

5. Efforts towards biological control of Striga should be intensified, and the Workshop endorses support for the specific proposals prepared by the Commonwealth Institute of Biological Control (Annex II).

6. The potentially valuable contribution made by the late Professor Alan Johnson and colleagues under finance from the International Development and Research Centre, in developing the "strigol analogues" for Striga control is noted by the Workshop and it is recommended that a quantity of at least 200 kg of "GR24" should be prepared to allow its full potential to be critically assessed in field experiments.

7. Basic studies on Striga should be supported at a range of institutions in both developed and developing countries where relevant expertise is available. Proposals for such studies should be invited and the projects coordinated as necessary (see Annex III for examples of some proposals already submitted).

Support for such projects should particularly include the provision of post-graduate studentships for agricultural scientists from developing countries, and fellowships should be established for work on basic research projects as outlined above and also for attachment to the ICRISAT field projects in India and Africa. After such relevant training, the personnel will be better able to contribute to National programmes as below (see point 8).

8. National *Striga* projects should be established, to test resistant varieties and integrated control systems across a wide range of agro-climatological conditions, and to involve the small farmer in this adaptive research and development work (see Annex IV). Such development work should include attention to seed production so that resistant cultivars can be reliably bulked and made available to farmers, and should be staffed by scientists specially trained under the fellowship scheme.

9. The importance of *Striga* should be much more widely publicized. IBN and other bodies should be asked to help in the preparation and dissemination of appropriate material; and articles on *Striga* should be written for the more popular scientific journals as well as national newspapers.

It should be noted that these conclusions and recommendations are the results of the deliberations of this Workshop only, and participants recognized the importance of other research projects being carried out by other organizations and groups.

ANNEX I : Proposed Striga Control Project

The ICRISAT West African Striga programme needs to be expanded substantially to develop integrated methods of Striga control which can be used by small farmers.

The expanded programme would require at least :

- a sorghum breeder
- a millet breeder
- an agronomist
- a crop physiologist

The objectives would include the following :

1. To increase the breeding effort on sorghum and millet, one plant breeder is needed for each crop. (The millet zone stretches right across Africa adjacent to the southern edge of the Sahara. The sorghum zone runs east-west and south of the millet zone. Increasing areas of maize occur in the sorghum zone towards the south).

2. To develop methods of Striga control which can be used by small farmers, an agronomist is needed. Activities would include evaluating low rates of nitrogen fertilizers, dates of planting, crop mixtures, crop sequences and safe herbicide use by simple methods.

3. To study weak points in the Striga life cycle, and to discover ways of exploiting them, a crop physiologist is needed. Activities would include monitoring the soil populations of Striga seed, the effectiveness of other crops in germinating Striga seed in the absence of a host plant, and the destruction of Striga in the soil using simple ethylene injection equipment, already developed in the USA.

4. Training. Training courses for breeders, agronomists and other workers for the National Programmes are urgently needed. These would be run by the professional scientists in the project.

The existing ICRISAT project is budgeted at US $992,120 over 3 years. At least US $2 million are required to develop an adequate programme.

ANNEX II : Biological Control

1. Surveys

Surveys have been made in South India and East Africa and work has begun in the Sudan. Although heavy insect damage has been reported in West Africa, no studies have been made to identify the causes of this damage and assess its impact on Striga spp. The results would indicate opportunities for introduction of missing species.

Minimum requirements would be an entomologist for 6 months in two years to visit selected sites in the Sahel and savanna zones during the cropping season, and for extensive sampling and rearing insects. If possible, national entomologists should be selected to undertake further studies of the impact of natural enemies on Striga spp. populations. Cost : US $30,000 to include salary, travel, identifications. Could be undertaken by CAB (Commonwealth Agricultural Bureau) Institutes, for example.

2. Exchange of Striga insects between India and Africa for trial as biological control agents

Eulocastra argentisparsa, a fruit feeding moth, has no counterpart in Africa. The Indian Smicronyx weevil does not attack fruits preferentially, whereas some African species do. There is also no counterpart of Ophiomyia strigalis in India. These insects should be screened for host specificity and if, as anticipated, they will not damage crops, they should be introduced as appropriate.

Requirement is support for entomologists in India (CIBC (Commonwealth Institute for Biological Control), Bangalore) and Sudan (University of Khartoum) to carry out screening and development of disease-free cultures, shipment and release of exchange material. Impact assessment would cost US $50,000 over 3 years with possible assistance of Institute of Virology, Oxford in eliminating disease.

3. Taxonomic study of African Smicronyx spp.

There are at least six species of Smicronyx associated with Striga spp. in Africa. They are of particular interest as biological control agents, as they are likely to be host specific and some species are specialist fruit gallers. At present only one can be identified. New collections are required to provide adequate specimens for study, and determination of geographical distribution and parts of host plant attacked. Material would be available from the West African and Sudan surveys with cooperation from entomologists elsewhere. An illustrated identification guide would be produced.

Required support for CIE (Commonwealth Institute for Entomology) taxonomist for 3 months during 2 years would cost US $10,000 for salary, visits to museums and publication.

ANNEX III : Basic Studies - Sample Proposals

1. Biochemical approach to the development of a Striga-specific herbicide

Work carried by the Plant Stress Metabolism Group in the Biology Department, Birkbeck College, University of London, has been directed towards determining the key characteristics of *Striga* biochemistry. Studies of carbon and nitrogen metabolism suggest the possibility of developing *Striga*-specific herbicides based on the occurrence of metabolic products not synthesized by the host plants. This work could be further developed through the selection and synthesis of mannitol analogues which would then be tested as control agents. Support in the form of a post-doctoral research associate, a technician and consumables would be essential (approximate cost $150,000 over 3 years).

2. Mechanism of Striga resistance and the development of biochemical methods of resistance screening

The control of *Striga* would be considerably assisted by the development of methods which would permit rapid screening for resistance. An approach which the Plant Stress Metabolism Group at Birkbeck College is pursuing is the analysis of changes which occur in parasitized host plant metabolism in order to identify "markers" of *Striga* infection which would be absent in resistant plants; a second approach is to use the technique of molecular genetics to isolate resistance genes which could be used as probes to screen germ plasm and varieties. This work would be greatly assisted by the appointment of further staff such as a post graduate and technician with appropriate research funding (approximate cost $100,000 over 3 years).

3. Development of Striga bioherbicide

Dr. Jane Nichlin and M. McQueen at Birkbeck College (PSM Group) are collaborating with Tate and Lyle Industries Ltd. in a project aimed at assessing the potential of fungi as biocontrol agents for *Striga* control. This work could readily be extended to assess the potential of bacteria and viruses. The easiest way in which this could be done would be to appoint one or two graduate students who could undertake this work as part of their Ph.D. programme. Ideally, such students should come from countries with a *Striga* problem and would be trained as part of Birkbeck's *Striga* project.

ANNEX IV : National Projects

National Striga farming systems research programmes in the main sorghum and millet growing countries, working in conjunction with the main project, are essential. They would test the field feasibility of the control methods devised under different small farmer conditions. They would greatly increase the effectiveness of the resistance breeding programme through multi-locational testing under a wide range of soils, soil conditions and Striga populations. Important countries for such national projects are the Sudan, Nigeria, Upper Volta and Ethiopia. The first three have projects on Striga in their national programme. The national programme in Upper Volta is not yet strong, and ICRISAT is doing much of the national programme research.

The Striga work in the other three countries is part-time, a component of a large cereals programme. The purpose of the suggested projects would be to strengthen the Striga work, so that at least one man is responsible full-time for the breading component, and another for the agronomy component, with sufficient funds to ensure that the trials can be properly planted at the right time and properly tended and recorded. Sufficient funds for extensive within-country travel would be needed. The scientists need not be highly qualified and experienced researchers: they would receive plenty of guidance and on-the-job training from the ICRISAT project scientists. The whole programme would be worked out together with ICRISAT.

These projects offer an opportunity to develop cropping/farming systems. Adaptive research with the farmer is essential, with a proper socio-economic component based on experience with the ACSN (Asian Cropping Systems Network). The serious effects of Striga, minimized by resistant variety and associated management practices, will make an excellent subject for farming systems work and extension.

III

OPENING ADDRESSES

OPENING ADDRESS

given by

Richard D. Keynes

Chairman, Internatonal Biosciences Networks

A few years ago, observing that many of the most pressing problems which face the developing countries are fundamentally biological in nature, the International Biological Unions* adhering to the International Council of Scientific Unions (ICSU) entered into discussions with Unesco as to how the international scientific community might play a more active part in tackling these problems. It was quickly agreed that the prime need was to help the developing countries to acquire their own scientific and technical expertise by training more biologists of every kind for them and otherwise strengthening their scientific infrastructure. This could best be achieved by setting up regional networks of existing research centres and individual scientists which could determine priorities and organize training programmes and joint research projects so that the strongest countries could help their weaker neighbours in the areas of biology considered to be of the greatest practical importance. A model for such networks was provided by the UNDP/Unesco Regional Programme for Postgraduate Training in Biological Sciences which had been in successful operation in South America since 1976, and an Asian Network for Biological Sciences had been established by COSTED (ICSU's Committee on Science and Technology in Developing Countries) in 1978. A Steering Committee for the International Biosciences Networks (IBN) was accordingly set up jointly by ICSU and Unesco with the object of establishing networks to cover all the countries of the Third World, to coordinate their general development so that each Regional Network could benefit from the experience of the others, and to assist in raising funds for their operations.

The major region of the world for which no network existed was Africa and a Symposium on the State of Biology in Africa was therefore held in Accra in April 1981, to consider the special problems of the African continent. It was attended by some 90 leading biologists and government representatives from seventeen African countries, together with representatives from a number of international and regional organizations. Priorities for biological research and training in Africa were discussed, and it was recommended that an African Biosciences Network (ABN) should be established at the earliest opportunity. With the aid of a grant from UNDP for the period 1984-86, the ABN has now come into being, and a part-time Coordinator has been appointed whose office is located at the Unesco Regional Office in Dakar.

On the recommendations of the ICSU Commission on the Application of Science to Agriculture, Forestry and Aquaculture (CASAFA), a problem of considerable economic importance to Africa which has received relatively less attention than others in the field of agriculture is that of the losses to farmers in the semi-arid parts of the continent caused by the parasitic weed *Striga*. It was accordingly agreed that a suitable topic for the first formal activity of the ABN would be a meeting of experts from Africa and elsewhere to consider the present state of knowledge on the basic biology of Striga and on measures which might be taken for its control under the conditions prevailing in Africa.

On behalf of the IBN, I wish to express gratitude to Dr. Balla Moussa Daffé, Minister of Scientific and Technological Research of the Republic of Senegal, for opening this Workshop, and to the International Development Research Centre of Canada (IDRC), CASAFA, ICSU and Unesco for their financial support.

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* The International Unions of Biological Sciences (IUBS), Physiological Sciences (IUPS), Biochemistry (IUB), Pure and Applied Biophysics (IUPAB), Pharmacology (IUPHAR), Nutritional Sciences (IUNS), Immunological Societies (IUIS), Microbiological Societies (IUMS) and Psychological Sciences (IUPsyS).

STATEMENT ON ABN

given by

Edward S. Ayensu
Chairman

It is my honour to welcome you on behalf of the African Biosciences Network (ABN). I would like to take this opportunity to describe very briefly the background and objectives of this organization.

Recently there has been a strong recognition among the international scientific community that something has to be done to strengthen the scientific and technological capabilities of developing countries. Stimulated in large part by the discussions of the Bio-unions of the International Council of Scientific Unions (ICSU), the International Biosciences Networks (IBN) was born in 1980 as a joint activity with Unesco. Discussions within the Bio-Unions and the ICSU-Unesco Coordinating Committee identified a variety of objectives, including :

1. The building up of scientific and technical manpower and the strengthening of their capability to identify and to contribute to the solution of development problems having science and technology components.
2. The upgrading of institutions in developing countries to become 'centres of excellence' and for such institutions to serve as the focal points for the training of scientists and technologists.
3. The establishments of linkages among national and regional scientific and technological institutions and between such institutions in the developed and the developing nations.
4. The establishment of regional networks in the biological and physical sciences.

With the earlier existence of the Latin American and Asian regional biosciences networks supported by UNDP and Unesco, the IBN Steering Committee, in 1980, convened a preparatory meeting to explore the possibility of forming an African Biosciences Network. The result of this meeting led to the organization of a Symposium on the State of Biology in Africa in April 1981 in Accra, Ghana, where the African Biosciences Network was officially inaugurated in the presence of representatives from various national, non-governmental and inter-governmental organizations.

The Symposium was convened to assess the state of biology in the various environments of Africa, including the humid tropics, the arid and semi-arid zones, and the aquatic ecosystems. The priority research areas examined included : i. forest resources, ii. insect pests, iii. plant breeding, iv. microbiology, v. water resources, vi. nutritional problems, vii. endemic diseases, viii. medicinal plants, and ix. the publication of appropriate biological textbooks for Africa.

The presentations made by the African scientists brought home quite clearly the gaps in our knowledge and the need to increase the quality of research in the various biosciences. It was also pointed out that the single most telling constraint plaguing Africa was the inadequate number of scientists and technologists. It was obvious from the various discussions at the Symposium that for any African country to fulfil its primary objective to develop a self-sustaining scientific and technical capacity, it was absolutely necessary that a critical mass of scientific manpower be developed in the shortest possible time so that they can participate effectively in the planning and execution of national objectives.

It is not uncommon, for example, to observe that the sharing of scientific ideas and information amongst scientists within a country is often lacking. The usual answer to this state of affairs is that there are no effective mechanisms to correct such an obvious problem.

Funding permitting, the African Biosciences Network hopes to help rectify such situations by organizing practical training courses, short-term fellowships, workshops, study groups, seminars, symposia and conference on regular bases in different regions on the continent.

The opening of the new ABN Secretariat here in Dakar, and the appointment of Dr. Amadou Tidiane Ba as the Coordinator will help to speed up plans to implement many of the objectives of the organization.

The Secretariat will also help the ABN to establish and foster a close working relationship with other scientific and technical organizations already in existence in Africa. For example, the ABN plans to increase communication with the relevant sections of the Economic Commission for Africa (ECA), the Organization of African Unity (OAU), the International Agricultural Research Centres (IARCs) of the Consultative Group of International Agricultural Research (CGIAR), and the programmes and organizations established under the aegis of the United Nations University, such as the Food and Nutrition Programme for Africa, as well as the proposed Institute for Natural Resources in Africa (INRA).

This present Workshop on the Biology and Control of Striga is the first collaborative type venture the ABN is holding with scientists from other international organizations to focus on a specific problem having relevance to food and fibre production in Africa.

It is my hope that the results of this Workshop will go a long way to stimulate interest in our attempt to reduce the influence of this parasitic weed on crops.

It is indeed an exciting opportunity and a challenge for this Workshop to come up with suggestions that will serve as the key to unlock the secrets that can help us to control Striga, not only in the agricultural fields of Africa, but also in all other regions where they occur.

STATEMENT ON CASAFA

by

J.H. Hulse

Chairman

The recent continuous severe drought which has depleted food crops and caused the demise of thousands of head of cattle and other livestock in eastern and southern Africa emphasises yet again the delicate balance that exists between nutritional need and food supply among many developing countries. In contrast, the impressive scientific advances made by the international agricultural research centres (IARCs) have led to significant increases in food grain production in several Asian, Middle Eastern and Latin American countries.

As was clearly illustrated in the recommendations of CHEMRAWN II (Chemical Research Applied to World Needs), if widespread malnutrition is to be avoided over the long-term future, a much greater investment in relevant research and in the application of practically useful results in the agricultural production and post-production sectors is essential.

A very meagre proportion of the world's scientific talent is directed towards improving agricultural sufficiency and stability. In an effort to find ways to focus the wide range of scientific talents encompassed by its members on the food situation, the International Council of Scientific Unions (ICSU) created in 1978, the Inter-Union Commission on the Application of Science to Agriculture, Forestry and Aquaculture (CASAFA).

This Commission is composed of a group of senior scientists together with representatives of several ICSU member Unions and such agencies as the Food and Agriculture Organization of the United Nations (FAO) and the United Nations Educational, Scientific and Cultural Organization (Unesco). Concentrating its efforts mainly on the needs of the developing countries, CASAFA pursues the following objectives :

- to direct the attention of the members of the ICSU family to agricultural problems and to the need for improving the ways in which basic research results can be applied to their solution;
- to collaborate, when feasible, with interested national or international organizations in studies that would assist in ensuring the more rapid application of basic scientific research to solving agricultural problems and to increasing food production;
- to act as a clearing house for suggestions for novel or inadequately supported research into agricultural problems; and
- to stimulate appropriate groups, both inside and outside ICSU, to undertake such research, and to suggest sources from which it might be possible to obtain financial support for such research.

To achieve these objectives, CASAFA has made contact with many research organizations, including national bodies in developing countries, and IARCs, to identify and set in order of priority specific areas of relevant research in which scientists in developed and developing countries could cooperate. Of particular interest are subjects that cross disciplines and encourage cooperation between agricultural scientists and those in disciplines not frequently associated with agriculture. CASAFA has also encouraged national academies of science to establish national committes whose purpose is to act as a two-way conduit in each country through which information on the needs for such research and on the facilities for undertaking it can flow. In addition, CASAFA, through the national committees, will help to stimulate cooperation between scientists in developed and developing countries.

The devastation caused by Striga spp. to the feed crops of the semi-arid tropics is eloquently described in the papers presented in this publication. CASAFA welcomed the opportunity to cooperate with the African Biosciences Network in sponsoring the Striga Workshop and will devote particular attention to pursuing the recommmendations made.

WELCOME FROM UNESCO

given by

K.A. Tuffour
Regional Hydrologist for Africa

On behalf of the Director General of Unesco, the Assistant Director General for the Science Sector of Unesco, the Director of Water Sciences, Unesco, the Director of the Regional Office for Science and Technology (ROSTA), the Director for Education (BREDA) of Unesco, I wish to thank you all for participating in this ABN and CASAFA Seminar on Striga.

I wish to congratulate the officials of the International Council of Scientific Unions for organising this meeting and their ability to bring together renowned scientists from all over the world. I wish to thank especially Professor Richard D. Keynes, Chairman of IBN, and Professor Edward S. Ayensu, Chairman of ABN, Dr. A.T. Ba, Coordinator of ABN, and Mme. Julia Marton-Lefèvre for their efforts. You are all most welcome.

Unesco, true to its basic functions and obligations, will play its role in effectively coordinating the efforts of the ABN, and in collaboration and cooperation with other institutions including ICSU, UNDP and other organizations, to ensure the successful operation of ABN.

Unesco as a world medium of education, science and information, among others, is as willing and ready to assist ABN as she has been with IBN and ICSU in promoting the biological activities of ABN within Unesco's terms of reference and obligations.

Unesco expects from the ABN a reciprocity in performance and the demonstration of the ability to tackle and to help in solving the biological problems and the development of programmes in Africa. A lot is expected of you and I hope this association with its noble ideals will not be a nine-day wonder.

On behalf of ROSTA, I would like to welcome ABN to the fold and to assure you of our unflinching support and cooperation in the true spirit of Unesco.

The countries and citizens of the world are linked by history and common land masses. We are also connected by dynamic systems of air masses, oceans and seas. We are therefore, connected by transferable problems, be it social, economic, political or scientific. We are each brother's keeper, each one's problem should be our common concern and the solutions to problems must be our common aspiration.

It is to this end that scientists here today and elsewhere are called upon to tackle the basic biological problems that threaten our very existence within and across their national boundaries. Indeed, the world through Unesco, ICSU, UNDP and others have placed enough confidence in you to ensure the success of the activities of the African Biosciences Network.

ABN as an operating arm of IBN is charged and indeed expected to make an impact in finding solutions to Striga - the parasite that is depriving humans of their rightful share of the right amount of nutrients in our staple foods. It is an affront to the scientists here and elsewhere. Through constant and tireless research efforts, Striga can be nipped in the bud.

OPENING ADDRESS

given by

The Hon. Balla Moussa Daffé
Minister of Scientific and Technological Research
Republic of Senegal

Distinguished Representative of the Director of the Unesco Regional Office for Education, Chairman of the International Biosciences Networks, Chairman of the African Biosciences Network, Chairman of CASAFA, ladies and gentlemen, dear friends.

I wish first of all, in the name of my President, his Government and in my own name to welcome all of you who have accepted (many of you from afar) to attend this important event marking at the same time the launching of the African Biosciences Network and the opening of a scientific meeting concerned with the parasitic weed Striga.

Mr. Chairman of the International Biosciences Networks, it is with pleasure and pride that we welcome the choice of our country as the headquarters of the African Biosciences Network. This, to us, signifies your confidence in Senegal, which we will do all in our power to merit, as we have done before on similar occasions, when our national scientific potential was given the occasion to be strengthened through international collaboration. I can personally assure you that the Government of Senegal, and especially my own department, will do all it can to ensure that this newcomer to the international scientific network will succeed.

In this connection I would like to congratulate the International Council of Scientific Unions, Unesco and the IBN for having conceived the ABN, and the United Nations Development Programme for so generously supporting it.

Thus, under such promising signs, it is for me a real pleasure to be here this morning to preside over the opening of the ABN and to tell you of the high hopes that we have placed on this young organisation.

It is a fact that recent developments in science and especially in biology have already brought and will continue to bring, I am certain, appropriate solutions to basic human problems. In Africa we must seize upon all the opportunities which arise to put science to work for development. Thus, the training of competent scientific personnel is more than ever our highest priority. We must also explore with the help of modern techniques of investigation, new avenues of research in order to assist man to live in the utmost harmony with his constantly evolving environment.

Although comparisons are not always correct, we cannot but be confident about the ABN when we note the remarkable results obtained by the Latin American and Asian Biosciences Networks.

The Symposium on the State of Biology in Africa held in Accra in 1981 gives evidence of the seriousness with which you have undertaken the task of looking at the situation of biological research and training on the continent. The conclusions and priorities identified in Accra correspond exactly with those identified by the Government of Senegal as a result of the National Days of Reflection on Science and Technology held in June 1982. These research priorities, in brief, were :

1. Attainment of independance and security in food and energy resources.

2. Deeper understanding of our physical, biological and human environments.

3. Study of our natural and sociological (urban and non-urban) ecosystems and their interaction.

4. The health and well-being of our population with emphasis on nutritional aspects, primary care and the eradication of endemic diseases.

4. Strengthening of our education and training sectors through adaption and generalization.

Thus, your own desire to find solutions to pressing problems in the agricultural sector, in pisciculture, medicine and education will always find a favourable response in this country.

In choosing to couple this formal ceremony of opening the African Biosciences Network with a scientific workshop on Striga, you have demonstrated your determination not to loose any time in beginning the scientific work of the ABN. This for me provides another reason for satisfaction to preside over this opening session, for Striga has been the cause in Senegal, and in fact in all of the Sahel, of serious losses in millet, the basic food crop of our rural populations. Although we are aware of Striga's harmful characteristics, we have been scientifically, technologically and materially unable to fight against this, especially as we are threatened by other parasites which are as economically devastating as Striga.

Since 1977, the University of Dakar has carried out a research programme on Striga, funded in part by my own department. This is to demonstrate to you the interest we have in this problem, and in the timeliness of your Workshop.

You have chosen to examine the Striga problem by inviting the most knowledgeable specialists from all over the world to this Workshop. We congratulate you in this choice, as this approach will not only provide the opportunity to evaluate past results but also to take an important step forward in defining new and efficient research areas more suitable to our needs. This in any case is our hope.

Permit me to express one small regret, and that is that this important meeting is being conducted only in English, as some of our own scientists may not be fluent enough in this language, which may affect the way in which they participate in your deliberations.

This does not in any way reduce our interest in your work. On the contrary, we await with impatience your findings which we hope to use in our fight against food crop parasites in order to help us attain as soon as possible our objective of independence in our food resources. It is for this reason that we wish you every success in your Workshop on the Biology and Control of Striga, as well as wishing all of you a pleasant stay in Senegal.

I therefore declare this Workshop open, wishing a long life and much success to the African Biosciences Network.

IV

SCIENTIFIC PAPERS

STRIGA - ITS BIOLOGY AND CONTROL AN OVERVIEW

H. Doggett

INTRODUCTION

The genus Striga belongs to the family Scrophulariacae. There are approximately 50 species of Striga, all of which are parasitic on other plants, the most troublesome being the obligate parasites. The species affecting cereals are S. hermonthica in Africa, S. asiatica both in Africa and Asia, and S. densiflora in Asia, especially in India. S. gesnerioides can be devastating on cowpeas, and serious on tobacco, occuring in both Africa and Asia. Sorghum, maize and the millets are all subject to Striga attack. (Hosmani, 1978).

These species of great economic importance are endemic to the continents in which they are found, with a widely distributed range of wild host plants. There can be no question of eliminating Striga, we have to learn how to live with it, controlling the Striga populations so that they cannot build up sufficiently to cause economic damage.

BIOLOGY

The Seed

The seeds are tiny, some 0.30 mm long and 0.15 mm broad, larger or smaller according to species. Estimates of seed production in the literature may be as high as 40,000 seeds per plant of S. hermonthica, and over 90,000 seeds per plant of S. asiatica. They can remain viable for many years under dry conditions, estimates vary from six months to 20 years according to climatic conditions. Most of the seeds, perhaps 80% occur in the top 30 cm of soil, and may give 20-50% germination. Some seeds occur down to a depth of 150 cm and seeds from this depth may show over 95% germination. (Andrews, 1945; Robinson & Kust, 1962).

Germination

Striga is beautifully adapted to the conditions of the semi-arid tropics. The seed requires a period of after-ripening, and so cannot germinate at the end of the rainy season in which it is produced. The seed requires a period of pre-treatment after it has imbibed water, lasting perhaps one to five weeks. It is therefore not ready to germinate until the rains begin and the host plants have had time to start growing. The pretreated seed requires a stimulant produced by the host plant before it will germinate. The majority of the seeds within 2 mm of the host root receive sufficient stimulant to germinate, so few seedlings are wasted through being too far away from a host root. Much of the seed which has imbibed water enters a period of "wet dormancy" if it is not stimulated to germinate. After they have dried out again at the end of the rains, many seeds revert to their original condition, and need pre-treatment again before they become responsive to the germination stimulant. (Saunders, 1933; Vallance, 1950, 1951a, 1951b; Reid & Parker, 1979).

Attachment

The radicle of the Striga seedling grows towards the host root - perhaps there is a weak chemotropic influence - and at the point of contact the tip of the radicle of the Striga seedling swells. It forms a papilla which penetrates between the cells of the cortex and flattens against the host endodermis. The ability of the endodermis to bar penetration by the parasite may differ according to genotype. Once a link is established with the host xylem and phloem, the parasite draws its supplies from the host. Although the Striga does turn green above ground, there is continued movement of carbohydrates, minerals and water from host to parasite. Growth hormones are also important. (Rogers & Nelson, 1962; Ramaiah & Parker, 1982).

Development

Many Striga plants may be attached to the same individual host plant; and some fail to emerge above ground, owing to competition for nutrients from the host. If the emerged plants are removed, then some of the subterranean Striga appear in their place. The total numbers of the parasite may be difficult to estimate from the number of green Striga plants actually above ground, but the condition of the crop is a good guide. (Doggett, 1965; Okonkwo, 1966; Yoshikawa et al, 1978).

CONTROL

Is Control Necessary?

As a generalisation, the poorer the land, the poorer the management, the fewer the inputs, then the greater is the amount of Striga damage. The parasite can be devastating. Yields of only 70-340 kg/ha have been recorded in Tanzania. In the Sudan, grain yield losses were quoted as 70% under severe infestation, 60% in Nigeria, 25,000 tons of sorghum grain annually are lost in the State of Andhra Pradesh, India. (Doggett, 1965; Hamdoun & El Tigani, 1977; Obilana, 1979; Gebisa, 1980; Rana et al, 1980; Hanumantha Rao et al, 1981; Ramaiah & Parker, 1982).

Good farming practices and ample inputs can keep down the Striga attack; but it should be noted that S. asiatica was introduced into the USA at the end of the last war, and some 200,000 ha were infested by Striga. Up until now, 90,000 ha have been freed from Striga. Progress has been slow, owing to limitations of funds. (Eplee, 1981). Who will provide the funds to clean up the Striga lands of Africa and India using the technology developed in the USA? Striga presents a desperate problem to small subsistence farmers. They must grow their cereals for food, population pressure requires more continuous use of the land, there is little money for inputs - so Striga increases and yields fall. Land has to be abandoned, or the cereal changed, e.g. by growing Pennisetum millet in the place of sorghum, yet the soil conditions may be too different. Millet is a crop for light, sandy soils, sorghum grows on heavier lands and can endure short periods of "wet feet", which millet cannot.

The problem for which we are trying to seek the road to a solution in this meeting is not the control of Striga as such - given sufficient resources, we know this can be done. Our problem is how to reduce Striga numbers and control the parasite on the smallholdings of the subsistence farmers over so much of Africa and India. Can we find out - not how to control Striga - we know a lot about that already - but how the small farmer can control Striga and find it worth his while to do so? These are two aspects, cleaning up the infested lands and maintaining control of the parasite afterwards.

CONTROL MEASURES

A. Reducing the Number of Striga Seeds in the Soil

The Stimulant

Striga is vulnerable because it is an obligate parasite, and can only produce seed on a suitable host plant. The need to supply the germination stimulant is the key here, if Striga seed can germinate in the absence of a suitable host, it will soon die. Small farmers in India have known this for many years. They rotate sorghum with cotton and the cotton stimulates the germination of some of the Striga seed in the soil. However, the parasite cannot emerge and flower on cotton. Other crops, especially legumes can do the same thing. In any case, the reduction in the numbers of Striga seeds is not substantial enough since very often a single sorghum crop will push the Striga numbers back up again. Evidently, crop rotation is important, but we do not know whether the small farmer has enough land to be able to achieve this. The cereal is his food supply. Can he afford to have only one half of his land under cereals? Can he manage the increased total area needed? Is the land available in the first place?

Another aspect of rotation referred to above indicates that in many places the Striga strain parasitizing on sorghum is not a problem on millet. Therefore such cereal rotation offers possibilities and could help to meet the need to have sufficient land area under cereals.

Chemists used extracts from cotton roots to identify a Striga-germinating stimulant, and called it "strigol". (It may or may not be the stimulant produced by cereals such as sorghum). It is complex and expensive to synthesize. Workers at Sussex University produced synthetic analogues of strigol which were much simpler, but production costs and clearance for toxicity have held up field experimentation. These chemicals can be applied with an ordinary knapsack sprayer, and may be expected to be very useful if sprayed on the "trap" crops in the rotation, augmenting the activity of that crop's roots. These analogues of strigol urgently need proper evaluation.

Ethylene acts very effectively as a stimulant to germinate Striga seed. Mechanical equipment for soil injection developed in the USA works well. The back-pack equipment, however, would take a very long time to cover one hectare. This is a potential method for reducing Striga seed in the soil. It is instructive to note that even in the USA funds have not been made available to use such equipment to cover a large enough area. Again we are forced to ask who would pay to use this technology on small subsistence farms of Africa and India?

Another way of using natural stimulant production is to grow a very susceptible cereal cultivar and to plough the crop under before the Striga flowers. This has been used very successfully by large farmers owning modern machinery. This method is mentioned last because it is completely beyond the capability of the small subsistence farmer. (Watt, 1893; Andrews, 1947; Last, 1960, 1961; Eplee, 1975, 1981; Cook et al, 1972; Johnson et al, 1976; Ramaiah & Parker, 1982).

B. Controlling the Parasite in the Growing Crop

Resistance Breeding

Striga resistance may be defined as the plant's capacity to produce a satisfactory grain yield in the presence of many Striga seeds in the soil, whilst at the same time carrying fewer flowering Striga above the ground than do susceptible crop types. (Tolerance is dangerous as tolerant plants produce similar numbers of flowering Striga to susceptible crops and thereby add as much Striga seed to the already large numbers in the soil).

Resistant cultivars represent the weapon which indigenous farmers use against Striga. Resistant crop types are to be found in many countries. This has been demonstrated very clearly in India, where the new HYV's and hybrids are very much more heavily attacked than the local land-races. Over the years, the Indian farmer has selected resistant races.

Modern breeding methods and the availability of the world germplasm collection have greatly improved the situation because better resistant types are becoming available. We shall be hearing of Framida, a selection made in South Africa from a Chad race many years ago. Its resistance was identified as being due to low stimulant production in 1959. Why has it not become popular with the farmers? Perhaps other characters of Framida are not liked by sorghum growers. The plant breeders are working on this. Dobbs was identified as resistant to Striga more that 30 years ago. Again, it has not been widely adopted. Much more plant breeding work is needed to obtain high levels of resistance in combination with better agronomic characteristics, especially yield and quality.

We are touching on the whole basic question of agricultural development for the small subsistence farmers. Resistance alone is not sufficient to control Striga. (Saunders, 1933; Williams, 1959; Doggett, 1965; Ramaiah, 1982, 1983).

Destruction of the Striga Plant

1. Handpulling. Uprooting the *Striga* by hand every 10 days to 2 weeks has been recommended. It can be a burdensome task and its effect is shortlived. If the *Striga* is already flowering and fruiting, viable seeds may well be broadcast by the uprooted plant. Handpulling is valuable where *Striga* plants in the crop field are few. It is a useless exercise in a heavily infested field. (Butler, 1957, 1958; Doggett, 1965).

2. Herbicides. The problem with the use of herbicide in fields of small farmers where the practice of intercropping is most prevalent. The non-cereal crop may be damaged by the herbicide. Chlorfenac has been found effective as a preplanting herbicide in the USA, but it is damaging to other crops. 2,4-D has been used successfully in the USA, India and the Sudan. In the USA, it has been effective when combined with paraquat at the end of the season. In India it has been used with atrazine. In the USA 2,4-D had to be applied for several successive seasons before there was any significant reduction in the field population of *Striga*.

   Spot-spraying with ametryne, using a handheld plastic squirter ("pistol grip" sprayer) showed promise in Nigeria. (Robinson, 1961; Robinson et al, 1967; Ogborn, 1974; Eplee & Langston, 1976; Yaduraju & Hosmani, 1979).

   The most interesting combination tested in the USA was that of the Sussex University strigol analogue GR 24 in combination with either the herbicides paraquat or goal (Oxyfluorfen), which was as effective as soil injection with ethylene when used on bare land. (Norris & Eplee, 1981).

3. Fertilizer. The use of farmyard manure in improving grain yields on *Striga* infected soil has long been known. The main effective component is nitrogen, and responses vary from place to place. In the USA very high dressings of ammonium nitrate controlled *Striga* in maize for the whole season (1,120 to 3,360 N kg/ha). In the Sudan, 90 N kg/ha trebled sorghum grain yields on lightly infested soils, to around 4,000 kg/ha. On heavily infested land grain yields were increased by a factor of 8 to around 1,700 kg/ha by the same level of nitrogen. On fertile land, the addition of nitrogen reduced the amount of witchweed emerging. On "infertile" land (i.e. badly infested land?) the addition of nitrogen increased the amount of *Striga* emerging above ground. This emphasises the need to think in terms of raising the fertility of the land. Nitrogen alone could not be used effectively on soils where levels of the other essential nutrients were very low. There must be at least sufficient phosphate before the continued use of nitrogen can be recommended.

   We shall be hearing of the successful use of *Striga*-resistant sorghum types in conjunction with the use of nitrogen at quite low levels and the way in which a little nitrogen enhances the resistance of at least some *Striga* resistant cultivars.

The use of a 20% solution of urea as a spray withers the parasite. Perhaps the "pistol grip" sprayer might be useful to apply this. (Saunders, 1933; Peat in Rounce, 1949; Jones, 1953; Butler, 1957, 1958; Last, 1960; Shaw et al, 1962; Chaudhuri, 1975; Ramaiah & Parker, 1982; Ramaiah, 1983).

4. Biological control has been suggested. Prospects of success are small. Striga populations are already in balance with the indigenous pests and diseases. The potential for moving Striga pests and diseases between India and Africa should be examined very carefully at some point, but the prospects of successful control by this method do not appear very good.

GENERAL REMARKS

The answer to successful crop production in areas where Striga is endemic lies in good farming practices. Farmers with ample resources can do this and have done it. The problem facing our workshop is how the small subsistence farmer can do this. There are two aspects : a) the development of the necessary technology, which must be a low input technology; and b) its application.

The development of the necessary technology requires research. For the small subsistence farmers of Africa and India, Striga and birds are the major problems of cereal growers and other witchweeds can be serious on other crops. Yet these two major problems have received negligeable attention from Donor Agencies. Over the years, research on Striga has been a part-time activity of interested individuals. For the past several years, the only Striga work in Africa has been supported by IDRC, a very effective Canadian Government funding agency. Even so, there is only one full-time agronomist, no plant pathology input, no plant physiology input. To me, this situation is unbelievable. Somehow, we have to find a way to bring to the notice of the donor agencies the urgent need for work in this area.

Realism demands low input technology. It must lie within the farmer's reach, and must be economically possible for him to use.

Resistance breeding is the obvious first step. We shall be hearing later of the excellent progress being made, let us pray that continued support for this work will be forthcoming so that it can be sustained for the period necessary to produce good, practical results.

The indications that at least some form of resistance can be augmented by the application of small amounts of nitrogen, demand more research. How does nitrogen work? How much is needed? Does this open up a line of research, looking at the mechanism by which resistance is augmented and finding out whether other substances will do the same thing as nitrogen, but more effectively? What other fertilizers need to be applied with nitrogen to ensure that its effects are maintained with continuous application? What is the smallest effective dose of nitrogen or nitrogenous supplement which still boosts resistance substantially?

More must be done on herbicides. Is there any possibility of finding a Striga-specific herbicide? Is anybody looking?

We need cheap strigol analogues. The combination of strigol analogue with herbicide needs much more research, it has only just begun. The use of strigol analogues has not yet been evaluated, because they have not been available in sufficient quantity. Their potential value on trap crops such as cotton or pulses used in a rotation may be great. Perhaps they could be included in with the pesticide sprays that cotton so often requires.

Many other areas may come to mind; pathology and physiology have not yet been mentioned. Yet the other few topics have been highlighted because they could be brought within the reach of the subsistence farmer.

Subsidies for fertilizer, herbicide and strigol analogues could yield big returns. Efficient seed multiplication of Striga-resistant HYV's is possible. The organisation for marketing and distribution so that all of these items could be close at hand for the farmer is possible.

The application of the research technology is an area where only general comments and questions are possible. This work can only be done by effective, indigenous, National Agricultural Research and Extension Services. Are we always sufficiently aware of the need to improve farming standards in countries dependent upon agriculture? Or is this forgotten because of the need to produce more cotton or more groundnuts? Do the price and marketing structures provide sufficient incentives for industrious farmers to be able to earn enough to encourage them to improve their farming yet further? Does our research begin with the realised needs of small farmers in their own fields, and are they involved sufficiently at all stages? Have we sufficient humility to be able to learn from small farmers? There is a wisdom which has enabled them to survive down the years with little infrastructure or outside help.

All these questions are becoming more insistent as populations increase and per capita agricultural production falls. At least, we must keep asking them until sufficiently highly-placed people realise that they need answers.

REFERENCES

ANDREWS, R.W. (1945), "The parasitism of Striga hermonthica Benth. on Sorghum spp. under irrigation", Ann. Appl. Biol. 32 : 193

ANDREWS, R.W. (1947), "The parasitism of Striga hermonthica Benth. on leguminous plants", Ann. Appl. Biol. 34 : 267

BUTLER, E.J. (1957), "Agronomy section, guinea-corn", Ann Rept. Dept. Agric. N. Nigeria 1953-54, pp. 17

BUTLER, E.J. (1958), "Agronomy section, guinea-corn", Ann Rept. Dept. Agric. N. Nigeria 1954-55, pp. 30

CHAUDHURI, S.D. (1975), "Striga can be controlled with urea spray", Sorghum Newletter 18 : 48

COOK, C.E., WHICHARD, L.P., WALL, M.E., EGLEY, G.H., COGGAN, P., LUTHAN, P.A. & McPHAIL, A.T. (1972), "Germination stimulants. 2. The structure of strigol - a potent seed germination stimulant for witchweed, (Striga lutea Lour.)", J. Amer. Chem. Soc. 9 : 6198

DOGGETT, H. (1965), "Striga hermonthica on sorghum in east Africa", J. Agric. Sci. 65 : 183

EPLEE, R.E. (1975), "Ethylene: a witchweed seed germination stimulant", Weed Sci. 23 : 433

EPLEE, R.E. (1981), "Progress on control of Striga asiatica in the United States", 2nd International Striga Workshop, Ouagadougou, Upper Volta, October 1981

EPLEE, R.E. & LANGSTON, M.A. (1976), "Developments in the control of Striga in the USA", PANS 22 : 61

GEBISA, E. (1980), "Status of sorghum improvement in the Sudan", Rept. ICRISAT-W.A. Co-op. Prog. Gezira Res. Stn., Wad Medani, Sudan

HAMDOUN, A.M. & EL TIGANI, K.B. (1977), "Weed control problems in the Sudan", PANS, 23 : 190

HANUMANTHA RAO, C., SANGHI, N.K. & RAO, U.M.B. (1981), "Screening technique and evaluation of sorghum for Striga tolerance", A.I.C. R.P.D.A., Hyderabad. Paper presented at the Annual Sorghum workshop, Navasari, India, May 11-14, 1981

HOSMANI, M.M. (1978), "Striga - a noxious root parasitic weed", University of Agricultural Sciences, Dharwar, India

JOHNSON, A.W., ROSEBERY, G. & PARKER, C. (1976), "A novel approach to Striga and Orobanche control using synthetic germination stimulants", Weed Research 16 : 223

JONES, K.W. (1953), "Relation of witchweed (Striga) to fertility in tropical soils", Nature, London 172 : 128

LAST, F.T. (1960), "Effect of cultural treatments on the incidence of Striga hermonthica and yields of sorghum in the Sudan", Ann. Appl. Biol. 48 : 207

LAST, F.T. (1961), "Direct residual effects of Striga control treatments on sorghum yields", Trop. Agric. 38 : 49

NORRIS, R.S. & EPLEE, R.E. (1981), "Effects of stimulant plus herbicide on Striga germination", Ann. Rep. Whiteville Methods Dev. Center, North Carolina, USA, 1981, USDA

OBILANA, A.T. (1979), "Search for Striga control through resistance in guinea-corn in Nigeria", 3rd NAFPP Workshop Sorghum/Millet/Wheat, National Centre, Zaria, Nigeria

OGBORN, J.E.A. (1974), "The control of Striga hermonthica in peasant farming", Samaru Research Bull. 207

OKONKWO, S.N.C. (1966), "Studies of Striga senegalensis III in vitro culture of seedling: establishment of cultures", Ann. J. Bot. 53 : 679

PEAT, J.E. in Rounch, N.V. (1949), "The agriculture of the cultivation steppe", Longman's, Capetown, pp. 22

RAMAIAH, K.V. (1982), "Striga research, breeding", Annual Report 1981, ICRISAT/Upper Volta Cooperative Programme, Ouagadougou

RAMAIAH, K.V. (1983), "Striga research, breeding", Annual Report 1982, ICRISAT/Upper Volta Cooperative Programme, Ouagadougou

RAMAIAH, K.V. & PARKER, C. (1982), "Striga and other weeds in sorghum", Sorghum in the Eighties, Int. Symp. ICRISAT, Patancheru, India, Nov. 1981, pp. 291

RANA, B.S., ENSERINK, H.J., RUTTO, J.K. & OCHANDA, N. (1980), "Progress Report 1980 L.R.", Busia, Field Document 6, UNDP/FAO Ministry of Agriculture, Nairobi, pp. 42

REID, D.C. & PARKER, C. (1979), "Germination requirements of Striga spp.", Proc. 2nd Int. Symp. Parasitic weeds, Raleigh, North Carolina, USA, pp. 201

ROBINSON, E.L. (1961), "Soil-incorporated pre-planting herbicides for witchweed control", Weeds 9 : 411

ROBINSON, E.L., DALE, J.E. & SHAW, W.C. (1967), "Herbicide, crop rotation for witchweeed control", Weeds, 15 : 243

ROBINSON, E.L. & KUST, C.A. (1962), "Distribution of Striga seed in the soil", Weeds 10 : 335

ROGERS, W.E. & NELSON, R.R. (1962), "Penetration and nutrition of Striga asiatica", Phytopathology 82 : 1064

SAUNDERS, A.R. (1933) "Studies in phanerogamic parasitism, with particular reference to Striga lutea Lour.", S. Africa Dept. Agri. Sci. Bull. 128, pp. 56

SHAW, W.C., SHEPHERD, D.R., ROBINSON, E.L. & SAND, P.F. (1962), "Advances in witchweed control", Weeds 10 : 182

VALLANCE, K.B. (1950), "Studies on the germination of the seeds of Striga hermonthica. I. The influence of moisture-treatment, stimulant dilution and after-ripening on germination". Ann. Bot. 14 : 347

VALLANCE, K.B. (1951a), "Studies on the germination of the seeds of Striga hermonthica. II. The effect of the stimulating solution on seed respiration", J. Exp. Bot. 2 : 31

VALLANCE, K.B. (1951b), "Studies on the germination of the seeds of Striga hermonthica. III. On the nature of pre-treatment and after-ripening", Ann. Bot. 15 : 109

WATT, Sir George, (1893), "A dictionary of the economic products of India", Vol. 6, part 2, pp. 127

WILLIAMS, C.N. (1959), "Resistance of sorghum to witchweed", Nature, Lond. 184 : 1511

YADURAJU, N.T. & HOSMANI, M.M. (1979), Striga asiatica control in sorghum, PANS 25 : 163

YOSHIKAWA, F., WORSHAM, A.D., MORELAND, D.E. & EPLEE, R.E. (1978), "Biochemical requirements for seed germination and shoot development of witchweed (Striga asiatica)". Weed Science 26 : 119

TAXONOMY AND BIOSYSTEMATICS OF STRIGA

L.J. Musselman and E.S. Ayensu

INTRODUCTION

This presentation is aimed at giving a general background of the taxonomy and biosystematics of Striga. It will indicate the need for more research on these parasitic weeds that affect the food resources of Africa. For a review on biosystematic studies see Musselman and Parker (1982).

TAXONOMY AND SYSTEMATICS

The genus Striga Loureiro (Scrophulariaceae) comprises approximately 30 species of the old world tropics and subtropics. Members of the genus are characterised by the distinctive bend in the corolla tube below the bilabiate limb, unilocular anthers and hispid and/or scabrous pubescence. All species that have been examined are parasites. Most are annual.

Wettstein's (1895) treatment of Striga in Engler and Prantl's Die Naturlichen Pflanzenfamilien, divides the genus into two taxonomic sections based on the number of ribs on the calyx-tube. The genus is in need of revision and L.J. Musselman is currently preparing a taxonomic revision of the genus with the cooperation of A. Raynal-Roques, Museum of Natural History, Paris, F.N. Hepper of the Royal Botanic Gardens, Kew, and C. Parker of the Tropical Weeds Group, Weed Research Organization, Oxford.

There are many species of Striga, including S. asiatica, having distinct physiological or ecotypic differences (Bharathalakshmi & Jayachandra, 1979; Musselman et al, 1982). Various strains of S. hermonthica are specific to sorghum and millet, based on responses to different seed germination stimulants in the respective crop exudates (Parker & Reid, 1979). S. gesnerioides has specialized physiological strains that may be restricted to one host species. There is a tobacco strain of this species in Zimbabwe, and in Nigeria there is a cowpea strain and a Tephrosia strain which differ in flower colour and other features (Musselman et al, 1982).

Being root parasites, Wettstein considered Striga among the most advanced members of the Scrophulariaceae and placed the genus in the Rhinanthoideae-Gerardieae. Only Harveya and Hyobanche with their scale-like leaves are considered more advanced than Striga and evolving towards the non-chlorophyllous Orobanchaceae.

Wettstein's sections of Striga are the Pentapleurae, having a 5-ribbed calyx-tube, and the Polypleurae with 5- to 10-ribbed calyx-tube. The reference is to ribs which terminate at the tip of one of the five lobes, rather than terminating in a sinus between calyx-lobes. Engler created another section Tetrosepalum. Saldanha (1963) observed that rib number is often an untenable characteristic for delimiting the species. For example, S. asiatica usually has 10 ribs, but may have up to 17. Also, S. gesnerioides may have 4 to 8 ribs, depending on the number of properly developed calyx-lobes. Despite this, rib number is a valuable taxonomic character.

The most recent nomenclature activity seems to have been fathered by the discovery of a witchweed for the first time in North America in the mid-1950's. This plant from the Carolinas was first determined as S. asiatica, and later as S. lutea (Smith, 1966), based on Saldanha's (1963) belief that the name S. asiatica was a misapplied source of botanical confusion and must be rejected under the Code of Botanical Nomenclature. The basionym, Buchnera asiatica L., was described by Linnaeus from material said to come from Ceylon and China, and Bentham (1835) observed that Linnaeus simply applied this name to 'all of the Strigae he was acquainted with' (Saldanha, 1976).

A decade later, in 1974, Hepper revived S. asiatica (L.) Kuntze and lectotypified it, based on one of five specimens on a sheet in the Linnean Herbarium. The type specimen of Buchnera asiatica was determined by Hepper's botanical detective work to have been collected by Olof Toreen on the island of St. Joanna in the Comoro Islands near Madagascar. Thus, Linnaeus had mistakenly attributed the plant to China (Hepper, 1974), although it must be said that Toreen in his 1759 voyage did go beyond the Comoro Islands to China. S. asiatica now infests around 1,400 farms with a total of 931,000 hectares in the Carolinas (Musselman, 1982).

There appears to be a continuum of reduction within the genus from such leafy specimens as S. euphrasioides, which does not have a specialized germination requirement to S. gesnerioides with its scale leaves and small size.

The genus Striga may be geographically arranged as shown in Table 1, although there is a certain amount of overlap in the range of some species.

SPECIES OF ECONOMIC IMPORTANCE

The economically important species of Striga are :

1. Striga asiatica. Witchweed, fireweed. A weed in 25 countries; parasitizing many crops, i.e. 60 species of grasses in 28 genera, most often damaging oats, rice, teosinte, wheat, rye, sorghum, millet (Italian, pearl, finger), Sudan grass, corn (Zea) and sugarcane. Up to 500,000 seeds per plant. Serious weed in South Africa and elsewhere. Occurs in India, Asia and Africa (USDA, 1976; Musselman, 1982; Holm et al, 1977; Ramaiah et al, 1983).

2. Striga densiflora. Common in cultivated fields, especially on sorghum, millet and sugarcane. Serious weed in India. Occurs in India, Mysore, Assam (Reed, 1977; Holm et al, 1983; Ramaiah et al, 1983).

3. Striga euphrasioides. On millet, rice, sorghum, sugarcane and other cultivated crops. Serious weed in India. Occurs throughout India, Punjab, southwards to Sri Lanka, eastwards to Khasia Hills, Pegu and Burma, Java, Africa (Reed, 1977; Holm et al, 1977; Ramaiah et al, 1983). There is some confusion about the correct name for this taxon (Musselman, 1984).

4. Striga forbesii. Giant mealie witchweed. Parasitizes grasses. Once a problem on maize. Occurs in Africa (Ethiopia, Natal, Zaire, Zimbabwe) and Malagasy Republic (Reed, 1977; Ramaiah et al, 1983).

5. Striga gesnerioides. Tobacco witchweed, cowpea witchweed. Parasitic on a wide range of dicot hosts, including Lepidagathis, Euphorbia, Dysophylla, tobacco, sweet potato (Ipomoea) and cowpea (Vigna). Serious weed in cowpeas in west Africa. Cowpea yields in west Africa may be reduced up to 50% in areas where all of the cowpeas are infested. Occurs from Cape Verde Islands through Africa and through the Arabian peninsula to India. In 1978, a legume strain, the indigo witchweed was discovered in the United States in central Florida (Polk County) at a disturbed mine site, parasitizing the introduced weedy legume species (Alysicarpus vaginalis and Indigofera hirsuta) (Musselman & Parker, 1981).

6. Striga latericea. Reported to cause serious damage to sugarcane in Ethiopia (Musselman, 1980).

ECOLOGY

The genus Striga is basically tropical and subtropical in distribution, usually occuring between latitudes 30°N and 30°S. It extends south of 30°S in Natal, growing on sugarcane, and grows at 34°N in the Carolinas (United States).

Striga asiatica tends to prefer light and sandy soils, whereas S. hermonthica in East Africa is more common on heavy soils. Although S. asiatica prefers light soils as in Tanzania and South Africa, it does appear to thrive in the heavy 'mbuga' soils of Sukumaland (Tanzania). The US Agricultural Research Service (1975) reported that in the Carolinas, S. asiatica grows predominantly on sandy soils of a light colour and ranging from coarse sands to fine sandy loams.

The size of S. asiatica is variable from one host crop to the other, under various environmental conditions, and in different geographical areas (Holm et al, 1977; Musselman et al, 1982). For example, in Burma it attains a height of 50 cm; in Zimbabwe, growing on corn, it is a branched plant 15 to 30 cm; and when growing on native veld grasses, it is a rather spindly, unbranched plant 15 to 20 cm tall.

Formerly it was thought that S. asiatica would not invade areas with a photoperiod longer that 14.5 hours of daylight. Experiments were made in South Africa growing sorghum and Striga in a 17-hour day (at 2,000 foot candles of light intensity), and thus it is now believed that the length of the photoperiod is not a limiting factor in the spread of S. asiatica (Holm et al, 1977). While this genus has not been reported from central America, South America, Mediterranean Europe or the Eurasian regions, the photoperiodic studies indicate that it is very possible that the species can spread, and it is capable of surviving under a variety of ecological conditions which would be a barrier to less aggressive species.

Witchweed cannot prosper in areas of high rainfall. In southern Africa, it is often found in the so-called 'Maize Triangle' in the summer rainfall area, having a low rate of 45.72 to 50.8 cm annual precipitation. In North and South Carolina where S. asiatica occurs, the average annual rainfall is 119.38 to 127 cm. In

South Africa, the optimum temperature for seed germination was found to be 86°F to 104°F, with no germination occurring at 59°F or lower, or at 113°F or higher.

In 1969, Aline Raynal-Roques of the Musée National d'Histoire Naturelle in Paris described two new species of Striga from Africa which show unusual ecological preferences. Instead of being rather widely distributed like a number of other species in the genus, they are geographically limited and ecologically specialised (Raynal, 1969).

Striga hallaei A. Raynal (Section Pentapleurae) from Gabon and Congo-Kinshasa (Kivu) appears to be the only species that grows in a humid equatorial rain forest; it was found growing in a blanket of moss on top of a granite 'inselberg' in Gabon, and near a river under forest shade on the Congo. In Africa, the Striga species that occur in equatorial regions, by contrast, grow in various savannas, often of the Sudanian type. Rain forest habitat was totally unknown before, and is a significant departure fom the normal habitat of the genus. This species resembles S. forbesii.

The other species described by A. Raynal is S. chrysantha (Section Polypleurae) from the Central African Republic and Congo-Kinshasa (Uele) where it is endemic to the dry fissures of rocks in a 'closed' savanna of restricted size. This environment is more inhospitable than the ground of the savannas in which other Striga species occur.

There are at least two distinct patterns of breeding within the genus. The first is allogamy which is well developed in S. hermonthica. In fact, this species is an obligate out-crosser (Safa et al, 1984) exhibiting sporophytic incompatibility. It is thus dependent upon insect vectors, which include bee flies (Diptera-Bombyliidae) and Lepidoptera in west Africa (Musselman et al, 1983), and Lepidoptera in Sudan (Musselman & Hepper, in preparation). Striga asiatica and S. gesnerioides, on the other hand are inbreeders which have a well developed system of autogamy (Musselman et al, 1982). Here no pollen vector in needed, the pollen is picked up by the elongating style and fertilization ensues. The likelihood of any cross pollination is small as the pollen is sticky and forms a plug on the bifid stigma, which effectively forms a barrier to any foreign pollen. In S. gesnerioides, at least, the barriers to outbreeding are mechanical, because crosses between strains of S. gesnerioides were successful (Musselman et al, 1982).

Much more information on breeding systems and genetics of Striga is needed. Chromosome numbers for most species are not even available. Research on a related genus, Aureolaria (Bell & Musselman, 1982) suggests that hybridization involves a self-incompatibility system with multiple S allelles at a single locus. In such a system, the pollen of the self-compatible (SC) plants will not grow on the stigma of the self-incompatible (SI), but the reciprocal cross would be effective and the cross would then be unilateral. Preliminary work in artifical hybridization between S. hermonthica and S. aspera indicates unilateral hybridization towards S. aspera, but further work is needed to see how this system relates to the genus as a whole.

CONCLUDING REMARKS

More intensive research is needed on several aspects of *Striga*, including :

- the taxonomy of the genus;
- the mechanisms of species-specific physiological strains;
- ecotypic variation;
- phylogeny of parasitic systems in the genus; and

It is our hope that this Workshop may inspire the African scientific community to undertake this challenge. Hopefully, these remarks will contribute to our understanding of *Striga* and to the ultimate eradication of these parasitic weeds.

Table 1 : Striga species and their distribution

1.	S. asiatica (L.) Kuntze - Africa, Arabian peninsula, India, Burma, China, Indonesia, Philippines, Malaysia, New Guinea, Australia (?), introduced into the United States (including S. lutea Lour., several other synonyms)
2.	S. gesnerioides (Willd.) Vatke - Africa, Arabian peninsula, India, introduced into the United States (including S. orobanchoides Benth., S. chloroleuca Dinter and other synonyms)
3.	S. densiflora (Benth.) Benth. - Arabia (where probably introduced), India, East Indies
4.	S. euphrasioides Benth. - east Africa, Oman, India, China. The relationship between this species and the next is not clear (Musselman, 1984) (including S. alba Pennell?, S. schlecteri Pennell?)
5.	S. masuria Benth. - India, China, Philippines, Malaysia, New Guinea
6.	S. sulphurea Dalz. ex Dalz and Gibbs - India
7.	S. curviflora Benth. (including S. spanogheana Mig.?) - Australia
8.	S. multiflora Benth. - Australia
9.	S. parviflora Benth. - Australia
10.	S. bilabiata (Thunb.) Kuntze - Africa (including S. thunbergii Benth., S. glandulifera Engl., several other synonyms)
11.	S. elegans Benth. - South Africa
12.	S. forbesii Benth. - Africa (including S. hallaei A. Raynal?)
13.	S. junodii Schinz - South Africa
14.	S. aequinoctialis Chev. ex Hutch and Dalz. - west Africa
15.	S. aspera (Willd.) Benth. - Africa
16.	S. baumanii Engler - west Africa
17.	S. brachycalyx Skan - Africa
18.	S. chrysantha A. Raynal - central Africa
19.	S. klingii (Engler) Skan - west Africa (including S. dalzielii Hutch.)
20.	S. fulgens (Engler) Hepper - Tanzania

Table 1 (cont.)

21. S. gracillima Melch. - Tanzania

22. S. hermonthica (Del.) Benth. - Africa, Arabian peninsula (including S. senegalensis Benth.)

23. S. latericea Vatke - Ethiopia and Somalia

24. S. ledermanni Pilger - Africa

25. S. linearifolia (Schumach. and Thonn.) Hepper - west Africa (including S. strictissima Skan)

26. S. macrantha (Benth.) Benth. - west Africa

27. S. passargei Engler - Africa, Arabian peninsula (?)

28. S. primuloides Chev. - Ivory Coast

29. S. pubiflora Klotzsch - Somalia

30. S. somaliensis Skan - Somalia, Ethiopia (?)

REFERENCES

BELL, C.R. & MUSSELMAN, L.J. (1982), "Unilateral hybridization in Aureolaria Raf. (Scrophulariaceae)", Amer. J. Bot. 69 : 647-649

BENTHAM. G. (1835), "Companion", Bot. Mag. 1 : 364

HEPPER, F.N. (1974), "Parasitic witchweeds : Striga asiatica versus Striga lutea (Scrophulariaceae)", Rhodora 76 (80) : 45-47

HOLM, L.G., PLUCKNETT, D.L., PANCHO, J.V. & HERBERGER, J.P. (1977), "The world's worst weeds - distribution and biology", University Press of Hawaii

BHARATHALAKSHMI & JAYACHANDRA (1979), "Physiological variations in Striga asiatica", pp. 132-143, in 2nd International Symposium on Parasitic Weeds, Raleigh, North Carolina State University, USA

MUSSELMAN, L.J. (1982), "Parasitic weeds of arable land", pp. 169-179. In Biology and Ecology of Weeds. W. Holzner and N. Numata eds. W. Junk Publishers, The Hague

MUSSELMAN, L.J. (1984), "Taxonomic problems in Striga with particular reference to Africa", Proceedings 3rd International Symposium on Parasitic Weeds, Aleppo, Syria

MUSSELMAN, L.J., NICKRENT, D.L., MANSFIELD, R.A. & OGBORN, J.E.A. (1979), "Field notes on Nigerian Striga", Sida 8 : 196-201

MUSSELMAN, L.J. & PARKER, C. (1981), "Studies on indigo witchweed, the American strain of Striga gesnerioides (Scrophulariaceae)", Weed Science 29 : 594-96

MUSSELMAN L.J. & PARKER, C. (1982), "Biosystematic studies in the genus Striga (Scrophulariaceae)", pp. 19-24. In K.V. Ramaiah and M.J. Vasudeva Rao eds. Proceedings of 2nd International Striga Workshop, Institute for Crop Research in the Semi-Arid Tropics, Patancheru, A.P. India

MUSSELMAN, L.J., PARKER, C. & DIXON, N. (1982), "Notes on autogamy and flower structure in agronomically important species of Striga (Scrophulariaceae) and Orobanche (Orobanchaceae). Beitr. Biol. Pflanzen 56 : 329-343

PARKER. C. & REID, D.C. (1979), "Host specificity in Striga species - some preliminary observations", pp. 79-90 in 2nd International Symposium on Parasitic Weeds, Raleigh, North Carolina State University, USA

RAMAIAH, K.V., PARKER, C., RAO, M.J. Vasudeva & MUSSELMAN, L.J. (1983) "Striga biology and control", 34 pp. Institute for Crop Research in the Semi-Arid Tropics, Patancheru, A.P., India

RAYNAL, A. (1969), "Deux nouveaux Striga africains (Scrophulariaceae)", Bull. Jard. Bot. Nat. Belg. 39 :373-382

REED, C.F. (1977), "Economically important foreign weeds", Agricultural Handbook No. 498. Washington D.C. : U.S. Department of Agriculture

SAFA, S.B., JONES, B.M.G. & MUSSELMAN, L.J. (1984), "Mechanisms favoring out-breeding in Striga hermonthica (Scrophulariaceae)", New Phytol. 96 : 299-305

SALDANHA, C.J. (1963), "The genus Striga Lour. in western India", Bull. Bot. Surv. India 5(1) : 67-70

SALDANHA, C.J. (1976), "Scrophulariaceae", pp. 515-528 in C.J. Saldanha & D.H. Nicolson, eds. Flora of Hassan District, Karnataka, India, New Delhi : Amerind Publishing Co.

SMITH, C.E. (1966), "Identity of witchweed in south eastern United States", Rhodora 68 : 167

U.S. Department of Agriculture (1976), "Selected weeds of the United States", Agriculture Handbook, No. 366, Washington D.C., USA

WETTSTEIN, R. von (1895), "Scrophulariaceae", pp. 39-107 in A. Engler and K. Prantl, eds. Die naturlichen Pflanzenfamilien IV (3b)

MORPHOLOGY, ANATOMY AND ULTRASTRUCTURE OF SOME PARASITIC SPECIES OF THE GENUS STRIGA (Scrophulariaceae)

A.T. Ba

INTRODUCTION

According to several authors, this genus includes some 25 to 60 species, all species that have been examined are root parasites. Striga asiatica, S. hermonthica and S. gesnerioides are particularly harmful to some cultivated cereals and legumes such as rice, millet, sorghum, corn and cowpea. The following study deals mostly with the morphology, anatomy and cytology of the above three species, with the major emphasis on ultrastructure.

1. Morphology

Some Striga spp. are perennial. The morphological structure of the vegetative, reproductive and parasitic system is almost the same for all species except S. gesnerioides. Therefore, only two examples (S. hermonthica and S. gesnerioides) will be taken to illustrate the morphology.

Striga hermonthica - aerial parts

Striga hermonthica is a chlorophyllous plant and grows up to 80 cm in Senegal. Its vegetative parts consist of a main axis which is circular at the base but quadrangular at about 2-3 cm above the ground. The main axis is prolonged by a terminal inflorescence which exerts apical dominance on the axillary buds. The leaves are linear and 3-10 cm long, sometimes more, and 5-20 mm wide. The size of the leaves and the plant vary according to environmental conditions and to the host plant. The stem and leaves are covered with short, stiff hairs. The inflorescence is a spike-shape raceme, bearing up to 60 flowers for the terminal, and 10-20 for the lateral inflorescence, and number 7 to 15 per shoot.

The flower is typically Scrophulariaceous and generally pink. Sometimes S. hermonthica has white flowers. Morphologically, it is not much different from that of S. gesnerioides.

Striga hermonthica - underground parts

The root system of S. hermonthica is fibrous. The radicle which emerges at germination produces a primary haustorium. Other roots, growing from the base of the stem develop on contact with the host root, producing numerous secondary haustoria. All the haustoria are approximately the same size (1-2 mm), whatever the ecological conditions. Nevertheless, haustoria are decidedly smaller on some hosts.

Generally, there are large numbers of haustoria, and as many as 80 or more can be counted on one Striga shoot.

Striga gesnerioides - aerial parts

The aerial part consists only of inflorescences from 15 to 20 cm high. The main axis bears, on its lower half, many secondary axes. The scale-shaped leaves, 0.5 to 0.7 cm long, are greenish, thick, and covered with white, stiff hairs. They are sub-opposite at the base of the main axis, but alternate at a higher level. The inflorescences are simple racemes. Solitary flowers are subtended by thick, hairy bracts. The short peduncle bears two bracteoles. Flowers up to 2 cm long are pentamerous and show a slight zygomorphy, typical of the Scrophulariaceae. The calyx is gamopetalous, jagged and covered with short hairs. The gamopetalous corolla has two lips, the upper 2-lobed, and the lower 3-lobed, and is bent at about two-thirds of its length. The corolla is generally purple and covered with a few hairs. The colour of the corolla seems to be variable. Besides a variety with a white corolla, Berhaut (1967) reported finding another with blue flowers. The stamens consist of one unilocular anther. Anthers are introrse and submedifixed. The ovary is superior, divided by a complete septum and has an axile placentation. The fruit, an oblong capsule with loculicidal dehiscence, contains a large number of seeds with an ornamented testa.

Striga gesnerioides - underground parts

These consist of a portion of the stem, the roots and the parasitic system. The underground part of the stem is white, as are the scale-leaves it bears. The root system, which is variable, has been the subject of controversy (Ozenda & Capdepon, 1972; Okonkwo & Nwoke, 1975). According to Tiagui (1956) the seedling would fix itself, by means of the radicle, to the host root and forms the haustorium. The primary haustorium grows and later becomes a tuber-shaped organ reaching the size of a cola-nut and weighing up to 150 g. Above the primary haustorium on the underground part of the stem, many adventitious roots emerge, often from the base of the young leaves. Those adventitious roots contact the host roots and form secondary haustoria.

The root and parasitic system described above may vary and the modifications may reflect the importance of the secondary roots of the host plant. When S. gesnerioides attacks Ipomoea pescaprae, its secondary roots are abundant and form a very thick tuft of branched roots, relatively short and intermingled, forming a sort of ball around the primary haustorium, which is sometimes totally covered. On the other hand, when it attacks such hosts as Indigofera diphylla, Tephrosia lupinifolia or Merremia spp., secondary roots are markedly less numerous or non-existent.

Conclusions

A succint review of the morphological features of some species of the genus Striga shows that it is a relatively homogeneous group. Only S. gesnerioides is distinguishable from the others because of its smaller size and its very reduced leaves. These particular characteristics of having all reduced leaves, morphologically places this species closer to the family Orobanchaceae. This is one of the reasons why some authors (Ozenda & Capdepon, 1972) have suggested their transfer into that family.

2. Anatomy and Ultrastructure of the Haustorium

Since the stem and the root of the species of the genus Striga have similar anatomical characteristics to other dicotyledons, they were not included in this presentation. The haustorium, on the other hand, forms the biological bridge between the parasite and its host, and is of considerable biological interest in the plant kingdom, and was studied in detail.

Anatomical investigations have been made of the haustorium of some species of Striga, particularly S. asiatica (Stephens, 1912; Saunders, 1933; Uttaman, 1950; Rogers & Nelson, 1962; Musselman, 1973; Musselman & Dickison, 1975), S. hermonthica (Okonkwo, 1966a; Ba, 1983), S. gesnerioides (Ozenda & Capdepon, 1972; Okonkwo & Nwoke, 1978; Ba, 1983). These studies show that the anatomical characteristics of the haustoria of S. asiatica and S. hermonthica have much in common, whilst that of S. gesnerioides is clearly distinguishable from the other two species.

Anatomical observations on the haustorium of parasitic species of the genus Striga are scanty (Ba, 1983). Therefore, the following study will concentrate on this aspect.

Ozenda and Capdepon (1979) simplified the models used by many authors to describe the haustoria of other parasitic flowering plants. A view of the longitudinal section of the haustorium illustrated four distinct characteristics :

i. the tracheid head (Musselman & Dickison, 1975) which consists of a mass of xylem from the mother root of the haustorium;

ii. the nucleus of central parenchymatous core, including vessels or vascular parenchymatous core, which consists of a group of parenchymatous cells more or less differentiated and embedded with vessels linking the host xylem to that of the parasite;

iii. the endophyte, the part of the haustorium inside the host root tissues;

iv. the intrusive cells, resembling palisade cells, constitute the terminal part of the endophyte.

These distinct characteristics are of interest because they promote ideas for assessing phylogenetic relationships among different types of haustoria and the different taxa of parasitic flowering plants. However, these characteristics do not present the full picture of the anatomy of the group.

Anatomy of the haustorium of Striga asiatica

In spite of its date, Stephens' study (1912) on the anatomy of the S. asiatica haustorium is still the most complete. Detailed and careful observations with clear and concise diagrams enabled her to locate the main structural differences of the haustorium.

- tracheid head

Stephens (1912) had not discerned the tracheid head, but it is possible to recognize it in her diagram. Musselman and Dickison (1975) have also noted that "in this species the vascular core is not readily discernible from the axial strand". However, their illustrations appear to show a structure which looks like the "radial system" in the haustorium of S. hermonthica (Ba, 1983). That "radial system" could be the lower limit of the tracheid head.

- parenchymatous vascular core

On Stephens' diagram (1912) the region that should correspond to this structure has been described by her as "a mass of transparent nucleated cells surrounded by a cortex of varying thicknesses. At the centre of the nucleus is a strand of tracheids linking the vascular system of the parasite to that of the host".

- endophyte

The endophyte consists of a few cells of the "nucleus", the terminal part of the tracheids of the haustorium vascularisation, and the instrusive cells.

- intrusive cells

Stephens (1912) calls them "papillae of the haustorium". They are elongated cells (up to ten times their width). Each has a dense cytoplasm with a distinctive nucleus.

Conclusions

Stephens (1912) noticed that "no sieve tubes are formed in the haustorium" and that "none have been found in the mother root". The lack of phloem in the haustorium of S. asiatica has been confirmed by authors such as Saunders (1933) and Uttaman (1950). The supposed lack of sieve cells in the mother root of the haustorium has been confirmed with the assistance of transmission electron microscopy and fluorescence microscopy.

Anatomy of the haustorium of Striga hermonthica

The haustorium of S. hermonthica consists of tracheid head, parenchymatous vascular core and the endophyte which is essentially composed of intrusive cells.

- tracheid head

The tracheid head is made up of tracheids located between the xylem of the mother root and the vascular "radial system", which is also formed of short tracheids disposed at right angles to the vascular axial strand of the haustorium.

- parenchymatous vascular core

The parenchymatous vascular core represents the main proportion of the haustorium and is divided into 3 structurally distinct areas :

i. the cortical parenchyma, which occupies an outer position and is made up of large cells with vacuoles and starch;

ii. the vascular axial strand, which consists of strands of tracheids with associated parenchyma. The strand runs from the "radial system" to the host xylem;

iii. the hyaline tissue, which is pear-shaped and made up of meristematic-like cells with intercellular spaces. The characteristics of some of the hyaline tissue cells (mitosis and gradient of vacuolization) indicate that the cortical parenchyma and at least some elements of the vascular axial strand could be differentiated from that tissue.

- endophyte

The endophyte is mainly composed of intrusive cells, associated with a few foremost cells of the hyaline tissue and of the terminal part of the vascular axial strand.

- intrusive cells

The intrusive cells are generally elongated with cellulosic or more or less lignified walls. These different aspects of the intrusive cell walls may correspond to a succession of cell differentiation, leading to the formation of tracheids which would be linked to the host xylem. Dobbins and Kuijt (1973) made such observations in the case of another Scrophulariaceae, <u>Castilleja</u> spp.

<u>Ultrastructure of the haustorium of Striga hermonthica</u>

For this study only the contact zone between the haustorium and host root tissues, the intertracheidal parenchyma, the hyaline tissue and the endophyte, including the intrusive cells were considered. The anatomical investigations in the haustoria of <u>S. hermonthica</u> did not reveal the phloem which was encountered in the host root. It was important to know how the tissues of the haustorium were linked to those of the host root. Connections between the parenchyma of the haustorium and the sieve cells of the host root have been observed. On the cell walls separating the sieve cells and parenchyma it has also been observed that there are many plasmodesmata, allowing communication between these two cell types.

- intertracheidal parenchyma

Investigations made with the transmission electron microscope and the fluorescence microscope did not reveal the presence of any sieve cells in the haustorium of <u>S. hermonthica</u>. Cells of the intertracheidal parenchyma have been investigated with the view to learning if they had any characteristics which could make them behave like sieve cells. In the "radial system" and the vascular axial strands, parenchymatous cells associated with the tracheids are perforated by many plasmodesmata, which are often gathered into a plate along the cell walls. They have a somewhat vacuolated cytoplasm containing many cell inclusions.

The presence of the large number of plasmodesmata gathered into plates could be interpreted as permitting interchanges between intertracheidal parenchyma cells and the tracheids of the vascular axial strand with which they are associated. Meanwhile, other cytological features of those cells, especially conspicuous cytoplasm, indicate that they cannot be true substitutes for the phloem.

- hyaline tissue

Hyaline tissue is composed of cells with dense cytoplasm containing many inclusions such as rough endoplasmic reticulum, ribosomes and polysomes, and a large nucleus which is often polylobed. Cells are separated by walls that are sometimes thin and sometimes with large intercellular spaces containing a dark substance, which is electron-opaque.

- endophyte

Intrusive cells are the main components of the endophyte of S. hermonthica. They are elongated cells with dense cytoplasm and inclusions such as ribosomes and rough endoplasmic reticulum. Slightly structured mitochondria and a very large, elongated nucleus, generally polylobed, are also present in the cytoplasm. These intrusive cells are generally preceeded by a fluid electron-opaque substance, which obviously exerts a dissolving action on the host cell walls, including those that are lignified.

Conclusions

Anatomical and ultrastructural study (Ba, 1983) describes the cytological features in some areas of the haustorium of S. hermonthica. It seems that communication between the parenchymatous cells of the haustorium and the sieve element of the host root is probably unique to the haustorium.

Finally, investigations undertaken with the transmission electron microscope, photonical microscope and fluorescence showed that phloem did not exist in the haustorium of S. hermonthica. It can therefore be concluded that the lack of phloem and the problem of translocation of organic compounds through the haustorium still remain unclear.

Anatomy of the haustorium of Striga gesnerioides

The anatomical structure of the haustorium of S. gesnerioides does not show a distinct tracheid head, but does show a parenchymatous vascular core and an endophyte.

- parenchymatous vascular core

The parenchymatous vascular core consists of parenchymatous cells with 2 to 4 vascular arcs. Outside the vascular arcs are located starch grains, embedded in parenchyma. Inside the arcs the parenchyma cells are devoid of starch. Next to the host root are meristematic-like cells arranged in 5 to 10 rows. These meristematic-like cells differentiate into parenchyma on one side and into intrusive cells on the other. This, therefore, is the mechanism for increasing the bulk of the haustorium. Old haustoria do not exhibit this cellular differentiation.

Unlike S. asiatica and S. hermonthica, the vascularisation of the S. gesnerioides haustorium is not composed of one single vascular strand, but consists of several strands, more or less branched, of which 2 to 4 of the more important ones are located at the periphery in an arc-shaped fashion. This type of vascularization can be compared to that of Aureolaria pedicularia, Seymeria pectinata and Castilleja coccinea, according to Musselman and Dickison (1975). It can also be compared to the vascularization of the haustorium of Alectra vogelii.

- endophyte

The endophyte is composed of intrusive cells and the ends of the tracheids from the vascular axial strand which are in contact with the host root xylem. These elongated cells of the parasite form the front of the invading tissue.

Ultrastructure of the haustorium of Striga gesnernioides

Meristematic-like cells have a dense cytoplasm with an abundant endoplasmic reticulum, often laying in rows. They have poorly developed plastids and mitochondria and a long elongated nucleus. They are separated by more or less large, intercellular spaces.

- intrusive cells

These cells are elongated (up to 30 microns) with a cytoplasm containing numerous endoplasmic reticulum lining the length of the cell. There are a few, poorly differentiated plastids and mitochondria. The cells are in an opaque fluid when viewed under the electron microscope. The fluid seems to dissolve the cell walls of the host plant.

- sieve cells

Sieve cells have been reported for the first time to occur in the transition zone between the meristematic-like cells and the parenchyma cells that have no starch grains. The phloem is therefore composed of typical sieve cells, very often associated with companion cells, and typical branched plasmodesmata. Using fluorescence microscopy, it has been possible to observe sieve-tubes in the parenchymatous vascular core and around the xylem strands. It clearly appeared that the phloem of the haustorium is connected to that of the host root. Nevertheless, it has not been possible to distinguish with certainty the relationship between the phloem of the haustorium and that of the host root.

Conclusions

This anatomical and ultrastructural study of the haustorium of S. gesnerioides has enabled us to describe histological and cytological features related to the physiology of the haustorium.

It appears that the meristematic-like cells which are at least partly responsible for the growth of the haustorium, have similar cytological features with cells of hyaline tissue of S. hermonthica, with which they could be homologous. An abundance of endoplasmic reticulum and ribosomes suggests that these cells could be the centre of synthesis directed towards differentiation of other cellular categories or protein formation.

Intrusive cells in haustoria of both S. hermonthica and S. gesnerioides show the same cytological features described on similar structures involved in the penetration of the host (Dobbins & Kuijt, 1973).

The presence of phloem in the haustorium of S. gesnerioides raises the question of the means of translocation of organic compounds from the host plant through the haustorium. It is interesting to note that the presence of phloem in the haustorium in this species is apparently unique to the genus Striga. As far as it is known, there is no organic connection between the phloem of the haustorium and the host plant.

DISCUSSIONS AND CONCLUSIONS

Structure and Ultrastructure of the Haustorium

The anatomy of the haustoria of European and North American parasitic Scrophulariaceae has been studied by many authors. Musselman and Dickison (1975) have summed up these studies in their publication. Tropical parasitic Scrophulariaceae have been less studied. For the two species considered here (S. hermonthica and S. gesnerioides), their anatomical investigations have been made earlier by Okonkwo (1966a), Okonkwo and Nwoke (1978). The results presented in this paper generally confirm those of other authors.

Vascularisation of the Haustorium

Generally a xylem bridge links the host xylem to that of the parasite in mature haustoria. The haustorium of S. hermonthica is connected by a single strand of xylem itself consisting of many strands. The axial strand is "interupted" near the host root by a transvere system of tracheids and the radial system. The vascularisation of S. gesnerioides haustorium is more complex than that of S.hermonthica and S. asiatica. This is related in part to the difference in haustorium size, but also to the nature of the relations each Striga spp. has with its host.

Striga hermonthica and S. gesnerioides are characterized by the lack of phloeotracheids. In fact, anatomical and ultrastructural investigations have permitted us to verify the lack of these imperforate vascular elements containing glycoprotein granules in the haustorium of some Santalaceae (Fineran, 1974; Fineran et al, 1978). We have observed granules in the tracheids of the parenchymatous vascular core of both S. hermonthica and S. gesnerioides, but those elements are perforated, therefore they do not correspond to the phloeotracheids.

The Phloem

The lack of phloem in the haustorium of S. hermonthica raises a question about the translocation of organic compounds through the haustorium. For this species it has been established that it takes up organic compounds from its hosts (Okonkwo, 1966b). More generally, Dobbins and Kuijt (1973), think that "all Scrophulariaceae, chlorophyllous or not, take up important quantities of organic compounds from their hosts". It is very likely that organic compounds of S. hermonthica thus taken up, could migrate, at least partly, through the intertracheidal parenchyma in the vascular axial strand which possesses sieve plates and plasmodesmata when viewed in traverse sections. This hypothesis is all the more plausible since neither phloeotracheids nor transfer cells could be found in the haustorium of S. hermonthica.

The presence of phloem in the haustorium of S. gesnerioides answered a classical question concerning the translocation of organic compounds through a haustorium. Phloem has been observed in the haustoria of other parasitic flowering plants like Phoradendron flavescens (Calvin, 1967), Viscum album (Sallé, 1976), Orobanche ramosa (Dörr & Kollmann, 1975), Cuscuta spp. (Sabine et al, 1980), Castilleja sulfurea (Kuijt & Dobbins, 1971), Alectra vogelii (Dörr et al, 1979) and S. gesnerioides (Ba, 1983). This list contains less than 10 of the 3,000 known parasitic phanerogams. The list will lengthen when modern methods are used to investigate the presence of sieve cells. Nearly half of the species known to possess phloem in their haustorium (Orobanche spp., Cuscuta spp., Alectra vogelii) have been discovered by the same authors (Dörr et al, 1979), who used classical anatomy, fluorescence microscopy and transmission electron microscopy in their studies. The same techniques enabled us to confirm the absence of phloem in the haustorium of S. hermonthica, and its presence in S. gesnerioides. It is therefore probable that other parasitic flowering plants which have not yet been studied using the above methods, may possess phloem in their haustoria.

This observation leads us to wonder about the presence or absence of phloem in the haustoria of these parasitic plants. Some authors have tried to answer that question through inferences. Kuijt and Dobbins (1971) who observed sieve cells in the haustorium of Castilleja sulphurea, concluded that such cells "appeared only in old haustoria". However, this is not the case for S. gesnerioides. Kuijt (1977), thought that the presence of sieve tubes in the haustorium of species belonging to the Santalaceae and mistletoes, such as Phorandendron flavescens and Viscum album could relate to the photosynthetic activity of the cortical cells than to the process of absorption of substances from the host. Sallé (1977), after the discovery of sieve tubes in the endophyte of Viscum album, presented a hypothesis indicating that sieve tubes occur only in parasitic phanerogams of large size, and only when they were hemiparasites. It is noteworthy to observe that S. gesnerioides, which is a hemiparasite of small size, and Cuscuta spp. which is not a hemiparasite, both possess phloem in their haustoria.

The number of species in which phloem has been oberved is still small. This group of species is not large enough to present any evidence of the distinctive characteristics that could separate them from the other parasitic phanerogams.

It is therefore necessary that research be undertaken on a larger number of species to determine the presence or absence of sieve tubes in haustoria.

Hyaline Tissue of Striga Hermonthica

This tissue has been called "nucleus" by Okonkwo (1966a). Stephens (1912) named the same tissue "nucleus" in the haustorium of S. asiatica. Both investigators borrowed the term from Barber (1906) who used it to mean a core of parenchymatous cells in the haustorium of Santalum album. Kuijt (1977), proposed that the term "nucleus" should not be used, in order to avoid confusion. Nevertheless some authors still use it. We prefer to use the term "hyaline tissue" to describe more accurately such tissue in the haustorium of Lathraea clandestina as described by Renaudin (1974), who also showed that the tissue stored protein. Rogers and Nelson (1962), working on S. asiatica arrived at the same conclusion on the possible role of the hyaline tissue. The alloxane-Schiff test administered on the hyaline tissue of S. hermonthica revealed the presence of proteins. Other aspects of our observations showed that the hyaline tissue manifested itself together with cortical parenchyma and certain elements of the vascular axial strand and intrusive cells. Except for this tissue, we have observed no other structure similar to the vascular cambium which Musselman and Dickison (1975) seem to consider as a structure common to parasitic flowering plants. The hyaline tissue therefore behaves as a cambium which differentiates into parenchyma, tracheids and intrusive cells. The amount of protein found in this hyaline tissue enables it to behave as a storage tissue. However, only further biochemical studies of this tissue, and the analysis of the evolution of its proteins during the development of the plant, can confirm its true nature.

The presence of callose on the hyaline tissue cell walls of S. asiatica led Rogers and Nelson (1962) to believe that such tissue could share similar features with the phloem. The same authors found that organic compounds taken up by the parasite from its host passed through the hyaline tissue. Using aniline blue as fluorochrome, we noticed the presence of callose on the cell walls of the hyaline tissue of S. hermonthica. Ultrastructural investigations showed clearly that those cells are not cytologically similar to sieve cells. The interpretation of Rogers and Nelson (1962) probably results from an error in the handling of the radioactive compounds applied, which may have migrated into the hyaline tissues.

To conclude, we hope that histophysiological studies will be undertaken to determine the function or functions of the tissue which serves as meristem and as storage tissue, according to the above authors.

Collenchyma

Dobbins and Kuijt (1973), and Musselman and Dickison (1975) asserted that collenchyma is a common tissue to parasitic Scrophulariaceae. However, this tissue was not observed either in the haustorium of S. hermonthica or that of S. gesnerioides. It is possible that these authors have mistaken the intercellular spaces around the cells of the hyaline tissue of S. hermonthica for parietal thickening of collenchyma cells. Renaudin (1974) studying Lathraea clandestina and Renaudin and Cheguillaume (1977) working on Thesium humifusum observed intercellular spaces instead of parietal thickening in the hyaline tissue of these two species.

Meristematic-like Cells of the Haustorium of Striga Gesnerioides

These cells are located in a subapical position in the endophyte. They differentiate into parenchymatous cells, tracheids and intrusive cells. The alloxane-Schiff test revealed the presence of proteins in this tissue. Callose was also found on the cell walls of the same tissue. These observations led us to conclude that the hyaline tissue of S. hermonthica, the meristematic-like cells of S. gesnerioides and similar tissues in haustoria of other parasitic Scrophulariaceae are anatomical structures that could be considered as secondary meristem. This particular secondary meristem, in addition to its normal role, may have other roles such as the storage of proteins, depending upon the character function and specificity of the haustoria of parasitic plants.

Intrusive cells

These cells have been recognized in the haustorium of many parasitic, flowering plants. According to many authors, these intrusive cells are different and are named as follows : palisade cells (Kuijt, 1969), columnar cells (Malcolm, 1966), appressorial cells (Williams, 1960), digitate cells or intrusive cells (Kuijt, 1977) and cellules absorbantes (absorbing cells) (Renaudin, 1974). In both S. hermonthica and S. gesnerioide they are characterized by their size and their content (Dobbins & Kuijt, 1973; Renaudin, 1974; Sallé, 1977). They always possess the same cytological features of secreting cells with a dense cytoplasm, a prominent endoplasmic reticulum, a large number of ribosomes and dictyosomes and a voluminous polyploid nucleus, often lobed.

Inside the haustorium, these intrusive cells are often preceded by a mucilaginous dark substance, opaque to electrons. According to Sallé (1977), this substance may be secreted by the intrusive cells and would be of a polysaccharidic nature. According to Musselman and Dickison (1975), the substance, which is stained red by safranin, is P.A.S. negative and so could not be of a polysaccharidic nature. Whatever its nature may be, many authors think that it may play an important part in the process of host penetration by preceding the action of intrusive cells.

Penetration and Fixation of the Parasite on the Host

Mechanisms involved in the process of penetration, and particularly the penetration of parasitic flowering plants are not completely understood. However, since we have no proof, many arguments forwarded lead us to think of an enzymatic or mechanical action of some sort. Most of the earlier authors suggest an enzymatic action (Leclerc du Sablon, 1887; Hocquette & Arsigny, 1931). Other authors think that the mechanical and enzymatic actions are associated with predominance of enzymatic action (Barber, 1906; Stephens, 1912; Saunders, 1933; Okonkwo, 1966a; Dobbins & Kuijt, 1973; Renaudin, 1974; Sallé, 1977). Nevertheless, very few authors have shown enzymes in the contact area between parasite and host tissues. Enzymes that may play a role in the degradation of cell walls of the host may be cellulases and pectinases. Only

Renaudin (1977) has revealed cellulases in the haustorium of Lathraea clandestina. We tried Renaudin's techniques on the haustoria of both S. hermonthica and S. gesnerioides, without success. Other authors have found other enzymes in the haustoria of some parasitic flowering plants. Enzymes discovered were mostly acid phosphates (Rodrigues & Pannier, 1967; Tripodi, 1970; Onofeghara, 1972; Toth & Kuijt, 1977; Renaudin, 1977; Ba & Kahlem, 1979). Toth and Kuijt (1977) think that acid phosphates would be secreted by the cells of the endophytes and would attack and soften the host cell. Our opinion is that these acid phosphates are not directly responsible for the degradation of the host cell walls, but are certainly involved in the catabolic process which are the origin of that degradation. These results are indirect arguments, but the proof of the existence of enzymes which are thought to act on the host cell wall, is not yet found. For so doing, histochemical techniques which take into account the low concentration of those enzymes will be needed.

Structures involved in the penetration include a dark substance and the enzymes that precede the action of intrusive cells. These intrusive cells ensure the penetration, but later are differentiated into tracheids. Multiplication and enlargement of meristematic cells localised behind the intrusive cells are responsible for the mechanical pressure exerted by the tissues of the parasite upon those of the host plant. Of the tissues in the host plant which are less resistant (cortical parenchyma) this action is more or less visible while it is always very striking on more resistant tissue like the endoderm.

The process of penetration and fixation of the parasites on their hosts is complex and still difficult to analyze. More investigations are necessary. It is hoped that the answers to some of the questions raised in this review will help us to understand how this type of parasitism operates. Perhaps researchers could find some clue to the eradication of these noxious plants through further investigation of the anatomy of the genus.

REFERENCES

BA, A.T. (1983), "Biologie du parasitisme chez deux Scrophulariadées tropicales Striga hermonthica and Striga gesnerioides", Thèse Doct. Sci. Nat., Dakar

BA, A.T. & KAHLEM, G (1979), "Mise en évidence d'activités enzymatiques au niveau de l'haustorium d'une phanérogame parasite : Striga hermonthica (Scrophulariaceae)", Can. J. Bot. 57 (22) : 2564-2571

BARBER, C.A. (1906), "Studies in root-parasitism. The haustorium of Santalum album 1. Early stages, up to penetration", Mem. Dept. Agr. India, Bot. Ser. 1 (1) : 1-30

BERHAUT, J. (1967), "Flore du Sénégal", Editions Clairafrique, Dakar

CALVIN, C.L. (1967), "Anatomy of the endophytic system of the mistletoe Phoradendron flavescens", Bot. Gaz. 128 : 117-137

DOBBINS, D.R. & KUIJT, J. (1973), "Studies on the haustorium of Castilleja (Scrophulariaceae - II. The endophyte", Can. J. Bot. 51 : 923-981

DORR, I. (1968), "Zur lokalisierung von zellkontakten zwischen Cuscuta hyphen", Protoplasma 67 : 123-137

DORR, I. & KOLLMAN, R. (1975), "Strukturelle grundlagen des Parasitismus bei Orobanche I. Die differenzierung des assimilat-leitungsbahn im haustorialgewebe", Protoplasma 83 : 185-199

DORR, I., VISSER, J.H. & KOLLMAN, R. (1979), "On the parasitism of Alectra vogelii. Benth (Scrophulariaceae), III. The Occurence of phloem between host and parasite", Z. Pflanzenphysiol. 94 : 427-439

FINERAN, B.A. (1974), "A study of phloeotracheids in haustoria of Santalaceous root parasites using scanning electron microscopy", Ann. Bot. 38 : 937-946

FINERAN, B.A., JUNIPER, B.E. & BULLOCK, S. (1978), "Graniferous tracheary elements in the haustorium of Santalaceae", Planta, 141 : 29-32

HOCQUETTE, M. & ARSIGNY, L. (1931), "Secrétion par le meristème caulinaire de Cuscuta epithymum de substances nocives pour les tissus de l'hôte", C.R. Acad. sc. Paris 192 : 764

KUIJT, J. (1969), "The biology of parasitic flowering plants", Berkeley Univ. Calif. Press. 246 pp

KUIJT, J. (1977), "Haustoria of phanerogamic parasites", Ann. Rev. Phytopathol. 15 : 95-118

KUIJT, J. & DOBBINS, D.R. (1971), "Phloem in the haustorium of Castilleja (Scrophulariaceae)", Can. J. Bot. 49 : 1735-1736

LECLERC DU SABLON, M. (1887), "Observations anatomiques sur la structure et le développement des suçoirs du Melampyrum pratense", Bull. Soc. Bot. Fr. 34 : 154-160

MALCOLM, W.M. (1966), "Root parasitism in Castilleja", Ecology, 47 : 179-186

MUSSELMAN, L.J. (1973), "On the anatomy of the haustoria of parasitic Scrophulariaceae", Proc. Eur. Weed. Res. Counc. Symp. Parasit. Weeds : 140-148

MUSSELMAN, L.J. & DICKISON, W.C. (1975), "Structure and development of haustorium in parasitic Scrophulariaceae", Bot. J. Linn. Soc. 70 : 183-212

OKONKWO, S.N.C. (1966a), "Studies on Striga senegalensis Benth. I. Mode of the host-parasite union and haustorial structure", Phytomorphology 16 (4) : 453-463

OKONKWO, S.N.C. (1966b), "Studies on Striga senegalensis Benth. II. Translocation of C-14 labelled photosynthate urea C-14 and sulphur-35 between host and parasite", Am. J. Bot. 53 : 142-148

OKONKWO, S.N.C. & NWOKE, F.I.O. (1975), "Observations on haustorial development in Striga gesnerioides (Scrophulariaceae)", Ann. Bot. 39 : 979-981

OKONKWO, S.N.C. & NWOKE, F.I.O. (1978), "Initiation, development and structure of the primary haustorium in Striga gesnerioides (Scrophulariaceae)", Ann. Bot. 42 : 455-463

ONOFEGHARA, F.A. (1972), "Histochemical localization of enzymes in Tapinanthus bangwensis : acid phosphatase", Am. J. Bot. 50 : 549-556

OZENDA, P. & CAPDEPON, M. (1972), "Recherches sur les phanérogames parasites: II. Une Scrophulariacée holoparasite méconnue, Striga gesnerioides", Phytomorphology, 22 : 314-324

OZENDA, P. & CAPDEPON, M. (1979), "L'appareil haustorial des phanérogames parasites", Rev. Gen. Bot. 86 : 235-343

RAO, L.N. (1942), "Parasitism in Santalaceae", Ann. Bot. 6 : 131-150

RENAUDIN, S. (1974), "Contributions à l'étude de la biologie des phanérogames parasites : recherches sur Lathraea clandestina L. (Scrophulariaceae)", Thèse Doct. Sc. Nat. 203 p

RENAUDIN, S. (1977), "Mise en évidence d'activités enzymatiques au niveau des suçoirs de Lathraea clandestina", Bull. Soc. Bot. Fr. 124 : 419-425

RENAUDIN, S. & CHEGUILLAUME, N. (1977), "Sur quelques aspects de l'ultrastructure des suçoirs de Thesium humifusum", L. Protoplasma 91 : 55-69

RODRIGUEZ, M.P. & PANNIER, P. (1967), "Etude de la distribution de la phosphatase acide dans l'haustorium primaire de Phthirusa pyrifolia", (H.B.K.) Eichl. (Loranthaceae), Rev. Gen. Bot. 76 : 625-635

ROGERS, W.E. & NELSON, R.R. (1959) "Studies on the translocation of minerals and carbon compounds between corn and Striga asiatica", J. Elisha Mitchell Sci. Soc. 75 : 67

ROGERS, W.E. & NELSON, R.R. (1962), "Penetration and nutrition of Striga asiatica", Phytopathology, 52 : 1064-1070

SABINE, I., DORR, I. & KOLLMANN, R. (1980), "Das phloem der haustorium von Cuscuta", Protoplasma, 103 : 309-321

SALLE, G. (1976), "Le phloème dans les cordons corticaux du Viscum album L. (Loranthacées)", Protoplasma 87 : 17-25

SALLE, G. (1977), "Etude cytologique, cytochimique et histo-autoradiographique du Viscum album L. (Loranthacées)", Thèse Doct. Sci. Nat. Paris

SAUNDERS, A.R. (1933), "Studies in phanerogamic parasitism with particular reference to Striga lutea Lour.", Dep. Agric. S. Afr. Bull. 128 : 1-57

STEPHENS, E.L. (1912), "The structure and development of the haustorium of Striga lutea Lour.", Ann. Bot. 26 : 1067-1076

TAIGUI, B. (1956), "A contribution to the embryology of Striga orobanchoides Benth. and Striga euphrasioides Benth.", Bull. Torrey Bot. Club 83 : 154-170

TOTH, R. & KUIJT, J. (1977), "Cytochemical localization of acid phosphatase in endophytic cells of the semi-parasitic angiosperm Comandra umbellata (Santalaceae)", Can. J. Bot. 55 : 470-475

TRIPODI, G. (1970), "Localization of tryptophan-rich proteins and glycerophosphatase activity in Cuscuta haustorial cells", Protoplasma 71 : 191-196

UTTAMAN, P. (1950), "A study of the germination of Striga seed and on the mechanism and nature of parasitism of Striga lutea on rice", Proc. Indian Acad. Sc. 32B : 133-142.

WILLIAMS, C.N. (1960), "Sopubia ramosa, a perennating parasite on the roots of Imperata cylindrica", Jour. W. Afr. Sci. Assoc. 6 : 137-141

ZIEGLER, H. (1955), "Lathraea ein Blutungssaftschmarotzer", Ber. Deuts. Bot. Ges. 68 : 311-318

STRIGA HERMONTHICA : ITS ADAPTATIONS AND DISTRIBUTION IN GHANA

E. Laing

INTRODUCTION

Striga hermonthica, like other species of the genus Striga (family Scrophulariaceae), is an important root parasite of a number of economically important crop plants in various parts of the tropics and sub-tropics of Africa (Dalziel, 1955; Doggett, 1970; Hepper, 1963; Irvine, 1974; Purseglove, 1975). The family Scrophulariaceae is noted for the range of modes of nutrition displayed by various members, some species being chlorophyll-less parasites, some chlorophyll-containing parasites (Lawrence, 1963). Biologically it is worth recognizing Striga's mechanisms of adaptation to its peculiar mode of existence. A knowledge of its distribution may assist in understanding its present agricultural importance, and in pointing to possible problems it can pose to intensified cultivation of various crop plants especially in the savanna areas of the country.

This note reviews the gross adaptive features of Striga spp., and summarizes some data available in the Ghana Herbarium on collections of S. hermonthica from various part of Ghana (and a few from outside Ghana).

ADAPTIVE FEATURES OF STRIGA

On a priori grounds, we would expect to find both structural and functional adaptations of any species to its mode of existence and also to find the adaptation reflected at all levels of organization of the anatomy and physiology of the species. In the case of Striga, the most striking gross adaptive features are outlined below.

Striga spp. display a high reproductive capacity, like many other parasites or species with precarious chances of survival before the reproductive stage. The fruit (capsule) contains a large number of small seeds (reminiscent of seed production in the orchids).

The seeds, partly on account of their size, are efficiently dispersed by animals and, inadvertently, by man. As contaminants of seeds or fruits of cultivated plants, the seeds must be transported by man over large distances - a situation that may be exacerbated by the efficiency of modern transport.

Survival of the seed is aided by its extensive longevity, especially in dry soil.

The seed is stimulated to germinate by the host plant, the potential victim of the parasite (Purseglove, 1975). This phenomenon is an impressive example of teleonomic design in adaptive strategy.

Agriculturally, the vegetative stage of the parasite may lead a cryptic subterranean existence, and hence may escape detection by farmers. The fact that under severe intra-specific competition among individuals of Striga the plants may remain subterranean, means that it is precisely when the parasite is most abundant and most damaging to a crop host plant species that it evades detection (Purseglove, 1975).

The haustorium is an important vegetative, anatomical and physiological adaptive mechanism, assuring the parasite of an efficient and secure attachment to the root of the host plant (Stephens in Metcalfe & Chalke, 1957).

Striga spp. display a wide host range, parasitizing species belonging to such taxanomically widely separated families as Gramineae, Papilionaceae, Compositae and Malvaceae (Dalziel, 1955; Irvine, 1974).

The geographical range is equally impressive. This is illustrated by S. hermonthica occurring in East, North and West Africa (Purseglove, 1975).

The occurrence of a series of chromosome numbers related as diploid and tetraploid among the parasitic species in the family Scrophulariaceae suggests the possibility of polyploid complexes (Kumar, 1941 in Darlington & Wylie, 1955). While Striga spp. have $2n = 40$ ($x = 10$), related parasitic species Odontites possess $2n = 20$ ($x = 10$), and Euphrasia has $2n \times 22, 44, 45$ ($x = 11$) (Darlington & Wylie, 1955).

REPRODUCTIVE POTENTIAL OF STRIGA HERMONTHICA

The Ghana Herbarium holds a number of vouchers of various species of the genus Striga. Those belonging to the species S. hermonthica, mainly collected within Ghana (but with a few collected in Nigeria) are listed with data on their inflorescence in Table 1.

To provide an idea of the reproductive potential of S. hermonthica, estimates were made of the actual and the potential output of capsules and of seeds per plant, the number of seeds per capsule, and the seed size, in the 20 Ghanian specimens in the herbarium. Potential seed output was based upon the estimated mean number of seeds per capsule and the number of flowers and fruits, i.e. assuming all flowers and fruits would yield seeds. The number of seeds per capsule, based on three capsules and the potential seed output per plant are shown in Table 2.

Seed size was measured on 30 dry seeds of Specimen GC 37954. The data are summarized in Table 3.

The number of capsules per plant was 19.4 (actual) and 25.8 (potential, i.e. flowers and fruits), with ranges 0 to 80 and 0 to 88 respectively. Potential number of seeds per plant (assuming all flowers and fruits would produce seeds) was 37,360 (range 7,840 to 84,392). The number of seeds per capsule was 644 (range 196 to 1,171). Seed dimensions were found to be 375 microns long (standard deviation 47 microns) and 163 microns wide (standard deviation 24 microns).

These data illustrate the high reproductive potential of S. hermonthica.

COMMENTS

Striga hermonthica occurs in the savanna of the northern third of Ghana. Other species of Striga also occur in the savanna of the Accra Plains and in the grassland of the Volta gap connecting the northern savanna and the coastal savanna (Hepper, 1976). It is obvious that the parasite is available in the area where the cultivation of cereals is being intensified, and hence, agriculture in this area must reckon in the future with possible crop losses from Striga attack.

The array of adaptive mechanisms displayed by Striga spp. must have been concentrated in the genus of its component species by recombination during the evolution of the genus. We suggest from this observation that the breeding system of Striga is likely to be versatile, and that evolution by mutation and hybridisation may be continuing in the genus, possibly aided by man. The grassland habitat of Striga is an area subjected to periodic fires and intense cultivation by man. Modern agriculture (with irrigation schemes) is likely to maintain this disturbance of the ecosystem, thus encouraging hybridisation of the habitat (Anderson, 1948), and also to introduce the possibility of wider dispersal by modern transport of the seeds of the parasite. These circumstances are likely to maintain the further evolution of the genus Striga.

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Table 1 : Striga hermonthica specimens in the Ghana Herbarium: Data on Inflorescence

Voucher Number (and year of collection)	Locality (and notes)	Number of Inflorescence Branches (and number on which flower and fruit counts are based)	Number of Flowers, Immature and Mature, and their Total	
GC 37855 (1967)	Bongo, near Bolgatanga	7 (1)	10, 0, 0	10
GC 37957 (1967)	Winkogo to Tongo (damp roadside)	15 (2)	8, 56, 24	88
GC 37954 (1967)	Winkogo to Tongo (wet grassland)	4 (1)	13, 23, 12	48
GC 36000 (1966)	Zause near Bawku (corn field)	6 (1)	17, 10, 12	39
GC 9876 (1953)	Ziong, Tamale Road (cultivated field)	7 (2)	7, 20, 13	40
GC 6214 (1951)	Tamale Rest House (guinea corn field)	19 (2)	10, 45, 0	55
A 1333 (1954)	Bawku (grassland on hill)	1 (1)	7, 0, 0	7
268 (1935)	Tamale agricultural station (parasitic on guinea corn root)	2 (2)	0, 0, 0	0
268 (1935)	Tamale agricultural station (parasitic on guinea corn root)	1 (1)	0, 0, 0	0
368 (1935)	Tamale agricultural station (parasitic on guinea corn root)	1 (1)	2, 0, 0	2
268 (1935)	Tamale agricultural station (parasitic on guinea corn root)	2 (2)	0, 0, 0	0
GC 30748 (1958)	Bunkpurugu (guinea corn field)	4 (2)	16, 0, 0	16
4107 (1950)	Paliba, near Oti River (among grass on edge of millet field)	13 (2)	0, 4, 24	28

Table 1 (cont.)

Voucher Number (and year of collection)	Locality (and notes)	Number of Inflorescence Branches (and number on which flower and fruit counts are based)	Number of Flowers, Immature and Mature, and their Total	
A 1394 (1954)	Gambaga (guinea corn field)	9 (2)	16, 0, 42	58
GC 400 (1965)	Savelugu (cultivated field)	3 (1)	8, 5, 8	21
Achimota Herbarium (1933)	Tamale agricultural station (parasitic on guinea corn root)	9 (2)	4, 22, 10	36
443 (1950)	Tongo, near Zuarungu (on orchid?)	10 (2)	0, 36, 22	58
Achimota Herbarium (1921)	Yendi	1 (1)	3, 0, 0	3
Achimota Herbarium (1958)	Bole (marsh)	1 (1)	3, 0, 0	3
40575 (1950)	Yendi	10 (1)	6, 0, 0	6
*FHI 64088 (1971)	Elekoyangan, Ilorin (Kwara State)	3 (1)	6, 18, 0	24
*IUH 15199 (1973)	Botany Dept. University of Ibadan	5 (2)	11, 70, 0	81
*FHI 62230 (1968)	Egbe, Yagba (Kabba Province)	9 (2)	4, 62, 0	66
*UIH 11431 (1968)	Gombe	2 (1)	6, 6, 0	12

The last four marked with an asterisk are Nigerian specimens

Table 2 : **Striga hermonthica: number of seeds per capsule**

Specimen	Number of Seeds per Capsule			Mean	Number of Flowers and fruits	Potential Seed Output
GC 9876	198	203	187	196	40	7840
HC 36000	232	224	219	225	39	8775
GC 37954	1241	1101	1171	1171	48	56208
GC 37957	817	929	1130	959	88	84392
4107	320	214	376	303	28	8484
A 1394	1312	801	912	1008	58	58464
	Overall			644	50	32307

The figures give the number of seeds in three capsules. Potential seed output is based on the mean number of seeds per capsule and the number of flowers and fruits

Table 3 : **Striga hermonthica: data on seed size, based on 30 dry seeds of Specimen GC 37954**

	Length (μm)	Width (μm)
Mean	375	163
Range	270 to 472	122 to 216
Standard deviation	47	24

REFERENCES

ANDERSON, E. (1948), "Hybridisation of the habitat". In Ehrlich, P.R., Holm, R.W. and Raven, P.H. (Ed.) 1969. Papers of evolution, Little, Brown & Co. Boston, 173-181, (originally in Evolution, 2, 1-9)

DALZIEL, J.M. (1955), "The useful plants of west Africa", Crown Agents for Overseas Governments & Administrations, London

DARLINGTON, C.D. & WYLIE, A.P. (1955), "Chromosome Atlas of flowering plants", George Allan & Unwin, London, pp. 519

DOGGETT, H. (1970), "Sorghum improvement in east Africa", in Leakey, C.L.A. (Ed.) 1970. Crop improvement in east Africa, Commonwealth Agricultural Bureaux, Farnham Royal

HEPPER, F.N. (1963), Scrophulariaceae", in Flora of west tropical Africa. Eds. Hutchinson, J. & Dalziel, J.M., Crown Agents for Overseas Governments & Administrations, London

HEPPER, F.N. (1976), "The west Africa herbaria of Isert and Thonning", Bentham-Moxon Trust, Royal Botanic Gardens, Kew

IRVINE, F.R. (1974), "West African crops", Oxford University Press

LAWRENCE, G.H.M. (1963), "Taxonomy of vascular plants", Macmillan, New York

METCALFE, C.R. & CHALK, L. (1957), "Anatomy of the dicotyledons", Vol. II, Clarendon Press, Oxford

PURSEGLOVE, J.W. (1975), "Tropical crops : monocotyledons", English Language Book Society & Longman, London, pp. 607

PATTERNS OF STRIGA RESISTANCE IN SORGHUM AND MILLETS WITH SPECIAL EMPHASIS ON AFRICA

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SUMMARY

Although host plant resistance in sorghum was demonstrated as early as 1920 both in Africa and India, its exploitation in breeding broad-spectrum stable resistant cultivars started only recently. In pearl millet, however, the existence of host plant resistance is not yet clearly demonstrated. *Striga*-resistant sorghum varieties are in general agronomically poor. Multi-locational evaluation in Africa revealed that Framida and N 13 are the most stable resistant varieties. These two varieties were resistant to both *S. asiatica* and *S. hermonthica*. Some of the varieties like Najjadh, 12610C and IS 9830 revealed a narrow spectrum of resistance when tested across different seed samples of *S. hermonthica*. Genetic analysis of field resistance in sorghum revealed that it is controlled predominantly by additive gene action and thus straight selection is effective. A pedigree approach to transfer resistance into elite agronomic backgrounds was successful. Several selections with promising levels of resistance, stable grain yields and good grain quality were identified and are now in 'on farm' tests. In millet, a few less susceptible lines have been identified. Intercrossing them and following the pedigree system of selection resulted in increased levels of resistance and grain yields. The need for integrated *Striga* management, including resistant cultivars and complementary agronomic control practices, is emphasised.

INTRODUCTION

Breeding for increased grain yields and quality in cereals has been known for several years. Spectacular yield increases were obtained in several cereal crops like wheat, rice, maize and sorghum, leading to the Green Revolution in several countries. Insect and other disease pests have drawn the attention of plant breeders to the fact that these pests are important yield-reducing factors. Relatively recently, work on the development of crop varieties resistant to those pests was initiated. *Striga* is still considered merely as a weed, but not as an important crop pest by farmers and administrators alike. As such, very little attention has been paid to its control. Many farmers are not even aware that *Striga* produces seed and that the seed production should be checked by weeding out *Striga* before it flowers. Resistant varieties of sorghum were identified as early as 1920, but serious efforts to exploit them and develop stable resistant cultivars with acceptable food quality and increased grain yields started only recently. *Striga* is widespread throughout the semi-arid tropical regions of Africa; it is very rare that one finds a filed of sorghum or millet without a *Striga* plant. Being an obligate parasite, it causes enormous damage to the host plant.

LOSSES DUE TO STRIGA

Striga hermonthica causes serious crop losses in sorghum and millet and it is present in most areas where these crops are grown. Yield loss estimates vary. In our own trials we found that yield reduction varied from 10-35%. In ordinary farm crops, the losses are much higher and often lead to total crop failure. Doggett (1965) estimated reduction in yield to be about 1 kg for every 1,000 plants of Striga. In one of our trials it was found that a yield reduction of 10% represented the presence of Striga density of 15,000/ha. In peasant farms the Striga densities are often much higher.

Sorghum and millet are the principal staple food crops in Africa and are grown in almost all African countries. The area under cultivation, average grain yields (kg/ha), and total production for sorghum, millet and maize and also the figures for all cereals, including wheat and rice are given in Table 1. The value of all the cereals in Africa is estimated at US $17.479 billion, based on 1983 prices for coarse grains. Striga can attack all the rainfed cereals in Africa, particularly sorghum, millet and maize. The approximate value of these three crops is US $12.438 billions. Yield losses due to Striga range anywhere from 10 to 100%. Thus, if Striga spreads to all the areas where these crops are grown, the value of the crop loss due to Striga may range from US $1.2 billions to total loss. Even though Striga is not present everywhere now, it is likely to spread to other non-infested areas in due course. Thus it is expected to pose a serious threat to the cultivation of rainfed cereals in Africa if adequate control measures are not taken immediately.

STRIGA CONTROL

Striga can be controlled in several ways, namely :

a) by methods which lead to the depletion of Striga from the soil, such as trap crops, catch crops, ethylene gas, strigol analogues, methyl bromide fumigation, etc., and
b) by those which limit and/or reduce Striga reproduction, such as hand weeding before flowering, herbicides, seed hardening, resistant varieties, fertilizers, irrigation, shading-intercropping, or mulching or high crop density, biological control, etc.

HOST PLANT RESISTANCE IN SORGHUM

Exploitation of host plant resistance in sorghum started in South Africa in the 1920's (Saunders, 1933) and then in Nigeria, Sudan, Ethiopia and in Upper Volta. The resistant varieties reported in South Africa, Zimbabwe, Tanzania, Sudan and Nigeria are listed in Table 2. Most of these varieties, with the exception of SRN 4841 (Framida), have local usefulness with narrow spectrum resistance. Varieties like 37R9, 37R29, 37R37, N Sorte and P 41 are not available now. An ICRISAT project, based in Upper Volta, has been testing several varieties of sorghum from the world collection in breeding programmes and from other programmes in Africa in its regional trials since 1977. A few varieties are identified as possessing satisfactory levels of resistance. The promising varieties are listed in Table 3. The agronomic characteristics of some of the promising varieties are given in Table 4. Among these varieties, IS 9830, Tetron and Entry 39 are low stimulant producers, whereas Framida is a low stimulant and has root cell wall thickenings (El Hiweris, personal communication). Other varieties such as N 13, Najjad and SPV 103 produce stimulants, and so are suspected of having other forms of resistance such as anti-haustorial factors, etc.

The stability analysis (Ramaiah, 1983a) of some sorghum varieties in several African countries revealed N 13 and Framida as the most stable varieties for Striga resistance as indicated by their very low mean emergence of Striga plants and a regression coefficient close to zero (Table 5).

Extensive field trials conducted in Upper Volta by breeders, agronomists and economists revealed that Framida, in addition to Striga resistance, has several other desirable traits like stable grain yields, excellent seedling establishment and early seedling drought resistance, acceptable food quality and is suitable for intercropping. The results of 'on farm' testing in 1980, 1981 and 1982 are presented in Table 6. In 1980, the results from several African countries revealed that N 13, and SPV 103 were resistant, whereas Framida exhibited moderate levels of resistance. Grain yields with Framida were, however, superior to all the varieties tested. N 13 and SPV 103 produced grain yields much inferior to the local varieties. Because of its higher yield potential, in 1981, Framida continued to be tested in Upper Volta on six fields which were heavily infested with Striga. In the presence of Striga, Framida's superior yield over the local varieties was very striking, showing an overall increase in yield of 80%. Encouragingly, Framida is attacked by only 25% Striga compared to the local varieties. In 1982, the results from ICRISAT's economic programme in Upper Volta demonstrated the stability of Framida under both traditional and improved managements.

RESISTANCE OF SORGHUM VARIETIES ACROSS STRIGA spp.

There are two major Striga spp., S. hermonthica and S. asiatica, for which host plant resistance is sought. There has been only one report that resistance of sorghum varieties to S. asiatica (South Africa) does not hold against S. hermonthica (Doughty, 1941). At the ICRISAT Centre in India, several varieties have been identified as resistant to S. asiatica (Indian). These were further tested at other locations, in India against S. asiatica and in several locations in Africa against S. hermonthica, The results (expressed as percentage of a standard susceptible variety) are presented in Table 7. Some of the varieties like Framida, N 13 and 16-3-4 have exhibited some level of resistance to both species of Striga whereas the other varieties were only resistant to S. asiatica as measured by the number of emerged Striga plants. It seems therefore, that there is a lack of general uniformity in the ways the crops are resistant to S. asiatica and S. hermonthica.

In the breeding programme, selections have been tested against both S. asiatica (at ICRISAT Cente, India) and S. hermonthica with the objective of finding crop cultivars resistant to both species. Much breeding material has been generated. The segregating generations have been simultaneously screened for resistance to both species. In this volume, Dr. Rao has presented a list of promising cultivars which were derived from crosses involving 148, 555 and Framida (SRN 4841) as parents. In Upper Volta, selected progenies were made from crossing involving E 35-1, Framida, etc. The derivatives of crosses involving 148 and 555, which are Indian varieties, did not adapt to African conditions. While these progenies were in general, short, early and low yielding, the progenies from crosses involving E 35-1 and Framida as parents were medium tall, partially photosensitive, and high yielding. Thus, apart from resistance to Striga there are other general adaptation characters which need to be taken into consideration.

One of the selections (entry no. 39 in ISRST-3) from a cross between 148 (an Indian variety) and Framida (an African variety) had shown good levels of resistance to both species and it also has good agronomic characters. 148 was moderately resistant to S. asiatica, whereas Framida is resistant to both species. The selection from this cross was a tan plant with white grain, like 148, and head-shaped with elongated internodes from Framida. Thus, by careful selection from judiciously planned crosses, one could select cultivars resistant to both species.

RESISTANCE OF SORGHUM VARIETIES TO STRAINS OF STRIGA HERMONTHICA

Striga hermonthica is a highly variable species because of cross pollination. There is clear evidence of the presence of at least two strains, one specific to millet and the other to sorghum (Wilson Jones, 1955; Zummo, 1975; Parker & Reid, 1979; Bebawi, 1981; Ramaiah, 1983). The crop specificity is reported to be based on germination stimulant compounds present in the host crop root exudates (Parker & Reid, 1979). The distribution of Striga strains in relation to ecological zones in west Africa indicates that millet and sorghum are the principal hosts in the Sahel and Sudan savanna zones respectively. However, in the northern Guinea savanna and a transition zone between the Sahel and Sudan savanna zones, both millet and sorghum act as hosts (Ramaiah, 1983).

Sorghum is extensively grown in the Sudan savanna zone where S. hermonthica perhaps has evolved different strains. In east Africa the presence of physiological strains in S. hermonthica attacking sorghum was suspected (Doggett, 1952), because two of the sorghum varieties, Dobbs and P 41, that were resistant in one location in Tanzania, were susceptible in another. Our multilocational trials in the Sudan savanna present similar results. It is important in a breeding programme to determine how variable a pathogen is in order to decide the breeding strategies to develop cultivars with stable and broad-spectrum resistance. The results of two of our pot experiments conducted in 1980 and 1981 (Table 8) indicate significant differences among the sorghum varieties and among Striga samples each year. The interaction between varieties and Striga samples was significant in 1981. Sorghum varieties resistant in one year were not resistant in another. For example, Najjad had shown resistance to all three Striga samples in 1980, but showed susceptibility to STS 6 in 1981. Similarly IS 9830 was resistant to all the strains in 1981 but showed susceptibility to STS 2 in 1980. However, IS 1261C had a similar response both years. Framida was consistantly resistant and CK60B was consistently susceptible in both the years. These results indicate the instability of resistance of some of the sorghum varieties and the probable presence of intracrop variants of S. hermonthica which threaten host-plant resistance in sorghum. Availability of varieties with stable resistance like Framida and N 13 (Ramaiah, 1983) indicates the possibility of breeding high yielding cultivars with stable broad-spectrum resistance.

GENETIC ANALYSIS OF FIELD RESISTANCE IN SORGHUM

There are no reports in the literature on the nature of inheritance of resistance to S. hermonthica in sorghum. During the 1982 crop season, the field resistance in some sorghum varieties was analyzed through generation means, diallel, and line x tester analyses. The results are presented in ICRISAT/Upper Volta, Annual Report, 1982. In this paper the results of a pot experiment of a 7x7 diallel are presented.

Seven varieties of sorghum, out of which N 13, Framida, SPV 103 and IS 9830 are resistant, and three varieties, IS 9849, VS 702 and BTx623, are susceptible, were crossed in all possible combinations without reciprocity. Parents and 21 crosses were planted in pots in a Randomised Block Design, with six replications. Observations were taken on the number of emerged Striga plants and their fresh weight.

Heterosis : the means of parents and crosses for the number of emerged Striga plants and Striga fresh weight are presented in Table 9, along with estimates of heterosis over the mid-parent (MP) value. A critical examination of the heterosis values indicate that those cross combinations (involving both resistant parents) which have exhibited maximum positive heterosis have the parents with different resistance mechanisms. Examples are N 13 x Framida, N 13 x IS 9830, Framida x SPV 103, and SPV 103 x IS 9830. On the contrary, crosses involving the parents with the same resistance mechanisms have not exhibited any heterosis. Table 4 shows resistance mechanisms of parents involved in the crosses. The observation that parents with two different resistance mechanisms exhibit positive heterosis in cross combination, indicates that they are probably controlled by different gene loci and that resistance is recessive. When they segregate, it is possible to select for recombinants with both the gene systems. IS 9830 as a female parent in crosses with susceptible varieties did not exhibit any heterosis and perhaps its resistance may be quantitatively inherited. IS 9849 exhibited negative heterosis with N 13, SPV 103 and VS 702.

Combining ability : was analyzed according to method 2 and Model 2 of Griffing (1956). The analysis of combining ability of Striga number and Striga fresh weight is presented in Table 10. For Striga number, both general and specific combining abilities were highly significant, whereas for Striga fresh weight only, general combining ability was significant. For both characters the general combining ability was more important as revealed by the ratio GCA/SCA. Thus, Striga resistance as measured by these two characters is predominantly controlled by the additive genetic factors and therefore straight selection to improve Striga resistance is quite effective.

The general combining ability effects (GCA) of the parents are presented in Table 11. Negative estimates indicate a tendency towards resistance, while positive values refer to susceptibility. All the resistant parents except Framida, produced a significant negative effect, and thus are good general combiners for resistance. Susceptible varieties like BTx623 and IS 9849 were poor combiners for number of Striga plants. For Striga fresh weight, SPV 103 and BTx623 produced significant negative and positive effects respectively. SPV 103 is the best combiner for both Striga number as well as Striga fresh weight.

HOST PLANT RESISTANCE IN MILLET

Pearl millet was not researched for resistance to S. hermonthica until 1979 when ICRISAT started to work on this crop in Upper Volta. Progress was rather slow. During the first few years, several west African local varieties and several introduced varieties were tested in Striga sick plots and selfed to isolate resistant inbred lines. Pot experiments are now being used to screen and isolate single plants from less susceptible varieties identified in the field trials. Two sick plots, one in northern Upper Volta (farmer's field) and one in Niger (Tarna Research Station in Maradi) are being used for screening in the rainy season. A few promising, less susceptible varieties are listed in Table 12, along with their grain yields over several locations and reaction to Striga when tested in Striga sick plots and in pots. Out of the 20 varieties tested, only results for nine are presented. In pot experiments, the Striga infestation was very high, resulting in the death of highly susceptible plants within two months of planting. To show the susceptibility, the number of killed plants was expressed as the percentage of the total number of plants established as seedling for each variety. In 1982, the susceptible check (ex-Bornu) was killed in all the pots; whereas in entry nos. 2, 3, 9 and 15, about 70% of the plants survived. 1983 pot experiments closely agree with the 1982 pot results as well as 1983 field screening. Over the three experiments the promising entries for resistance are 3 (P 2661-3-5), 9 (P 449-1-29) and 15 (P 2627-1-19). They are in general poor grain yielders. In contrast, some of the high yielding entries like 6 (P 2627-2-11), 20 (local) and IS (P 2627-2-18) supported more Striga. Considerable breeding work is required to intercross and select high yielding progenies with less susceptibility.

RESISTANCE IN SEMI-WILD MILLETS (SHIBRAS)

Parker and Wilson (1983) reported semi-wild millets (shibras) collected from Niger as showing promising levels of resistance. Four of their most promising progenies were tested in our pot experiments in 1983, using millet strain of S. hermonthica, collected from the northern region of Upper Volta. A susceptible variety (82W214) was included as a check. Ten plants (one plant in each pot) for each variety were tested. All five varieties showed a high level of susceptibility as indicated by the number of emerged Striga plants and the percentage of millet plants killed in each variety when observed eleven weeks after sowing. A few plants in each variety survived, which were selfed for further testing.

BREEDING STRATEGIES

Breeding procedures largely depend on the nature of gene action controlling a particular character under selection. In sorghum fields, resistance to Striga is controlled predominantly by additive gene action. Selection procedures like pedigree, back cross and recurrent selection systems should be very effective. Similar procedures should also be useful in pearl millet, although population improvement through recurrent selection is easy and effective.

Pedigree Approach

Sorghum : improvement of resistant varieties of sorghum for various agronomic traits was initiated using pedigree and back cross procedures. In the African ICRISAT Striga programme, the main focus has been the improvement of Framida for grain colour (from red to white), resistance to insects and disease and improvement of E 35-1 for resistance to Striga, good seedling establishment and good panicle exsertion.

Over the past four years, several progenies from crosses involving Framida and E 35-1 as parents were tested in several African locations for Striga resistance and grain yield. They were also screened in pots in 1982 and 1983. Some of the promising entries were also tested for cooking quality (Tô). The results are presented in Table 13.

Two selections from crosses involving E 35-1 and IS 8785, a Striga resistant variety from Kenya, emerged as the best. They are 82-S-50 |(IS 8785 x E 35-1)-1-4-2|, and 82-S-47|(IS 8785 x E 35-1)-1-4-3|. They not only out-yielded E 35-1, but also exhibited very good levels of Striga resistance, good seedling establishment, superior food quality and non-senescent sweet stems. In our 'on farm' tests conducted in 1982, 82-S-50 produced 50% more yield (2,098 kg/ha) than E 35-1 (1,400 kg.ha). In 1983 'on farm' tests in Upper Volta, 82-S-50 and 82-S-47 had exhibited excellent levels of resistance to Striga compared to the local varieties.

Among the crosses involving Framida, entry no. 7 |(Framida x SPV 329)-2-1| had shown some promise. It is an early cycle variety and has coloured glumes. There are now several selections involving Framida with tan plant colour and grain mould resistance.

Millet : some of the less susceptible selections identified in 1979 and 1980 were intercrossed and advanced as a pedigree system. The segregating F_2 populations were screened for downy mildew resistance. Good selfed plants were tested in Striga sick plots in Aourèma (Upper Volta) and Maradi (Niger) in 1982. A few selected progenies were advanced in 1982 winter and selfed. 45 F_5 progenies were again screened in both locations in 1983.

A sandwich technique in which two test varieties (2x2 = 4 rows) are placed between two plants (2x2 rows) of ex-Bornu on either side is used for assessing the intensity of Striga infestation. Striga emergence on each variety is expressed as the percentage of that on the adjacent plot of ex-Bornu. This trial was replicated four times. Actual number of emerged Striga plants was analyzed after log transformation. The selected progenies are listed in Table 14.

Striga infestation at Maradi and Aourèma was satisfactory. The best entries in both the locations were 45, 20, 26, 14 and 21. It is encouraging that we are able to obtain levels of resistance comparable to that of Aourèma local variety (this variety used to be the best in all our trials from 1980-82) and increase the yields substantially. Our selections are about two weeks earlier than the local.

Population Improvement

Population improvement through recurrent selection offers good scope in both sorghum and millet. In sorghum, male sterile genes are used to facilitate crossing.

Millet : several crosses were made between less *Striga* susceptible varieties, the F_1 bulk was random-mated three times and grown out in *Striga* sick plots in Aourèma and Maradi in 1983. Full-sibs were made and at harvest only those full-sibs where one or both the parents were free from *Striga* were retained. Several S_1s and half-sibs free from *Striga* were also selected at harvest. All the three recurrent selection procedures, i.e. S_1, full-sib and half-sib testing will be compared.

Sorghum : a procedure similar to that of millet is proposed. Several crosses were made onto genetic male steriles and are being random mated.

SCREENING TECHNIQUES

It is not intended to review here the problems of screening in the field and in the laboratory. Planting of susceptible variety (indicator rows) at frequent intervals as local control appears to be the best approach at present. There are field layouts called sandwich technique and checker board layout. In sandwich technique, two rows of a susceptible variety are planted on either side of two test varieties, whereas in checker board layout, each test variety is surrounded by a susceptible variety on all four sides. Sandwich technique is more practical when the sick plot area is limited and test varieties are numerous. However, if only a few varieties are to be tested, and if there is enough sick plot area available, checker board layout is a better choice. Hill plot technique was also used in Nigeria to advantage. This is useful for screening large numbers of pure line varieties if one could use several susceptible plots as local control.

Laboratory screening is only available now for identifying low stimulant varieties or progenies (Parker et el, 1977). Although most of the low stimulant varieties from germplasm supported a lot of *Striga* when field tested, several of the breeding progenies involving low stimulant varieties retained the low stimulant character when selected after repeated field testing (Rao et al, 1983). Any one resistance mechanism may not confer complete field resistance to *Striga* because of significant influences of soil and climatic factors. Thus the laboratory should be able to identify varieties with various components of resistance, such as low stimulant compounds, haustorial initiation factors, anti-haustorial, antibiosis and some as yet unknown factors. This would enable the breeders to put these various resistances together using appropriate breeding procedures. The segregating progenies need to be screened again, thus a good screening laboratory is a necessary complement for an effective breeding programme.

RESISTANT VARIETIES IN INTEGRATED *STRIGA* MANAGEMENT

Host plant resistance is used as a component in an integrated programme of insect control in several crops. For example, in cotton, the traits of 'earliness' and 'nectariless' are valuable components in the management of cotton insects. A good level of resistance to greenbug is available in sorghum, but insect control is obtained only when resistant hybrids are grown in areas where predators can have a significant impact on the greenbug population.

For Striga, partial resistances are available in sorghum, and they should be used in combination with other methods to achieve complete control. There are several agronomic management systems that could be used very successfully with the resistant cultivars. They include optimum date of planting, rotation with trap crops, N-fertilizers, tied ridges with mulch, etc. Some of the results are reported in ICRISAT/Upper Volta Annual Report, 1982. They are briefly described below.

1. Resistant cultivars and hand weeding : resistant varieties support significantly fewer numbers of Striga plants compared to susceptible varieties. Smaller numbers of Striga plants can more easily be pulled out or sprayed with herbicides using pistol-grip sprayers. Both these practices were found to be tedious and not practicable with the high density of Striga infestation associated with susceptible varieties.

2. Resistant varieties in crop rotation : this is perhaps the best long term solution of Striga eradication. Resistant varieties reduce Striga build-up significantly. Rotation with trap crops helps to get rid of Striga seed reservoirs from the soil.

3. Resistant varieties and N-fertilizers : nitrogen fertilizers in general reduce Striga infestation. Very high doses of nitrogen are required to bring about an economic increase in yield and significant reduction in Striga infestation. Our results, using resistant and susceptible varieties, indicate that a very low dose of 14 kg/N/ha is enough to reduce Striga infestation and increase grain yields significantly with resistant varieties like Framida. A high dose of 150 kg/N/ha is required to suppress Striga in susceptible varieties. In Africa, where the farmers in some countries have started to use N-fertilizers, the Striga problem is going to increase if they use their local susceptible varieties. It is evident that improved sorghum varieties that are recommended for cultivation should possess some level of resistance to Striga.

4. Tied ridge with mulch : high soil moisture reduces or delays Striga emergence. Heavy rains or continuous irrigation are not favourable to Striga growth. Striga do not attack crops like rice, under irrigation.

   In west Africa irrigation facilities for sorghum and millet are almost absent. Tied ridges, to conserve soil moisture, in sorghum and millet resulted in almost doubling of crop yields (ICRISAT/Upper Volta Annual Report, 1982). Our experiments in 1982, using tied ridges in Striga sick plots, did not reduce Striga significantly. In 1983 tied ridge with mulching significantly increased Striga growth where the sorghum crop on control plots (flat planting) completely failed because of the drought. Tied ridges in west Africa therefore means better conditions for crop growth as well as for Striga. However, they do not provide sufficiently wet conditions to reduce Striga emergence. Resistant varieties in this context are evidently required.

In addition, there are a whole range of control methods which have proved impractical and uneconomical and which can be made more economical and practicable with the resistant varieties. Striga-resistant cultivars with appropriate complementary agronomic practices should be the most ideal control package.

Table 1 : Production figures of cereals grown in Africa

	Area (000 ha)	Grain Yield (kg/ha)	Production (000 t)	Crop Value* (US $ m)
Sorghum	15,312	730	11,174	2,558
Millet	16,691	616	10,282	2,355
Maize	22,583	1,455	32,860	7,525
All cereals	73,056	1,045	76,329	17,479

(FAO Production Yearbook, 1981 data)

* 1 t = US $229 (based on 1983 prices for sorghum, millet and maize in Ouagadougou, Upper Volta). The value of "all cereals" shown in the Table is a lower estimate since they include rice and wheat, whose prices are generally much higher than sorghum, millet and maize

Table 2 : *Striga* resistant sorghum varieties identified in Africa

Resistant variety	*Striga* species	Country	Reference
37RP*, 37R29, 37R27	S.a.	South Africa	Saunders (1942)
N Sorte*	S.a.	Northern Rhodesia	Moore (1933)
Dobbs & P 41	S.h.	Tanzania	Doggett (1952 & 1954)
Najjad	S.h.	Sudan	Kambal (1974)
SRN 4841, Framida & SRN 6838A	S.h.	Nigeria	Zummo (1975)

*Not available now

S.a. = *Striga asiatica*
S.h. = *Striga hermonthica*

Table 3 : Sorghum varieties resistant to Striga for different African countries

Country	Resistant varieties
Sudan	IS 9830, Entry 39, Tetron, Framida
Ethiopia	N 13, Framida, SPV 103, 12610 C
Kenya	N 13, Framida
Cameroun	N 13, Framida, NJ 1515, IS 8785
Nigeria	N 13, Framida, SRN 6838A, L 187
Niger	N 13, Framida
Upper Volta	N 13, Framida, SPV 103, Entry 39
Mali	N 13, Framida, IS 2203
Ghana	N 13, Framida, Najjad, IS 9830, Entry 39
Mauritania	N 13, Framida, IS 9830, SPV 103, Najjad

Table 4 : Agronomic characteristics of some Striga resistant sorghum varieties

Variety	Origin	Days to Flower	Plant Height (cm)	Grain Yield (kg/ha)	Grain Colour	Mechanism of Resistance
N 13	India	89	306	760	Yellow	Anti-haustorial factors
Framida	Africa	80	253	1930	Brown	Low stimulant + mechanical barriers*
IS 9830	Sudan	61	281	920	White	Low stimulant + moderate root cell wall thickening*
SPV 103	India	65	153	910	White	Anti-haustorial factors(?)
Najjad	Sudan	78	216	1010	White	Anti-haustorial factors(?)
Ent.39 (148xFramida)	India	70	150	1500	White	Low stimulant

*El Hiweris, personal communication

(?) Both varieties are stimulant positive but field resistant. They are suspected of having anti-haustorial factors or some other mechanisms of resistance

Table 5 : Stability analysis of some sorghum varieties for Striga resistance

Variety	Stability Parameters		
	Mean no. of Striga plants	bi	sdi
N 13	7.1	-0.82	2.2
Framida	7.7	0.01	2.4
IS 5603	12.4	1.87	1.3
2219 B	13.2	1.40	1.6
1202 B	16.0	1.74	11.2
CK60B	17.7	0.65	7.3

Table 6 : Results of multilocation on-farm testing of a few <u>Striga</u> resistant sorghum varieties

	1980[a]		1981[b]		1982[c]	
	Susceptibility (% local)	Grain yield (kg/ha)	No. of Striga/ha	Grain yield (kg/ha)	Grain yield (kg/ha) Traditional Management	Improved Management
N-13	16	778 (78)[d]				
SPV 103	28	743 (54)				
Framida	60	1281 (119)	28,625 (25)	1630 (181)	412 (125)	880 (131)
Local	100	997 (100)	116,688 (100)	903 (100)	300 (100)	672 (100)

a = Based on 4-15 locations in Africa (Annual Report 1980, ICRISAT/Upper Volta)

b = Based on 6 locations in Upper Volta (Annual Report, 1981, ICRISAT/Upper Volta)

c = Based on 69 locations in Upper Volta for Framida and 60 for local variety (Annual Report 1982, ICRISAT/Upper Volta)

d = Figures in parentheses are percentages compared with the local variety

Table 7 : Resistance of some sorghum varieties across two species of Striga. The number of emerged Striga plants/pots of test varieties are expressed as percentage of susceptible check variety used in each trial

	Striga hermonthica					Striga asiatica (Indian)					
	Ethiopia (1977)	Ethiopia (1978)	Cameroun (1977)	U. Volta (1979)	Mean ± SD	Akola (1977)	B'Sagar (1977)	Parbhani (1978)	Dharwar (1978)	Nandyal (1978)	Mean ± SD
Framida (SRN4841)	9	33	9	3	13.5±11.5	0	1	30	16	-	11.8±12.3
N-13	0	39	17	37	23.3±15.9	0	2	4	8	8	4.4± 3.2
555	46	47	38	53	46.0+ 5.3	8	11	31	9	9	13.6± 8.7
IS 4242	5	43	62	16	31.5±22.4	0	1	2	32	5	8.2±12.0
IS 5218	32	53	34	62	45.3±12.7	5	1	1	3	2	2.4± 1.5
IS 9985	70	133	94	117	103.5±23+8	0	0	4	6	11	5.8± 3.7
IS 4202	14	31	62	100	51.8±32.7	0	1	4	7	3	3.0± 2.4
16-3-4	5	22	35	25	21.8±10.8	10	-	30	23	4	16.8±10.3
Suscept-ible check	100(22)	100(84)	100(225)	100(428)		100(10)	100(472)	100(300)	100(96)	100(143)	

Figures in parentheses are actual number of emerged Striga plants/plot

Table 8 : **Resistance of some sorghum varieties against a few samples of *Striga hermonthica* tested in pots**

	Striga samples[a]						Variety means[b]	
	STS-9 Gas-Tougan		STS-6 Kokologo		STS-2 Farako-Bâ			
	1980	1981	1980	1981	1980	1981	1980	1981
IS 12610 C	0.6	0.2	0.8	1.2	1.4	0.7	1.05	0.69
IS 9830	0.6	0.0	0.2	0.2	1.1	0.1	0.80	0.14
CK60B	1.4	0.6	1.3	1.3	1.4	1.1	1.36	1.00
Framida	0.4	0.0	0.5	0.5	0.7	0.1	0.65	0.20
Najjad	0.4	0.0	0.3	1.2	0.5	0.4	0.68	0.55
Striga means[c]	0.65	0.18	0.63	0.90	1.00	0.47		

		1980	1981
a =	LSD (5%) for Striga at same variety level	0.66	0.38
	LSD (5%) for varieties at same Striga level	0.65	0.39
b =	LSD (5%) varieties	0.32	0.14
c =	LSD (5%) Striga	0.30	0.17

Table 9 : Mean and heterosis for Striga number (SN) and Striga fresh weight (SF) in 7x7 diallel in pots

Parent/Cross		Mean/Pot SN	SF	Heterosis over MP SN	SF
N 13		5.7	7.1		
Framida		4.0	5.4		
SPV 103		2.5	2.6		
IS 9830		9.7	2.7		
IS 9839		33.0	7.7		
BTx623		46.8	12.3		
VS 702		19.5	8.0		
N 13	x Framida	15.5	7.0	221	12
	x SPV 103	4.8	3.8	18	-22
	x IS 9830	15.0	6.3	96	29
	x IS 9849	10.0	5.3	-48	-28
	x BTx623	51.2	12.2	95	26
	x VS 702	15.2	4.8	21	-36
Framida	x SPV 103	13.2	4.4	613	10
	x IS 9830	4.7	4.9	-32	21
	x IS 9849	28.8	10.1	56	54
	x BTx623	55.3	10.6	118	20
	x VS 702	13.5	6.4	15	-5
SPV 103	x IS 9830	12.0	8.3	97	215
	x IS 9849	15.7	6.7	-12	30
	x BTx23	4.2	0.4	-83	-95
	x VS 702	29.3	4.4	256	-16
IS 9830	x IS 9849	21.3	7.0	0	34
	x BTx623	25.3	7.6	-10	1
	x VS 702	14.2	5.0	-3	-6
IS 9849	x BTx623	49.8	9.3	25	-7
	x VS 702	14.8	7.7	-44	-2
BTx623	x VS 702	38.7	8.4	17	-17
Mean	20.85	6.65			
SE ±	7.01	2.18			

Table 10 : Analysis of variance table for combining ability analysis of sorghum varieties for Striga resistance

Source of variation	DF	Mean sum of Squares	
		Striga Number	Striga Fresh Wt
General combining ability (gca)	6	648.606*	17.627*
Specific combining ability (sca)	21	123.142*	5.025
Error	135	49.182	4.763
GCA/SCA		5.267	3.508

* Significant of 1% probability level

Table 11 : General combining ability effects (gca) of parents for Striga resistance in sorghum

	Striga number	Striga fresh wt
N 13	-4.860*	0.040
Framida	-1.970	0.100
SPV 103	-8.070**	-2.240**
IS 9830	-6.100**	-0.990
IS 9849	4.430*	0.920
BTx623	16.820**	2.220**
VS 702	-0.230	-0.040
SE (gi)	+2.164	+0.674
SE (gi-gj)	+3.306	+1.029

* Significant of 5% probability level

** Significant at 1% probability level

Table 12 : Striga resistance and grain yield of a few selected millet varieties

Entry No.	Pedigree	Grain Yield (kg/ha) - 1982						Striga			
		Aouréma U.Volta	Kamboinsé U.Volta	Farako-Bâ U.Volta	Maradi Niger	Louga Senegal	Mean	Aouréma 1983 (Mean No/plot[a])		In Pots[b] (% killed) 1982	1983
18	P2627-2-18	806	1440	730	2254	525	1151	2.2	(51)[c]	67	67
15	P2627-1-19	273	1116	703	2138	462	938	2.3	(67)	29	40
7	Inbred 5258-1-10	172	1602	730	1242	424	834	2.3	(61)	50	-
3	P2661-3-5	398	807	839	1546	321	782	1.9	(31)	14	7
2	Inbred 5258-1-19	715	452	573	1502	435	735	2.1	(63)	33	60
9	P449-1-29	299	1044	495	953	153	589	2.1	(49)	33	40
6	P2627-2-11	649	1698	1094	2499	664	1321	2.6	(80)	57	60
20	Local	420	-	896	3192	633	1285	2.2	(60)	100	60
	Ex-Bornu (susceptible check)							494[d]			
	Mean	433	1202	732	1828	507		2.3			
	SE ±	±164.7	±339.6	±360.2	±334.0	±251.1		±0.28			

a = Log transformed data

b = Number of plants killed expressed as percentage of total number of plants in each variety

c = Expressed as percentage of four adjacent plots of ex-Bornu in a checker-board layout

d = Number of emerged Striga plants/plot (6 m^2) averaged over 136 plots in four replicationss in the checkerboard

Table 13 : Grain yield, Striga resistance, and food quality of a few sorghum cultivars

Entry No	Origin	Pedigree	Grain yield[a] (kg/ha)	Number of Striga[b]				Food quality[c]	
				Kamboinsé	Pabré	Farako-Bâ	Sudan	Elasticity	Taste
6	82-S-50	(IS 8785xE 35-1)-1-4-2	1044	1.7	2.3	1.5	1.2	67	73
7	82-S-51	(Framida x SPV 329)-2-1	949	1.8	1.8	1.7	1.4	NT	NT
5	82-S-49	(IS 8785xE 35-1)-1-4-1	887	1.0	2.0	1.9	1.7	NT	NT
3	82-S-47	(IS 8785xE 35-1)-1-4-3	809	1.8	1.9	1.8	1.7	80	80
18	82-S-53	(Framida x GG)-1-1-1	792	2.2	1.8	1.5	1.2	NT	NT
8	82-S-52	(Framida x SPV 105)-2	717	1.6	1.6	1.7	1.3	NT	NT
16	-	E 35-1	766	1.9	1.8	1.6	1.9	80	73
17	-	Framida	602	1.5	2.5	1.5	1.0	87	90
		Mean		1.81	1.91	1.70	1.51		
		SE ±		±0.23	±0.39	±0.49	±0.49		

a = Mean over seven locations in four African countries

b = Log (X+1.1) transformation of number of emerged Striga plants/plot

c = Food Quality (Tô) is based on test by 15 villagers
Local variety is 93% and 100% for elasticity and taste respectively

NT = Not tested

Table 14 : Striga resistance and grain yield of a few selected F_5 progenies of millet

Entry No.	Origin	Pedigree	Number of Striga[a] Maradi		Number of Striga[a] Aouréma		Grain yield (kg/ha) Auoréma	
45	82W213	(80R351-6-1xP 508-1)-1	1.2	(17)[c]	2.2	(59)[c]	122	(271)[b]
26	194	(Sel.Thiou-2-1-6xP 1538-1)-3	1.6	(39)	2.3	(62)	179	(398)
20	188	(P23-1-18xSerere 2 A-9-2-23)-4	1.3	(25)	2.1	(85)	202	(499)
14	182	(Sel.Thiou-4-1-4xSerere 2 A-9-2)-1	1.4	(25)	2.1	(59)	288	(640)
33	201	(Sel.Thiou-2-1-6xP1538-1)-7	1.1	(27)	1.9	(74)	197	(438)
34	202	(P 1527-1-4xP 23-1-2)-25	1.5	(31)	2.1	(51)	116	(258)
21	189	(P 354-3-24xP 2861-1-1-3)-6	1.7	(32)	1.8	(24)	139	(309)
8	176	(P 357-3-4xSerere 2 A-9-2-8)-4	1.7	(33)	2.1	(78)	286	(636)
46		Local	2.07	(78)	2.22	(59)	118	(262)
		Ex-Bornu (susceptible check)[d]	34		23			
	Mean		1.79		2.21		169.5	(377)
	SE ±		±0.32		±0.31		±76.29	

a = Log transformation of number of emerged Striga plants/plot

b = In parentheses kg/ha

c = In parentheses - number of Striga plants expressed as percentage of adjacent indicator row plot in sandwich layout

d = Mean number of emerged Striga plants/m^2, averaged over 120 plots in 4 replications in sandwich layout

REFERENCES

BEBAWI, F.F. (1981), "Intra-specific physiological variants of Striga hermonthica", Experimental Agriculture, 17 : 419-423

DOGGETT, H. (1952), "Annual Report of the Botanist, Ukiriguru, for the year 1950", Tanganyika Dept. Agr. Annual Report, pp. 222-241

DOGGET, H. (1954), "Botanist's Annual Report - 1951-52 Season", Tanganyika Dept. Agr. Annual Report 1952. Section III : 61-67

DOGGETT, H. (1965), "Striga hermonthica on sorghum in East Africa", J. Agric - Sci. 65 : 183-94

DOUGHTY, L.R. (1942), "A note on Striga investigations at Amani", East Afr. Agric. J. 8 : 33-38

GRIFFING, B. (1956), "Concept of general and specific combining ability in relation to diallel crossing systems", Australian Journal of Biological Sciences - 9 : 463-492

KAMBAL, A.E. (1974), "Breeding sorghum varieties for resistance to Striga", 11th Agric. Res. Colloqium on Cereal Crops in the Sudan, Wad Medani, Sudan

MOORE, T.C. (1933), "Some indigenous crops of northern Rhodesia", Northern Rhodesia Dept. Agric. Ann. Bulletin, 2 : 35-50

PARKER, C., HITCHCOCK, A.M. & RAMAIAH, K.V. (1977), "The germination of Striga spp. by crop root exudates : techniques for selecting resistant cultures", Proc. 6th. Asian Pacific Weed Science Society Conference, Djarkarta, Indonesia, pp. 67-74

PARKER, C. & REID, D.C. (1979), "Host specificity in Striga spp. - some preliminary observations", Proc. 2nd. International Symposium on Parasitic Weeds, Raleigh, North Carolina, USA, pp. 79-90

PARKER, C. & WILSON, A.K. (1983), "Striga - resistance identified in semi-wild 'Shibra' millet (Pennisetum spp.)", Proc. 35th Int. Symp. Crop Protection, Ghent, Belgium, May 1983

RAMAIAH, K.V. (1983), "Striga research at ICRISAT/Upper Volta", Proc. 2nd Int. Striga Workshop, 5-8 Oct. 1981, Ouagadougou, Upper Volta

SAUNDERS, A.R. (1933), "Studies on phanerogamic parasitism with particular reference to Striga lutea", South African Dept. of Agricultural Science Bulletin No. 128, pp. 56

SAUNDERS, A.R. (1942), "Field experiments at Potchefstroom. A summary of investigations conducted during the period 1903-1940", South African Dept. Agric. & Forestry Science Bulletin, No. 14 : 19-21

RAO, M.J. Vasudeva, CHIDLEY, V.L., RAMAIAH, K.V. & HOUSE, L.R. (1983), "Breeding sorghum genotypes with resistance to Striga asiatica at the ICRISAT Centre", Proc. 2nd. Int. Striga Workshop, 5-8 Oct. 1981, Ouagadougou, Upper Volta

WILSON JONES, K. (1955), "Further experiments on witchweed control. II. The existence of physiological strains of Striga hermonthica", Emp. J. Exp. Agric. 23 : 206-13

ZUMMO, K. (1975), "Annual Report, cereal pathology", Inst. for Agr. Res. Ahmadou Bello Univ. Zaria, Nigeria, pp. 158

PATTERNS OF RESISTANCE TO STRIGA ASIATICA IN SORGHUM AND MILLETS, WITH SPECIAL REFERENCE TO ASIA

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INTRODUCTION

Striga, an old world root parasite of cereals and legumes, has attracted much attention of late, as a causative agent for serious losses in crop production in the semi-arid tropics. There are three general options available for its control : a) genetic (using resistant varieties); b) agronomic (using cultural manipulation and chemicals); and c) biological (using insect pests and pathogens). The genetic option appears to be economically the most viable because a resistant variety that can avert the subterranean damage by Striga is a non-cost input for the farmer. In this paper the distribution and nature of the Striga problem in different Asian countries is briefly described, with special reference to sorghum and pearl millet.

1. Striga in Asia

Striga is reported to occur in almost all sorghum-growing semi-arid parts of Asia, including India, Pakistan, China, Japan, Indonesia, Thailand and Burma. Striga is a serious problem in India and certain parts of Pakistan on sorghum and pearl millet. In other countries, Striga is a recognized yield reducer on crops such as maize (Thailand), sugarcane (Australia), and rice (Burma, Indonesia, Thailand). In addition to being a major problem on sorghum and pearl millet in restricted areas in India, Striga is also a problem on sugarcane, maize, rice and minor millets.

There are at least two morphotypes of S. asiatica occurring in Asia. White-flowered S. asiatica is reported from India, Pakistan and Burma, and a yellow-flowered variety is reported from Thailand and Indonesia. There are also reports of yellow-flowered types of S. asiatica in the Malnad tract of Karnataka state in India (Hosmani, 1978). There could be some implications of this with reference to host reactions and consequently on breeding of resistance lines.

2. Striga in India

In India, which has the largest area under sorghum in Asia, Striga was a problem with marginal economic implications for traditional farmers using local cultivars. The problem has, however, grown in magnitude since the introduction of hybrids, as all the released hybrids are highly susceptible. In several places sorghum cultivation has been abandoned because of Striga after some years of hybrid cultivation (House & V. Rao, 1982). Under traditional farming systems using local varieties, some Striga seed is always present in the soil because most local varieties are tolerant and yield well in spite of Striga infestations. Even though some local cultivars have evolved resistance because of their cohabitation with Striga over centuries, they are not immune. Consequently, when susceptible hybrids are introduced, the level of Striga infestation in the soil, which hitherto remained low, increases considerably. However, a few years are required to build up economically-damaging Striga levels, so hybrids were accepted in the initial years of introduction when their yields were good in spite of Striga. The problem assumes economic proportions only after a few years of continuous hybrid cultivation in the same field. Consequently, the Striga problem has followed the spread of the hybrids. The gravity of the problem was strongly stressed by a working group meeting of scientists from the Indian Council of Agricultural Research (ICAR) and the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) at the ICRISAT Centre, Patancheru in September-October 1982. This meeting also recommended an increase in the research thrust to counter this increasingly severe problem on sorghum in India and to define the future research strategy on Striga in the region. In addition to S. asiatica, S. densiflora and S. euphrasioides occur in India. S. densiflora is a recognized problem in the post-rainy season sorghums in parts of Karnataka and Maharashtra states. In view of its increasing importance, the working group meeting recommended additional research input on S. densiflora.

In the Asian region pearl millet is grown to a large extent only in India. Striga is recognized as a serious problem in Gujarat and Rajasthan states in Sikar, Jhunjhunun, Nagour and Alwar districts. Striga is also reported to damage pearl millet in Andhra Pradesh in south India (Sivaramakrishnaiah et al, 1968). In the pearl millet growing regions of India, Striga is more serious on the relatively lighter types of soils, this is also true for sorghum.

Striga is also reported to cause damage to upland rice in Nellore district, Andhra Pradesh state (G. Rao et al, 1953), on the Malabar Coast, Tamil Nadu state (Uttaman, 1949), and in Quillon district, Kerala state (K. Karunakaran, personal communication). S. asiatica and S. euphrasioides are reported as causing the damage. Losses of 80-90% are reported (Uttaman, 1950).

Of late, Striga has also been reported to cause damage to sunflower in Tamil Nadu and Karnataka States (N.M. Prasad, personal communication). The species involved is presumed to be S. asiatica, but detailed studies are required to verify this.

3. Striga in Thailand

Teerawatsakul (1975) reported that in Thailand, Striga occurred before 1974 on wild plants in uncultivated areas. However, in 1974, it was first noticed attacking maize at Nam Yuen, Ubon Ratchathani, where maize cultivation was extensive. Nearly 7,000 hectares is infested with Striga in this area. It was named 'Yah Jew' (a tiny weed) and 'Yan Maemod' (witchweed). Furthermore, Teerawatsakul and Kanjanajirawong (1977) reported that Striga attacks field maize cv 'Suwan 1', sorghum cv 'Late Hegari', sugarcane and sweet corn.

4. Striga in Indonesia

Pancho and Mangoesoekardjo (1975) recorded S. asiatica as a parasite of rice. They reported that it caused an estimated 50-60% yield reduction in upland rice.

5. Striga in Pakistan

Mohyuddin et al (1965) reported that S. asiatica and S. euphrasioides attack sorghum in West Pakistan. The white-flowered S. asiatica is also a serious problem on sorghum in Deraghazi Khan district in Punjab State (M. Ali Bajwa, personal communication)

6. Striga in Burma

Aubert (1910) and McKerral (1912) recorded the white-flowered S. asiatica as a problem constantly threatening the cultivation of sorghum.

CURRENT RESEARCH PROGRAMMES ON STRIGA IN ASIA

Research on Striga has been sporadic throughout the world. Among the various Asian countries where Striga is a menace, only India has on-going Striga research programmes. A strong research project is located at the ICRISAT Centre, Hyderabad. The All India Coordinated Sorghum Improvement has coordinated Striga resistance trials and agronomic trials, and some of the Indian universities also have limited programmes on Striga control.

PATTERNS OF RESISTANCE TO STRIGA - SORGHUM

1. Past Efforts in Asia

India is the only country in the world other than South Africa, where work on breeding for Striga resistance in sorghum was initiated as early as the 1930s. Hosmani (1978) reviewed the past Indian work on resistance breeding activities in sorghum. Several varieties were reported resistant to S. asiatica by different workers (Table 1). Most Striga research efforts in the past had short-term objectives and were not adequately sustained. The progress in breeding for Striga resistance in the past was slow. Possible reasons are the absence of long-term support, both fiscal and physical to sustain the continuity of research efforts; the absence of immunity to Striga in sorghum, coupled with the lack of valid field screening techniques, which resulted in the terms 'resistant' and 'tolerant' being used indiscriminately. Follow-up studies of early reports have not been able to confirm the results mainly due to the absence of a reliable screening methodology.

2. Screening for Resistance Mechanisms

Two approaches were adopted by past researchers : screening for the individual mechanism which confers resistance to the host; or screening for field resistance. Three resistance mechanisms have been identified in sorghum : low stimulant production; mechanical barriers (anti-haustorial factors); and antibiosis factors. At the ICRISAT Centre, nearly 15,000 germplasm accessions have been screened for their capacity to stimulate the germination of S. asiatica from the Patancheru area, and 640 low stimulant accessions have been identified. Only N 13, a high stimulant and a highly stable field resistant line has been identified as having mechanical barriers. Little work has been carried out on the third mechanism although it is indicated to exist (Saunders, 1933).

The usefulness of low stimulant production as a prediction of the field resistance of sorghum lines has often been questioned. Initial efforts to correlate Striga numbers in the field and stimulant production indicated a low, but positive correlation. Further studies have lead to the following conclusions (V. Rao et al, 1982a) :

i. the proportion of field resistant line among low stimulant lines is higher than that among the high stimulant lines;

ii. simple correlation coefficients between Striga numbers and stimulant production obtained from different trials were positive and at some locations and trials very high - indicating that stimulant production could be a useful indicator of field reaction (Table 2).

GENETICS OF STRIGA RESISTANCE

1. Inheritance of Low Stimulant Production

The first report on inheritance of low stimulant production was from the ICRISAT Centre (ICRISAT, 1978). It indicated that a single recessive gene, 'sal', controlled stimulant production. Further analysis indicated that the character was also amenable to quantitative genetic variance (V. Rao et al, 198a). Shinde and Kulkarni (1982) in a 7-parent complete diallel, while confirming the higher additive gene action for this character, also reported reciprocal differences indicating maternal effects. IS 2221, S 1841 and SPV 86 were reported to be good combiners for low stimulant production.

2. Inheritance of Field Resistance

Studies on the inheritance of field resistance are plagued by two main difficulties, the absence of a field technique that assures a uniformly high level of Striga challenge for each host plant and the interpretation of data based on a single external manifestation (emerged Striga counts) of reaction which is the result of actions and interactions of one or more resistance mechanisms, each of which are likely to be controlled by different genes. Chandrasekharan and Parthasarathy (1953) reported that Striga resistance was dominant while Narasimhamurthy and Sivaramakrishnaiah (1963) reported that the nature of inheritance varied with the parents involved in a cross. 23-4, N 13 and NJ 1515 in their crosses showed dominant resistance and in crosses with IS 6942 there was partial dominance. A preliminary study at ICRISAT using line x tester analysis has indicated that susceptibility is dominant over resistance (V. Rao et al, 1983). Shinde and Kulkarni (1982), using a 7-parent diallel, reported that field resistance was controlled by both additive and non-additive gene actions with a preponderance of additive gene action, and suggested that pedigree selection was effective for field resistance.

There is no work on the inheritance of mechanisms other than low stimulant production.

TRANSFER OF RESISTANCE

Concerted efforts have been made since work began at ICRISAT to identify stable resistant lines by multi-locational testing. Although there is no absolute resistance or immunity to S. asiatica there are stable low susceptible lines such as N 13, 555, IS 2203, IS 4202, IS 7471 and IS 9985 (V. Rao et el, 1983). Crosses are made every year among resistance lines and between resistant lines and high yielding susceptible lines. The absence of reliable single plot screening techniques to differentiate resistant and susceptible plants in the segregating generation is a major drawback. However, the segregating generations are grown and advanced in Striga-sick fields. The best looking plants are selected and once they attain some uniformity, they are processed through a three-stage screening (see below). The best advance generation progenies are being identified as SAR (S. asiatica resistant) lines. SAR 1, 2, 10 and 16 are lines with good levels of Striga resistance that have moderate yield levels even under the most severe Striga infestations (Table 3). SAR 1 and 2 are currently undergoing farmers' field testing in Manarashtra State.

Breeding for Stable Resistance

Striga is a versatile parasite capable of adapting to different hosts and different environments in a short time. There are different levels of organization within the genus Striga, i.e., with reference to differences between species, morphotypes within a species, and host-specific races within a morphotype. Taxonomically-distinct species like S. asiatica, S. densiflora and S. euphrasioides coexist in India. Variations in morphological characters among plants of S. asiatica existing in the same field have been noticed (V. Rao et al, 1983). Recent observations near Anantapur, Andhra Pradesh state, indicated that in a restricted area, Striga attacks pearl millet. From cross inoculation tests, using Striga from sorghum and pearl millet collected in the same area, it has been found that pearl millet-Striga parasitized both sorghum and pearl millet, while the sorghum-Striga could only parasitize sorghum (Table 4).

These observations point to the necessity to breed for 'stable' resistance, i.e., resistance of the host across different Striga spp., morphotypes and host-specific races.

The stability of resistance with reference to Striga pressures, as expressed in the number of emerged Striga plants per unit area has also been studied at ICRISAT. Data from an advanced Striga resistance trial conducted at five locations in India using a checkerboard layout was used to plot the number of emerged Striga plants in test entries against the positional check average (average of four check plots surrounding each test entry plot). Three representative varieties were studied (Figure 1). N 13, a very stable variety, held its resistance even at the highest pressure recorded, while SRN 4841, a moderately resistant variety held its resistance under low Striga pressure, but became susceptible at higher pressures. T233B, a susceptible variety, showed high Striga counts even at low pressures. It was found that a graphical approach using the multi-location checkerboard layout data is a very useful way to identify varieties with stable resistance (Gilliver et al, 1983).

In addition to breeding stable resistant varieties, it is important to protect the products of breeding, i.e., the Striga-resistant varieties, from losing their resistance. In the past, excellent resistant varieties such as 'Radar' failed to maintain resistance apparently due to outcrossing (Grobbelaar, 1952). At present, there are no specific procedures for monitoring the seed production of varieties bred for specific resistance. Stringent seed production procedures may have to be developed to avoid the breakdown of resistance due to mutation, outcrossing or other reasons. This procedure will become even more crucial when Striga-resistant sorghum hybrids are developed.

PATTERNS OF RESISTANCE TO STRIGA - PEARL MILLET

Breeding for Striga resistance in pearl millet has received much less research input than sorghum. Consequently, very little information is available on patterns of resistance. However, since pearl millet and Striga have coexisted for a long time, it is to be expected that resistance to Striga exists in the host and a concerted effort to identify resistant lines would be worthwhile.

Sivaramakrishnaiah et al (1968) screened six pearl millet hybrids and their parental lines against Striga near Anantapur and reported that TIF23A was highly resistant and that this resistance was transmitted to its hybrids. Mathur and Bhargava (1971) studied the resistance of 19 hybrids (with TIF23A as the female), 12 inbreds, 14 established lines, HB1 and TIF23A as checks in pots at Jaipur, Rajasthan state. They also notices that TIF23A is highly resistant. Among the 12 Durgapura inbreds (DB series) tested in crosses with TIF23A, only six hybrids were resistant.

Obviously much work is still required on screening pearl millet for Striga resistance.

SCREENING METHODOLOGY

Lack of proper screening methodology has hindered significant progress in Striga resistance breeding activities in the past. The main problems to be countered are variability in infestations as measured by the emerged Striga counts from year to year and variability from spot to spot in the field in any one year. The emerged Striga count is an unknown percentage of the subterranean Striga numbers. Major efforts at the ICRISAT Centre have been directed to solving the latter problem. A 'three-stage' screening methodology specifically suited to Striga-resistance breeding activities (Figure 2) has been developed (V. Rao et al, 1982b). The three stages are :

Stage 1 - Observation Nursery. This consists of a single replication of a large number of breeding lines with a frequently-repeated (one in five plots) susceptible check. A minimum of two rows of each entry are grown and susceptible lines are rejected based on Striga counts relative to the closest check.

Stage 2 - Preliminary screening. The entries, advanced from Stage 1, are tested at more than one location in three row plots and repeated at least three times with checks arranged in such a way that every test entry plot will have one check adjacent to it (Figure 2). Striga counts are determined on the central row of each plot. Trials are classified as all-zero, some-zero or no-zero based on Striga emergence in the susceptible check plots. In the all-zero trial, where Striga has not appeared in the susceptible check, trial data may be used for yield evaluations. In the some-zero trials, where Striga has appeared in some parts of the trial and not in other parts, data may be analyzed using a 'single-unit comparison' system (V. Rao et al, 1983), wherein comparison between test entries are limited to a unit of eight plots with the susceptible check being in the centre. In the non-zero trials, where Striga appears in all check plots, the reactions of test entries are computed as Striga counts percent of the susceptible check, in the same unit. Data are then analyzed as per the experimental design.

Stage III - Advanced screening. Resistant entries from Stage II are tested in five row plots arranged in such a way that every test entry plot is surrounded by susceptible check plots on four sides, giving the field a checkerboard appearance (hence the name). This layout provides a useful opportunity to estimate grain yields from replicated test entry plots in Striga-sick fields, and at the same time to monitor, estimate and use the information in Striga infestations in the susceptible check plots which are regularly interspersed in the experimental area for assessing the variability of Striga infestation. Statistical procedures involve either plot assessment, co-variance analysis or a graphical approach (Gilliver et al, 1983).

The three-stage screening methodology is fully operational at the ICRISAT Centre and has been found quite useful in identifying resistant lines. The checkerboard layout has been adopted by the All India Sorghum Improvement Project in their multilocation coordinated Striga trial.

Farmers' field testing. A procedure which involves sowing of resistant and susceptible lines in alternate strips (Figure 3) has also been developed to test resistant lines in farmers' fields. The length and width of each strip is variable. The alternate strips are very convenient for use in farmers' fields and very convincing when Striga is seen on either side of resistant strips. Data on Striga counts and yields may be collected from two to five random samples from each strip.

FUTURE RESEARCH PRIORITIES

1. The current research input on Striga is grossly inadequate, and is not commensurate with the magnitude of the problem. It requires not only a concerted effort on the part of each organization involved in Striga research, but also strong international coordination between organizations so that there is more effective research to control this menace across crops, species, morphotypes and host-specific strains.

2. A very strong input is requires on breeding for resistance, not only in sorghum and pearl millet, but also in other crops which host Striga. Breeding programmes can produce results only if there is a well-established network of testing centres located in places where the different species and morphotypes occur.

3. More effort is required to understand the mechanisms conferring resistance to the host and their action and interactions between themselves and with the environment.

4. Intensified effort is required to develop more efficient methods for screening single plants for resistance. This will help speed up progress in breeding. Field screening methodology needs to be improved to obtain reliable Striga infestations year after year. Studies are required on the management of Striga-sick fields.

5. More studies are required on the biology of Striga to determine the biochemical interactions involved between the parasite and its hosts.

6. Systematic surveys are required in the Asian countries to locate Striga 'hot-spots', to identify the species and morphotypes occurring and to understand the host range and magnitude of the problem.

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Table 1 : Varieties reported to be resistant to Striga asiatica from India

Variety	Place	Reference	Remarks
Bilichigan	Temburni Maharashtra	Gadgil(1933)	Selection from Maldandi
Mudinandyal Burma K.K. Burma Y.K. Agikodal Malleswar	Poona Maharashtra	Jenkins(1944)	Resistant in pot tests
S.versicolor S.purpureosericeum S.nitidum	Poona Maharashta	Deodikar(1951)	
AS 4003(Boganhilo) AS 4693(Bilichigan) CO-7 CO-11 CO-20(AS 9028)	Coimbatore Tamil Nadu	Sivaraman(1952)	
N 13(Culture 109)	Nandyal Andhra Pradesh	Nagur et al(1962)	Selection from local 'Patchajonna'
BH 4-1-4	Bailhongal Karnataka	Kajjari et al(1967)	Also resistant to SDM
BO-1	Akola Maharashtra	Anonymous(1979)	Selection from local NJ-156
PS-13 PJ-16K Khedi 2-2-10	Parbhani Maharashtra	Chopde et al(1973)	

Table 2 : **Simple correlation coefficients between low stimulant production and field reaction to Striga asiatica**

Season	Trial No.	No. of entries	Location	'r' Value	Remarks
Rainy '81	53	13	Akola	0.91**	Checkerboard layout
			Bhavanisagar	0.65**	" " " "
			Bijapur	0.34	" " " "
Rainy '82	71	15	Akola	0.85**	" " " "
			Bijapur	0.70**	" " " "
			Indore	0.86**	" " " "
			Parbhani	0.57	" " " "
			Patancheru	0.85**	" " " "
Rainy '82	72	78	Akola	0.51**	Preliminary Stage
			Bijapur	0.36**	Screening
			Parbhani	0.58**	" " " "
			Patancheru	0.47**	" " " "
Rainy '82	73	54	Akola	0.32*	" " " "
			Bijapur	0.28*	" " " "
			Patancheru	0.023	" " " "
Rainy '82	74	20	Akola	0.27	" " " "
			Bijapur	0.39	" " " "
			Patancheru	0.56**	" " " "

Table 3 : *Striga* reaction (SR)[1] and grain yield (kg/ha) of 15 breeding lines and 5 source lines in multilocation testing (checkerboard layout, rainy season 1982)

Origin	Pedigree	Patancheru		Akola		Indore		Parbhani		Bijapur		Average	
		SR	Gr.Yd.	SR	Gr.Yd.	SR	Gr.yd.	SR	Gr.Yd.	SR	Gr.Yd.	SR	Gr.Yd.
SAR-1	(555x168)-1-1	0.1	3967	4.2	2281	0.2	1543	5.7	2250	1.4	2130	1.9	2434
SAR-2	(555x168)-16	0.5	3367	3.9	2593	1.3	1605	10.2	1958	1.8	2120	3.0	2328
SAR-5	(148x555)-1-2	0.7	3956	3.6	2474	12.4	988	6.2	1958	2.6	1527	4.2	2180
SAR-6	(148x555)-33-1-3	0.2	3678	3.2	2178	1.0	2130	13.3	2450	0.5	1814	3.0	2450
SAR-9	[SRN-4841x(WABC xP-3)]-7-3	1.1	4844	1.5	1074	4.9	2346	4.0	2083	12.8	1425	4.1	2354
SAR-10	[555x(PDxCS-3541) -29-3]-5-2-1	0.5	4111	1.1	2578	0.6	2625	6.8	2625	0.8	2166	1.7	2502
SAR-11	(555xAwash-1050) -2-2	2.2	1556	5.7	1785	11.1	818	11.5	1667	3.9	1731	6.0	1511
SAR-12	(SRN-4841xSPV-104)-17	4.1	3500	5.3	1044	8.8	2160	9.3	2208	8.3	1129	7.1	2008
SAR-13	(555x168)-1	0.8	4600	1.7	2267	1.1	1728	5.6	1958	2.1	1601	2.0	2430
SAR-14	(Framida x148)-21 -2-2-4	0.3	4367	4.7	1067	13.0	710	3.8	2125	1.7	1296	3.9	1913
SAR-15	(555x168)-23 -2-2-3-2	0.8	4211	5.0	2400	4.6	1759	28.6	1708	1.3	2138	6.9	2443
SAR-16	(555x168)-19-2-7	0.8	4344	5.2	2700	18.2	664	8.7	2450	2.3	1500	6.4	2331

Table 3 (cont.)

Origin	Pedigree	Patancheru		Akola		Indore		Parbhani		Bijapur		Average	
		SR	Gr.Yd.	SR	Gr.Yd.	SR	Gr.yd.	SR	Gr.Yd.	SR	Gr.Yd.	SR	Gr.Yd.
SAR-17	(N-13x269)-5-2	3.2	2656	10.3	2207	10.1	864	2.6	2000	6.2	1712	5.7	1887
SAR-18	(N-13x2KX6)-1-2 -1-2	3.2	4211	20.9	1674	4.2	988	9.9	2083	11.7	1129	8.7	2017
T-233B	T-233B	128.1	2356	141.3	1659	156.9	710	31.1	1874	23.5	777	85.6	1475
N613	N-13	0.1	1288	0.3	2192	1.1	771	2.9	1374	0.8	2851	0.9	1695
555	555	4.9	1166	10.3	2533	10.3	1033	4.0	1708	1.2	2148	5.2	1717
SRN-4841	SRN-4841	11.4	2211	6.8	-	10.3	1280	11.0	458	22.7	1231	10.5	1036
IS-4202	IS-4202	0.2	1688	3.8	2222	1.4	1975	4.3	1916	2.9	861	2.1	1732
IS-7471	IS-7471	0.8	-	12.9	-	25.5	-	9.5	-	0.9	1638	8.4	327
CSH-1[2]	Mean	230	4041	67	1307	222	1471	36	2131	501	804		
(Suscep-	Min	82		7		4		13		189			
tible control)	Max	434		380		1047		101		817			
	'r' bet^{n} Striga counts and yield/plot		-0.43**		-0.49**		-0.57**		-0.39*		-0.32*		
	R^2		0.18		0.24		0.33		0.15		0.10		

1 : SR of test entries expressed as emerged Striga counts percent of positional check value, averaged over two replications

2 : SR of CSH-1 expressed as number of emerged Striga/M^2 averaged over 40 CSH-1 plots in the checkerboard

Gr. Yd : Grain Yield

Table 4 : Cross-infection of Striga asiatica from sorghum and pearl millet hosts

Test host	Number of Striga plants/flats	
	Sorghum Striga	Pearl Millet Striga
Sorghum (Cv. Swarna)	169	15
Pearl millet (IP8551)	0	27

Kharif 1981; 75-day counts; wooden flats; average of three repeats

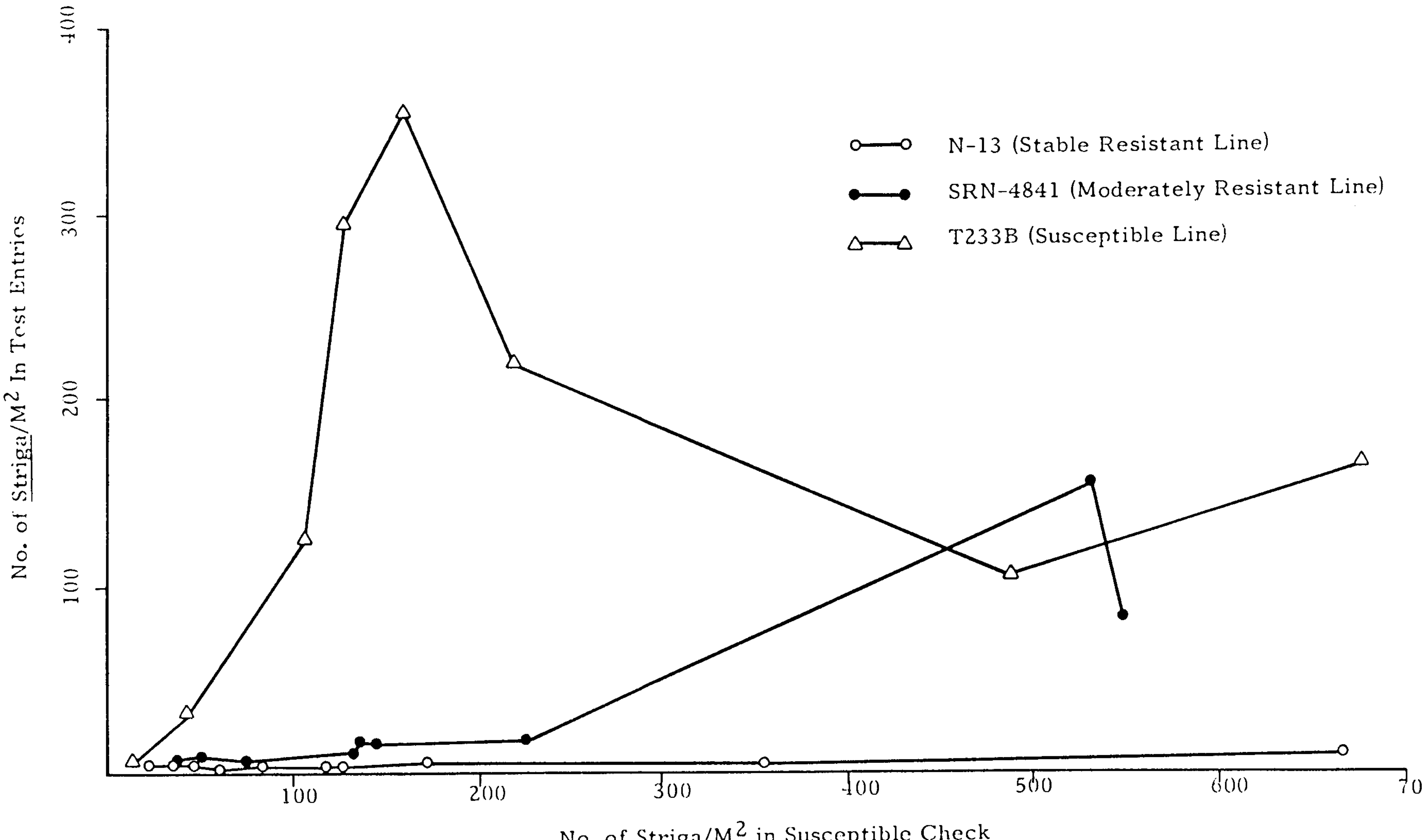


Figure 1 : Association between Striga numbers in test entries and the Striga intensity in the soil measured by the number of Striga with a susceptible check (Gilliver et al, 1983)

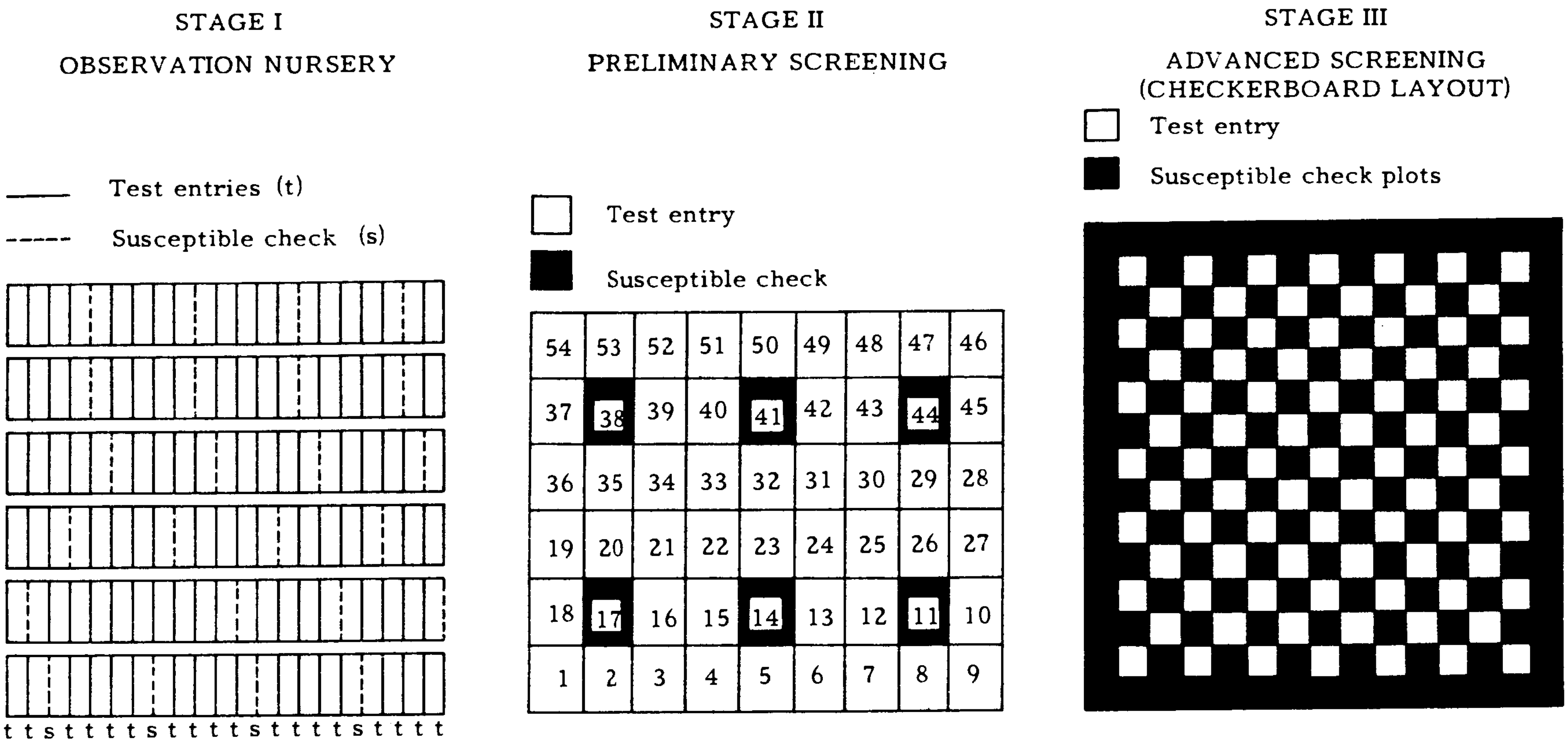
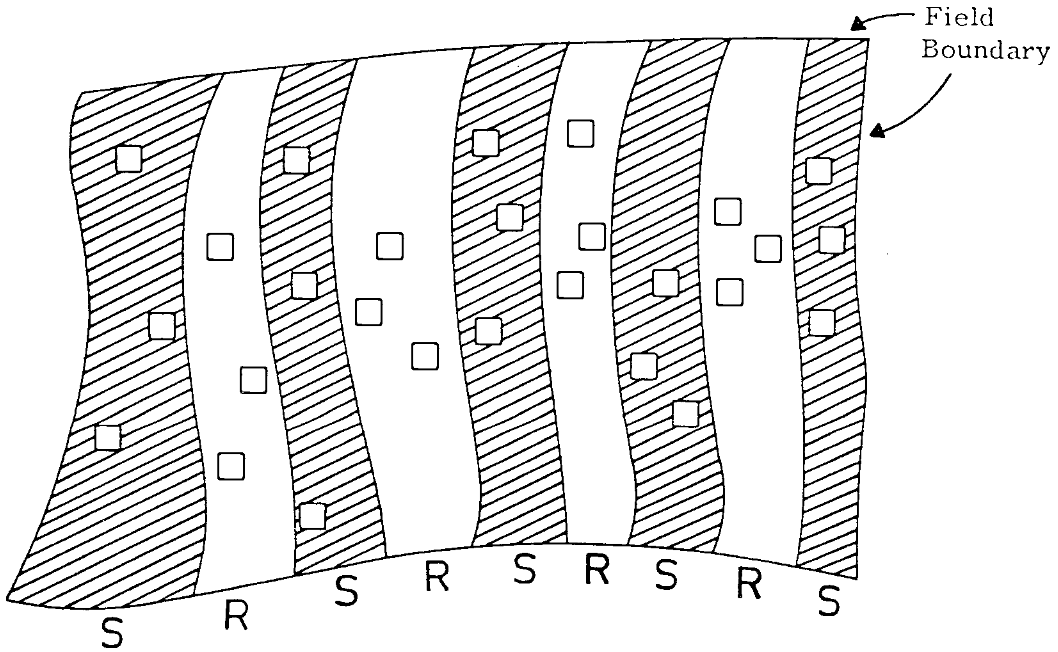


Figure 2 : A three-stage screening methodology for <u>Striga</u> resistance breeding in sorghum (Rao, M.J.Vasudeva et al, 1983)



S = Susceptible check

R = Resistant varieties

□ = Sample area for Striga counts and yield estimation

Figure 3 : Farmers' field testing of Striga resistant varieties in alternate strips

Slide 1 : A resistant line of sorghum bred at the ICRISAT Centre, Hyderabad, India, shows much less Striga compared to a mat of Striga present on the susceptible hybrid (at left)

REFERENCES

ANONYMOUS (1979), "Investigations into biology of Striga lutea, obnoxious weed on sorghum and evaluation of Striga-tolerant varieties and hybrids", Annual Report of Project, Punjabrao Krishi Vidyapeeth, Akola, Maharashtra, India

AUBERT, L. (1910), "Andropogon sorghum - its cultivation and some of its enemies", Agr. J. India, 5 : 222-230

CHANDRASEKHARAN, S.N. & PARTHASARATHY, S.V. (1953), "Cytogenetics and plant breeding", P. Varadachary & Co., Madras, India

CHOPDE, P.R., SHINDE, V.K. & SEWLIKAR, A.L. (1973), "Screening sorghum varieties for resistance to Striga (Striga lutea Lour.), Sorghum Newsletter, 16 : 57-58

DEODIKAR, G.B. (1951), "Sorghum versicolor - species highly resistant to Striga", Current Science, 20 : 135-136

GADGIL, V.V. (1933), "Summary of work done under the Deputy Director of Agriculture, South Central Division, Poona, for the year 1931-32", Bombay Dep. Agric. Ann. Rep., pp. 71-121

GILLIVER, B., RAO, M.J. Vasudeva & VENKATESWARLU, P. (1983), "A design and methods of analysis to monitor crop growth conditions illustrated with sorghum screening trials for resistance to Striga", Statistics Unit Report No. 5/83, ICRISAT, Patancheru, A.P., India

HOSMANI, M.M. (1978), "Striga - a noxious root parasitic weed", Univ. Agri. Sci. Dharwar, India

HOUSE, L.R. & RAO, M.J. Vasudeva (1982), "Striga - problems and prospects", Proceedings of the ICRISAT-ICAR Working Group Meeting on Striga Control, 30 Sept.-1 Oct. 1982, ICRISAT Centre, Patancheru, A.P. India, Departmental Report SB-4, pp. 10-18

ICRISAT (1978), "ICRISAT Annual Report 1977-78", Hyderabad, India

JENKINS, W.J. (1944), "Research work on crop protection", Bombay Dept. Agri. Ann. Rep. pp. 14-17

KAJJARI, N.B., HIREMATH, P.S. & RENUKARYA, M.K. (1967), "Sorghum variety BH 4-1-4 tolerant to witchweed, downy mildew and rust", Sorghum Newsletter, 10 : 51-53

McKERRAL, A. (1912), "Yamethin District", Burma Dept. Agri., Agr. Surveys 3:32, (from Hosmani, 1978)

MATHUR, R.L. & BHARGAVA, L.P. (1971), "Screening of pearl millet (Pennisetum glaucum) varieties against Striga lutea", Ind. Phytopath, 28 : 804-806

MOHYUDDIN, A.I., GALOCH, G.M., MUJAHID, A.A. & QURESHI, M. (1965), "Studies on the insect enemies of noxious weeds in Pakistan", Final Report 1960-65, Pak. Stn. Commonwealth Inst. Biol. Control, Rawalpindi, Pakistan, 149-151

NAGUR, T., SREERAMULU, C. & SIVARAMAKRISHNAIAH, M. (1962), "Striga resistant culture No. 109", Andhra Agri. J. 9 : 145-148

NARASIMHAMURTHY, B.L. & SIVARAMAKRISHNAIAH, M. (1963), "Modern trends of agricultural research with reference to Striga resistant sorghum types for maximum food production", Andhra Agri. J. 10 : 6-11

PANCHO, J.V. & S. (1975), "Notes of witchweed, Striga lutea, a potential pest of rice in South East Asia", Proc. of the 3rd Indonesian Weed Sci. Conf., Bandung, Indonesia, 207-211

RAO, Govinda P., RAO, Narasimha M. & NAIDU, C.A. (1953), "A short note on Striga euphrasioides on paddy and its control", Madras Agric. J. 40 : 381-382

RAO, M.J. Vasudeva, CHIDLEY, V.L. & HOUSE, L.R. (1982a), "Genetic control of Striga asiatica in sorghum", Proceedings of the ICRISAT-ICAR Working Group Meeting on Striga control, 30 Sept.-1 Oct. 1982, ICRISAT, Patancheru, A.P., India, Departmental Report, SB-4, pp. 22-39

RAO, M.J. Vasudeva, CHIDLEY, V.L. & HOUSE, L.R. (1982b), " A three-stage screening methodology for Striga resistance screening in the field", Unpublished, Paper presented to the Annual Workshop of All India Coordinated Sorghum Improvement Project, 17-19 May 1982, Puna, India

RAO, M.J. Vasudeva, CHIDLEY, V.L. & HOUSE, L.R. (1983), "Genetics of field resistance to Striga asiatica (L.) Kuntze in sorghum", Sorghum Newsletter

RAO, M.J. Vasudeva, CHIDLEY, V.L., MUKURU, S.Z. & HOUSE, L.R. (1983), "Screening methodology and breeding sorghums resistant to Striga asiatica (L.) Kuntze at the ICRISAT Centre", Paper presented at the Nat. Sem. on Breeding Crop Plants for Resistance to Pests and Diseases, TNAU, Coimbatore, Tamil Nadu, India, 25-27 May 1983

RAO, M.J. Vasudeva, CHIDLEY, V.L., RAMAIAH, K.V. & HOUSE, L.R. (1983a), "Breeding sorghum genotypes with resistance to Striga asiatica at the ICRISAT Centre", Proc. 2nd International Workshop on Striga, Ouagadougou, Upper Volta, 5-8 Oct. 1981, pp. 61-76

SAUNDERS, A.R. (1933), "Studies in phanerogamic parasitism with particular reference to Striga lutea Lour.", South Africa Dept. Agric. Sci. Bull. 128

SHINDE, V.K. & KULKARNI, N. (1982), "Genetics of resistance to Striga asiatica in sorghum", Proceedings of the ICRISAT-ICAR Working Group Meeting on Striga Control, 30 Sept.-1 Oct 1982, ICRISAT Centre, Patancheru, A.P. India, Departmental Report, SB-4, pp. 134-141

SIVARAMAN, M.S. (1952), "Administration report of Agriculture Department for fasli (cropping) year 1950-51, Madras", pp. 140

SIVARAMAKRISHNAIAH, M., RAO, C. Raghunatha, & RAO, G.N. Shankaranarayana (1968), "Striga resistance of male sterile lines and hybrids of pearl millet", Andhra Agri. J. 15(6) : 180-181

TEERAWATSAKUL, M. (1975), "Discovery of witchweed (Striga lutea Lour.), a root parasite of corn in Thailand, II. Studies on witchweed control", Ann. Rep. Thailand Natl. Crop & Sorghum Prog. pp. 192-199

TEERAWATSAKUL, M. & KANJANAJIRAWONG, S. (1977), "Progress report on witchweed (Striga asiatica (L.) Kuntze), a root parasitic weed of corn in Thailand", Ann. Rep. Thailand Natl. Corn and Sorghum Prog. pp. 211

UTTAMAN, P. (1949), "An introduction to the study of Striga lutea as a root parasite of rice in Malabar", Madras Agric. J. 36 : 303-307

UTTAMAN, P. (1950), "Parasitism of Striga lutea Lour., on rice and methods to protect rice plants against Striga", Madras Agri. J. 37 : 99-118

CHEMICAL CONTROL OF STRIGA

R.E. Eplee

INTRODUCTION

The comments presented below are based on work with Striga asiatica eradication in the USA. It should, however, be applicable to other Striga spp.

The use of chemicals to control Striga can be divided into two general categories. The first category is vegetation control. This is a control of the Striga plant prior to its emergence (pre-emergence), or after the Striga has emerged (post-emergence). A second category is chemical control which uses a fumigant to kill the seeds in the soil, or a stimulant to induce suicidal germination of seeds in the soil. Another subject area that is critical to effective chemical control of Striga is application methodology.

Vegetation Control (pre-emergence)

A group of herbicides that have been effective in the control of Striga before it emerges above ground are the dinitroaniline compounds. Representative herbicides in this family of chemistry include Treflan, Prowl, Basalin and Balan. The trade names are used for convenience only. A list of common and chemical terms is given at the end of the text. These compounds act as a 'barrier' to Striga emergence. Striga will grow underground but cannot penetrate the herbicide shield.

Other pre-emergent Striga herbicides are Goal, and a new material from ICI called Flex. These herbicides appear to work systematically, as the Striga reaches the treated soil.

The herbicide, Fenac, showed promise early in the US Striga programme, but its use was discontinued because of damage to susceptible crops the following year. Two other materials, Dacthal and Casoron have also shown some pre-emergence activity for Striga suppression. All of these herbicides permit Striga to parasitize and inflict damage to the host. Crop susceptibility and other use restrictions govern the extent to which these herbicides can be used to control Striga.

Vegetation Control (post-emergent)

The most effective method for chemical control of Striga is by applying a herbicide to the emerged Striga plants. The most commonly-used herbicides for this purpose in the USA is the Phenoxy material 2,4-D. This herbicide is relatively less expensive than other herbicides and does an excellant job when the foliage of the Striga is covered with an application of the material. The mode of activity to the Striga is systemic, thus providing effective kill of the Striga to which it is applied. Phenoxy materials cannot be applied in mixed cropping situations where susceptible crops such as cowpeas are interplanted.

The Triazine herbicide, ametryn is effective as a foliar herbicide, but it also has potential for damage to susceptible interplanted crops.

The Diphenyl Ether compounds, Goal, Flex and an expermiental herbicide, PPG 884, trade named Cobra, also have excellent post-emergent Striga activity. These are the most promising herbicides for control of Striga plants. These compounds also provide some residual pre-emergence activity as discussed previously.

The use of the desiccant herbicide paraquat or gramaxone has proved to be a very effective Striga control material. Care must be exercised with paraquat to ensure that the herbicide contacts only the target weed.

Gramoxone, glyphosate and others of the chemicals mentioned above can also be used under certain circumstances to control Striga host vegetation. This use procedure is host avoidance. Without a host, Striga cannot reproduce. In the USA, this technique is used to prevent Striga seed production on grassy weeds in idle lands and in crops that are not a host to Striga.

It must also be added that, almost without exception, the successful use of post-emergent herbicides is enhanced by the use of a surfactant to aid the absorption and penetration of these materials into the pest weed.

All of the pre-emergent and post-emergent herbicides are designed to stop Striga seed production. They have minimum benefit in protecting the currently infested crop. Several years of no seed production may be required to significantly reduce a Striga seed population. A herbicide that can protect the current crop is still elusive.

Seed Active Materials (fumigants)

At present the only way to protect a crop from Striga is to rid the soil of its seeds. Unfortunately, there is no economical way to devitalise seed in the soil. Nevertheless, the technology presently available that can be used to devitalize Striga seeds in the soil will be discussed.

The most effective fumigant for killing seeds in the soil is methyl bromide. This very expensive treatment requires the use of about 500 kg/ha of the fumigant. The treatment must be entrapped under a gastight cover for a couple of days to retain the chemical and insure its biological activity.

Another material, Vapam, can be drenched or incorporated into the soil with quite acceptable results. The same active ingredient in granular form is sold as Mylone. This material is applied to the soil surface and carried into the soil with rainwater. Although these fumigant treatments are expensive and technically demanding in application, they may have a place in ridding soils of Striga in research plots and other special institutions.

Seed Active Materials (stimulants)

By far the most promising method of ridding the soil of Striga seeds is the use of seed germination stimulants. The only proportional Striga seed germination stimulant to date is ethylene (C_2H_4). This material, applied as a compressed gas, is injected into the soil at a time when the seeds are preconditioned and capable of germination. The ethylene gas readily diffuses through the soil, triggering the germination of Striga seeds. Striga seeds can survive after germination for no more that 4 days unless attachment to a host occurs. A suitable host root must be within 4 mm of the seed for attachment to occur. Even in the presence of a host, the probability of Striga making a successful attachment after ethylene stimulation is rare. Thus the ethylene-induced germination of Striga seeds is suicidal. Research has indicated that a single ethylene treatment can rid the soil of approximately 90% of the viable preconditioned Striga seeds.

The price of ethylene is quite reasonable for a pesticide. But no treatment is without its problems. Ethylene is a gas under relatively high pressure. The transport and application equipment may present problems. We have resolved these problems for the USA. However, a system of handling and applying ethylene has yet to be developed in other infested countries, especially in developing countries. This is certainly an area of challenge.

Other non-gaseous compounds have been formulated to induce suicidal germination of Striga seeds. These are the strigalogs - analogs or compounds with an active moiety of the natural Striga stimulant. Unfortunately, development of these compounds is practically non-existent.

Application Methodology

We have found that as much as 80% of the success of a chemical control treatment is associated with application methodology. Therefore, in considering chemical control technology, brief mention should be made of the technology which has been developed to ensure that chemicals available reach the target area and provide the desired results.

The elements of herbicide application consist of a transport system, a carrier or diluent, the delivery energy source and the spray nozzles. The transport equipment may be a simple bottle, a hand sprayer or backpack. From these simple one-man transport units one can advance up to tractor-mounted and self-propelled specialized sprayer equipment. The single function of all of this equipment is to transport the spray material to the pest infected area. The size, form and complexity of the 'sprayer' is determined by the individual situation.

The carrier or diluent for the herbicide is used to ensure proper dispersal of the chemical. It permits appropriate coverage of the target and/or enhances movement of the chemical into the activity site. Water is the most common carrier solution, but there are uses for which oil is a preferred carrier. The quality of the carrier is important, but the volume of the carrier need not exceed that which is sufficient to achieve the movement of the pesticide to the target area in the required coverage manner.

The herbicide and carrier are moved through the sprayer and out through the nozzle by gravity pressures or a variety of designs of pumps, or in the case of the

CDA systems, by the spinning action of an electric motor. Regardless of the system, the need is for sufficient volume movement of the spray solution at the proper pressure to operate the nozzles and provide tank agitation if needed.

The key to effective chemical dispersal is the spray nozzle. This component of the delivery system is perhaps the most neglected part of the system. It determines not only the volume of chemical applied, but equally important, the uniformity of delivery and particle size.

The four basic nozzle styles that have been used in herbicide application are the flat fan, flood jet, whirlchamber and spinning disc. Each nozzle style has advantages and limitations. Greater use of the whirlchamber has been made in the Striga programme than any of the others. The whirlchamber nozzle is much preferred for many reasons over the CDA or other nozzles. The primary reasons are droplet size (250 microns), low pressure operation, wear factor and freedom from clogging. It is vital to successful chemical application that the proper nozzle be selected for the job that is to be done.

Important operational considerations of application methodology are nozzle operation pressure, travel speed, swath width and nozzle size selection. The most effective chemical available cannot be effective unless it is properly applied.

The chemicals, equipment and technology to deal with Striga in the United States have been developed. The extent to which these developments can be used for Striga control in the developing countries is yet to be determined.

Table 1 : Herbicidal efficacy for Striga asiatica

Ratings: 1 = no effect; 2 = poor; 3 = fair; 4 = good; 5 = excellent; - = not used this way

	GRASS				WITCHWEED			BROADLEAF	
			POST						
Herbicide	PPI	PE	1-3"	3-12"	PPI	PE	POST	PE	POST
Alanap	2	2	-	-	1	1	-	3	-
* Amex 820	5	-	-	-	4	-	-	3	-
Atrazine	2	3	2	1	1	1	3	5	3
* Balan-EC	5	-	-	-	4	-	-	4	-
* Balan "G"	4	3	-	-	4	3	-	3	-
Banvel	-	3	-	2	-	5	4	4	5
Basagran	-	1	1	1	-	-	2	-	4
* Basalin	5	-	-	-	4	-	-	3	-
Benazolin	-	3	-	1	-	3	3	-	3
Bicep	-	4	-	-	-	1	-	5	-
Bladex	-	4	3	2	-	2	4	5	4
* Blazer	-	4	4	3	-	3	4	4	4
* Casoron "G"	-	3	-	-	-	4	-	5	-
Cobra(PPG-844)	-	2	-	1	-	3	5	-	5
Cotoran	3	4	3	2	1	2	3	5	4
* 2,4-D	-	1	1	1	-	2	5	-	5
* 2,4-DB	-	1	1	1	-	1	3	-	3
* Dacthal	-	3	1	1	-	4	-	3	-
Dalapon	-	3	5	5	-	2	3	-	3
Devrinol	4	4	-	-	1	-	-	4	-
* Dinitro	-	2	3	2	-	2	3	3	4
Dual	3	4	-	-	1	2	-	4	-
Dyanap	-	3	3	1	-	2	3	4	4
* Enide	-	3	1	1	-	2	-	4	-
* Eptam	4	-	-	-	1	-	-	4	-
* Evik	-	3	5	3	-	2	4	4	4
Flex	-	5	-	1	-	5	5	5	5
Fusilade	-	-	-	5	-	1	1	-	1
Glean	-	5	-	2	-	5	5	-	2
* Goal	-	5	4	3	-	5	5	5	4
* Gramoxone	-	-	5	4	-	-	5	-	4
Hoelon	-	4	-	4	-	1	1	1	1
Karmex	-	4	4	3	-	2	4	5	4
Lasso	3	4	-	-	1	2	-	4	-
Lorox	-	3	4	3	-	1	3	4	4
MSMA	-	-	4	3	-	1	2	-	3
* Mylone	5	5	-	-	5	5	-	5	-
Oust	-	5	-	-	3	5	-	5	-

Table 1 (cont.)

Ratings: 1 = no effect, 2 = poor, 3 = fair, 4 = good, 5 = excellent, - = not used this way

	GRASS				WITCHWEED			BROADLEAF	
			POST						
Herbicide	PPI	PE	1-3	3-12"	PPI	PE	POST	PE	POST
* Paarlan	5	-	-	-	4	-	-	3	-
* Paraquat	-	-	5	4	-	-	5	-	4
Poast	-	2	-	5	-	1	1	-	1
* Prefar	4	-	-	-	1	-	-	3	-
* Probe	-	3	4	3	-	2	4	3	4
* Prowl	5	4	-	-	4	3	-	3	-
Ronstar	-	4	-	-	-	3	5	4	4
* Roundup	-	-	5	5	-	-	3	-	4
Sencor	3	3	3	2	-	1	2	5	4
Simazine	2	3	-	3	1	1	3	5	3
Sonar	-	5	-	-	-	3	-	-	5
Stam	-	3	-	2	-	3	3	3	3
* Surflan	-	5	-	-	-	3	-	3	-
Sutan	5	-	-	-	1	-	-	3	-
Tackle	-	5	-	3	-	5	5	5	4
Tenoran	-	2	2	2	-	2	3	-	4
Tillam	4	-	-	-	1	-	-	3	-
TOK	-	2	-	2	-	3	4	3	3
* Tolban	5	-	-	-	5	-	-	4	-
* Treflan-EC	5	-	-	-	5	-	-	4	-
* Treflan-G	5	5	-	-	5	4	-	4	-
* Vapam	5	5	-	-	5	5	-	5	-
* Vernam	5	-	-	-	1	-	-	3	-
Vistar	-	-	-	-	-	2	1	-	-

*Denotes herbicides which are included in witchweed control recommendations

PPI - Pre-plant incorporated (incorporated in the soil)
PE - Pre-emergence (surface spray)
POST - Post-emergence (applied to vegetation)

Prepared by the Whiteville Methods Development Center, October 1983

Table 2 : Vegetative control
Pre-emergent materials
Dinitroaniline herbicides

Common Name	Trade Name	Chemical Name
Trifluralin	Treflan	a,a,a-Trifluoro-2,6-dinitro-N,N-dipropyl-p-toluidine
Pendimethalin	Prowl	N-(1-ethylpropyl)-3,4-dimethyl-2,6-dinitrobenzenamine
Fluchloralin	Basalin	N-(2-Chloroethyl)-a,a,a-trifluoro-2,6-dinitro-N-propyl-p-toluidine
Benefin	Balan	N-Butyl-N-ethyl-a,a,a-trifluoro-2,6-dinitro-p-toluidine
	Diphenyl ether	
Oxyfluorfen	Goal	2-chloro-1-(3 ethoxy-4-nitrophenoxy)-4-(trifluoromethyl) benzene
Fomesafen	Flex	sodium salt of 5-|2-chloro-4-(trifluoro-methyl)-2-nitrobenzamide|
Fenac	Fenac	(2,3,6-Trichlorophenyl)acetic acid
	Miscellaneous	
DCPA	Dacthal	Dimethyl tetrachloroterephthalate
Diclobenil	Casoron	2,6-dichlorobenzonitrile
	Post-emergent control	
	Phenoxy	
2,4-D	2,4-D (salts) of	2,4-Dichlorophenoxyacetic acid
2,4-D	2,4-D (Esters) of	2,4-Dichlorophenoxyacetic acid
Dicamba	Banvel	3,6-Dichloro-o-anisic acid
	Triazines	
Ametryn	Evik	2-(ethylamino)-4-isopropylamino-6-methylthio-s-triazine

Table 2 (cont)

Common Name	Trade Name	Chemical Name
	Diphenyl Ethers	
Oxyfluorfen	Goal	2-chloro-1-(3-ethoxy-4-nitrophenoxy)-4-(trifluoromethyl) benzene
Fomesafen	Flex	Sodium salt of 5-|2-chloro-4-(trifluoro-methyl)-2-nitrobenzamide|
PPG-844	Cobra	------
Paraquat	Gramoxone	1,1-Dimethyl-4,4'bipyridinium ion
	Host Avoidances	
Paraquat	Gramoxone	1,1-Dimethyl-4,4'bipyridinium ion
Glyphosate	Roundup	N-(phosphonomethyl) glycine
	Seed Active Materials	
	Fumigants	
Methyl bromide	Methyl Bromide	Bromomethane
Metham	Vapam	Sodium N-methyldithiocarbamate
Dazomet	Mylone	Tetrahydro-3,5-dimethyl-2H-1,3,5-thiadiazi 2-thione
	Stimulants	
Ethylene	Ethylene	Ethylene C_2-H_4
GR-24	GR-24	2-methyl-4-(2-oxo-2,3,3a,8b-tetrahydro-4H-ideno |1,2-b| furan-3-ylidenemethoxy) but-2-en-4-olide
GR-7	GR-7	3-||(2,5-dihydro-4-methyl-5-oxo-2 furanyl) oxy| methylene|-3,3a,6,6a-tetrahydro-2H-cyclopenta|b| furan-2-one

Prepared by the Whiteville Methods Development Center, October 1983

Slide 1 : Portable ethylene compound applicator in use in Striga-infested fields in the USA

PUBLICATIONS

COOK, C.E. (1966), "Germination of witchweed (Striga lutea Lour.). Isolation and properties of a potent stimulant", Science:1189-1190

COOK, C.E., WICHARD, P., WALL, M.E., EGLEY, G.H., COGGAN, P., LUTHAN, P.A. & McPHAIL, A.T. (1972), "Germination stimulants. II. The structure of strigol - a potent seed germination stimulant for witchweed (Striga lutea Lour.). J. Am. Chem. Soc. 94 : 6198-6199

EPLEE, R.E. (1975), "Ethylene: A witchweed seed germination stimulant", Weed Science, 23 : 433-436

EPLEE, R.E. (1979), "The Striga eradication program in the United States of America", 2nd International Symposium on Parasitic Weeds, pp. 269-272

EPLEE, R.E. (1981), "Striga's status as a plant parasite in the US", Plant Disease 65 (12) : 951-954

EPLEE, R.E. & CARTER, E.M. (1968), "Direct spray applicator", Abstracts of Weed Science Soc. of America, pp. 110-129

EPLEE, R.E. & CARTER, E.M. (1972), "Nozzle support for high clearance sprayer", APHIS 81-1

EPLEE, R.E., CARTER, E.M. & MOODY, A.V. (1976), "Backpack ethylene applicator", APHIS 81-25

EPLEE, R.E. & LANGSTON, M.A. (1970), "Use of paraquat in late season weed control", Proc. of So. Weed Science Soc. pp. 127-128

EPLEE, R.E. & LANGSTON M.A. (1971), "Contact soil fumigation", Proc. of So. Weed Science Soc. pp. 194-195

EPLEE, R.E. & LANGSTON, M.A. (1976), "Developments in the control of Striga in the USA", PANS 22 : 61-64

GARRIS, H.R. & WELLS, J.C. (1956), "Parasitic herbaceous annual associated with corn disease in North Carolina", Plant Disease Reptr. 40 : 837-838

JOHNSON, A.W., ROSEBERY, G. & PARKER, C. (1976), "A novel approach to Striga and Orobanche control using synthetic germination stimulants", Weed Res. 16 : 223-227

LANGSTON, M.A., ENGLISH, T.J. & EPLEE, R.E. (1979), "Witchweed (Striga asiatica) eradication in the United States of America herbicides", 2nd International Symposium on Parasitic Weeds, pp. 273-227

LANGSTON, M.A. & EPLEE, R.E. (1974), "The use of glyphosate in witchweed control", Abstracts of Weed Science Soc. of America, pp. 115

LANGSTON, M.A., EPLEE, R.E. & GOSSETT, B.J. (1972), "Witchweed suppression in dinitroaniline herbicides", Abstracts of Weed Science Soc. of Amer. pp. 83

SAUNDERS, A.R. (1933), "Studies in phanerogamic parasitism with particular reference to Striga lutea Lour.", South Africa Dept. Agric. Sci. Bull. 128

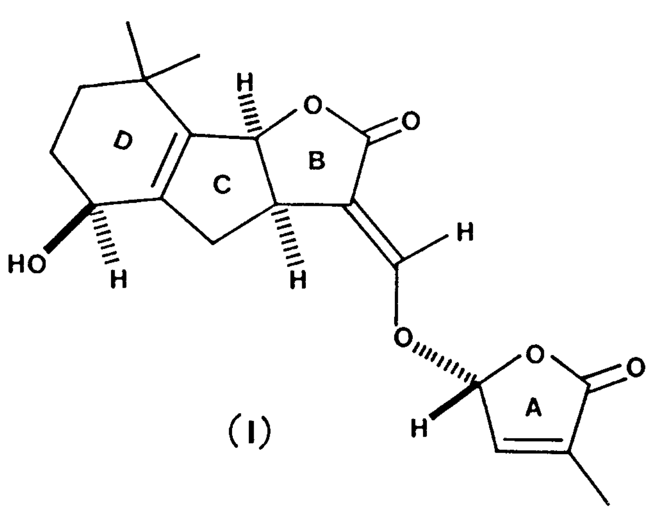
SHAW, W.C., SHEPHERD, D.R., ROBINSON, E.L. & SAND, P.F. (1962), "Advances in witchweed control", Weeds, Volume 10 (3) : 182-191

STRIGOL ANALOGUES : SYNTHETIC ACHIEVEMENTS AND PROSPECTS

A. Hassanali

INTRODUCTION

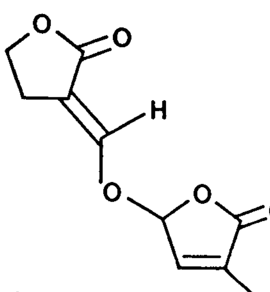
The possibility of Striga control by using synthetic compounds modelled on natural seed germination stimulants has been recognized since the early 1950's when first attempts were made to isolate and identify stimulants from host roots (Brown, 1959; Brown et al, 1949, 1951a, 1951b, 1952, 1954). Cook and his co-workers (Cook et al, 1966, 1972) described the isolation of a few milligrammes of a crystalline compound, strigol, from the root exudates of cotton (Gossypium hirsutum L.) which is not in itself a host of Striga spp. Nevertheless, strigol was found to be highly potent in stimulating the germination of S. asiatica, demonstrating activity at concentrations lower than 10^{-12}M. Some years later, the structure (I) was established by X-ray crystallography (Coggan et al, 1973) and this prompted synthetic studies in a number of laboratories. Several partial (Dolby & Hanson, 1976; Cooper & Dolby, 1979; Pepperman, 1981; Brooks & Kennedy, 1983) and two total syntheses (Heather et al, 1976; MacAlpine et al, 1976) of (±)-strigol have so far been reported, some of which have succeeded in providing gramme quantities of the stimulant for biological evaluation. However, unless there is an appreciable improvement in the efficiency of the synthesis of (±)-strigol, this compound is unlikely to be of economic significance. Between 1973 and 1981 the International Development Research Centre sponsored a project at the University of Sussex to synthesize and evaluate a series of synthetically simpler analogues of strigol. This presentation gives a summary of that work as well as points out possible future directions.



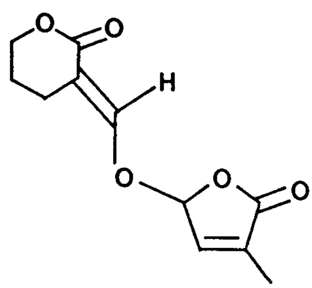
(I)

INITIAL SYNTHETIC WORK

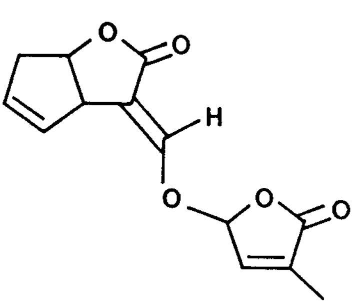
Initial synthetic design at Sussex was based on investigating the possibility that only a portion of the strigol molecule might be primarily responsible for biological activity. Accordingly, the first screening work undertaken by Dr. G. Roseberry (Johnson et al, 1976) involved the syntheses of various mono- and bis-lactones modelled on rings A, A-B and A-B-C of strigol. Laboratory bioassays showed that the minimum structural requirement for activity was a bis-lactone comprising rings A and B, structure (II), labelled 'GR5'. A minor departure from this structure, e.g. the use of a 6-membered B-ring lactone (III), led to an appreciable loss of activity. The tricyclic bis-lactone (IV), labelled 'GR7', which incorporates three of the four rings of strigol was found to be much more potent (active even at 10^{-6}-10^{-7}M). Epoxidation of the ring-C double bond or its hydrogenation gave analogues (compounds (V) and (VI)) with a reduced germination activity. As a bonus, (IV) was active in germinating seeds of Orobanche spp. as well as Alectra vogelli. Kilogramme quantities of this compound were therefore prepared for field and pot evaluation against both Striga and Orobanche spp.



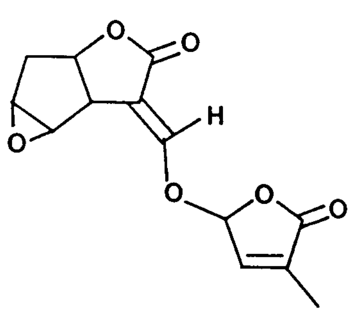
(II) "GR5"



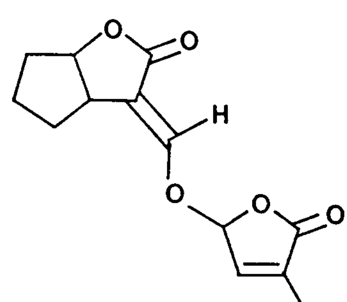
(III)



(IV) "GR7"



(V)



(VI)

Despite some encouraging results from pot/field trials, the results were generally disappointing. Field collaborators in the project attributed the problem to low soil stability of (IV). The bis-lactones had been shown to be rather unstable in alkaline media, although relatively stable in moderately acidic pH values (Johnson et al, 1976). Multivalent cations in the soil could conceivably catalyse the hydrolytic cleavage of these lactones and incubation experiments in sterilized and unsterilized soils clearly showed that microbial breakdown of (IV) was an important factor (Roseberry & Hassanali, unpublished).

SEARCH FOR MORE EFFECTIVE ANALOGUES

Further design of other analogues of strigol was based on two considerations :

1. modification of the structure of (IV) by buttressing the molecule with benzene rings and various ways in the hope of producing compounds with greater resistance to hydrolytic as well as microbial attack;

2. production of compounds which were structurally more closely related to strigol, without loss of the preparative simplicity of (IV) in the hope that these would be even more potent than (IV).

Structures of compounds so produced are shown on the following page.

Laboratory bioassays showed the presence of benzene rings in the butenolide side significantly decreased the activities of the compounds (VII), (VIII), (X), (XII) and (XIV) relative to the one containing the 3-methylbutenolide moiety. However, the presence of benzene rings in the oxymethylenelactone side (compounds (IX) and (XI)) appeared to be advantageous. Thus, compound (XI) which has a benzene ring in the same relative position as the double bond in (IV) was somewhat more active than the latter*. The most active compounds, as expected, were (IX) and (XIII) (Hassanali & Johnson, 1978; Johnson et al, 1981). Both these compounds contain Π-systems in the same relative positions as in strigol (I). Laboratory observations showed (XIII) to be chemically somewhat unstable whereas (XI) showed high relative stability. The reasons for these differences are not clear. Of the analogues so far investigated (XI) would appear to be by far the best candidate for more extensive field trials.

In another variation of the oxymethylenelactone moiety, analogues derived from oxymethyleneindolin-2-one, e.g. (XV), its N-methyl, 5-nitro- and N-methyl-5-nitro-derivatives were also prepared. None of these compounds however, had activity comparable to the more active bis-lactones described above.

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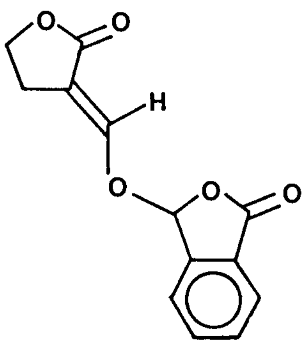
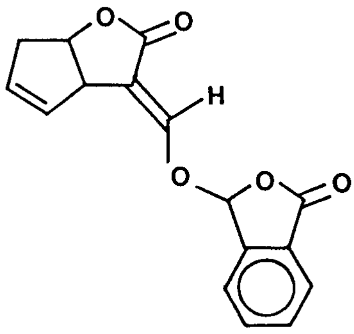
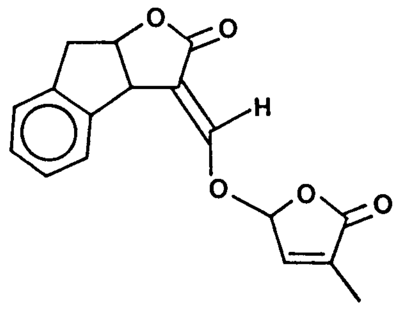
* The two diastereoisomers of (IX), 'GR18', m.p. 119-20°C (faster-moving isomer) and 205°C (slower-moving isomer) were almost equally active as germination stimulants)



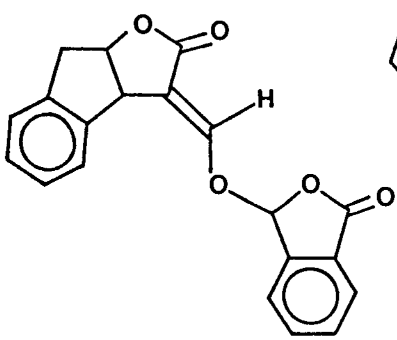
(VII)



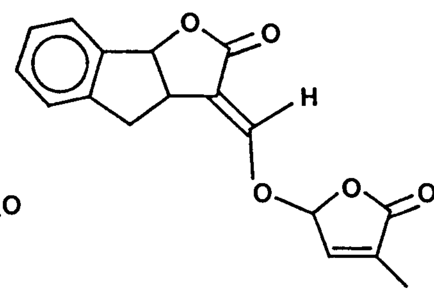
(VIII)



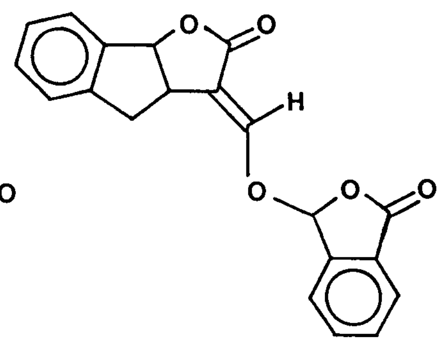
(IX) "GR 18"



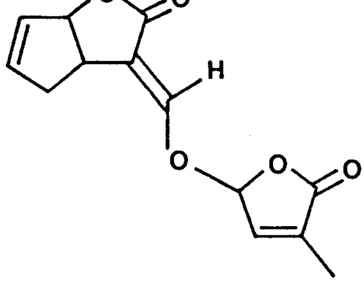
(X)



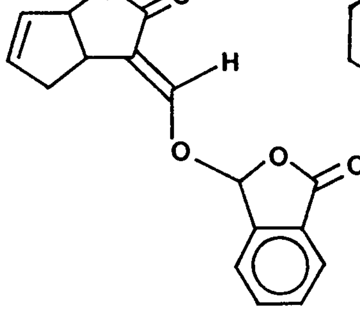
(XI) "GR 24"



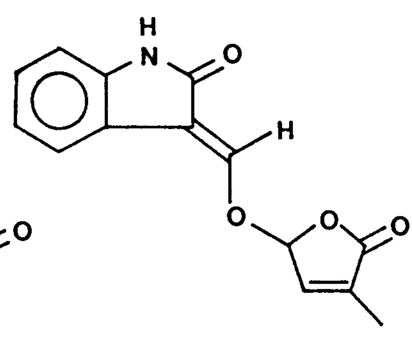
(XII)



(XIII) "GR 28"



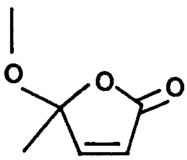
(XIV)



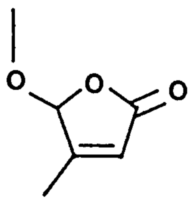
(XV)

Other structural variants

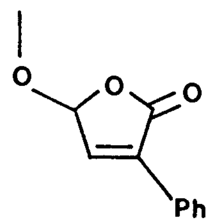
In the course of the project, various 2-, 3- and 4-substituted butenolides were prepared for assessment of structural variation of this moiety on the activities and stabilities (particularly in alkaline media) of the derived strigol analogues (Johnson et al, 1981). The variation involved is shown in the following partial structures:



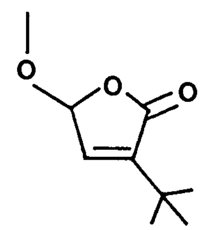
(XVI)



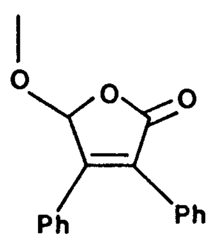
(XVII)



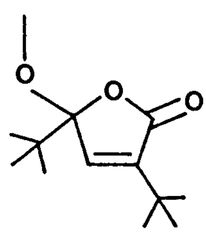
(XVIII)



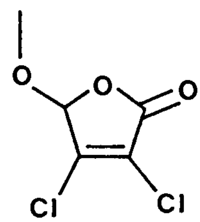
(XIX)



(XX)



(XXI)



(XXII)

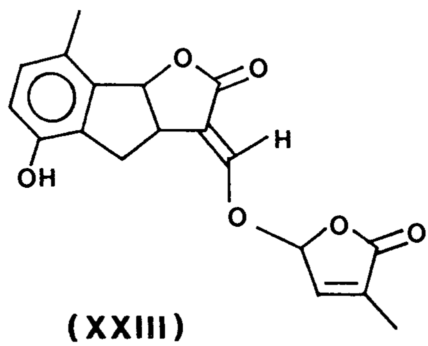
Significant germinating activity was observed only with analogues containing monosubstituted 3-methyl- and 2-t-butylbutenolides. The greater alkaline stability conferred to the analogues (Johnson et al, 1981) by these butenolide moieties merits further attention as this may have implications in calciferous soils.

Other work on strigol analogues

Cook and his co-workers (Kendall et al, 1979) have described the preparation of the bis-lactone (XXIII) which is related to 'GR24'. Surprisingly, however, this compound has been reported to have rather low activity relative to strigol*. Similar compounds are being synthesized by a graduate student at the University of Dar-es-Salaam, aimed at studying the effect of electron enrichment/depletion at the position in the benzene ring which corresponds to the olefinic bond of the

* Two diastereoisomers of (XXIII) have widely different activities, unlike our own results with 'GR7' and 'GR18'

cyclohexane ring of strigol. In another synthetic project, the University of Dar-es-Salaam is collaborating with Professor B. Zwanenburg of the University of Nijmegen, the Netherlands, in the preparation of analogues in which the two lactone moieties are linked by sulphur atoms. These compounds have not yet been biologically evaluated.



(XXIII)

CONCLUSIONS

Do strigol analogues represent a viable option for Striga control in Africa? Which direction, if any, should further chemical work on the analogues take? The answers to these questions would depend firstly on more extensive field evaluation of the more promising analogues, e.g. 'GR7', 'GR18' or 'GR24'. The most widely field evaluated strigol analogue so far has been 'GR7'. On the other hand 'GR24' has been found to be more effective both in the laboratory as well as in limited trials (Hassanali & Johnson, 1978; Johnson et al, 1981; Eplee, 1984). Sufficiently large quantities of 'GR24' need to be manufactured for proper evaluation. A factor that fuelled continued search for 'more stable analogues' was an assumption that the available compounds may not be sufficiently persistent in the soil. Results reported by some participants in this Workshop suggest that this may not be true (Eplee, 1984; Ogborn, 1984). Some quantitative data on the rate of deactivation of strigol analogues in different soil types on which Striga thrives may be useful in the evaluation process.

Secondly, the synthetic route to 'GR24' needs to be optimised to allow a meaningful prefeasibility study on the manufacture of the compound to be carried out. The study should preferably explore the possibility of a simple, small-scale, batchwise process in an African country with some chemical technological capacity. Contrary to general impression, the medium-scale synthesis of strigol analogues could be done by a combination of relatively straightforward unit operations. Moreover, simple structural variants of 'GR24', e.g. one containing an unsubstituted butenolide group (readily prepared from cheaply available furfuraldehyde) could be synthesized for evaluation.

The simple devices developed in the USA for the fumigation of Striga-infested soils with ethylene appear very attractive and practical. A parallel evaluation of ethylene would help in the assessment of the relative strengths of the two technologies in the African context.

Acknowledgement

This paper is dedicated to the memory of my mentor, the late Professor Alan W. Johnson, who spent over a decade on the elusive Striga and Orobanche germination factors, and who later initiated the synthetic work described here.

REFERENCES

BROOKS, D.W. & KENNEDY, E. (1983), "Efficient synthesis of methyl 3-oxo-2,6,6-trimethylcyclohex-1-ene-1-carboxylate, an A-ring intermediate for (±)-strigol", J. Org. Chem. 48 : 277-278

BROWN, A.P. (1959), "Studies in germination stimulants", Ph. D. Thesis

BROWN, R., GREENWOOD, A.D., JOHNSON, A.W., LANSDOWN, A.R., LONG, A.G. & SUTHERLAND, N. (1952), "The Orobanche germination factor. 3. Concentration of the factor by counter-current distribution", Biochem. J. 52 : 571-574

BROWN, R., GREENWOOD, A.D., JOHNSON, A.W. & LONG, A.G. (1951a), "The stimulant involved in the germination of Orobanche minor Sm. 1. Assay technique and bulk preparation of the stimulant", Biochem, J. 46 : 559-564

BROWN, R., GREENWOOD, A.D., JOHNSON, A.W., LONG, A.G. & TAYLOR, G. (1951b), "The stimulant involved in the germination of Orobanche minor. Sm. 2. Chromatographic purification of crude concentrates", Biochem, J. 48 : 564-568

BROWN, R., JOHNSON, A.W., ROBINSON, E. & TODD, A.R. (1949), "The stimulant involved in the germination of Striga hermonthica", Proc. Roy. Soc. 136 : 1-12

BROWN, R., JOHNSON, A.W., ROBINSON, E. & TAYLOR, G. (1952), "The Striga germination factor. 2. Chromatographic purification of crude concentrates", Biochem. J. 50 : 596-600

COGGAN, P. LUTHAN, P.A. & McPHAIL, A.T. (1973), "Crystal and molecular structure of the germination stimulant, strigol by X-ray analysis", J. Chem. Soc., Perkins Trans. 2 : 465-469

COOK, C.E., WICHARD, L.P., TURNER, B., WALL, M.E. & EGLEY, G.H. (1966), "Germination of witchweed (Striga lutea): Isolation and properties of a potent stimulant", Science, 154 : 1189-1190

COOK, C.E., WICHARD, L.P., WALL, M.E., EGLEY, G.H., COGGAN, P., LUTHAN, P.A. & McPHAIL, A.T. (1972), "Germination stimulants. 2. The structure of strigol - a potent seed germination stimulant for witchweed (Striga lutea Lour.)", J. Am. Chem. Soc. 94 : 6198-6199

COOPER, G.K. & DOLBY, L.J. (1979), "Convenient synthesis of the 2-methyl-4-hydroxybut-2-enolide moiety of strigol", J. Org. Chem. 44 : 3414-3416

DOLBY, L.J. & HANSON, G.J. (1976), "A convenient synthesis of a hydrindan percursor to strigol", J. Org. Chem. 41 : 563-564

EPLEE, R.E. (1984), "Chemical Control of Striga", Paper presented at ABN-CASAFA Workshop on the Biology and Control of the Parasitic Weed Striga, Dakar, Senegal, 14-17 November 1983

HASSANALI, A. & JOHNSON, A.W. (1976), "Butenolide derivatives", Brit. Pat. Appl. No. 2740801 (Chem. Abstr. 1978, 88, 190581)

HEATHER, J.B., MITTAL, R.S.D. & SIH, C.J. (1976), "Synthesis of the witchweed seed germination stimulant (±)-strigol", J. Am. Chem. Soc. 98 : 3661-3669

JOHNSON, A.W. & HASSANALI, A. (1980), "Novel compounds and process for their preparation", U.S. Patent No. 123257

JOHNSON, A.W., GOWDA, G., HASSANALI, A., KNOX, J., MONACO, S., RAZAWI, Z. & ROSEBERY, G. (1981), "Preparation of synthetic strigol analogues", J. Chem. Soc. Perkin I. 1934-1943

JOHNSON, A.W., ROSEBERY, G. & PARKER, C. (1976), "A novel approach to Striga and Orobanche control using synthetic germination stimulants", Weed Res. 16 : 223-227

KENDALL, P.M., JOHNSON, J.V. & COOK, C.E. (1979), "Synthetic route to an aromatic analogue of strigol", J. Org. Chem. 44 : 1421-1424

MacALPINE, G.A., RAPHAEL, R.A., SHAW, A., TAYLOR, A.W. & WILD, H.J. (1976), "Synthesis of the germination stimulant (±)-strigol", J. Chem. Soc. Perkins Trans. I : 410-416

OGBORN, J.E.A. (1984), "Striga : research priorities with specific reference to agronomy", Paper presented at ABN-CASAFA Workshop on the Biology and Control of the Parasitic Weed Striga, Dakar, Senegal, 14-17 November 1983

PEPPERMAN, A.B. (1981), "Improved yield preparation of 3-oxo-2,6,6-trimethylcyclohex-1-ene-1-carboxylic acid, an important intermediate in the synthesis of (±) strigol", J. Org. Chem. 46 : 5039-5041

THE NATURAL ENEMIES OF STRIGA Spp. AND THE PROSPECTS FOR THEIR UTILISATION AS BIOLOGICAL CONTROL AGENTS

D.J. Greathead

INTRODUCTION

Most organisms have natural enemies which can be important mortality factors limiting their abundance. The basis of biological control is the exploitation of natural enemies of pest species, and a prerequisite for the assessment of the prospects for biological control is a knowledge of the natural enemies and their effect on the population dynamics of the host. There have been few studies on the natural enemies of Striga spp. and no systematic observations on their impact on populations of the host plants, so that prospects for their utilisation for biological control cannot be fully assessed. However, sufficient is known to indicate the kinds of insects and pathogens which are likely to be encountered and to speculate on ways that they may be exploited alone or as part of an integrated management programme.

The discovery of S. asiatica in the USA in 1956 (Garriss & Wells, 1956) stimulated interest, and observations on insects began to be reported in Africa (Williams & Caswell, 1959; Davidson, 1963), and India (Khan & Murthy, 1955). The USDA (through PL-480) funded a major study of insects and pathogens by the CIBC in India (Sankaran & Rao, 1966; Nag Raj, 1966; CIBC, 1974), and a less extensive survey of insects by the CIBC in Pakistan (CIBC, 1966). In eastern Africa, the CIBC carried out an extensive survey of insects for the government of Tanzania (Greathead & Milner, 1971). The results of this work were assessed by Girling et al, (1979) who advocated an integrated programme using biological control in combination with other available methods.

Insect Natural Enemies

Numerous insects feeding on Striga spp. have been collected (Table 1) notably in India (Sankaran & Rao, 1966) and eastern Africa (Greathead & Milner, 1971). Many of them are polyphagous species, some are important pests of crops, e.g. Spodoptera spp., Heliothis armigera spp. and others, not previously reared, were so scarce as to suggest that Striga spp. are not their principal host plants and therefore were of no interest as potential biological control agents. Discussion will be confined to the remainder which are found regularly in substantial numbers and for which there is some evidence that they have a narrow host range, i.e. are oligophagous.

Smicronyx spp., weevils, are recorded galling Striga spp. in India and Africa. In India, there seems to be a single species, Smicronyx albovariegatus, which galls all parts of the plants (Sankaran & Rao, 1966). In Africa, several species have been reared from stem or fruit galls but it is not possible to obtain a name for all of them at present. Although a number of species have been described, mostly from specimens collected as adults without associated host plant records, there is no revision or key permitting ready identification of these species and unfortunately voucher specimens relating to most of the published records are no longer available. Dr. M.L. Cox has examined the material available in the British Museum (Natural History) and arrived at the following preliminary conclusions. S. umbrinus, known from Senegal, Sierra Leone, Nigeria, Upper Volta and the Sudan, has been reared from fruit galls in Upper Volta (C. Parker, personal communication) and the Sudan (Musselman, 1983). This was probably the species reared by Williams and Caswell (1959) in Nigeria. A similar, but distinct unnamed species is represented by specimens reared from fruit galls in Ethiopia (Tadesse Ghebremeddin, personal communication) and Uganda (the smaller species of Greathead & Milner, 1971). In addition, there is the larger fruit galling species from Uganda and the root galling species from Tanzania found by Greathead & Milner (1971) which are not represented by specimens.

Most of the Smicronyx spp. which have been reared feed as larvae in the stems or fruits of Cuscuta spp. or herbaceous dicotyledons, especially Compositae. The type of feeding and the tendency for feeding to be associated with gall formation (Anderson, 1982) support the belief that each species oviposits on a single plant genus only. This has been borne out in feeding tests on S. lutulentus, a species from Mexico being released for control of the composite weed, Parthenium hysterophorus, in Queensland, which attacked only Parthenium spp. (McClay, 1981).

As far as it is known, the life cycle of the Smicronyx spp. that feed on Striga spp. is similar. The adults live in the soil leaving it to feed and ovipost on the host plant. The eggs are inserted into plant tissue at the feeding sitte. Feeding causes the development of a gall which is vacated when the larvae are full grown. Pupation takes place in an earthen cell in the soil. Appearance of adults in the field is synchronised with the presence of the host plant and there appears to be a single annual generation. In Uganda, the dry season was passed in the pupal stage but in Nigeria development was rapid. In India, Smicronyx albovariegatus survived for six months in the laboratory implying that this species can survive the dry season as an adult.

Parasitoids of larvae of S. albovariegatus in India and of Smicronyx spp. in Uganda have been recorded. In Uganda, it was estimated that parasitism by the pteromalid wasp, ?Spintherus spp. ranged between 3-59%; the impact of the weevils will be limited when rates of parasitism are high. Adult feeding has no impact in Striga spp. Likewise, the presence of galls is not correlated with reduced vigour (Sankaran & Rao, 1966) but no seed is produced from galled fruits. In Uganda at localities where Smicronyx spp. were present, a mean of 62.5% Striga hermonthica were galled, affected plants bore 2-16 galls but galled plants were not noticeably weakened. Thus Smicronyx spp. appear to have little impact on seed production by Striga spp. in Uganda, possibly because of the action of parasitoids, but in the Sahel up to 80% destruction of fruits has been observed (C. Parker, personal communication).

Eurytoma spp. was the chief gall former (on stems) in western Kenya (Davidson, 1963). In one year, 10% of plants were galled but in another very few were affected, and during the surveys of Greathead & Milner (1971), although

Eurytoma spp. was present, only small numbers were reared. This insect is probably host specific and so of potential interest as a biological control agent.

Ophiomyia strigalis, an agromyzid fly, was described from specimens reared from S. hermonthica collected in western Kenya by Davidson (1963). It has since been found elsewhere in Kenya, and in Uganda and Tanzania, in S. hermonthica, S. asiatica and related parasitic Scrophulariaceae: Alectra asperrima and Rhamphicarpa montana. Agromyzidae usually have a narrow host range (Spencer, 1973) so it is anticipated that O. strigalis will be found to be confined to Striga spp. and related genera. So far, it has not been detected outside eastern Africa.

The flies insert their eggs beneath the epidermis of the stem, close to the ground. The larvae mine down the stem and into the roots beneath the epidermis, returning to above ground level to pupate. The life cycle requires less than one month and does not seem to be extended during the dry season. Usually one, but up to 28 individuals have been reared from single S. hermonthica plants. Damage is slight except when infestation is heavy and the mines become infected by pathogens. Up to 90% plants infested have been recorded by Davidson (1963) at the end of the season, but the rate is usually lower and did not exceed 49% in mid-season samples (Greathead & Milner, 1971). Parasitoids are abundant in most samples and killed an average of over 30% larvae in northern Uganda.

Junonia orithya, a butterfly, frequently cited as Precis orithya, is the most conspicuous and widespread insect in Striga spp. It is widespread in the Old World tropics and several sub-species, based on colour pattern, have been described but do not seem to have biological significance. In Africa, J.o. madagascariensis occurs throughout the tropical savanna regions and has been reared in Uganda and Tanzania (Greathead & Milner, 1971) and Upper Volta (C. Parker, personal communication); J.o. orithya occurs in India and Pakistan (Sankaran & Rao, 1966; CIBC, 1966) and J.o. minagara in Java (Boonitee, 1977). The larvae have been found on all species of Striga which have been investigated, and there are records from other plants, chiefly Acanthaceae and Scrophulariaceae, but including Convolvulaceae, Lamiaceae, Plantaginaceae and Thunbergiaceae. Related species are similarly polyphagous (J.D. Holloway, personal communication). However, preliminary screening by Boonitee (1977) suggests that it has a strong preference for ovipositing on Striga spp., but its host plant relations require further investigation. It is of interest that in the USA, where S. asiatica is now established, J. coenia, the very similar North American counterpart of J. orithya, causes severe defoliation. Although the eggs are laid singly, the larvae do considerable damage because of their large size (up to 6.5 cm) but are always at a low density so that although individual plants may be destroyed, the effect on overall plant density is slight. The life cycle is completed in 4-6 weeks and there is no evidence of delayed development during the dry season.

In Africa and Asia, a number of polyphagous parasitoids cause considerable larval and pupal mortality.

Stenoptilodes taprobanes, a plume moth, was described from Sri Lanka and has been identified from many localities in the Oriental and Afrotropical regions and

Queensland. However, critical examination of the genitalia is required to confirm that they are conspecific - African specimens from Striga spp. show some differences and their identity has not been confirmed (J.D. Bradley, personal communication). New World records probably refer to a distinct species. It has been reared in India from Striga angustifolia, S. asiatica and S. densiflora, and in eastern Africa it is the most widespread insect reared from S. asiatica and S. hermonthica and has also been reared from Alectra asperrima and Antirrhinum majus. In India, it has been reared from several other genera of Scrophulariaceae and there are single records from Primulaceae and Solanaceae. Thus, these moths seem to show a preference for herbaceous Scrophulariaceae and are not confined to the genus Striga.

The eggs are laid in small batches on the young leaves. The larvae mine in them during the first instar, but complete development feeding externally on the young leaves and inflorescence. Usually, only one or two larvae survive per shoot which may be severely damaged and prevented from setting fruit. The life cycle takes 5-7 weeks with no indication of arrested development. There are few records of parasitoids.

Damage can be quite severe when young plants are attacked and may prevent or severely curtail flowering, but on older plants, especially of S. hermonthica, the damage is negligible.

Two very similar species of the moth genus Eulocastra, E. argentisparsa with green larvae and E. undulata with brown larvae have been found feeding on all three Striga spp. in India (CIBC, 1974). The first feeds chiefly on the fruits while the other prefers leaves but also feeds on fruits (Sankaran et al, 1969); otherwise the life histories are very similar. Related species occur in Africa (E. aethiops) and Australia (E. fasciolata) but they have not been reared from Striga spp. or any other plants.

The eggs are laid singly on the stems and leaves. The larvae are active and move from plant to plant. E. argentisparsa consumes about 100 fruits before completing development, after which pupation takes place in the soil. The life-cycle occupies 4-9 weeks without arrested development.

Larval density of the two species was always low, never exceeding three per 10 plants, and usually less than one. Sankaran et al (1969) attributed this low density to heavy infection by a cytoplasmic polyhedrosis virus and microsporidia, which cause heavy mortality in laboratory colonies.

In preliminary feeding tests, which included Antirrhinum majus, neither fed on any plant other than Striga spp., but E. undulata has also been found in the field on Sopubia delphinifolia, another parasitic member of the Scrophulariaceae; otherwise no other host plants for either species have been found. E. argentisparsa larvae were unable to feed on S. delphinifolia in starvation tests (CIBC, 1974).

Pathogens

Less work has been done on micro-organisms associated with Striga spp. than on insects. No records of bacteria or viruses have been traced but several authors have isolated fungi. Nag Raj (1966) reported on fungi detected during the CIBC surveys in India and in subsequent papers, he and co-authors have listed further records. There are a number of published records from Africa but only Zummo (1977) specifically sought potential biological control agents. However, surveys have begun in the Sudan to find pathogens for further investigation as bioherbicides (J. Nicklin, personal communication). In the USA, Meister & Eplee (1971) isolated fungi from diseased S. asiatica and made preliminary tests on infectability and pathogenicity. Most records do not indicate the status of the fungi isolated and in few instances were attempts made to confirm pathogenicity by inoculating healthy plants. Further, there is little indication of the frequency of occurrence of diseased plants. However, most of the records (Table 2) are of plurivorous (i.e. polyphagous) or weak pathogens and saprophytes. Only these which are more likely to be specific to Striga spp. and capable of causing significant damage are discussed.

Sphaerotheca fuliginea, a powdery mildew, has been isolated in India and Africa. Oidium is the imperfect state of this and other powdery mildews. In India it is recorded as causing premature drying up of Striga densiflora, and less often S. asiatica (Nag Raj, 1966). It is an obligate pathogen but usually not very damaging but would weaken the plant and possibly reduce seed production. Host specific forma speciales are known crop pests so that maybe strains attacking Striga spp. are specific. Powdery mildew infestations tend to be more severe at low humidities and so Sphaerotheca fuliginea is a potentially useful biological control agent in semi-arid zones.

Phoma spp. have been recorded in Africa and Asia causing leaf and stem lesions, and, in Zimbabwe, killing plants (Bates, 1958). In Nigeria, ?Phoma spp. caused stunting but not the death of plants (Zummo, 1977). Since some species or strains of Phoma can be virulent pathogens and the spores are water-borne, they could be useful bioherbicides if suitable strains are found.

Cercospora spp. have been reported from India and several African countries but in only one instance has the species been identified so that it is not known how many species are involved. The disease develops as leaf spots and can spread to the stem where it is more damaging (Nag Raj, 1966). In Nigeria, heavily infected plants, attacked at an early stage, produced little seed, 10-15% plants were infected in mid-season and over 50% later (Zummo, 1977). These foliar pathogens tend to exist as host-specific species or strains and so are of interest as potential bioherbicides.

Drechslera longirostrata is a seed-borne pathogen identified from the Sudan. Drechslera spp. are usually associated with grasses, and host specific strains are known. The record is thus of interest and merits further investigation to determine the pathogenicity of the isolate to Striga spp. and its host range.

Of interest is the presence in Nigeria of a white rod-shaped gram-negative bacterium in S. hermonthica tissue which was found to inhibit infection in vivo and mycelial growth in vitro, and appears to be an important factor in protecting the plants from infection (Zummo, 1977).

Biological Control

Biological control of weeds by introduction and permanent establishment of host-plant-specific insects has been practised since the importation of insects attacking Lantana camara into Hawaii from Mexico in 1902 (Perkins & Swezey, 1924), but did not achieve spectacular results until the 1930s when prickly pear cactus (Opuntia spp.) was controlled in over 60 million acres in Queensland (Dodd, 1940). Since then, introductions have been made against some 86 species of weeds in 44 countries and satisfactory control achieved on at least 49 occasions up to 1979 (Julien, 1982). Most of these successes have been achieved with insects, but recently rust fungi have been successfully used against skeleton weed (Chondrilla juncea) in Australia and blackberries (Rubus spp.) in Chile, and a leaf spot fungus against Ageratina riparia in Hawaii. These results have given confidence that plant pathogens can be safely used and research is expanding rapidly (Hasan, 1983). Less progress has been made using native natural enemies against weeds. In part, this is because such agents must be cultured and released repeatedly in quantity to achieve control which can be expensive and must be done with precision in timing and quantity of inoculum to be effective. However, there is at least one product registered in the USA for application against weeds and a number of others are under evaluation.

Thus, biological control is established as a viable method of weed control but it is necessarily specific to the target weed. This selectivity is advantageous where a single weed is dominant but where, as in young crops on arable land, there is a complex of weed species which must be controlled simultaneously, selectivity is a hindrance and biological control is usually impracticable. As a result, the considerable research effort required to develop biological control is only justified where a single species or a group of closely related species is of major importance, and the losses caused outweigh the research costs. Harris (1979) has shown how these economic considerations can be quantified. He conveniently costs research in scientist years and estimates that 2-3 scientists years are required per agent with 3-4 agents being necessary to control each weed. Monetary values can be put on these estimates as appropriate, and used as a yardstick to cost projected biological control programmes.

Experience has shown that in introduction programmes, weeds are seldom controlled by a single agent. Usually several are required, each adding stress and reducing competitive advantage. The agents used are chosen, as far as possible, to be complementary, i.e. to do different kinds of damage rather than to compete when the additive effect would be reduced.

In choosing biological control agents it is first necessary to carry out literature and field surveys to determine the natural enemy complex affecting the target weed. Usually the richest complex will be found in the area of origin of the weed, or where it is of little economic importance. Choice of survey areas will be modified by accessibility and the need to match climate and conditions with the area where control is required. A very close match need not be sought as in most instances natural enemies are able to adapt to a broad range of conditions, but care is needed to detect limiting factors which may be of crucial importance (e.g. incidence of frost, length of dry season).

Survey results are evaluated to choose agents for further study. Known polyphagous species, often crop pests, are rejected immediately. Those thought to be specific or narrowly oligophagous are then rated according to their likehood of success - importance of damage, range of conditions under which they thrive, fecundity, dispersal ability, etc. Harris (1973) has developed a convenient scoring system for this purpose.

Next, detailed life history studies and screening trials are carried out on promising species. Screening is crucial to determine that the organism is incapable of damaging crops, or other useful plants, in the target area. Formerly, this was done using starvation tests (insects) and inoculation tests (pathogens) or oviposition tests (insects) in the laboratory. However, these tests can be misleading as under artificial, no-choice conditions, some organisms appear less specific than in the field. Hence, multiple choice tests are now favoured when screening insects, and more attention is given to field data from the area where the candidate organism originated. Since it is impracticable to test the entire flora of the target area, or even all the economically important species, test plants must be selected. Therefore, a scheme of centrifugal testing has been developed (Wapshere, 1975). In this, the candidate agent is first tested against varieties of the target weed, then representatives of the same species group, genus, tribe, subfamily and so on, until only negative results are obtained. As checks, a selection of unrelated plants with similar secondary chemicals or morphological characters, and crop plants, especially those not previously exposed to the candidate agent, are also tested. Only agents which pass these tests and appear to be compatible with the environmental conditions of the target area are subjected to field trials. For alien species, clearance from the national quarantine or plant import regulating agency must be obtained before importation.

So far, as indicated, most biological control has been by the method of introduction and permanent establishment of alien species. These are often more effective in new areas freed of their natural enemies than in their areas of origin. The method has the advantage of producing control indefinitely at no recurrent cost and so, when possible, should be favoured. When not feasible, native organisms can be effective but this requires periodic intervention to maintain control. It may be sufficient to augment field populations by timely releases when seasonal build-up is slow. This method involves modest recurrent costs to maintain cultures and organise releases. Otherwise, inundative methods may be needed, where the agent is applied as a biological herbicide for short-term control. This involves large-scale production of the agent and is usually only practicable using microbial agents which can be manufactured in vitro and stored until required. Finally, naturally occurring agents can be made more effective by taking measures to conserve them and enhance their numbers, e.g. avoidance of deleterious pesticide applications, development of uncultivated refuges, modified agronomic practice.

Biological Control Attempts

Only one attempt to implement biological control of Striga has been made. In Ethiopia, Smicronyx albovariegatus and Eulocastra argentisparsa were imported from India through the CIBC in 1974. Both were released on Striga hermonthica at Humera on the Setit River close to the Sudan border, but recovery surveys were not made because the area was overrun by the Eritrean Liberation Front shortly afterwards (T.J. Crowe, personal communication). A further importation of Smicronyx albovariegatus was made in 1978 and adults were released at Kobbo in Welo Province. Recoveries were made in September 1979 (Tadesse Ghebremeddin, personal communication) but no further information is available.

Prospects for Biological Control of Striga spp.

Striga spp. are not ideal targets for biological control as they are short lived annuals, produce vast numbers of very small seeds which remain viable for years and each plant is individually very damaging to its host and the greater part of the damage is done before it emerges above the ground. However, control is difficult by any means so that any action which tends to reduce the density of plants overall and reduce crop infestation is worth pursuing.

Surveys for natural enemies made to date are incomplete but do allow some conclusions and suggestions for further action. Insects (Sankaran & Rao, 1966) and fungi (Nag Raj, 1966) have been studied in south India and insects in east Africa (Greathead & Milner, 1971). Observations elsewhere have not so far added important new groups of natural enemies. Since the greatest diversity of Striga spp. is to be found in the Afrotropical Region, it is reasonable to assume that this is where the genus evolved and to expect it to harbour the most diverse assemblage of oligophagous co-evolved natural enemies. However, S. asiatica has a wider distribution than other species and could have been brought to Africa by traders crossing the Indian Ocean around 2,000 years ago when several crops are known to have been carried between India and Africa. The possibility that Striga spp. may have evolved in both Africa and the Indian sub-continent is suggested by a comparison of the principal insect enemies in the two areas. In particular, Striga-feeding Eulocastra spp. appear to be absent from Africa, although similar species, known only from adult specimens, are present, but overall Africa has a more diverse assemblage of insects on Striga spp. The greatest diversity has been collected around Lake Victoria, but surveys elsewhere have not been so intensive. New surveys are needed in the Sahel where there are many species of insects not found in eastern Africa and preliminary observations suggest that insect damage to Striga spp. is comparatively severe. There is also a need for more effort to be put into searching for insects damaging the stem base and root as most existing records are of species damaging the above-ground parts of the plants.

Knowledge of pathogens is less complete and systematic surveys in Africa are only now beginning, but the records to date do suggest that host specific fungi exist. New surveys should be concentrated on locating strains of those genera which are likely to have a restricted host range and, above all, on searching for rusts and other obligate parasites which have not yet been recorded on Striga spp.

Some opportunities exist for exchanging insects between regions, as indicated in Table 3, and spreading those with a restricted distribution into new areas, e.g. from east to west Africa. Before this is done, further host specificity testing is required. The most interesting candidates (Table 4) have been scored according to the criteria of Harris (1973) to suggest priorities but it should be remembered that more information is needed to provide reliable scores for all characters and that the weightings given by Harris do not meet with complete agreement among other investigators. For example, I feel that insufficient weight is given to the effect of galling in sequestering nutrients which might otherwise contribute to seed production.

Biological control by augmentation and inundation using insects seems impracticable in the tropics where resources are scarce and the high cost could not be tolerated by farmers. However, pathogens which can be manufactured in vitro are ideal for inundative biological control if highly pathogenic strains can be found which do not affect crops and can be readily cultured, formulated and stored until they are required. For this purpose, organisms are required which will infect Striga spp. under regularly encountered field conditions and which are not rapidly destroyed by insolation or high temperatures or, as with fungi, require unusual weather conditions for infection to take place. For example, Meister & Eplee (1971) found that pathogens which they isolated from Striga spp. would not kill inoculated plants unless the relative humidity was held at 90% for four days.

Natural enemy conservation methods which could be implemented as part of an integrated management programme require investigation. Notably, the effects of pesticide applications on infested crops need to be carefully considered and, if necessary, timed to avoid killing ovipositing insects or pathogens of Striga spp. Ecological studies might indicate other means of enhancing natural enemy attack, e.g. by identifying alternative host plants which could be preserved to act as reservoirs of natural enemies, or plants which are important sources of food for adult insects which could be encouraged to grow in field margins. Races and species of Striga which are pollinated by insects present a problem in that insecticides applied to kill or deter pollinators would affect beneficial insects, besides the probable pollinators are not specialists (Musselman et al, 1983) and are in other respects beneficial, so that attempts to reduce pollination using insecticides could have undesirable side-effects.

SUMMARY

1. Studies on insect natural enemies of Striga spp. have been made in India and east Africa and some records are also available from elsewhere in Asia and Africa. The most important natural enemies which show potential as biological control agents are : Smicronyx spp. (Coleoptera, Curculionidae), fruit and stem gallers from India and Africa; Eurytoma spp. (Hymenoptera, Eurytomidae), stem galler from Kenya; Ophiomyia strigalis (Diptera, Agromyzidae), stem miner from east Africa; Junonia orithya (Lepidoptera, Nymphalidae), defoliator from southern Asia and Africa; Stenoptilodes taprobanes (Lepidoptera, Pterophoridae), inflorescence feeder from India and Africa; Eulocastra argentisparsa (Lepidoptera, Noctuidae), fruit feeder from India.

2. Studies on pathogens have been made in India and records are available from Africa and the USA. Of possible interest as bioherbicides are a powdery mildew, Sphaerotheca fuliginea, Phoma spp. causing leaf and stem rot, Cercospora spp. causing leaf spot and Drechslera longirostrata, a seed borne

pathogen. All except the last, identified from the Sudan, have been found in India and Africa.

3. Biological control is well established as a means of supressing major weeds where host-plant-specific agents are available. Most effort has been made by the introduction of insects to achieve long-term control but fungi are now being used increasingly. Host-specific pathogens have potential as bioherbicides and at least one has now been registered and is commercially available in the USA.

4. Smicronyx albovariegatus from India has been introduced and established in Ethiopia for biological control of Striga hermonthica but the final outcome is not known. Otherwise no attempts have been made to achieve biological control of Striga spp.

5. Opportunities for further biological control effort are discussed but further research is needed before their feasibility can be assessed :

a) Host specifity screening of insects and pathogens.

b) Taxonomic studies to confirm the identity and distribution of the more important insect natural enemies, especially a revision of the African Smicronyx spp., most of which cannot be named at present.

c) Consideration of exchange of insect natural enemies between Asia and Africa and introductions into the USA.

d) Intensive surveys of natural enemies and damage levels in West Africa.

e) Quantative study of impact of natural enemies on Striga spp. in selected areas.

f) Evaluation of pathogens as potential bioherbicides.

g) Field workers to keep a particular look out for categories of natural enemies not yet known from Striga spp., notably stem and root borers and rust fungi which are proving important biological control agents against other weeds.

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Table 1 : Insects recorded feeding on Striga spp. (*Oligophagous species and others common on Striga spp. which are discussed in the text)

Insect	Country (overall distribution)	Striga hosts (overall host range)	Damage caused (remarks)	Reference
THYSANOPTERA: PHLAEOTHRIPIDAE				
Haplothrips sp.	India	asiatica	sucks shoots (occasional)	Sankaran & Rao (1966)
THRIPIDAE				
Chloethrips sp	India	angustifolia, asiatica	sucks shoots (occasional)	Sankaran & Rao (1966)
Dendrothrips ipomaea Bagnall	India (widespread tropics)	angustifolia (polyphagous)	sucks shoots (occasional)	Sankaran & Rao (1966)
Franklinella schultzei Trybom	India Upper Volta	angustofolia hermonthica	sucks shoots (occasional)	Sankaran & Rao (1966) BM (NH)
Trichromothrips bellus Priesner	India	angustifolia	sucks shoots (occasional)	Sankaran & Rao (1966)
HEMIPTERA: LYGAEIDAE				
Megalonotus sp.	India	Striga sp	sucks shoots (only once)	Sankaran & Rao (1966)
Nysius ceylanicus Motsch.	India	Striga sp.	sucks shoots (one adult only)	Sankaran & Rao (1966)
Nysius sp.	India	asiatica	sucks shoots (rare)	Sankaran & Rao (1966)

Table 1 (cont)

Insect	Country (overall distribution)	*Striga* hosts (overall host range)	Damage caused (remarks)	Reference
PENTATOMIDAE				
Antestia cincticollis Schaum	Uganda (eastern Africa)	*hermonthica* (Rubiaceae,Compositae)	sucks shoots (occasional)	Greathead & Milner (1971)
Hermolaeus robustus Dist.	India	*asiatica*, *angustifolia*, *densiflora*	sucks shoots (occasional)	Sankaran & Rao (1966)
Veterna patula Dist.	Uganda	*hermonthica* (minor pest of sesame)	sucks shoots (occasional)	Greathead & Milner (1971)
HOMOPTERA: CERCOPIDAE				
Poophilus costalis (Wlk.)	Uganda (tropical Africa, India)	*hermonthica*	sucks shoots (ocasional)	Greathead & Milner (1971)
CICADELLIDAE				
Yasumatsuus mimicus (Dist.)	India	*angustifolia*	sucks shoots (rare)	Sankaran & Rao (1971)
FLATTIDAE				
gen. near *Cyphopterum* sp.	India	*asiatica* (grasses)	sucks shoots (rare)	Sankaran & Rao (1971)
Aphis gossypii Glover	India (cosmopolitan)	*angustifolia*, *asiatica* *densiflora* (polyphagous)	sucks shoots (rare)	Sankaran & Rao (1971)

Table 1 (cont)

Insect	Country (overall distribution)	Striga hosts (overall host range)	Damage caused (remarks)	Reference
LEPIDOPTERA: OLETHREUTIDAE				
Lobesia aeolopa Meyr.	Uganda	hermonthica (polyphagous)	defoliates (rare)	Greathead & Milner (1971)
TORTRICIDAE				
Archips micaceana (Wlk.)	India	asiatica, densiflora (polyphagous)	rolls leaves (rare)	Sankaran & Rao, 1966)
PTEROPHORIDAE				
Platyptilla sp. near molopias Meyr.	Pakistan	Striga spp.	destroys flowers	A.I. Mohyuddin (personal communication)
Stenoptilia zophodactyla (Dup.)	Tanzania	Striga spp.	?	Le Pelley (1959)
* Stenoptilodes taprobanes (Feld.)	India	angustifolia, asiatica densiflora	destroys inflore-scences & fruits	Sankaran & Rao (1966)
	Kenya, Tanzania, Uganda Sudan (Oriental, Afro-tropical, Queensland)	asiatica, hermonthica hermonthica (Scrophulariaceae)		Greathead & Milner (1971) Musselman (1983)
NYMPHALIDAE				
Junonia coenia (Hb.)	USA (N. America)	asiatica (Scrophulariaceae etc.)	defoliates	Musselman et al (1983)

Table I (cont)

Insect	Country (overall distribution)	Striga hosts (overall host range)	Damage caused (remarks)	Reference
J. oenone (L.)	Tanzania (Afrotropical)	Striga sp. (Acanthaceae)	defoliates (occasional)	Greathead & Milner (1971)
* J. orithya (L.)	Tanzania, Uganda	asiatica, forbesii, hermonthica	defoliates	Greathead & Milner (1971)
	Sudan	hermonthica		Musselman (1983)
	Upper Volta	hermonthica		C. Parker (personal communication)
	India	angustifolia, asiatica, densiflora		Sankaran & Rao (1966)
	Indonesia	asiatica		Boonitee (1977)
	Pakistan	Striga sp.		CIBC (1966)
	Thailand	asiatica		Napompeth (1982)
	(Afrotropical, Oriental)	(Acanthaceae, Scrophulariaceae, etc.)		
J. westermanni (Westw.)	Tanzania	asiatica, hermonthica (Acanthaceae, Labiatae, Amaranthaceae)	defoliates (occasional)	Greathead & Milner (1971)
GEOMETRIDAE				
Scopula actuaria (Wlk.)	India	Striga sp.	defoliates (rare)	Sankaran & Rao (1966)
S. adeptaria (Wlk.)	India	Striga sp.	defoliates (rare)	Sankaran & Rao (1966)
S. emissaria (Wlk.)	India	Striga sp.	defoliates (rare)	Sankaran & Rao (1966)

Table 1 (cont)

Insect	Country (overall distribution)	*Striga* hosts (overall host range)	Damage caused (remarks)	Reference
LYMANTRIIDAE				
Euproctis xanthorrhoea (Koll.)	Pakistan	*Striga* sp. (polyphagous)	defoliates	CIBC (1971)
ARCTIIDAE				
Diachrisia investigatorum (Karsch)	Tanzania, Uganda (Afrotropical)	*asiatica*, *forbesii*, *hermonthica* (polyphagous)	defoliates	Greathead & Milner (1971)
NOCTUIDAE				
Chrysodeixis chalcites (Esp.)	India Pakistan (temperate & tropical Old World)	*asiatica* *Striga* spp. (polyphagous)	defoliates	Sankaran & Rao (1966)
Ctenoplusia albostriata (Brem. & Gray)	Pakistan (oriental)	*Striga* spp. (polyphagous)	defoliates	CIBC (1966)
* *Eulocastra argentisparsa* Hamps.	India	*angustifolia*, *asiatica*, *densiflora*	destroys fruit	Sankaran et al (1969)
* *E. undulata* Snellen	India (oriental)	*angustifolia*, *asiatica*, *densiflora* (*Sopubia delphinifolia*)	destroys leaves and fruits	Sankaran & Rao (1966)
Heliothis armigera (Hb.)	India, E. Africa (temperate & tropical Old World)	*asiatica* (polyphagous)	destroys fruits (occasional)	Greathead & Milner (1971)

Table 1 (cont)

Insect	Country (overall distribution)	Striga hosts (overall host range)	Damage caused (remarks)	Reference
Spodoptera exempta (Wlk.)	Tanzania (tropical Old World)	hermonthica (polyphagous)	defoliates (rare)	Greathead & Milner (1971)
S. exigua (Hb.)	Tanzania Pakistan (cosmopolitan except S. America)	asiatica Striga sp.	defoliates (rare)	Greathead & Milner (1971) CIBC (1966)
S. littoralis (Boisd.)	Tanzania, Uganda (S.Europe, Africa)	asiatica, hermonthica	defoliates (occasional)	Greathead & Milner (1971)
S. litura (F.)	India (Tropical Asia, Pacific	asiatica (polyphagous)	defoliates	Sankaran & Rao (1966)
DIPTERA: CECIDOMYIIDAE				
gen. et sp. indet.	India	angustifolia	in Smicronyx galls	Sankaran & Rao (1966)
AGROMYZIDAE				
Melanagromyza sp.	India	asiatica	adults from caged plants	Sankaran & Rao (1966)
* Ophiomyia strigalis Spencer	Kenya, Tanzania, Uganda	asiatica, hermonthica (Alectra, asperrima, Rhamphicarpa montana)	mines stems & roots	Davidson (1963)
CHLOROPIDAE				
Meromyza capensis Lw	E. Africa (Afrotropical)	asiatica, hermonthica	?saprophyte after Ophiomyia	Greathead & Milner (1971)

Table 1 (cont)

Insect	Country (overall distribution)	Striga hosts (overall host range)	Damage caused (remarks)	Reference
Pachylophus proximus Adams	E. Africa	asiatica, hermonthica	?saprophyte after Ophiomyia	Greathead & Milner (1971)
CHYLIZIDAE				
Chyliza sp.	E. Africa	asiatica, hermonthica	?saprophyte after Ophiomyia	Greathead & Milner (1971)
ANTHOMYIIDAE				
Atherigona sp.	E. Africa	asiatica, hermonthica	?saprophyte after Ophiomyia	Greathead & Milner (1971)
HYMENOPTERA: EURYTOMIDAE				
* Eurytoma sp.	Kenya	hermonthica	galls stems	Davidson (1963)
COLEOPTERA: APIONIDAE				
Apion sp.	India	angustifolia	2 adults on root	Sankaran & Rao (1966)
Apion sp.	India	densiflora	adults feeding on leaves	Sankaran & Rao (1966)
Conapion sp.	India	angustifolia	one adult on stem	Sankaran & Rao (1966)
CURCULIONIDAE				
Alcidodes fabricii (F.)	India	angustifolia (polyphagous)	one adult on root	Sankaran & Rao (1966)

Table 1 (cont)

Insect	Country (overall distribution)	Striga hosts (overall host range)	Damage caused (remarks)	Reference
Nematocerus sp.	Uganda	asiatica, hermonthica	adults feed on leaves (occasionally)	Greathead & Milner (1966)
* Smicronyx albovariegatus Faust.	India	angustifolia, asiatica densiflora	galls fruit, stems and roots	Saṇkaran & Rao (1966)
	Ethiopia (introduced)	hermonthica		T. Ghebremeddin (personal communication)
* S. quadritubulatus Hustache	Upper Volta (Nigeria)	hermonthica	mating on flowers	BM (NH)
* S. umbrinus Hustache	Nigeria	Striga sp.	galls fruit	Williams & Caswell (1959)
	Upper Volta	hermonthica		C. Parker (personal communication)
	Sudan (also Senegal)	hermonthica		Musselman (1983)
* Smicronyx sp. (small)	Tanzania, Uganda	asiatica, hermonthica	galls fruits	Greathead & Milner (1971)
	Ethiopia	hermonthica		T. Ghemremeddin (personal communication)
* Smicronyx sp. (large)	Uganda	hermonthica	galls fruits	Greathead & Miller (1971)
* Smicronyx sp.	Tanzania	hermonthica	galls stems	Greathead & Milner (1971)

Table 1 (cont)

Insect	Country (overall distribution)	*Striga* hosts (overall host range)	Damage caused (remarks)	Reference
SCOLYTIDAE				
Hypothenemus eruditus (Westw.)	India	*Striga* spp. (polyphagous)	larvae in dead stems (rare)	Sankaran & Rao (1966)
CHRYSOMELIDAE				
Dactylispa dilaticornis (Duv.)	Pakistan	*Striga* spp.	adults on leaves	CIBC (1975)
Monolepta signata (Oliv.)	India	*Striga* spp. (polyphagous)	adults feed on flowers (occasional)	Sankaran & Rao (1966)

Table 2 : Fungi recorded on Striga spp.

Fungus	Country	Host	Symptoms	Status (comments)	Reference
ASCOMYCOTINA : PLECTROMYCYTES					
*Sphaerotheca fuliginea (Shlecht. ex Fr.) Poll	India	asiatica, densiflora	leaf & stem lesions	-	Nag Raj & Ponappa (1970)
	?	hermonthica	- (powdery mildew)	- (obligate pathogen)	Herb. IMI
PYRENOMYCETES					
Leptosphaerulina australis McAlpine	India	densiflora	leaf spots	only transmitted in wounds (plurivorous minor pathogen)	Ponappa (1975)
DEUTEROMYCOTINA : COELOMYCETES					
Macrophoma sp.	India	asiatica	shoot blight	-	Nag Raj & Ponappa (1970)
Macrophomina phaseolina (Tassi)Goid.	India	densiflora	shoot blight (charcoal rot)	- (plurivorous, probably no host specific strains)	Nag Raj & Ponappa (1970)
Neottiospora sp.	India	asiatica		associated with Phoma sp	Nag Raj (1966)
Phaeosphaera eustoma (Fuckel) L.Holai	India	asiatica	stem lesions	only transmitted in wounds	Ponappa (1975)
*Phoma sp.	India	asiatica, densiflora	leaf & stem spots	cultured on medium (can be significant pathogens)	Nag Raj (1966)
*Phoma sp.	Zimbabwe	asiatica	leaf & stem spots	kills plants	Bates (1958)
*?Phoma sp.	Nigeria	hermonthica	stem lesions	isolated from diseased tissue	Zummo (1977)

Table 2 (cont.)

Fungus	Country	Host	Symptoms	Status (comments)	Reference
Urohendersonia mysorensis Nag Raj & Kendrick	India	asiatica	diseased stems	-	Nag Raj & Kendrick (1971)
HYPHOMYCETES					
Alternaria sp.	India	asiatica	-	isolated from diseased tissue	Nag Raj (1966)
Aspergillus flavus Link ex Fries	Sudan	Striga sp.	-	- (not a significant plant pathogen)	Herb. IMI
A. fumigatus Fresenius	Sudan	Striga sp.	-	-	Herb. IMI
*A. niger van Tieghem	Sudan	Striga sp.	-	- (some pathogenic strains)	Herb. IMI
A. terreus Thom.	Sudan	Striga sp.	-	- (not a significant plant pathogen)	Herb. IMI
*Cercospora strigae Nag Raj, Govindu & Thirumalachar	Nigeria	hermonthica	-	- (possibly host specific)	Herb. IMI
*Cercospora sp.	Cameroun, Ghana, Niger, Nigeria, Senegal	hermonthica	leaf spots	transmitted to plants in field	Zummo (1977)
*Cercospora sp.	India	asiatica, densiflora	leaf spots & necrotic patches on stems	-	Nag Raj (1966)

Table 2 (cont.)

Fungus	Country	Host	Symptoms	Status (comments)	Reference
*Cercospora sp.	Zimbabwe	asiatica	-	-	Bates (1958)
Curvularia geniculata (Tracy & Earle) Boeidijn	USA	asiatica	leaf & apical necrosis	transmitted in lab.tests (usually saprophytic)	Meister & Eplee (1971)
Curvularia sp.	India	asiatica	-	not pathogenic	Nag Raj (1966)
*Drechslera longirostrata (Subram.) Ram Nath, Neergard & S.B. Mathur	Sudan	Striga sp.	-	(seed borne pathogen ?specific)	Herb. IMI
Fusarium equisiti (Corda) Sacc.	Nigeria	hermonthica	vascular wilt	transmitted to plants in field (not usually pathogenic)	Zummo (1977)
F. roseum Link.	USA	asiatica	stem-base necrosis	transmitted in lab.tests (plurivorous soil-borne pathogen)	Meister & Eplee (1971)
F. solani (Mart) Sacc.	India	asiatica	-	-	Herb. IMI
	USA	asiatica	stem-base necrosis	transmitted in lab.tests (plurivorous soil-borne pathogen)	Meister & Eplee (1971)
Myothecium roridum Tode ex Fries	India	densiflora	shoot blight	-	Nag Raj & Ponappa (1970)
*Oidium sp.	India	asiatica, densiflora	powdery mildew on leaves & stems	- (imperfect state of Sphaerotheca & Erysiphe)	Nag Raj (1966)

Table 2 (cont.)

Fungus	Country	Host	Symptoms	Status (comments)	Reference
Rhizoctonia solani Kuehn	Zimbabwe	asiatica	root rot	-	King (1966)
	USA	asiatica	stem base rot	transmitted in lab.tests (plurivorous soil-borne pathogen)	Meister & Eplee (1971)
Sclerotium rolfsii Sacc.	USA (lab)	asiatica	stem necrosis	lab.tests only (plurivorous soil-borne pathogen	Meister & Eplee (1971)
MASTIGOMYCOTINA : OOMYCETES					
Pythium ultimum Trow.	South Africa	Striga sp.	wilt	- (unspecialised soil-borne pathogen)	Wager (1931)
ZYGOMYCOTINA : ZYGOMCETES					
Rhizopus oryzae Went & Prinsen Geerligs	Sudan	Striga sp.		- (not a significant pathogen)	Herb. IMI

*Species of possible interest discussed in the text

Table 3 : Comparison of principal insect enemies of *Striga* spp. in India and East Africa

Guild	India	East Africa
Defoliator	*Junonia orithya*	*Junonia orithya*
	Eulocastra undulata	-
Stem galler	-	*Ophiomyia strigalis*
	-	*Eurytoma* spp.
	Smicronyx albovariegatus	*Smicronyx* spp.
Inflorescence feeder	*Stenoptilodes taprobanes*	*Stenopilodes taprobanes*
Fruit feeder	*Eulocastra argentisparsa*	-
Fruit galler	(*Smicronyx albovariegatus*)	*Smicronyx* spp.

Table 4 : Rating of oligophagous insects from Striga spp. as potential biological control agents for introduction. Scored according to criteria of Harris (1973)

	Smicronyx albovariegatus	S. umbrinus	Eurytoma sp.	Ophiomyia strigalis	Junonia orithya	Eulocastra argentisparsa	E. undulata	Stenoptilodes taprobanes	Remarks
1. Host specificity	3	3	1	3	3*	3	3	3*	*? insufficiently host specific
2. Direct damage	0	5	0	0	2	5	2	5	fruit gallers ranked as seed destroyers
3. Indirect damage	0	0	3	3	0	0	0	0	incompletely known
4 Phenology of attack	4	4	3	3	4	3	3	4	all well synchronised
5. Number of generations	0	0	0?	4	4	0	0	4	uncertain
6. No. of progeny/generation	0	0	0	0	0	0	0	0	all believed below 500
7. Extrinsic mortality	4	4	0	0	3	4	4	0	incompletely known
8. Feeding behaviour	0	0	0	2	2	2	2	0	
9. Compatibility	2	2	2	2	2	2+	2	2+	+potential competitors with Smicronyx spp.
10. Distribution	2	4	0	0	6	2	2	6	
11. Effectiveness	0	0	0	0	0	0	0	0	not effective in area of origin
12. Size	0	0	0	0	2	2	2	0	
TOTALS	15	22	9	17	28	23	20	24	

REFERENCES

ANDERSON, D.M. (1962), "The weevil genus Smicronyx in America, north of Mexico", Proceedings of the United States National Museum, 113 : 185-372

BATES, G.R. (1958), "Branch of Botany, Plant Pathology and Seed Testing", Introduction pp 79-83. In Federation of Rhodesia and Nyasaland Report of the Secretary to the Ministry of Agriculture for the year ended 30 September 1957. Government Printer, Salisbury.

BOONITEE, W. (1977), "Biocontrol studies of Striga asiatica (L.). O. Kuntze in Java", Report submitted to BIOTROP, Bogor, 15 pp. (multigraph)

CIBC (1966), "Studies on the insect enemies of noxious weeds in Pakistan, May 1964-April 1965", Commonwealth Institute of Biological Control, Rawalpindi : 68 pp. (multigraph)

CIBC (1974), "US PL-480 Project: Evaluation of natural enemies associated with witchweed, nutsedge and several other aquatic weeds occurring in India; Final Technical report, June 21, 1968 to February 20, 1974", Commonwealth Institute of Biological Control, Bangalore 56 pp. (multigraph)

DAVIDSON, A. (1963), "Insects attacking Striga in Kenya", Nature, London, 197 : 923

DODD, A.P. (1940), "The biological campaign against prickly pear", Commonwealth Prickly Pear Board, Brisbane, 177 pp

GARRIS, M.R. & WELLS, J.C. (1956), "Parasitic herbaceous annual associated with corn disease in North Carolina", Plant Disease Reporter, 40 837-838

GIRLING, D.J., GREATHEAD, D.J., MOHYUDDIN, A.I. & SANKARAN, I. (1979), "The potential for biological control in the suppression of parasitic weeds", Biocontrol News Information, 7-16

GREATHEAD, D.J. & MILNER, J.E.D. (1971), "A survey of Striga spp. (Scrophulariaceae) and their natural enemies in east Africa with a discussion on the possibilities of biological control", Tropical Agriculture, Trinidad, 48 : 111-124

HASAN, S. (1983), "Biological control of weeds with plant pathogens - status and prospects", Proceedings of 10th International Congress of Plant Protection, Brighton, UK, 20-25 November 1983, 2 : 759-766

HARRIS, P. (1973), "The selection of effective agents for the biological control of weeds", Canadian Entomologist, 105 : 1495-1503

HARRIS, P. (1979), "Cost of biological control of weeds by insects in Canada", Weed Science, 27 : 243-250

JULIAN, M.H. (Editor) (1982), "Biological control of weeds. A world catalogue of agents and their target weeds", Commonwealth Agricultural Bureax, Slough, 108 pp.

KHAN, M.Q. & MURTHY, D.V. (1955), "Smicronyx albovariegatus Faust (Curculionidae Coleoptera): on Striga spp.", Indian Journal of Entomology, 17 : 362

KING, L.J. (1966), "Weeds of the world. Biology and Control", Leonard Hill, London, 526 pp.

LE PELLEY, R.M. (1959), "Agricultural insects of east Africa", East Africa High Commission, Nairobi, 307 pp.

McCLAY, A.S. (1981), "Studies on some potential biocontrol agents for Parthenium hysterophorus in Mexico", Proceedings of 5th Symposium on Biological Control of Weeds, Brisbane, Australia, 22-29 July 1980, 471-482

MEISTER, C.W. & EPLEE, R.E. (1971), "Five new fungal pathogens of witchweed (Striga lutea)", Plant Disease Reporter, 55 : 861-863

MUSSELMAN, L.J. (1983), "Striga in Sudan : Summary of work from September 1982 to April 1983", 7 pp. (multigraph)

MUSSELMAN, L.J., MATTESON, P.C. & FORTUNE, S. (1983), "Potential pollen vectors of Striga hermonthica (Scrophulariaceae) in West Africa", Annals of Botany, 51.: 859-862

NAG RAJ, T.R. (1966), "Fungi occurring on witchweed in India", Commonwealth Institute of Biological Control, Technical Communication, No. 7, 75-80

NAG RAJ, T.R. & KENDRICK, B. (1971), "Genera coelomycetarum 1. Urohendersonia", Canadian Journal of Botany, 49 : 1853-1862

NAG RAJ, T.R. & PONAPPA, K.M. (1970), "Some interesting fungi occurring on aquatic weeds and Striga spp. in India", Journal of the Indian Botanical Society, 49: 64-72

NAPOMPETH, B. (1982), "Biological control research and development in Thailand", Proceedings: International Conference on Plant Protection in the Tropics, Kuala Lumpur, 1-4 March 1982, 301-323

PERKINS, R.C.W. & SWEZEY, O.H. (1924), "The introduction into Hawaii of insects that attack lantana", Bulletin of the Hawaiian Sugar Planters' Association Experimental Station, No. 16, 83 pp

PONAPPA, K.M. (1975), "Ascomycetes occurring on witchweed (Striga spp.) in India", Beiheft zur Nova Hedwigia, 47 : 565-569

SANKARAN, T., RAJENDRAN, M.K. & RANGANATH BHAT, Y. (1969), "The biology of Eulocastra argentisparsa Hampson (Lep.: Noctuidae) with special reference to the occurrence of dimorphism", Commonwealth Institute of Biological Control Technical Bulletin, No. 11, 31-43

SANKARAN, T. & RAO, V.P. (1966), "Insects attacking witchweed (Striga) in India", Commonwealth Institute of Biological Control Technical Bulletin, No. 7, 63-73

SPENCER, K.A. (1973), "Agromyzidae (Diptera) of economic importance", Junk, The Hague, 418 pp

WAGER, V.A. (1931), "Diseases of plants in South Africa due to members of the Pythiaceae", Union of South Africa, Department of Agriculture, Science Bulletin, No. 105, 43 pp

WAPSHERE, A.J. (1975), "A protocol for programmes for biological control of weeds", Pesticide Articles and News Summaries, 21 : 295-303

WILLIAMS, C.N. & CASWELL, G.H. (1959), "An insect attacking Striga", Nature, London, 184 : 1668

ZUMMO, N. (1977), "Diseases of giant witchweed, Striga hermonthica in west Africa", Plant Disease Reporter, 61 : 428-430

ASPECTS OF THE BIOCHEMISTRY OF STRIGA

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INTRODUCTION

It is surprising that the biochemistry of *Striga* has received relatively little attention, given its very specialised mode of nutrition and agricultural importance. Little information relating to its basic biochemical pathways or to its secondary metabolism is available, although such information is important for the development of new chemical controls and in the selection-breeding of resistant host varieties. The recent review by Musselman (1980) indicates that apart from investigations of germination, haustorial formation and host recognition, little biochemical work is being pursued.

In this contribution we will consider some studies from our Plant Stress Metabolism Group which have had as their objective the characterisation of biochemical processes in *Striga* (particularly *S. hermonthica*) and the influence of *Striga* on the metabolism of its host. Our approach has been to :

a) identify features of *Striga* biochemistry which distinguish it from the host and which would therefore serve as 'target' in the design of novel chemical control measures;

b) to characterise the metabolic response of the host to *Striga* parasitism with the objective of identifying characteristics which might facilitate the selection and breeding of resistant varieties.

Here we will consider three areas of *Striga* biochemistry :

i. water relations and mineral metabolism;
ii. nitrogen assimilation-metabolism;
iii. carbon metabolism;

and their relationship to the response of the host to *Striga* parasitism. Areas where further studies are necessary will be identified and new approaches suggested.

WATER RELATIONS AND MINERAL METABOLISM

Water Relations

Striga is generally regarded as a xylem parasite and as such can be thought of as being nutritionally similar to, but in competition with the host shoot. In this type of association the water pathway can be represented as follows :

$$\text{Soil} \quad \text{Host root} \begin{array}{l} \nearrow \text{Host xylem} \rightarrow \text{leaf} \rightarrow \text{atmosphere} \\ \searrow \text{Parasite xylem} \rightarrow \text{leaf} \rightarrow \text{atmosphere} \end{array}$$

The implication of a direct xylem connection between host root and parasite is that there is competition for water between the Striga shoot and that of its host. The competitive success of Striga is usually ascribed to it having a greater osmotic pressure than its host (Kuijt, 1969) and a low stomatal resistance which results in high transpiration rates (Musselman, 1980).

The water relations of a plant can be represented by the following equation :

$$\psi = \psi p + \psi s + \psi m$$

where ψ can be the water potential of a cell, tissue, organ or shoot and (pP), (S) and (M) are the hydrostatic pressure (turgor), osmotic or solute potential and matrix potential respectively. Water potential ψ, rather than osmotic pressure is generally regarded as the fundamental measure of plant water status (Hsiao, 1973) and can be regarded as the driving force for water movement into Striga shoots. Determinations of leaf water potentials of Striga and host are shown in Table 1. These results indicate that in watered plants the leaf of Striga is 0.1 to 0.37 MPa lower than that of its host and they suggest water will therefore be supplied more rapidly to the Striga shoot system than that of the host. There is no indication from these results that parasitism by either S. asiatica or S. hermonthica induces water stress in their host as judged by the sorghum leaf ψ which are similar to those of control plants. Moreover, under conditions of water stress, the leaf ψ of Striga decreases more markedly than that of its host and this is accompanied by a large loss of water. These results suggest Striga is perhaps less able than its host to maintain a favourable water balance under conditions of severe water stress.

The above discussion relates only to the water relations of emerged Striga plants, those of unemerged plants will be somewhat different. Transpiration of pre-emergent plants will be low and it would seem likely that the development of host root pressure at night, and guttation by the young Striga plant supply many of the necessary solutes for what may be a prolonged period of completely heterotrophic growth. Detailed investigations of the water relations and solute composition of pre-emergent plants are necessary.

Mineral Metabolism

There is little experimental evidence relating to the mineral nutrient requirements of Striga although there is no a priori reason to suppose that its qualitative requirements are any different from autotrophic species. Culture studies (Okonkwo, 1966b; Yoshikawa et al, 1978) indicated commonly employed standard culture solutions are adequate to meet its mineral requirements. In parasitic emerged plants the apoplastic nature of xylem should ensure a ready supply of mineral elements, including those which are relatively immobile in the phloem. The supply of mineral elements prior to emergence may be more problematical and should be examined.

Analyses of emerged Striga shoots (Table 2) show that they are characterised by the presence of large amounts of potassium and magnesium. The amounts of iron, manganese and calcium are similar to those of its host (sorghum) while its nitrogen content is somewhat higher. The zinc content of Striga was found to be appreciably lower than that of sorghum. There is little evidence from these results that parasitized plants of sorghum are any lower in essential minerals than non-parasitized plants. Such changes as are evident would seem insufficient to account for the very marked reduction in sorghum shoot growth which is brought about by Striga parasitism.

The potassium/calcium ratio of Striga is higher than that of its host, similar results have been obtained with other xylem parasites and this phenomenon is particularly characteristic of phloem parasites such as Orobanche and Cuscuta (Ansiaux, 1958). Both potassium and magnesium are phloem-mobile compared with calcium (Baker, 1983). However, Horack (1974) has suggested that the higher potassium/calcium ratio found in mistletoes and other xylem parasites compared with their hosts results from an active potassium transport from host to parasite.

The accumulation of large amounts of potassium is of interest in relation to its proposed role in osmoregulation (Cram, 1976). The concentration of potassium salts in Striga are of the order of 300-350 mm and as such must make a major contribution to the osmotic potential of the cell (between -1.24 and -1.45 MPa).

Wyn Jones et al (1979) have suggested that in the cytoplasm of eukaryotic cells the concentrations of potassium are maintained in the range of 100-120 mm. Assuming the cytoplasm of a Striga cell to comprise 10% of the total cell water there will be a large discrepancy in the osmotic potential between cytoplasm and vacuole resulting from a cytoplasmic potassium concentration of 100 mm and a vacoular concentration of 322 mm. In other organisms in which there is this differential ion compartmentation, compatible organic solutes accumulated in the cytosol provide a mechanism for osmotic adjustment (Wynn Jones et al, 1977; Stewart & Ahmad, 1983). The possible role of mannitol in osmoregulation will be considered below.

The presence of large amounts of potassium necessitates the accumulation of a counter ion to maintain cation-anion balance. This could be provided via the xylem or by endogenous synthesis. At present we have little information on the anion composition of Striga although nitrate ions are not accumulated. Further work is needed to characterise the inorganic-organic anions which maintain the cation-anion balance.

NITROGEN ASSIMILATION AND METABOLISM

Nitrate and Ammonia Assimilation

For most plants, inorganic nitrogen compounds in their soil solution are the available nitrogen source for growth, parasitic plants such as Striga are different in so far as they have access also to reduced organic nitrogenous compounds synthesized by their hosts. Nitrate is the most commonly available form of nitrogen utilised by higher plants including some parasitic species (Govier et al, 1967; Lee & Stewart, 1978; Stewart & Orebamjo, 1980). Nitrate assimilation requires the active uptake of nitrate ions from the soil solution (Butz & Jackson, 1977), their subsequent reduction by nitrate and nitrite reductases to ammonia (Hewitt, 1975) and its incorporation into organic nitrogenous compounds.

Ammonia assimilation occurs via the so-called glutamine synthase cycle in which glutamine synthetase and glutamate synthetase catalyse an ATP-dependent synthesis of glutamate (Miflin & Lea, 1980). We have examined the occurence of these enzymes in various species of Striga (Table 3). Low activities of nitrate reductase were detectable in S. asiatica and S. hermonthica but not in S. gesnerioides. Substantial amounts of glutamine synthetase were present in all of the Striga spp. examined. Ferredoxin-dependent glutamine synthetase was present in S. hermonthica and S. gesnerioides.

The level of nitrate reductase in most plants is determined by the availability of nitrate, the enzyme being substrate-inducible (Hewitt, 1975). Feeding nitrate to excised shoots of S. hermonthica and S. asiatica did not induce any increase in nitrate reductase activity (Table 3). The application of high nitrate concentrations to sorghum plants parasitized by Striga was also ineffective in inducing nitrate reductase in Striga. A few days after nitrate application, the leaves of Striga blackened and subsequently the plants died. These results contrast with results obtained for Tapinanthus which had an inducible nitrate reductase (Stewart & Orebamjo, 1980). Nitrate ions seems not to be an important nitrogen source for parasitic Striga plants, which have little potential to reduce nitrate. Moreover, nitrate ions may be toxic to Striga.

The assimilation of ammonia ions absorbed from the soil appears to occur exclusively in the root system. This restriction arises from the need to regulate pH, since hydrogen ions are produced during ammonia assimilation. Plants have little capacity to store hydrogen ions or to neutralize them biochemically. Consequently the release of hydrogen ions from root cells to the soil solution is thought to be the only feasible means of pH control in plants absorbing and assimilating ammonia (Raven & Smith, 1976). Ammonia ions are unlikely therefore to be a nitrogen source for emerged Striga plants.

However, it has been realised recently that a major source of intracellularly-produced ammonia is the decarboxylation-deamination of glycine which occurs in photorespiration (Keys et al, 1978). It has been suggested that the rate of ammonia production in photorespiration could be as much as ten times that associated with nitrate reduction (Wallsgrove et al, 1983). Keys et al (1978) have described the reactions leading to the formation and reassimilation of ammonia in photorespiration as the photorespiratory nitrogen cycle. There is now evidence that the reassimilation of photorespiratory ammonia occurs via the glutamate synthase cycle (Woo et al, 1982). Two forms of glutamine synthetase are present in many plants (McNally et al, 1983a). One localised in the cytoplasm, the other in chloroplasts. In the Keys et al model of the photorespiratory nitrogen cycle the first step in ammonia reassimilation is catalysed by the cytoplasmic isoform of glutamine synthetase.

Ion exchange chromatography of leaf extracts of Striga spp. shows that in common with many other higher plants, two peaks of glutamine synthetase are present (McNally et al, 1983b) one of which is localised in the chloroplast. The relative proportions of the two isoforms in Striga are different from those in many other plants (Table 4) in so far as the chloroplastic isoform is the minor component, comprising less than 20% of the total activity. The ratios of GS_1 to GS_2 in Striga is in fact similar to that found in etoilated plants of rice (Guiz et al, 1979).

Although Keys et al (1978) originally suggested photorespiratory ammonia to be reassimilated by the cytoplasmic isoform, recent evidence suggests it is the chloroplast isoform which is active in photorespiration (Bergman et al, 1981; Woo & Osmond, 1982; McNally et al, 1983a). Our results with Striga suggest it conforms to the original Keys et al model. An alternative explanation is that rates of photorespiration are low and consequently there is little synthesis of the chloroplast isoform. The capacity for ammonia detoxification would appear low and this may have important implications with respect to the use of N-fertilizers in the control of Striga.

We are continuing to investigate the role of chloroplastic glutamine synthetase in Striga and it would seem worthwhile to examine the occurence and characteristics of photorespiration.

Nitrogen Transport

In parasitic plants of Striga the apparent lack of any appreciable capacity for nitrate assimilation implies the utilization of alternative nitrogen sources. Analyses of the bleeding sap (assumed to represent the xylem fluid) obtained from cut stumps of Striga shoots shows the presence of a number of organic nitrogen compounds but very little nitrate (Table 5). The major compounds present are glutamate and glutamine, which account for up to 85% of xylem nitrogen.

In addition to nitrogen-rich solutes such as ureides and amides which are derived from current assimilatory activity, roots can load the xylem stream with other nitrogenous compounds, these non-assimilatory products are thought to arise from catabolic processes within the root (Pate, 1980). They can account for 10-15% of the nitrogen exported from the root and include compunds such as valine, the leucines and alanine which are present in Striga xylem fluid. The occurrence of large amounts of glutamate in the bleeding sap of Striga is interesting since its amide glutamine is a more frequently present as a nitrogen-transport compound.

We have begun to investigate the origin of this glutamate using ^{15}N-labelled compounds. The labelling pattern of soluble amino compounds in the shoot of S. hermonthica parasitizing sorghum roots which have been fed $^{15}NH_4$ is shown in Table 6. Glutamate and glutamine are the most highly-labelled compounds and the labelling pattern of glutamate follows closely that of glutamine, suggesting that there is no input of unlabelled (that is non-assimilatory) glutamate via the xylem.

Raven (1983) has recently drawn attention to the substantial transfer of carbon which occurs when nitrogenous organic compounds are transferred from root to shoot and he suggests that the 'obligatory' carbon flux may account for **at least** one-fifth of the total carbon in a parasite. The carbon/nitrogen ratio of the nitrogenous solutes in the xylem fluid is between 3 and 6:1 (depending on host and developmental age). These values suggest that 17% to 25% of the carbon in a Striga plant is derived from the transfer of nitrogenous solutes from its host. One implication of these observations is that there may be a considerable 'sparing' effect on Striga photosynthesis.

Accurate measurements of carbon transfer from the host are highly desirable and Raven (1983) has suggested this could be obtained by measuring the carbon isotope ratio. Plants with the C_4 photosynthetic pathway have a lower $\delta^{13}C$ half than plants having only the C_3 pathway (O'Leary, 1981). Consequently, any substantial input of carbon from sorghum will result in a less negative $\delta^{13}C$ value for Striga compared with other C_3 species. The $\delta^{13}C$ values obtained for S. bilabiata on Eragrostis racemosa was -25.4 compared with a value of -12.9 for the C_4host (de la Harpe et al, 1981). The results for Striga are similar to those for other C_3 plants and are not indicative of any very marked carbon transfer from the host.

Carbon Metabolism

The dependence of Striga on its host for carbon alters during its lifecycle. Following attachment, the growth of the Striga plants is completely dependent on carbon from its host. After emergence and the appearance of chlorophyll the capacity of photosynthesis develops, and presumably the parasite becomes less dependent on carbon transfer from the host. It is evident from the earlier discussion that even in photosynthetically-active Striga there is a substantial 'obligate' carbon transfer from the host. Carbon transfer after exposure of the host to $^{14}CO_2$, [^{14}C] urea and [^{14}C] glucose has been demonstrated in S. asiatica (Rogers & Nelson, 1962) and S. hermonthica (Okonkwo, 1966a), although the radioactive products transported are not known. The rates of photosynthesis exhibited by S. bilabiata are barely sufficient to meet its carbon requirements (de la Harpe et al, 1981). Lack of more information concerning rates of photosynthesis are carbon transfer from the host is a serious limitation to our understanding of the quantitative aspects of Striga parasitism.

Analysis of the free carbohydrates in Striga leaves has shown that mannitol is the major low molecular weight carbohydrate (Table 7). Mannitol has been reported in other parasitic members of the Scrophulariaceae as well as in species of the Orobanchaceae (Smith et al, 1969). It has been suggested that angiosperm parasites which obtain their carbon predominantly from their host synthesize soluble carbohydrate reserves which differ from the major soluble carbohydrate reserves of the host and from the form in which carbon is transported from host to parasite (Smith et al, 1969). Another possible function for mannitol is as an osmotic solute, Smith et al (1969) suggest polyol accumulation could facilitate water movement from host to parasite.

Another polyol, sorbitol has been implicated in intracellular osmotic adjustment in the halophytic angiosperm Plantago maritima (Ahmad et al, 1979). The high potassium content found in Striga leaves would seem, as discussed earlier, to require the synthesis of some form of compatible cytoplasmic solute and mannitol could well serve in this role.

Recently it has been demonstrated that compatible solutes such as proline, glycine betaine and sorbitol can act as protectants, stabilizing enzymes against, for example, heat denaturation (Paleg et al, 1981; Nash et al, (1982); Smirnoff & Stewart, 1983). The results in Table 8 show that mannitol, in common with other compatible solutes protects various enzymes against heat denaturation.

Increased heat resistance may be of significance in the life-cycle of Striga at the period of pre-emergence when high soil temperature might be encountered and later if the transpirational cooling effect is reduced during a period of water stress.

Mannitol would seem then to be of importance in osmoregulation and could also be implicated in heat resistance. It is not a metabolite which we have found in either sorghum or millet and its metabolism would seem to be a 'target' for enzyme-directed herbicides. An examination of existing herbicide libraries for compounds with a structural similarity to mannitol or its precursors would seem a worthwhile starting point for a Striga-selective herbicide.

Host Metabolism

Substantially more information relating to the effects of Striga on the metabolism of its host would seem essential for the development of methods capable of screening large numbers of germplasm or breeding lines, and for understanding the dramatic effects of Striga on the growth of its host. The reduced yield and stunting of the shoot system are apparent well before the above-ground emergence of Striga and before any substantial transfer of nutrients and water have occurred (Williams, 1961a,b). Changes in hormonal balance, decreased cytokinins and gibberellins, and increased abscisic acid of the sorghum shoot have been implicated in the growth effects (Drennan & El Hiweris, 1979). It is not clear, however, if the hormonal changes cause or simply reflect the growth effects.

Comparative studies of metabolite changes in parasitized and control plants of varieties differing in their resistance are being carried out, with the emphasis being placed on identifying potential defence compounds or phytoalexin-like compounds. Most of the analytic procedures are elaborate and time consuming and we have recently begun to investigate the potential of proton nuclear magnetic resonance ('H-NMR) spectroscopy to screen plants. This is a technique for determining the different chemical environments of the various forms of hydrogen atoms present in organic molecules (e.g. - CH_3; = CH_2; - CHO etc.). Dried or freeze dried plant samples are dissolved in deuterium oxide (to prevent swamping by a large signal from the protons in water). The spectra from various samples can be compared to see if any large changes in organic solute can be detected. A preliminary identification of the types of compound accumulating can be made, and then subjected to more intensive analysis by gas or liquid chromatography. The technique has the advantage of measuring all organic solutes, but the disadvantage of lacking sensitivity. However, the results shown in Figure 1 give an 'alternative' picture of what a Striga plant looks like.

Another way in which host response and resistance is being studied is by looking for changes at the protein level. In this we are using SDS - polyacrylamide gel electrophoresis to examine protein extracts from control and parasitized root and shoot tissue of different sorghum varieties. In addition we have begun to examine the activity of specific enzymes in parasitized and control plants. preliminary results indicate that the activity of biosynthetic enzymes is reduced in parasitized plants while the levels of catabolic enzymes remained unchanged or increased. For example, the levels of two of the enzymes of arginine biosynthesis ornithine acetyl transferase and ornithine carbamyl transferase in parasitized plants are 30-40% of those in control plants while the activity of arginase and ornithine amino transferase is similar in control and parasitized plants. Detailed studies of arginine metabolism are being undertaken since parasitized plants of sorghum exhibit an increase in amine content. Arginine is the precursor of the diamine, putrescine and the polyamines spermidene and spermine. Putrescine appears to be the major amine in sorghum, but in parasitized plants the spermine content is 3-5 fold (60-500 n mol g fw^{-1}) higher than in control plants. Severely parasitized plants contain small amounts of cadaverine (indicative perhaps of the death of the shoot system!). The principal amine of Striga is spermine which is present in quite large amounts (1,400 n mol gfw^{-1}). Some of the amines have been implicated in growth regulatory phenomena and may have a role in protein synthesis (Smith, 1980). Their role in Striga parasitism is being investigated in collaboration with C. Parker and his group at the WRO, Oxford.

A new approach to the Striga problem which would seem to have great promise is the application of some of the techniques of molecular biology. Studies of the in vitro translation products of parasitized and control plants could provide a useful starting point for such work. Techniques for examining in vitro translation products are now well developed and could be applied to poly(A) RNA isolated from sorghum root and shoot tissue. Examination of $[^{35}S]$ methionine labelled products by one or two dimensional polyacrylamide gel electrophoresis might reveal changes occurring gene expression in parasitized plants. Extension of such studies to varieties differing in their Striga resistance might provide information relating to the existence of "resistance gene products". Success in these experiments could be followed up by molecular genetical studies. The construction of genomic libraries of Striga and sorghum together with the preparation of cDNA from poly(A)RNA could open the way to constructing cDNA probes to examine varieties for resistance genes. And the possibility of engineering Striga resistance into varieties acceptable to the farmer may in the future simplify the plant breeders problems of satisfying the agronomic and gastronomic interests.

CONCLUSIONS

Studies at the biochemical level show that Striga exhibits a number of unusual features, some of which may be important in relation to its control. There are, however, a number of areas which require more detailed study and the application of new techniques.

The metabolism of mannitol should be investigated in relation to the possible development of chemical controls targeted on this area. More general studies of carbon metabolism should include measurement of Striga photosynthesis and the quantitative determination of carbon transfer.

The possibility of host defence compounds should be investigated, this may require culture studies to identify host lines which inhibit Striga development. The role of polyamines in relation to chemical defence is one possible line of investigation. Another potentially useful line would be to study the metabolism of phenolic compounds in the host, particularly since these have effects on germination and haustorial development (M. MacQueen, unpublished results; Riopel).

In addition we suggest that studies at the molecular level should be undertaken as a high priority. Genomic libraries of Striga and sorghum should be constructed and using in vitro translation, cDNA synthesis, hybridization and cloning techniques studies of resistance genes should be initiated.

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Table 1 : Leaf water potentials[a] of *Striga* and its host Sorghum

	Watered	6 Days no Watering
Sorghum vulgare control	-1.02	N.D.
Sorghum parasitized by *Striga hermonthica*	-1.01	-1.86
Striga hermonthica on *sorghum*	-1.11	-2.30
	(90.3%)[b]	(76.9%)
Sorghum parasitized by *Striga asiatica*	-1.03	N.D.
Striga asiatica on *sorghum*	-1.40	N.D.
Pennisetum parasitized by *Striga hermonthica*	-0.93	-2.9
Striga hermonthica on *Pennisetum*	-1.06	-3.3

a : was determined by dew point hygrometry using Wescor Model HR-33T hygrometer coupled to a Wescor C-52 sample chamber

b : Figures in parenthesis are leaf water contents

Table 2 : Mineral nutrient status of *Striga and Sorghum***
(mg gdw-1)

Element	Sorghum Control	Sorghum Parasitized	*Striga*
Calcium	1.30	1.30	1.80
Iron	0.40	0.40	0.30
Magnesium	5.00	5.10	15.00
Manganese	0.10	0.13	0.14
Nitrogen	1.01	0.98	1.88
Potassium	9.00	10.10	54.00
Zinc	0.21	0.20	0.08

* Analyses were performed on leaf tissue from 9-week old associations of *Striga hermonthica* - *Sorghum vulgare* (var Ras Girid) grown in soil

Table 3 : Enzymes of nitrogen assimilation in *Striga* shoot tissue

μ mol hour-1 gfw-1

Species	Nitrate Reductase	Glutamine Synthetase	Glutamate Synthase
Striga asiatica	0.2	31.0	N.T.
Striga hermonthica	0.1	41.5	20.1
Striga gesnerioides	0.1	31.3	12.3

Enzyme assays were described by Stewart and Orebamjo (1980). Plants of *S. asiatica* and *S. hermonthica* were parasitizing *Sorghum vulgare*, and *S. gesnerioides* was parasitizing *Indigofera*.

Table 4 : Glutamine synthetase isoforms in *Striga* shoot tissue

% Total activity

Species	GS_1(cytoplasmic)	GS_2(chloroplastic)
Striga asiatica	95	5
Striga hermonthica	78	22
Striga gesnerioides	85	15

Ion exchange chromotography was carried out as described by McNally et al (1983b)

Table 5 : Nitrogenous compounds in the xylem fluid of *Striga hermonthica*

Compound	nmol cm^3
Nitrate	10
Alanine	10-20
Asparagine	25-50
Glutamate	500-1500
Glutamine	50-750
Glucine	trace
Isoleucine	trace
Leucine	10-20
Serine	trace
Threonine	trace
Valine	5-30

Amino acid analysis were as described by Rhodes et al (1981)

Table 6 : Time course of $^{15}NH_4$ incorporation into shoots of *Striga hermonthica*

^{15}N Abundance (%)

Compound	6	12	20 hours
Aspartate	23	29	22
Asparagine	14	22	27
Glutamate	25	32	28
Glutamine	21	32	37

ImM $^{15}NH_4Cl$ (99% ^{15}N abundance) was fed to pots containing *Sorghum vulgare* (Ras Girid) parasitized by *Striga hermonthica*. Analyses were as described by Rhodes et al (1981).

Table 7 : Analyses of the low molecular weight carbohydrates in leaves of Striga hermonthica

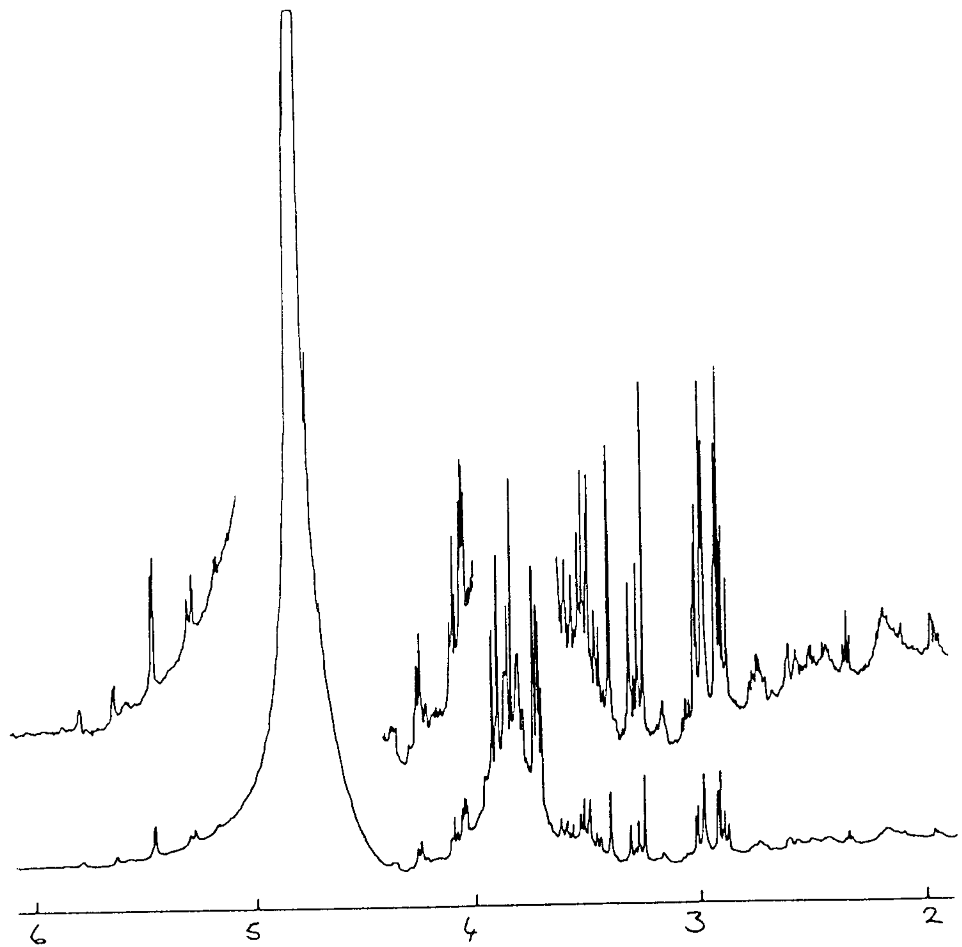
Compound	$umolgfw^{-1}$
β -Glucose	2.3-5.0
Mannitol	22.0-48.0
Sucrose	4.0-8.0

Plants were extracted with hot alcohol (80%) and sugars determined by gas chromatography of their TMS-derivatives

Table 8 : Effect of Mannitol on heat stability of Striga enzymes

% Residual activity of 50° (10 mins)

Enzyme	Control	+0.5m Mannitol	+1m Mannitol
Acid phosphatase	50	80	85
Aspartate aminotransferase	51	65	89
Glutamine synthetase (GS_1)	10	26	53
Malate dehydrogenase	67	100	100



Striga leaf tissue was dried at 40° and suspended in 99.8% D_2O. An ^{1}H-NMR spectrum was run on a Brukker AM 500 spectrometer at 500 MHz (500 l sample in a 5 mm tube), referenced to an external standard, at 298K, and is the result of 48 scans. The spectrum was obtained using a 70° pulse and a total repetition rate of 0.7 Hz. The results were obtained in collaboration with Dr. P.J. Sadler and Dr. D.P. Higham (Department of Chemistry, Birbeck College, London) and the Medical Research Council Biomedical NMR Centre, Mill Hill, London

REFERENCES

AHMAD, I., LARHER, F. & STEWART, G.R. (1979), "Sorbitol, a compatible osmotic solute in Plantago maritima", New Phytologist, 82 : 671-678

ANSIAUX, J.R. (1958), "Sur l'alimentation minèrale des phanérogames parasites", Bull. Acad. R. Belg., 44 : 787-793

BAKER, D.A. (1983), "Uptake of cations and their transport within the plant", In "Metals and micronutrients: uptake and utilization by plants". Ed. D.A. Robb & W.S. Pierpoint, pp 3-20, Academic Press, London

BERGMAN, A., GARDERSTROM, P. & ERICSON, I. (1981), "Release and refixation of ammonia during photorespiration", Physiol. Plant., 53 : 528-537

BUTZ, R. & JACKSON, W.A. (1977), "A mechanism for nitrate transport and reduction", Phytochemistry, 16 : 409-417

CRAM, W.J. (1976), "Negative feedback regulation of transport in cells. The maintenance of turgor, volume and nutrient supply", In "Encyclopaedia of plant physiology, Vol. 2. Transport in plants, Part A, Cells", Eds. U. Luttage & M.G. Pitman, pp. 284-316, Springer-Verlag, Berlin

DE LA HARPE, A.C., VISSER, C.J.H. & GROBBELAAR, N. (1981), "Photosynthetic characteristics of some South African parasitic plants", Zeit. Pflanzen Physiologie, 103 : 265-275

DRENNAN, D.S.H. & EL HIWERIS, S.O. (1979), "Changes in growth regulator substances in Sorghum vulgare infected with Striga hermonthica", in 2nd International Symposium on Parasitic Weeds, pp. 144-155, North Carolina State University, Raleigh, USA

GOVIER, R.N., NELSON, M. & PATE, J.S. (1967), "Hemiparasitic nutrition in angiosperms. I. The transfer of organic compounds from host to Odontites verna (Bell.) Dum. (Scrophulariaceae)", New Phytologist, 66 : 285-297

GUIZ, C.D., HIREL, B., SHEDLOFSKY, G. & GADAL, P. (1979), "Occurrence and influence of light on the relative properties of two glutamine synthetases in rice leaves", Plant Science Letters, 15 : 271-277

HEWITT, E.J. (1975), "Assimilatory nitrate-nitrite reduction", Annual Review of Plant Physiology, 26 : 73-100

HORACK, O. (1974), "Vergkeichenda Mineralstoff-Analysen eingen loranthaceen und deren wirtpflanzen", Zeit. Pflanzen Physiologie, 73 : 461-466

HSIAO, T.C. (1973), "Plant responses to water stresses", Annual Review Plant Physiology, 24 : 519-570

KEYS, A.J., BIRD, I.F., CORNELIUS, M.F., LEA, P.J., WALLSGROVE, R.M. & MIFLIN, B.J. (1978), "Photorespiratory nitrogen cycle", Nature, 275 : 741-742

KUIJT, J. (1969), "The biology of parasitic flowering plants", pp. 246, University of California Press, Berkeley

LEE, J.A. & STEWART, G.R. (1978), "Ecological aspects of nitrogen assimilation", Advances in Botanical Research, 6 : 1-43

McNALLY, S.F., HIREL, B., GADAL, P., MANN, A.F. & STEWART, G.R. (1983a), "Glutamine synthetase of higher plants: evidence for a specific isoform content related to their possible physiological role and their compartmentation within the leaf", Plant physiology, 72 : 22-25

McNALLY, S.F., OREBAMJO, T.O., HIREL, B. & STEWART, G.R. (1983b), "Glutamine synthetase isoenzymes of *Striga hermonthica* and other angiosperm root parasites", Journal of Experimental Botany, 34 : 610-619

MIFLIN, B.J. & LEA, P.J. (1980), "Ammonia assimilation", in Biochemistry of Plants, Vol. 5. Ed. B.J. Miflin, pp. 169-203, Academic Press, New York

MUSSELMAN, L.J. (1980), "The biology of *Striga*, *Orobanche* and other root parasitic weeds", Annual review of phytopathology, 18 : 463-489

NASH, D., PALEG, L.G. & WISKICH, J.T. (1982), "Effect of proline, betaine and some other solutes on the heat stability of mitochondrial enzymes", Australian Journal of Plant Physiology, 9 : 45-47

OKONKWO, S.N.C. (1966a), "Studies on *Striga senegalensis*. II. Translocation of $C^{14}C$-labelled photosynthate, urea ^{14}C and sulphate^{35} between host and parasite", American Journal of Botany, 63 : 142-148

OKONKWO, S.N.C. (1966b), "Studies on *Striga senegalensis*. IV. *In vitro* culture of seedlings. Effects of various sugars and glutamate", American Journal of Botany, 53 : 679-682

O'LEARY, M.H. (1981), "Carbon isotope fractionation in plants", Phytochemistry, 20 : 533-568

PATE, J.S. (1980), "Transport and partitioning of nitrogenous solutes", Annual Review of Plant Physiology, 31 : 313-340.

PALEG, L.G., DOUGLAS, T.J., van DAAL, A. & KEECH, D.B. (1981), "Proline and betaine protect enzymes against heat inactivation", Australian Journal of Plant Physiology, 8 : 107-114

RAVEN, J.A. (1983), "Phytophages of xylem and phloem: a comparison of animal and plant sap-feeders", Advances in Ecological Research, 13 : 136-235

RAVEN, J.A. & SMITH, F.A. (1976), "Nitrogen assimilation and transport in vascular land plants in relation to intracellular pH regulation", New Phytologist, 76 : 415-431

RHODES, D., MYERS, A.C. & JAMIESON, G. (1981), "Gas chromatography-mass spectrometry of N-hepta fluorobutyl isobutyl esters of amino acids in the analysis of the kinetics of $|^{15}NH_4^+|$ assimilation in Lemna minor L.", Plant Physiology, 68 : 1197-2005

ROGERS, W.E. & NELSON, R.R. (1962), "Penetration and nutrition of Striga asiatica", Phytopathology, 52 : 1064-1070

SMIRNOFF, N. & STEWART, G.R. (1983), "Stress metabolites and their role in coastal plants", Vegetatio (in press)

SMITH, T.A. (1980), "Plant amines", Secondary Plant Products, Vol. 8, pp. 433-460, Encyclopedia Plant Physiology (Ed. E.A. Bell & B.V. Charlwood), Springer Verlag, Berlin

SMITH, D.C., MUSCATIVE, L. & LEWIS, D. (1969), "Carbohydrate movement from autotrophs to heterotrophs in parasitic and mutualistic symbiosis", Biological Reviews, 44 : 17-90

STEWART, G.R. & OREBAMJO, T.O. (1980), "Nitrogen status and nitrate reductase activity of the parasitic angiosperm Tapinanthus bangwensis (Engl. & K. Krause). Danser growing on different hosts", Annals of Botany, 45 : 587-589

STEWART, G.R. & AHMAD, I. (1983), "Adaptation to salinity in angiosperm halophytes". In "Metals and micronutrients: uptake and utilization by plants", Eds. D.A. Robb & W.S. Pierpoint, pp. 33-50, Academic Press, London

WALLSGROVE, R.M., KEYS, A.J., LEA, P.J. & MIFLIN, B.J. (1983), "Photosynthesis, photorespiration and nitrogen metabolism", Plant, Cell and Environment, 6 : 301-309

WILLIAMS, C.N. (1961a), "Growth and morphogenesis of Striga seedlings: effects of light, gibberelic acid and kinetin on growth and morphogenesis of Striga seedlings", Nature, 189 : 378-381

WILLIAMS, C.N. (1961b), "Tropism and morphogenesis of Striga seedlings in the host rhizosphere", Annals of Botany, 25 : 407-415

WOO, K.C. & OSMOND, C.B. (1982), "Stimulation of ammonia and 2-oxoglutarate dependent O_2 evolution in isolated chloroplasts by dicarboxylate and the role of the chloroplast in photorespiratory nitrogen cycling", Plant Physiology, 69 : 591-596

WOO, K.C., MOROT-GAUDRY, J.F., SUMMONS, R.E. & OSMOND, C.B. (1982), "Evidence for the GS/GOGAT pathway during photorespiratory nitrogen cycle in spinach leaves", Plant Physiology, 70 : 1514-1517

WYN JONES, R.G., STOREY, R., LEIGH, R.A., AHMAD, N. & POLLARD, A. (1977), "An hypothesis on cytoplasmic osmoregulation", In "Regulation of cell membrane activities in plants", Eds. E. Marie & O. Ciferi, Elsevier, North Holland, Biomedical Press, Amsterdam

WYN JONES, R.G., BRADY, C.J. & SPEIRS, J. (1979), "Ionic and osmotic relations in plant cells". In "Recent advances in the biochemistry of cereals", Eds. D.L. Laidman & R.G. Wyn Jones, Academic Press, London & New York

YOSHIKAWA, F., WORSHAM, A.D., MORELAND, D.E. & EPLEE, R.E. (1978), "Biochemical requirements for seed germination and shoot development of witchweed (Striga asiatica)", Weed Science, 26 : 119-122

THE PHYSIOLOGY OF STRIGA spp.: PRESENT STATE OF KNOWLEDGE AND PRIORITIES FOR FUTURE RESEARCH

C. Parker

INTRODUCTION

In this background paper, I shall review the present state of knowledge of different aspects of the physiology of Striga spp., discuss the current research in progress and finally suggest priorities for future research. Accepting some risk of overlap with other Workshop contributors, I shall cover : 1) germination and other aspects of the pre-attachment phase; 2) attachment, penetration and development; 3) effects on the host; and 4) factors involved in host resistance. Unless otherwise indicated, generalisations will apply to S. hermonthica (Del.) Benth., and S. asiatica (L.) Kuntze. Much less is known, of other species but there will be some comment on S. gesnerioides (Willd.) Vatke., S. densiflora Benth. and S. angustifolia (Don) Saldanha (= S. euphrasioides Benth.). Where appropriate, use has been made of material in previous reviews (e.g. Parker, 1983).

STATE OF KNOWLEDGE AND RESEARCH NEEDS

1. Phases up to Germination

a) After-ripening and induced dormancy. Saunders (1933) stated that S. asiatica in South Africa required a resting period of at least six months following shedding, after which, germination would steadily improve up to 18 months when a plateau was reached. Fresh seed would only germinate to a level of about 5%. He did not state under what conditions of seed storage these observations were made. Kust (1963), however, has published results of detailed tests with S. asiatica in the USA, which confirm that freshly harvested seed gives very low germination percentages and that the length of the after-ripening period varies from 4-6 weeks at 35°C, to about 12 weeks at 24°C and 40 weeks at 0°C. Vallance (1950a) compared the germination of seeds of S. hermonthica of different ages (but also from different sources) and concluded that this species also has an after-ripening requirement. Unpublished observations at the Weed Research Organization (WRO) also indicate a tendency for samples of S. hermonthica from West Africa to give relatively low germination in the first six months after collection, but at least one sample of S. hermonthica from Abu Naama, Sudan, has given over 80% germination within three months of collection, so no generalisation can be made concerning this requirement. Attempts to overcome the after-ripening requirement of the west African seed by various temperature and desiccation treatments were not successful (Reid & Parker, 1979).

I am not aware of current research on after-ripening and from a practical viewpoint, assuming seed in the field has usually after-ripened by the following rainy season, it may only be a problem to researchers. Academically it is, however, of considerable interest and it would be useful if any parallel could be established with the induced dormancy which has been observed for both S. asiatica (R.E. Eplee, personal communication) and S. hermonthica (A.G.T. Babiker, personal communication), when already after-ripened seeds have been buried deep in the soil. Under these conditions (of low oxygen availabilty?) it has been observed that seed may acquire a form of dormancy which is not broken by the usual pre-conditioning and stimulant treatment (see below). It may take some months for seed to resume normal behaviour, and it may be that the process of recovery is the same as that required for after-ripening. It is not clear whether such induced dormancy is the same as the 'wet dormancy' arising after prolonged pre-conditioning (see below). Research continues in Sudan and we await further reports with interest.

b) Pre-conditioning. Several different terms have been used for the requirement of the seed to be imbibed for a period before it is exposed to stimulant. 'Pre-conditioning' is perhaps the most frequent, but 'pre-treatment' or 'conditioning' have also been used.

The optimum temperature and length of pre-conditioning were studied in detail for S. hermonthica by Vállance (1950a), who showed a temperature of 22°C to be more favourable than 27°C or 32°C. A lower temperature of 12°C resulted in slower conditioning but eventually gave higher levels of germination than 27°C or 32°C. The pre-conditioning period was shorter and the germination levels reached were generally greater for samples of seed 4 to 6 years old. Under the best conditions only a few days of the required temperature were needed for good germination and the optimum length of time varied from 7 to 21 days. In almost all instances, some decline of germination was observed after 21 days, which he referred to as 'wet dormancy'. He was able to show that viability was not necessarily lost, as ungerminated seeds following pre-conditioning at 22°C could be dried, pre-conditioned again and subsequently made to germinate. At higher temperatures the effect was not so readily reversible and hence perhaps analogous to the effect of deep burial, referred to in the previous section.

Reid and Parker (1979) confirmed that 23°C was a more favourable pre-conditioning temperature than 33°C for a wide range of samples of S. hermonthica from both west and east Africa and from both sorghum and millet hosts. For S. asiatica however, from both Indian and South Africa, they showed that the higher temperature of 33°C was the more effective. S. densiflora Benth. from India and S. gesnerioides (Willd.) Vatke. from west Africa also showed slightly better response to the higher pre-conditioning temperature, but results were less conclusive (Reid & Parker, 1979).

Reid and Parker (1979) confirmed the 'wet dormancy' phenomenon for S. hermonthica, especially when seed was pre-conditioned at 33°C for more than 4-6 weeks, but they did not find a comparable phenomenon in S. asiatica even after 8 weeks at 33°C.

Some recent results have shown that pre-conditioning in the presence of either natural (strigol) or synthetic (GR 7) germination stimulants greatly reduces the capacity of S. asiatica to germinate, even if fresh stimlulant is later supplied

(Hsiao et al, 1979; Pavlista et al, 1979). Comparable results have now been reported for S. hermonthica using GR 7 (Babiker & Hamdoun, 1982) and ethephon (Babiker & Hamdoun, 1983). These results could perhaps have been predicted on the basis of Vallance's earlier work (Vallance, 1950b) which showed that exposure to stimulant at any stage tended to stimulate respiration and that the higher the respiration during early stages of pre-conditioning (as in non-after-ripened seed) the lower the subsequent germination (Vallance, 1951). It might be supposed from this that anaerobic conditions during pre-conditioning would favour subsequent germination, but, at least for the related parasite Alectra vogelii Benth., it is known that anaerobic conditions prevent normal pre-conditioning (Botha, 1950). These phenomena are not only of great academic interest but also of enormous practical importance in relation to the use of artificial germination stimulants and trap cropping.

Striga angustifolia does not have a known conditioning requirement, but germination is improved by prolonged leaching of the seed (Rangaswamy & Rangan, 1966).

c) Germination. In all the Striga spp. under discussion, other than S. angustifolia, germination is normally triggered by substances leaking from the roots of potential host plants. Sunderland (1960) showed that in maize (Zea mays L.), leakage was greatest in a zone 3-6 mm behind the root tip. The natural stimulant substances are highly active, but are present in root exudates at such low levels that their separation, purification and identification have proved extremely difficult. Only two natural stimulants, strigol and strigol acetate, have so far been identified (Cook et al, 1972). Strigol can cause 50% germination of S. asiatica at a dilution of 10^{-11}M. Both substances were isolated from cotton (Gossypium hirsutum L.) root exudates and it is uncertain whether they are also produced by maize (Zea mays L.) or sorghum (Sorghum bicolor (L.) Moench). It is clear from the work of Visser and Botha (1974) that there are a number of natural stimulants, and their work with high pressure liquid chromatography shows at least three different substances in the root exudates of each of a range of host and trap crops.

A number of other natural and synthetic compounds have been shown to stimulate germination of Striga spp. to some extent. Before strigol had been identified it was shown that thiourea and allylthiourea had some stimulant activity (Brown & Edwards, 1945) and also some coumarin-type compounds (Worsham et al, 1959) and cytokinins such as kinetins and zeatin (Yoshikawa et al, 1978). Later it was demonstrated that ethylene would stimulate S. asiatica (Egley & Dale, 1970) and this natural gas is now being used on a substantial scale in the USA at about 1.5 kg/ha, to trigger 'suicidal' germination and so deplete the numbers of dormant seed in the soil and hasten the eradication process (Eplee, 1982). Ethephon has also been shown to stimulate both S. asiatica and S. hermonthica (Chancellor et al, 1971) but has not been used as a practical field treatment.

After strigol had been described by Cook et al (1972), the International Development and Research Centre (IDRC) sponsored a project to synthesize simpler analogues and several have proved highly active. GR 5 and GR 7 were described by Johnson et al (1976) and recently GR 24 has been found to be somewhat more active (Norris & Eplee, 1982).

Apart from the presence of a stimulant, Striga germination also requires a suitably high temperature, optima are generally between 30 and 35°C. Few workers have investigated the influence of light, but Kumar and Solomon (1940) showed that light appreciably decreased germination of S. asiatica and, although it is not completely inhibitory, it has a tendency to depress germination of both S. asiatica and S. hermonthica when applied either during pre-conditioning or at the time of exposure to stimulant.

Striga angustifolia does not require a stimulant, in keeping with its reported ability to develop without a host, i.e. as a facultative parasite. The seed is significantly larger than that of the other species, approximately 0.5 mm rather than 0.3 mm, and Reddy and Rao (1980) have described the development of cotyledons, never seen in unattached stages of other species (Rao & Reddy, 1982). As the seed is so small, however, it is not surprising that it germinates only in response to light, i.e. near the soil surface where it has a chance of emerging (Kumar & Solomon, 1940).

There is now considerable evidence for the existence of 'physiological strains' within S. hermonthica and S. asiatica, differing in their ability to attack different host species. Wilson-Jones (1955) was the first to demonstrate that there were strains of S. hermonthica in Sudan differing in their ability to attack sorghum and millet (Pennisetum americanum (L.) K. Schum.). He states that this specificity was **not** due to differences in germination requirement but did not present data to support his conclusion. Parker and Reid (1979) have since confirmed the existence of distinct strains in west Africa, which attack either sorghum or millet and do not normally parasitize the other. In this instance the specificity could be explained by different germination requirements, the sorghum root exudates failing to stimulate the strain from millet and vice versa. It is possible that the specific germination requirements of each strain are reinforced by an inability to develop on the alternative host even after germination, but this has not yet been confirmed. In India, there are also claims of some degree of host specificity of strains of S. asiatica on sorghum, millet and Paspalum scrobiculatum L., the specificity being to some extent based on differential germination requirements (Bharatalakshmi & Jayachandra, 1979).

These specificities are presumably due to the sensitivity of particular strains to particular root exudate substances (and their insensitivity to others). There are current research efforts in the USA and in India to identify more of the stimulants and clarify their relationships but there are difficulties of reproducibility and progress is likely to be slow.

The mode of action of the stimulants has not been explained, in spite of efforts by various workers in the USA and Europe. Vallance (1951) concluded that the stimulant probably had an influence on membrane permeability, but there is no full understanding of the phenomenon.

Research needs in phases up to germination

A better understanding of the temperature, moisture and gas requirements for effective conditioning and germination of Striga seeds in the soil, is vital to the successful use of either the natural stimulants released by trap crops, or artificial stimulants in the form of ethylene or strigol analogues. It should also help to explain 'wet dormancy' or whatever other phenomena are responsible for the seasonal patterns of *Striga* development in different regions. Some of this work could be done in laboratories, but it needs to be supported by quite detailed monitoring of seed under natural field conditions. Different species and strains of *Striga* may vary in requirement and may then need separate study.

Better understanding of the germination stage, particularly the mode of action of strigol, ethylene, etc., could lead to still more potent synthetic stimulants, but this cannot be seen as a priority in view of the difficulty of use of chemicals in most of the worst field situations.

More practical and important perhaps is the whole topic of trap crops, the stimulants that they produce, the time at which they produce them, and their persistence in the soil. The possibility of increasing the exudation of stimulants from the roots of trap crops, e.g., by inexpensive chemical treatments might also be worthwhile.

2. Post-germination Phases

a) *Chemotropism*. The importance of chemotropism remains unclear. Saunders (1933) claims to have observed a bending of *S. asiatica* radicles towards the host root, and Williams (1961) observed the same for seedlings germinating within 4 mm of the root. More recent studies, however, have failed to confirm anything more than a barely significant tendency for seedlings to grow towards, rather than away from the root (Dixon & Parker, 1984; Riopel, USA, personal communication). Considering the complex germination requirements, ensuring germination only when close to a potential host root, it seems surprising that there is not a very pronounced chemotropism to ensure that the seedling makes the earliest possible contact with the root. Perhaps techniques such as those used by Whitney and Carsten (1981) for *Orobanche* involving dilute agar are not suitable for some reason. Saunders (1933) points out that the effect is seen more clearly at lower moisture levels, and if this could be confirmed it could perhaps contribute to our understanding of the reduction of *Striga* attack under wet conditions.

b) *Haustorial initiation*. The initiation of the haustorium on contact with the host root was largely taken for granted until Atsatt et al (1978) and Riopel (1979) began to explore the phenomenon in *Orthocarpus* and *Agalinis* spp. They showed that gum tragacanth, a wound resin exuded by *Astragulus* spp., contained a highly active substance later identified and named xenognosin (Lynn et al, 1981). Structure activity relations have since been explored, and a considerable range of phenolic and flavonoid substances are now known to have activity in stimulating haustorial initiation in *Agalinis* and in *Striga* spp.

The degree of specificity of haustorial initiating substances to particular species or genera of parasite has not yet been clarified, but Nickrent et al (1979) have reported that *S. asiatica* normally forms no haustoria on the roots of *Phaseolus vulgaris* L. but will do so, and then form parasitic attachments when treated with gum tragacanth extract. Hence, a specific requirement for a haustorial initiator is here a factor in host specificity. It has not yet been shown that lack of haustorial initiation is ever a factor in varietal resistance within sorghum or millet, but it remains a possibility.

As haustoria do not usually form until the Striga radicle is virtually in contact with the root surface, it is assumed that the active substances are relatively insoluble and concentrations are only great enough at the root surface (unlike the germination stimulants which are active up to several mm from the root). Initiation of the haustorium is almost invariably associated with a cessation of radicle growth of the Striga. Hence a possible practical application of this new research is that suitably powerful initiators of haustoria might be used to trigger formation of haustoria **before** seedlings have made contact with the root surface, and reduce the number of contacts and attachments.

c) Attachment. It is now believed that the attachment of the haustorium to the root, or to any other surface, is a purely physical 'glueing', rather than a more subtle process involving 'host recognition'. It has been demonstrated that haustoria will attach to almost any inert surface and work is in progress in the USA to identify the chemical nature of the 'glue' involved (J.L.Riopel, personal communication). The adhesive substance is apparently associated with the hair-like protrusions on the haustorium.

d) Penetration. Soon after attachment, a small zone of the haustorium develops into an intrusive organ which penetrates the epidermis and cortex of the root, apparently separating whole cells enzymically, and growing between them, rather than crushing or penetrating the cells themselves. As the haustorium expands within the root, however, some crushing of cells may subsequently occur. The enzymes involved in the penetration process have not been precisely identified but are assumed to include pectinases.

To achieve effective parasitization, the haustorium has to establish contact with the host stele, which entails penetration through the endodermis. It is believed that difficulty of penetration through the endodermis may be a factor in varietal resistance, and Saunders (1933) associates this with thickened walls. He also describes varieties in which the endodermis is readily penetrated but tissues within the stele apparently offer mechanical resistance to further penetration. The possibility of such mechanical barriers being responsible for varietal resistance to sorghum and millet has been explored in recent years by ICRISAT and at WRO, but correlation of resistance with particular root anatomy has not been clearly established and it is suspected that physiological incompatibility or 'antibiosis' is also of importance in at least some varieties of sorghum as well as being an important factor in the resistance of non-hosts such as soyabean (Glycine max (L.) Merr.) (Saunders 1933).

Research needs on post-germination phases

Further research on chemotropism and haustorial initiation is in progress in the USA and the UK, but both topics deserve more study. Such research could lead to chemical treatments which, as noted above, might not be widely appropriate, but there are also possibilities for identifying crop varieties which have resistance associated with failure of one of these vital processes. It is also possible that the so-called 'Striga-chasers' (e.g. Cassia, Crotalaria spp.) may act by interference with one of these processes.

One of the most urgent research requirements of all is a better understanding of resistance mechanisms in sorghum, millet and cowpea, basic to the most rapid and effective selection and breeding of resistant crop varieties. The relative importance of stimulant exudation, chemotropism, mechanical resistance and physiological incompatibility need systematic study.

3. Development of Striga and Effects on the Host

a) Early development. Only after the *Striga* seedling has penetrated the root does further development of the plumular end of the seedling occur. This observation has indicated that the parasite is dependant on the host, at least initially, for a supply of cytokinin to trigger its shoot development (Yoshikawa et al, 1978), but Okonkwo (1966) provides evidence that no elaborated organic substances are needed from the host, other than sugars, and presumably the supply of sugar enables the parasite to synthesize its own cytokinin.

The nature of the connections with the host stele will also be the topic of other papers, but it may be briefly observed that the connections between phloem of host and phloem of parasite are obscure or at least somewhat indirect, raising the question whether the parasite gains most of its sugars from the host phloem or in a much more dilute form from the xylem, with which the connection is clear and direct.

In most *Striga* species the primary haustorium remains small (never larger than 1-2 mm in diameter), but from a very early stage, the seedling begins to produce adventitious roots which form a quite extensive system on which secondary haustoria develop laterally, wherever there is contact with other host roots. These secondary haustoria therefore greatly increase the capacity of the parasite to absorb materials from the host. The relative abundance or importance of these secondary haustoria in different species or under different conditions has never been systematically observed.

The importance of the adventitious roots of *Striga* in absorbing water or nutrients direct from the soil has never been clearly established. No doubt some absorption occurs, but as root hairs are not generally formed it would seem that their main function is to form further parasitic connections with the host.

Striga gesnerioides in contrast, develops a relatively massive primary haustorium, more comparable to that of *Orobanche* spp., and it probably relies on this for most of its absorption from the host, but does form some secondary haustoria (Okonkwo & Nwoke, 1975).

b) Effect on the host. The damaging effects of *Striga* can begin to appear even before the emergence of the parasite from the soil, and Parker (1984) has shown how the total dry weight of a sorghum host may be decreased by several grammes when the weight of parasite is only about 100 mg. It is clear that there is a toxic or pathological effect rather than a mere deprivation of water and nutrients. The only work to indicate the nature of the toxic action is that published by Drennan and El Hiweris (1979), showing that infection by *S. hermonthica* causes a drastic change in the natural growth regulators in the xylem sap, involving about 90% reduction in gibberellins and cytokinins and an approximate doubling of the inhibitors abscisic acid (ABA) and farnesol. This change alone could largely explain the pronounced reduction in shoot development, particularly stem elongation, which is a characteristic effect of all Striga spp. on cereal hosts. A concurrent effect first reported by Parker (1976) and since confirmed by others for both S. asiatica and S. hermonthica is the stimulation of the host root system. This could be a 'passive' phenomenon resulting from diversion of photosynthates not being utilised by the inhibited shoot, since photosynthesis does not appear to be immediately reduced to any very marked degree as a result of infection. It is clearly not a 'hormone-directed-transport' effect, as it is the whole root system which benefits, rather than the root with attachments. It seems probable therefore that it arises from a general change in the hormonal system controlling root:shoot ratio.

How the parasite triggers the changed hormone balance has not been explained but it may be significant that Drennan and El Hiweris (1979) showed a very close parallel beteen the effect of S. hermonthica and that of drought stress, and there are other reasons for looking more closely at the relationships between drought stress and Striga. Hosts infected by S. hermonthica do not generally show any enhanced wilting or other symptoms of drought. S. asiatica, however, characteristically induces wilting in sorghum and maize even when soil moisture is not seriously limiting. In both cases the transpiration of the host is decreased as a result of infection and it is understandable that the parasite is effectively reducing the competition of the host for water, and perhaps more importantly reducing the tension in the xylem so that water plus nutrients can move freely from host to parasite.

Apart from the effect on hormones and water balance, S. hermonthica shows evidence of producing (or inducing?) a toxic substance which causes yellowish chlorotic blotches in the foliage. This symptom is not seen with infection by S. asiatica.

Research needs in post-attachment phases

A better understanding of the damaging effects on the host may not directly contribute to control measures but could have two important implications. Firstly, if the nature of the 'toxic' effect is understood, it could permit rapid and effective screening procedures to be developed for 'tolerance', that is the ability of a crop to grow and yield normally in spite of parasite attack. Tolerance alone has not been regarded as a wise and worthwhile end of research, particularly by ICRISAT, but if it could be simply identified and selected for it could be a valuable adjunct of more genuine resistance.

Secondly, an understanding of the toxic effects of Striga on the host, particularly in biochemical terms, could yield ideas for protection of the host from the toxic effect and so enhance tolerance, again preferably in conjunction with a degree of resistance or other means to reduce infestation. This area of research is desirable and it will be particularly interesting to learn why the effect of S. asiatica differs from that of S. hermonthica but it is not a particularly high priority from a practical viewpoint.

4. Factors in Striga Growth and Host Resistance

a) Light. There is conflicting evidence for the requirement of Striga for light. Some experiments have suggested that Striga can complete its development and flower in total darkness, provided that the host is well illuminated (Rogers & Nelson, 1962). On the other hand, it is generally observed in the field that a densely shading crop greatly supresses Striga development. While the first observation has rarely been reported and needs confirmation for more host/parasite combinations, it should not be unexpected that a plant capable of developing as a total parasite below ground can continue to develop as one above ground. It is therefore necessary only to question how direct is the influence on the Striga of changed light intensity in the densely shaded crop. A common observation in the field is of a fringe of emerged Striga around the edge of a dense crop stand and very little even emerged within the stand. Thus the shade has not only slowed the development of the emerged parasite but also prevented emergence. The cause of supression must therefore be sought, for example, in lower soil temperatures reducing germination, or a change in the physiology of the host in a dense stand, particularly its root : shoot ratio and the downward movement of photosynthates from lower leaves.

Further understanding of the 'shade' effect could be valuable in devising control techniques. If, for instance, it is mainly an effect of soil temperature, a similar effect might be achieved by mulching, especially with light coloured material. Hence, perhaps an explanation of the belief in Cameroon of a benefit from spreading ash (O. Gwathmey, personal communication).

b) Inorganic nutrients. It has long been known that high levels of fertilizer, particularly nitrogen, can help to reduce the Striga problem, yet the mechanism of its action is still not clear. One possibility for which Teferedegn (1973) found evidence, was that N reduced or at least delayed stimulant exudation by the young sorghum seedling, but attempts to confirm this effect have not always been successful (Sheriff & Parker, unpublished).

The possibility of a direct effect of N-fertilizers on Striga germination and development has been proposed by Pesch and Pieterse (1982), but this has not so far been supported by any other studies. N may contribute to the shade effect described above simply by increasing leaf area but it is also perhaps significant that N has a tendency to promote shoot growth at the expense of root development, so reversing the influence of the Striga and resulting in less downward flow of photosynthate. Other possibilities for the influence of N include some indirect effects via the encouragement of rhizosphere microflora pathogenic to the Striga and increased resistance in the host, whether structurally or biochemically. Some attempts continue at WRO to resolve this problem but there is a need for much more work. The effects of other nutrients have not usually been as pronounced as that of nitrogen. Saunders (1933) among others showed little of no benefit from superphosphate while more recent observations in South Africa suggest that K may, if anything, increase infestation of S. asiatica (P.E.L. Thomas, personal communication). This latter observation may deserve further study.

c) Water. The importance of soil moisture in relation to conditioning and germination of Striga has already been emphasised, but its influence on the host/parasite relationship at the later stage may also be important. Striga generally thrives under conditions of limited moisture availability and its development on most host types is enhanced by modest drought stress. As with the effect of N, this may be at least partly linked to the effect of moisture on root : shoot ratio, in this case the dry conditions encouraging downward flow of photosynthates and hence favouring the parasite. It has also been observed, however, that some of the more Striga-resistant sorghum cultivars tend to show their resistance best under conditions of moderate to severe drought stress and perform less well under higher rainfall (Ramaiah & Parker, 1983). The relationship between Striga-resistance, drought-stress and drought-resistance are the subject of continuing study at WRO.

Research needs on factors in host resistance

So far no cereal variety has shown total resistance to Striga in the field. It is also clear from field experiments and observations that resistance varies greatly from site to site and season to season. A better understanding of the factors influencing the resistance of the host, or, conversely the virulence of the parasite could lead to great improvements in the reliability of resistant or semi-resistant varieties.

It may not be possible to manipulate the moisture and drought stress, but understanding any relationships between Striga and the way the crop responds to drought could help towards the incorporation of useful drought response characteristics into resistant varieties.

Nutrient and light are under more direct control and it is thus particularly important to understand more about the way each of these factors influence the host/parasite system.

CONCLUSIONS

Three main areas of research stand out as requiring priority attention :

i. Study of the environmental factors influencing after-ripening, pre-conditioning and germination of Striga spp.; in particular the influence of gas, moisture and temperature levels on seeds at different depths in the soil. Such studies are vital to a better understanding of the natural seasonality of Striga germination and emergence, and to a more effective use of germination stimulants whether artificially applied or produced naturally by trap crops.

ii. Study of resistance mechanisms, particularly in selected resistant lines of crops but also in non-hosts. Only with a better understanding of such mechanisms can the development of improved resistant cultivars be accelerated.

iii. Study of the environmental factors influencing the host-parasite relationship, in particular those influencing host resistance. This is again of importance in relation to the process of selection of resistant cultivars and their testing, but also to the optimum integration of such varieties with other controllable inputs, including nitrogen applications and shading.

None of the above are new areas of research, but in the past they have either been done under relatively artificial conditions in temperate countries, or with relatively primitive facilities in naturally infested areas. There is a particular need to establish well-equipped research projects in several affected regions to study different species of *Striga* on their various hosts, under various climatic conditions.

REFERENCES

ATSATT, P.R., HEARN, T.F., NELSON, R.T. & HEINEMANN, R.T. (1978), "Chemical induction of haustoria in Orthocarpus purpurascens (Scrophulariaceae)", Annals of Botany, 32 : 1117-84

BABIKER, A.G.T. & HAMDOUN, A.M. (1982), "Factors affecting the activity of GR 7 in stimulating germination of Striga hermonthica (Del.) Benth." Weed Research, 22 : 111-115

BABIKER, A.G.T. & HAMDOUN, A.M. (1983), "Factors affecting the activity of ethephon in stimulating seed germination of Striga hermonthica (Del.) Benth.", Weed Research, 23 : 125-131

BHARATALAKSHMI & JAYACHANDRA (1979), "Physiological variations in Striga asiatica", in Proc. 2nd Int. Symp. on Parasitic Weeds, Raleigh, North Carolina, USA, 1979, 132-143

BOTHA, P.J. (1950), "The germination of the seeds of angiospermous root-parasites. Pt 1 The nature of the changes occurring during pre-exposure of the seed of Alectra vogelii Benth.", Journal of South African Botany, 16 : 23-28

BROWN, R. & EDWARDS, M. (1945), "Effects of thiourea and allylthiourea on the germination of the seed of Striga lutea", Nature, 155 : 455-456

CHANCELLOR, R.J., PARKER, C. & TEFEREDEGN, T. (1971), "Stimulation of dormant weed seed germination by 2-chlorethyl-phosphonic acid", Pesticide Science, 2 : 35-37

COOK, C.E., WHICHARD, L.P., WALL, M.E., EGLEY, G.H., COGGAN, P., LUTHAN, P.A. & McPHAIL, A.T. (1972), "Germination stimulants. 2. The structure of strigol - a potent seed germination stimulant for witchweed (Striga lutea Lour.)", Journal of Am. Chem. Soc. 94 : 6198-6199

DIXON, N.H. & PARKER, C. (1984), "Aspects of the resistance of sorghum varieties to Striga spp.", in Proc. 3rd. Int. Symp. on Parasitic Weeds, Aleppo, Syria, 1984, pp. 123-132

DRENNAN, D.H. & EL HIWERIS, S.O. (1979), "Changes in growth regulator substances in Sorghum vulgare infected with Striga hermonthica", in Proc. 2nd Int. Symp. on Parasitic Weeds, Raleigh, North Carolina, USA, 1979, pp. 144-155

EGLEY, G.H. & DALE, J.E. (1970), "Ethylene, 2-chloroethyl-phosphonic acid and witchweed seed germination", P. 327, abstract in Proc. 23rd Ann. Mtg. Southern Weed Science Society, Atlanta, Georgia. Available from Dept. of Botany, Auburn University, Alabama 368303, USA

EPLEE, R.E. (1982), "Progress in control of Striga asiatica in the United States", in Proc. 2nd. Int. Striga Workshop, Ouagadougou, Upper Volta, 1981, pp. 99-102

HSIAO, A.I., WORSHAM, A.D. & MORELAND, D.E. (1979), "Factors affecting conditioning and germination of witchweed (Striga asiatica (L.) Kuntze.) seeds under laboratory conditions", in Proc. 2nd Int. Symp. on Parasitic Weeds, Raleigh, North Carolina, USA, 1979, pp. 193-201

JOHNSON, A.W., ROSEBERY, G. & PARKER, C. (1976), "A novel approach to Striga and Orobanche control using synthetic germination stimulants", Weed Research, 16 : 223-227

KUMAR, L.S.S. & SOLOMON, S. (1940), "The influence of light on the germination of species of Striga", Current Science, 9 : 541

KUST, C.A. (1963), "Dormancy and viability of witchweed seeds as affected by temperature and relative humidity during storage", Weeds, 11 : 247-250

LYNN, D.G., STEFFENS, J.C., KAMAT, V.C., GRADEN, D.W., SHATANOWITZ, J. & RIOPEL, J.L. (1981), "Isolations and characterizations of the first host recognition substance for parasitic angiosperms", Journal of the American Chemical Society, 103 : 1868-1870

NICKRENT, D.L., MUSSELMAN, L.J., RIOPEL, J.L. & EPLEE, R.E. (1979), "Haustorial inititation and non-host penetration in witchweed (Striga asiatica)", Annals of Botany, 43 : 233-236

NORRIS, R.S. & EPLEE, R.E. (1982), "Effects of stimulant plus herbicide on Striga germination", In Proc. 2nd Int. Striga Workshop, Ouagadougou, Upper Volta, 1981, pp. 43-46

OKONKWO, S.N.C. (1966), "Studies on Striga senegalensis (Striga hermonthica). 3. In vitro culture of seedlings. Establishment of culture", American Journal of Botany, 53 : 679-687

OKONKWO, S.N.C. & NWOKE, F.I.O. (1975), "Observations on haustorial development in Striga gesnerioides (Scrophulariaceae)", Annals of Botany, 39 : 979-981

PARKER, C. (1976), "The influence of the parasitic Striga spp. on the host crops sorghum and maize", Abstract in Annals of Applied Biology, 83 : 330

PARKER, C. (1983), "Factors influencing Striga seed germination and host-parasite specificity", in Proc. 2nd Int. Striga Workshop, Ouagadougou, Upper Volta, 1981, pp. 31-35

PARKER, C. (1984), "The influence of Striga spp. on sorghum under varying fertilization nitrogen", in Proc. 3rd Int. Symp. on Parasitic Weeds, Aleppo, Syria, 1984, pp. 90-98

PARKER, C. & REID, D.C. (1979), "Host specificity in Striga spp. - some preliminary observations", in Proc. 2nd Int. Symp. on Parasitic Weeds, Raleigh, North Carolina, USA, 1979, pp. 70-90

PAVLISTA, A.D., WORSHAM, & MORELAND, D.E. (1979), "Witchweed seed germination. II. Stimulatory and inhibitory effects of strigol and GR7, and the effects of organic solvents", in Proc. 2nd Int. Symp. on Parasitic Weeds, Raleigh, North Carolina, USA, 1979, pp. 228-237

PESCH, C. & PIETERSE, A.H. (1982), "Inhibition of germination in Striga by means of urea", Experientia, 38 : 559-560

RAMAIAH, K.V. & PARKER, C. (1983), "Striga and other weeds in sorghum", in Proc. Int. Symp. Sorghum in the Eighties, Hyderabad, India, 1981, 291-302

RANGASWAMY, N.S. & RANGAN, T.S. (1966), "Effects of seed germination stimulants on the witchweed Striga euphrasioides (Vahl.) Benth.", Nature, 210 : 440-441

RAO, P.N. & REDDY, B.V.N. (1982), "Name correction of Striga asiatica as Striga angustifolia", Current Science, 51 : 945

REDDY, B.V.N. & RAO, P.N. (1980), "Colleters on the cotyledons of in vitro-raised seedlings of witchweed - Striga asiatica (L.) Kuntze.", Current Science, 49 : 595-597

REID, D.C. & PARKER, C. (1979), "Germination requirements of Striga spp.", in Proc. 2nd Int. Symp. on Parasitic Weeds, Raleigh, North Carolina, USA, 1979, pp. 202-210

RIOPEL, J.L. (1979), "Experimental studies on induction of haustoria in Agalinis purpurea", in Proc. 2nd Int. Symp. on Parasitic Weeds, Raleigh, North Carolina, USA, pp. 165-173

ROGERS, W.E. & NELSON, R.R. (1962), "Penetration and nutrition of Striga asiatica", Phytopathology, 52 : 1064-1070

SAUNDERS, A.R. (1933), "Studies in phanerogamic parasitism, with particular reference to Striga lutea Lour.", South African Dept. of Agriculture, Science Bulletin, University of Pretoria, 128, 60 pp.

SUNDERLAND, N.C. (1960), "Germination of the seeds of angiospermous root parasites", Biology of Weeds, Symp. of the British Ecological Society, pp. 83-93

TEFEREDEGN, T. (1973), "Stimulation of Striga (Benth.) germination with sorghum root exudate", Master of Technology Thesis, Brunel University, Uxbridge, UK, 33 pp

VALLANCE, K.B. (1950a), "Studies on the germination of the seeds of Striga hermonthica. I. The influence of moisture-treatment, stimulant-dilution, and after-ripening on germination", Annals of Botany, 14 : 347-363

VALLANCE, K.B. (1950b), "Studies on the germination of the seeds of Striga hermonthica. II. The effect of the stimulating solution on seed respiration", Journal of Experimental Botany, 2 : 31-40

VALLANCE, K.B. (1951), "Studies on the germination of the seeds of Striga hermonthica. III. On the nature of pre-treatment and after-ripening", Annals of Botany, 15 : 109-128

VISSER, J.H. & BOTHA, P.J. (1974), "Chromatographic investigations of the Striga seed germination stimulant", Zeitschrift für Pflanzenphysiologie, 72 : 352-358

WHITNEY, P.J. & CARSTEN, C. (1981), "Chemotropic response of broomrape radicles to host root exudates", Annals of Botany, 48 : 919-921

WILLIAMS, C.N. (1961), "Growth and morphogenesis of Striga seedlings", Nature, 189 : 378-381

WILSON-JONES, K. (1955), "Further experiments on witchweed control. II. The existence of physiological strains of Striga hermonthica", Empire Journal of Experimental Agriculture, 23 : 206-213

WORSHAM, A.D., MORELAND, D.E. & KLINGMAN, G.C. (1959), "Stimulation of Striga asiatica (witchweed) seed germination by 6-substituted purines", Science, 130 : 1654-1656

YOSHIKAWA, F., WORSHAM, A.D., MORELAND, D.E. & EPLEE, R.E. (1978), "Biochemical requirements for seed germination and shoot development of witchweed (Striga asiatica)", Weed Science, 26 : 119-122

STRIGA : RESEARCH PRIORITIES WITH SPECIFIC REFERENCE TO AGRONOMY

J. Ogborn

INTRODUCTION

When the control of a parasitic weed by agronomic techniques is reviewed, it seems clear that control can be achieved by the integration into simple control routines appropriate to local farming systems. All relevant fundamental information about the parasite and its host species must therefore be included.

Ways of eradicating Striga spp. were known and successfully used by large scale commercial farmers in southern and eastern Africa during the colonial era. They primarily used sole crop rotations, catch cropping and rigorous hand-pulling with the abundant and cheap hand labour which they could then deploy (Vernon, 1980). These farmers had access to financial credit which enabled them to accept the medium term cost penalties involved in catch cropping and hand-pulling.

The most important unsolved Striga spp. control problem in Africa is the attack of S. hermonthica (and to a lesser degree S. asiatica) on sorghum and pennisetum millet crops grown by smallholders who cannot afford heavy short term costs or to deliberately sacrifice part of their annual staple food harvest in the course of control operations. The smallholders, usually depend on a stable family labour force and cannot deploy extra labour for the control of Striga spp. when this conflicts with some other seasonal peak labour demand.

All of the other cereal staple crops can be attacked in certain areas during some seasons. The most economically damaging are the sporadic and unpredictable failures of the maize crops in areas with variable rainfall. Upland rice can also be seriously damaged, but the conditions which intensify the attack on this crop have not been defined.

Striga orobanchiodes can also devastate the cowpea crops in certain localities in many seasons, but so far this parasite has had relatively little research attention.

This review is therefore devoted mainly to the control of Striga spp. in smallholder farming systems in Africa.

CONTROL TECHNIQUES WHICH CAN BE USED

The available control techniques may be divided into 'crop protection' methods which protect the current susceptible host crop (and must produce a profitable increase in yield) and 'infestation reduction' or 'eradication' methods which reduce the infestation of Striga seed in the soil when applied in the absence of a susceptible host.

The tools available to date are listed in Table 1.

HAND-PULLING AND OTHER MANUAL STRIGA CONTROL TECHNIQUES

Hand-pulling is almost the only universally prescribed control technique for Striga spp. Nearly all sorghum extension leaflets include a recommendation to 'Control Striga by pulling out all emerged shoots before they flower', or something similar. A recent example appeared in the 1981 Report from the Gambia. This universally recommended panacea is almost unanimously neglected by smallholders! In view of their often desperate need for an effective control it must be concluded that they find this simple method less than satisfactory. The comment on this method in Table 1 explains their dissatisfaction. Table 2 shows just how labour intensive this technique can be when it is performed as recommended!

There seem to be no recent publications about the labour required for the intensive hand-pulling of S. asiatica. The older publications about either species do not specify the exact growth stage at which Striga was removed in experiments, although it must be assumed that it was meant to be 'before flowering' (Gisborne, 1953; Butler, 1953-5; Watson, 1956-8). It is extremely difficult to supervise experiments closely enough to ensure that Striga is pulled at this stage when it is so difficult to see. Practical experience suggests that most of the recorded long-term experimental crop responses must, in practice, have been obtained by hand-pulling Striga after flowering. Smallholders generally hoe out Striga after flowering when 'late' weeding forms part of their normal system. They are aware that S. hermonthica pulled before flowering breaks off at the soil surface and sprouts again 'worse than before' within a fortnight! This explains the dramatic increase in emergence recorded in Table 2.

The foregoing explains the general disregard of the standard extension recommendation for early hand-pulling. Removal of Striga spp. at a more mature stage cannot be expected to produce comparable yield increases or to prevent completely some ripening of Striga seed. The results from the northern Guinea savanna of Nigeria presented in Table 1 are probably representative of what can be expected in other endemic Striga areas.

One of the important research priorities for all endemic Striga-infested areas should therefore be local investigations as to whether smallholders are still continuing to perform any late general weed control in their Striga infested cereal crop mixtures. It is probable that this practice was almost universal in the past and there is still a need to evaluate the effectiveness of any incidental Striga control which may result from it. It is difficult to estimate the actual benefit experienced by small holders who still practice late weeding but I have observed that typically they are able to maintain their Striga infestation at a low level considered to be tolerable (Ogborn, 1977a).

HOST GENETIC CHARACTERS USED IN STRIGA CONTROL

During the meeting we have experienced some difficulty in distinguishing between 'tolerance', 'resistance' and 'immunity'. It is therefore necessary to define these terms in order to clarify the following discussion : 'Tolerance' implies the ability of the host crop to produce an acceptable yield in the presence of heavy Striga infestation. It is difficult to define 'acceptable'. A subsistence smallholder may regard a yield of less that 1 tonne/ha as acceptable whereas it is clearly not profitable for a high input production project where a tonne of grain may be insufficient to pay for the cost of production. An alternative definition of tolerance which certainly distinguishes between the present maize varieties in west Africa and sorghum and millet, is that a tolerant crop is able to survive a heavy early Striga attack and possible produce some grain, whereas a 'susceptible' crop such as maize may be killed even before Striga emerges. 'Resistance' implies the ability to resist and reduce the number of successful parasitic connections which permit the Striga to produce viable seed in the field. 'Immunity' similarly implies the possession of resistance of such quality that no successful parasitism occurs in the field.

Tolerance. This is a neglected research topic. Tolerance to Striga attack has not been a primary objective of cereal breeders in the past, although it is arguable that this is the most urgent need in maize varieties grown by smallholders. All traditional and most new varieties do, in practice, develop some tolerance to Striga attack as a result of involuntary selection on Striga infested experimental sites. In recent years some breeders have started the routine screening of selected varieties for Striga tolerance before they are issued to the smallholders. This falls well short of the probable benefit of a formal breeding programme specifically intended to produce tolerant varieties for use by smallholders in endemic Striga areas for which adapted resistant varieties are not yet available. This logically appears to be their most urgent need, their primary short term objective is surely to produce the maximum yield of acceptable quality grain rather than to reduce the Striga challenge to a very low level.

The availability of traditional locally adapted tolerant varieties does, however, make the integrated control of Striga spp. by agronomic means much easier, in spite of the fact that rather higher inputs are required than would be needed to supplement the resistance of a genuinely highly resistant variety. These local tolerant/resistant varieties can, in practice, be used as a basis for the introduction of a range of control measures selected from Table 1, pending the introduction of new 'breeders' resistant varieties. At present, this resource is almost completely neglected in West Africa and the Sudan.

A tolerance breeding programme for maize is particularly needed because the search for sources of Striga resistance in this species has been so unfruitful. There is some evidence that sources of tolerance exist in USA maize varieties (Langston & English, 1981), and the longer period of exposure to Striga attack suggests that better sources of tolerance may exist among locally adapted African maize varieties.

A common criticism of the use of tolerant varieties is that their use allows the unrestricted growth of the Striga infestation. Historically, this did not occur in the traditional smallholder farming systems partly because of their generally low intensity grain production and also because of the natural biological control. The most serious danger of unrestricted Striga population growth evidently occurs when a susceptible variety is grown intensively with high levels of pest control (exemplified by the Indian experience with susceptible sorghum hybrids). I therefore reiterate the need for more attention to be devoted to tolerance breeding to provide local short-term solutions before the adapted resistant varieties are generally available.

Resistance. By far the greatest research effort has gone into the identification of sources of resistance and their incorporation into locally adapted varieties. We have discussed some of the problems of using new resistant varieties in local peasant farming systems in earlier sessions. Quite apart from the problems of developing varieties which are locally adapted both to the local environment and to local palates without weakening the original genetic resistance, general historical experience with resistant varieties has been that their original high level of resistance declines in the field as soon as they are widely cultivated (Doughty, 1941). This has often been attributed to the loss of genetical purity in the resistant variety and there is little doubt that this has sometimes occurred, but smallholders are usually successful in retaining the identity of those varieties which they consider to have special qualities. The sorghum variety 'Framida', for example, has been grown by Sudanese smallholders in the clay plains, apparently for at least two decades and is still markedly resistant. The general complaint by smallholders in the Sudan and elsewhere is that resistant varieties lose their extreme resistance when grown for several seasons on the same site. In the absence of clear contrary evidence, I attribute this loss of extreme resistance mainly to changes in the local Striga populations under the extreme selection pressure which inevitably occurs when only a small fraction of the original population is able to multiply by parasitizing the resistant host.

If the above hypothesis is correct, some caution is necessary when extrapolating the performance of new varieties which show extreme resistance in experiments as compared with susceptible control varieties. The level of resistance may fall somewhat when they are grown for several seasons on the same site by smallholders. This practice is common in those areas where cereal based crop mixtures are grown. It is also noteworthy that the traditional sorghum and millet varieties are invariably tolerant and usually display some resistance. The benefit from introducing resistant host varieties into an area where traditional adapted varieties are being grown is therefore likely to be disappointing as compared with India where the intensive use of susceptible hybrids has built up very high populations of Striga spp. This is not a reason to reduce the effort put into breeding resistant vareties, but it does illustrate the need to extend their period of maximum resistance by introducing them as a component in a package of other Striga control practices which ensure that no fresh Striga seed is produced from the new variety. There are no published references describing this practice.

Immunity. The ultimate objective of resistance breeding is hopefully to develop immune varieties, but there seems to be general agreement that it is unlikely that a variety will be bred from a generally susceptible host species which will display perfect in vitro immunity to Striga spp. It may well be physiologically impossible.

There is field evidence that Striga parasitism can develop both on the 'wetting curve' at the beginning of the rains and on the 'drying curve' after the rainfall peak (Ogborn, 1972a) when the Striga seed passes through the condition in which it can germinate in response to the stimulus from natural or synthetic germinators. The economic importance of each of these periods of potential

Striga attack obviously depends on the local cropping and weather patterns. In certain environments the traditional smallholders have exploited this phenomenon to intensify host Striga resistance to the level of immunity

There are several reported examples of practical immunity in particular local environments. I am most familiar with the case of the day length neutral millet (dln) variety ex-Bornu in the Northern Guinea savanna (Ogborn, 1977b). North of a well-defined boundary there is a change to a different Striga population which attacks both millet and sorghum. This boundary corresponded closely to the southern boundary of the Sudan ecological zone (Mansfield, 1979). This is a particular case of the general zonal differentiation in west Africa described by Ramaiah (1981). Our detailed observations at Samaru indicated that this was not just a simple case of 'sorghum only attacked south and both species attacked north of the boundary'. Millet varieties of a similar dln type which are not locally adapted can be heavily attacked when sown on the same date as ex-Bornu when the season is favourable to an uncharacteristically early Striga attack.

One dramatic example was shown to some of the participants at this meeting in a 1979 experiment where ex-Bornu was the local control in a breeding trial of material from ICRISAT. Most of the ICRISAT provenance was very heavily attacked, whereas only one Striga spp. emerged in the discard of an ex-Bornu plot and all of the rest of this variety where unattacked. This type of millet comes to harvest at the end of July and in August when the rainfall is so heavy that emerged Striga spp. cannot survive the attacks of the naturally occuring pathogenic fungi. The unusual rainfall distribution in 1977 permitted Striga spp. to emerge and ripen seed at this season. This confirms that the Striga population in the northern Guinea savanna has been selected not to attack dln millet varieties, and in particular, not to attack the **locally adapted** varieties of dln millet. The similar unadapted millet varieties appeared to have little tolerance to the Samaru (sorghum strain) Striga population. The identical ex-Bornu variety was heavily attacked by Striga spp. in a trial near Torit in the southern Sudan whereas an adjacent plot of local millet was very lightly attacked.

I conclude that there is no simple relationship between local populations of Striga spp. and the adapted host varieties which display tolerance to their attacks. There is, in particular, a need to record relationships of the type described above where the local climate has effectively selected local Striga populations not to attack the locally adapted varieties. An examination of the circumstances in which susceptible species display local immunity in environments where another host species is heavily attacked may indicate ways in which local field immunity could be obtained elsewhere.

The routine use of a rainfall peak to develop local immunity is probably only practicable where there is a single intense rainfall mode. Striga outbreaks are particularly difficult to predict in those transitional areas where the rainfall is essentially monomodal in some seasons, but definitely bimodal, with a distinct inter-modal drought in others. The southern Guinea savanna is an example of such an area where the seasonal changes in the climate lead to bewildering changes in the prevalence of Striga spp. These changes are most extreme in the case of the present local maize varieties which have no detectable genetical resistance or tolerance. In a particular area, there may be a succession of seasons in which the maize is completely free from attack (evasive immunity) even in sites where the locally adapted day length sensitive (dls) sorghums are regularly attacked. Eventually however, a season occurs in which the maize is generally attacked and quite often completely destroyed. This is a disaster for the local smallholders and a major setback to large-scale mechanized maize projects which may have been cropped successfully for several seasons before experiencing crop failure. The research input needed here is the early classification of each season as monomodal, intermediate or bimodal in time for operational decisions to be made and implemented. When the classification predicts a damaging attack on timely sown maize, it may be possible to sow some other crop or else to protect the maize by sowing it later. It is noteworthy that heavy damage to maize always results from a heavy early Striga attack. This is in contrast to sorghum and millet which can often tolerate a heavy **early** attack providing that it is followed by heavy rain. I have observed that maize which has evaded any early Striga attack seems to display field immunity to the 'drying curve' attack which causes most of the economic damage to tolerant dls sorghum and millet in this zone (Ogborn & Mansfield, 1979). Field observations suggest that Striga parasitism on maize may be expected when the crop is sown early relative to the start of the rains. It is probable that the Striga seed has time to pre-wet but not to become wet dormant as it probably does in most seasons when maize evades attack. This is not proven, but it demonstrated the need for a fundamental study of the interaction between climate and the incidence of Striga attacks on all susceptible species. The availability of satellite weather reports enables the movements of the Inter-Tropical Convergence Zone to be traced and rapidly predicted. Providing that the necessary quantitative information about the local intensity and occurence of Striga spp. can be collected and correlated with the meteorology, it should be possible to develop predicted Striga attacks in time for cereal growers to take appropriate action. Practical proposals to implement this need should be formulated at this meeting for implementation by ABN and CASAFA.

THE AGRONOMIC USE OF ABORTIVE FORCED GERMINATION (IMMUNE HOST SPECIES, STRIGOL ANALOGUES AND ETHYLENE)

Immune Host Species

Although the use of Striga-susceptible catch crops which have to be destroyed to control the parasite is out of the question for smallholders for both operational and economic reasons, there is scope for the use of immune hosts (trap crops) in many of their farming systems. In fact, many of the typical west African savanna crop mixtures include at least one effective trap crop for S. hermonthica. Groundnuts, pigeon peas, chick peas, haricot beans, field peas, cowpeas, cotton and many species of cucurbits have been reported to produce active root exudates which stimulate Striga spp. to germinate. When these crops are grown on the same site each season, they certainly contribute to reducing the reserve of Striga seed in the soil, but unfortunately the traditional mixtures in the infested areas invariably contain at least one staple food species which is a susceptible host.

Where there is only one susceptible host crop in the mixture, it is technically possible to control Striga spp. by withdrawing this component from the mixture to be grown as a sole crop in which direct Striga control measures can be profitably applied (Ogborn, 1977a). The residual crop mixture remaining after this withdrawal can certainly be expected to reduce the level of Striga infestation each season. Crops such as cotton or groundnuts which can be grown as high input cash crops are often recommended to be grown sole and are then particularly valuable for reducing the seed reserve of Striga spp. in the soil.

In the last two decades in some territories, it has been realised that sole cropping of cash crops is often less profitable to the smallholder than their production in modified crop mixtures. Their potential role for Striga control is a counter argument in favour of sole cropping them in endemic Striga areas, particularly if they are rotated round the holding. Regrettably in Africa at least, there appears to be no conscious use of rotational cropping of mixtures and sole cash crops with the deliberate intention of controlling Striga spp. The standard recommendations in extension leaflets for control by 'sole crop rotations' never seems to be worked out in terms of what is practicable in the smallholder systems and therefore has little hope of being accepted by smallholders! It is to be hoped that this is an unduly pessimistic view of the current position in the field.

For the practical implementation of rotational control by immune hosts, the research priority is clearly to set up comprehensive examinations of the traditional systems in each area to observe which of them can be modified by the withdrawal of susceptible crops and/or the introduction of immune host cash crops to act as effective trap cropping phases in the systems.

Approximately the same final result would be achieved by the introduction of direct 'crop protection' measures which can only be profitably applied in sole crops, but unless there is a specific recommendation to withdraw susceptible crops from mixtures, experience suggests that smallholders will continue to sow them while they produce an acceptable level of multiplication of the sown seed.

Strigol Analogues (Johnson et al, 1976)

The most logical use of Striga germinators would be to apply them in a non-susceptible mixture or sole crop or even a mixture containing immune host crops as described above. It is difficult to develop techniques which effectively utilise these potentially valuable control tools in smallholder systems where susceptible crops are sown every season and are often the earliest crops to be sown in the season. Originally there was a hope that an application in the dry season might lead to the abortive germination of a high proportion of the Striga seed during the earliest rains as soon as the Striga seed had pre-wetted (Ogborn & Mansfield, 1979). The few available field observations suggest that this type of application reduced this germinability of the Striga seed instead of enhancing it! This would be expected from the in vitro observation that Striga seed pre-wetted in the presence of strigol analogues had a lower forced germination rate than when pre-wetted before the analogues were added (Babiker & Hamdoun, 1983).

The 'window of opportunity' for applying both the strigol analogues and ethepon before susceptible crops were sown was therefore restricted to the short period after sufficient rain had been received to pre-wet the Striga and the timely sowing date of the susceptible crop. The strigol analogue treatment giving the most profitable results was a dosage of the order of 0.1-0.2 kg.a.i/ha applied about a week before the susceptible crop was sown. The strigol analogue was lightly incorporated during the normal seedbed preparation. The crop usually responded with improved vegetative vigour, an increase in grain yield and (usually) a small reduction in emergence of Striga spp. at the end of the season. Higher dosages applied at the same time produced reductions in crop vigour and yield but a large increase in Striga emergence. The latter could be directly attributed to the action of the germinator because the reduced vigour of the crop would normally also have reduced Striga emergence. I believe these results showed that the germinators actively promoted the germination of Striga spp. for as long as each dosage persisted in the soil. The inherent variability of Striga field experiments reduced the statistical significance of these responses so that several more seasons of experimentation on a larger number of sites would be required to confirm any hypothesis. The interactions between additional fertilizer nitrogen and rates of strigol analogue were complicated, but in accordance with the general hypothesis that high nitrogen status effectively increased the resistance of both sorghum and maize varieties than the host crop roots until the applied dosage had decomposed. It was noteworthy that very large increases in emergence of Striga spp. occurred on occasions following the stimulation with low dosages of strigol analogues. This would only be the result of the synthetically-stimulated Striga forming effective haustoria with the host crops.

Shortage of active ingredient very much restricted the amount of field experimentation which could be undertaken when the strigol analogues were first introduced. The few references to their recent use in the field suggest that this is still a problem. GR7, GR45 and GR24 were all used in different seasons in Nigeria for no other reasons than current availability. A comprehensive field evaluation to justify large scale manufacture still remains to be carried out. Ironically, the delay in carrying out this programme in Nigeria was partly due to a shortage of active ingredients. It is now clear that a major multinational programme lasting at least five seasons is necessary. The evaluation of strigol analogues would be only one component in the project, but would entail the production of a batch of several tonnes of active ingredients before field work can commence. It is never going to be possible to evaluate any Striga control method for use in smallholdings by means of a few limited trials in a few experimental centres. This is because the local farm systems strongly influence the nature of the local problems with Striga spp. and hence the methods of control which are locally preferable.

Ethylene

Rather similar results to those obtained with the strigol analogues were also obtained with ethepon (Chancellor et al, 1970), except that variations in dosage appeared to have little differential effect on the crop response. This was presumably because the ethylene produced by hydrolysis of the ethepon at all dosages did not persist in the soil. In the strigol analogue experiments a single dosage of 1.6 kg ethylene equivalent/ha was used for comparison with rates of strigol. This gave results comparable to the 0.1-0.2 kg.a.i. dosages of strigol analogues but unfortunately the importance of applying the germinators after the Striga seed had pre-wetted was not appreciated when most of these experiments were performed. As a result, it is possible that the ethylene generated by hydrolysis of the ethepon may have reached buried Striga seeds by rapid diffusion before they were fully pre-wetted. This is much less likely to have happened with the strigol analogues which could only reach the Striga seeds by diffusion following the wetting front in dry soil. Hence, comparison between two types of germinator was not always 'in the presence of pre-wetted Striga seed' and the results may give a misleading impression of the comparative ineffectiveness of the ethepon treatment in these experiments. There can be no doubt of the very strong activity of GR7 and GR45 in the Nigerian field experiments.

The direct injection of ethylene (Eplee et al, 1976) into soils of African or Asian smallholdings has not yet been tested but the comparative simplicity of the technology suggests that it could be effectively transferred through an external aid project. Ethepon and ethylene treatments appear to be operationally preferable to strigol analogues in the presence of Striga-susceptible crops because the very short persistence of ethylene widens the 'window of opportunity' during which applications can be safely made with no risk of the germinated Striga spp. attaching to the host roots. In contrast, the analogues appear to be much more effective in germinating Striga spp. in non-susceptible crop mixtures because of their greater period of persistance.

Although there were no very large increases in Striga emergence following ethepon application, the field evidence suggested that S. hermonthica (unlike S. asiatica in Carolina) is able to form haustoria on maize and sorghum roots after being stimulated to germinate by ethylene.

The Design of On-farm Striga Control Experiments

There is no need for elaborate experimental designs at each centre because there are effectively only two environments in which Striga germinators can be used in smallholdings. They can be applied in the absence of a susceptible crop both on the seasonal soil wetting of drying curves and also pre-sowing to a susceptible host crop after the Striga seed has pre-wetted. At each centre it would be necessary to have a single replicate of all the possible Striga control treatments (including a single replicate of each rotation). The number of Striga seed in the soil of each treatment plot would need to be measured each dry season and the yields of all crops grown in each treatment should also be recorded annually. Where resources permitted, the Striga emergence should be recorded for correlation with the local rainfall records. The need to make the Striga seed assays of soil samples from each plot would add to the already high cost of large scale dispersed field experiments. At this meeting we have heard of improved techniques for the direct counting of Striga seed in the soil which can be used in simple field experimental centres. I suggest that the setting up of Striga seed counting units is essential wherever the agronomic control of Striga in smallholdings is being attempted and is suitable for a direct aid project. The ability to count Striga seed populations is the only way in which the success of integrated control of Striga spp. in smallholder farming systems can be unambiguously evaluated. If the Striga populations consistently decline throughout the experimental project period, there will be promise that when continued for long enough, the integrated control routine under test will eventually reduce Striga damage to insignificant levels on the site. In Africa and Asia where Striga spp. are endemic, reinfestation from wild hosts makes it very difficult to eradicate Striga even in a limited area.

When the application of Striga germinators is made pre-sowing to Striga-susceptible crops, it will be almost inevitable that the susceptible crop will be grown sole and closely spaced because the value of the crop yield response will be maximised and have a greater chance of profitability.

The solubility of the various strigol analogues in soil solutions of different acidities should critically affect their practical use in semi-arid areas where the soil dries out completely before the rains commence. A very insoluble material will move more slowly than the wetting front in the dry soil when applied shortly after the beginning of the rains. This will ensure that there is no danger of the germinator reaching buried Striga seed before it has been conditioned but will involve the risk of susceptible crop roots reaching the analogue while it is still actively germinating Striga seed. The ideal solubility will ensure that the analogue moves through the soil in a compact band behind the wetting front stimulating all the Striga seed as soon as it is conditioned. It is probable that different solubilities will be required for different soil textures. The acidity of the soil solution will affect the solubility of the analogue compound as well as its chemical stability. The limited field evidence from the Nigerian experiments suggested that GR7 at least was too insoluble and could persist in the surface soil throughout the rainfall peak.

Although the timing of the ethylene/ethepon applications is less critical in order to avoid the enhancement of a Striga attack on a susceptible crop, the timing of the application to ensure that the ethylene stimulated the maximum possible population of Striga seeds will be critical. If applied too early, some of the Striga seeds will still not be fully conditioned, whereas when applied later, some of the Striga seed may already have become wet dormant.

The timing of the application of Striga germinator materials in relation to the amount and intensity of the early rains is therefore clearly a priority research investigation.

OTHER SOIL-APPLIED STRIGA spp. CONTROL TREATMENTS

Herbicides

Soil active herbicides have been identified which give partial control of both S. hermonthica and S. asiatica before they emerge from the soil (Kasasian & Parker, 1971) but there are many difficulties which militate against their use by smallholders. Very few of the active materials have a wide enough spectrum of selectivity to permit their use in the common crop mixtures. The selectivity of the cheapest materials is not always adequate in the cereal food crops. 2,4-D for example, is quite toxic to many of the traditional west African sorghums at the dosages required for effective control. There are a number of other herbicides which give general weed control as well as control of Striga spp. and are therefore useful when the main Striga infestation develops on the wetting curve, but are difficult to utilise when it develops on the drying curve at the end of the rains. There are additionally all the problems connected with accuracy of application, supply and storage which occur when any soil active herbicides are introduced into smallholder systems. The cost of the herbicide is not usually prohibitive, but the cost of the supply and service organisation combined with the uncertainity of obtaining a profitable crop response make the use of soil active herbicides, specifically for control of Striga spp., too risky for routine areas with an intensive rainfall peak. The most promising areas for their use have single mode rainfall of less than one metre and a heavy enough soil texture to ensure that a pre-sowing or pre-emergent herbicide application will have disappeared before the onset of the next dry season. 'Cereals only' mixtures or cereal sole crops are more common in this climatic zone for a number of agronomic reasons, but unfortunately the crops tend to have low potential yields and therefore little scope for increasing the cost of inputs. Field experience suggests that soil active herbicides may be a viable supplementary option only when nitrogen fertilizer (applied alone) gives a profitable response. It is therefore concluded that soil active herbicides are not a priority research topic for control of Striga spp. in smallholdings. There is, of course, everything to be said for using them for general selective weed control in cereal mixtures or sole crops when this use is profitable and practicable. The selection of a Striga-active substance in preference to a non-active substance may then be expected to give partial Striga control and increased profitability in seasons when Striga damage is severe.

There is a need to identify selective soil applied herbicides for the control of S. orobanchiodes parasitizing cowpeas because there are few, if any, promising crop protection methods of control.

Extra Fertilizer Nitrogen

This may be defined as the application of fertilizer nitrogen just before Striga infestation starts at a dosage well above the normal economic level recommended in uninfested soils. This use of fertilizer nitrogen for Striga control in cereals is the most practicable and attractive method for the smallholder. It has been traditional knowledge for many years that the application of organic manure to infested stands reduced the emergence of Striga spp. and increased the crop yield. This ancient truth is constantly reiterated by extension agents or project workers (Gambia, 1981) who tend to suggest that control of Striga spp. is a simple matter of conserving organic matter for use in Striga control. In practice there is never enough organic manure to protect more that a small fraction of the crop from Striga spp. The alternative application of extra nitrogen fertilizer which is potentially available in large quantities at present world prices, should be profitable even when used at the end of a long overland supply route. It is a high technology product which should be attractive to overseas aid donors. It is not poisonous and can be safely stored on smallholdings.

The nitrogen acts in at least two ways, systematically by increasing the tissue nitrogen of the host root to a level at which parasitism by Striga spp. is directly inhibited (there is now some evidence as to the mechanisms of this effect (McNally & Stewart, 1982) as well as Professor Stewart's significant paper to this

Workshop) and indirectly by reducing light intensity at the soil surface as a result of the denser crop canopy. This second effect is most easily obtained with the tall and medium tall traditional varieties. The high yielding dwarf varieties of 1 m or less in height do not form a dense enough canopy to exclude light sufficiently unless sown at a very close spacing. The best levels of Striga control are therefore obtained with traditional varieties in sole crop.

The systematic effect can be effectively used by itself with traditional varieties in widely-spaced crop mixtures and is potentially of great value because it is the only control method using a placed soil application as opposed to an overall soil application. When nitrogen is used in this way in crop mixtures, the vigorous traditional cereal varieties are likely to compete with the other crops when the application is first introduced. It may be expected that smallholders will adapt the spacing of their crops in mixture as they become accumstomed to the method. There is also some in vitro evidence that soil-applied urea may directly inhibit germination of Striga spp. (Pesch & Pieterse, 1982).

In each climatic zone there is a need to determine the timing and the appropriate extra nitrogen dosage application for each host crop (and in the case of sorghum for each height class). Very tall varieties such as Fara-fara tolerate a lower dose than the medium height varieties before they are at risk of lodging at wide spacing in crop mixtures. This is less of a problem in sole crop even with the very tall varieties because of the degree of mutual support they afford each other. Even when high winds do cause general lodging, the reduced light intensity at the soil surface is usually maintained together with the Striga control effect.

One very important practical point is that when extra fertilizer nitrogen is applied for Striga control it should always be in the non-acidifying form of 'calcium ammonium nitrate (CAN)' and never in the strongly acidifying form of ammonium sulphate. Application of fertilizer N at the levels required (60-100 kg/N) for Striga control rapidly acidifies the generally poorly buffered soils of the typical areas where Striga is endemic and can in a few seasons cause far greater loss of crop than the Striga infestation which it is intended to control.

FOLIAR APPLICATIONS FOR CONTROL OF STRIGA spp.

Foliar Nitrogen Applications

In theory, it should be possible to increase host tissue nitrogen by repeated foliar applications of urea, but the few field observations produced no clear responses in control or increased grain yield. One suggested technique has been to drop urea granules into the funnel of well-established cereal plants in the hope of increasing tissue nitrogen to the level at which it would inhibit Striga parasitism. This intriguing suggestion is worth examination if only because it involves a simple hand application which only needs to be carried out once during the growth of the crop.

Foliar Crop Herbicides

There are a large number of foliar active herbicides which kill S. hermonthica and S. asiatica at low dosages (Ogborn, 1972b). Highly selective formulations have been identified for most of the susceptible host cereal species, but there are apparently no herbicides giving satisfactory control of S. orobanchoides in cowpeas. In this latter crop, foliar control is complicated because the Striga spp. has little chlorophyll and therefore tolerates herbicides which act mainly by inhibiting photosynthesis. The parasite also grows relatively much larger than the cereal Striga spp. before emerging and is then well protected from sprays by the cowpea leaves.

The tolerant cereal hosts suffer comparatively little damage before Striga emergence unless the infestation is unusually severe, but there is a very large increase in total parasite dry matter after emergence. The increase is often well over a hundredfold, for example, 1.5 gm of underground Striga spp. were estimated to produce an average of over 210 gm of mature Striga dry matter/stand in a typical Samaru experiment (Ogborn, 1970). As most of this increase takes place at the end of the rains when the host is suffering from water strain it is easy to see why such large losses in the potential yield occur in the grain crop which is bulking up at the same time.

Oleo-ametryne was identified as a herbicide which was sufficiently selective when spot-applied to Striga spp. in crop mixtures at 800 ppm field concentration to kill the Striga and to be tolerated by the usual range of crops grown in the mixtures. Linuron and bromoxynil actually kill Striga spp. faster but have smaller ranges of tolerant crops.

Modes of Foliar Herbicide Application

The main purpose of foliar herbicide applications is to kill emerged Striga populations before they can produce viable seed. The applications always produce some increased crop vigour and small yield increases. These yield increases are minimum estimates of the losses caused by the Striga. Even when the infestation is very light, the response to spraying is rarely less than 15% of the total potential yield.

There are two practical modes of application. In crop mixtures it is essential to use directed applications in order to avoid waste of herbicide on bare ground and non-host components of the crop mixture. The Intermittent Directed Foliar Application (IDFOLA) technique recommended for this mode of application in Nigeria (Ogborn, 1972b) is the only proven method of direct Striga control in crop mixtures apart from hand-pulling and has the further advantage that it does not stimulate Striga emergence like the latter control method. Although developed as long ago as 1971 it has never been widely adopted or given a thorough socio-economic investigation. It is readily accepted by smallholders in pilot scale on-farm trials, but appears to be a difficult technique for extension staff to understand and to extend. The essential features of performing the application at walking speed in emerged infestations not exceeding 100,000 ha tend to be ignored and there is a tendency to attempt to control more numerous emerged populations making this method unacceptably slow in execution.

These heavier emergences rarely occur in widely spaced crop mixtures and are fortunately usually confined to 'all cereal' mixtures or sole crops. These are most economically controlled by an overall application of one of the same range of selected herbicides recommended for IDFOLA in sole crops. Almost any normal form of applicator can be used provided that the plane of the herbicide swath is kept below the level of the growing points of the cereal host. The best technique which has given excellent control in sorghum (Mansfield, 1979) is to use a standard spinning disc herbicide applicator treating every inter-row of the crop stand.

For both modes of application the best time to apply the herbicide is 'as soon as possible after the emergence of the Striga'. Because this is operationally difficult, it is expedient to apply the herbicide as soon as the conspicuous Striga flowers are visible. A single application made overall at the time of first flowering usually kills about 85-95% of the potential emerged Striga population for the season. This should result in a net reduction in the Striga seed reserve in the soil even if it is not repeated during the growth of the crop.

The same overall application technique is useful for killing the emergence which sometimes develops on the stubble of millet or sorghum after harvest. It is better to kill the Striga directly rather than indirectly by killing the stubble with an application of dalapon or glyphosate. Paraquat does not always kill the stubble roots satisfactorily and is not very active against S. hermonthica. (Another reported difference from the behaviour of S. asiatica in Carolina). This should rule out its use for Striga control even without taking account of toxicity hazards which are involved for smallholder users.

BIOLOGICAL CONTROL

Insect Predators

There are many references to insect pests which attack Striga spp. and which have been described in great detail in D. Greathead's paper to this Workshop. There is little doubt that they constitute an important natural control to the rapid multiplication of Striga spp. But it is difficult to see how they could be integrated into an agronomic Striga control system. Perhaps the most important need is to avoid the use of agronomic techniques which can be expected to weaken natural insect predation. Parker (1979), for example, observed that insecticidal spraying of experimental sorghum plots to control stem borers in west Africa had also controlled a locally important insect Striga predator and visibly increased the level of Striga attack on the crop.

Pathogens as Bioherbicides

There have been a number of observations on pathogens which attack emerged Striga spp. during periods of high atmospheric moisture. At first sight these seem to have little relevance to agronomic control because the infestations develop naturally whenever the ambient atmosphere is suitable. D. Greathead's paper suggests that at least one strain of powdery mildew specific to Striga spp. may have potential as a practical bioherbicide. It is particularly promising because its attacks tend to be more severe at low humidities. There is also some promise that moderately specific pathogenic fungi may be multiplied on other non-parasitic Scrophulariaceae for use as foliar bioherbicides to replace chemical herbicides. In view of their zero mammalian toxicity and long shelf life, such formulations are inherently suited for use by smallholders. Their development should therefore be given priority. It is possible that some progress has already been achieved (Kalidas, 1981) although it is not clear from the abstract whether this is the case, a fungal extract or a suspension of spores was actually applied.

CONCLUSION

This review shows that there are a number of proven techniques which can be used by smallholders for control of Striga spp. I have suggested a number of individual research priorities which need urgent attention. Most of these entail simple location-specific adaptive research in the endemic Striga areas to develop integrated Striga control systems based upon the use of existing local tolerant/resistant cereal varieties (already grown by smallholders) supplemented by the use of nitrogen fertilizer and foliar herbicides. There is really no need to await the maturation of the current resistance breeding programme or more fundamental information about the parasite-host relationship before developing sound local Striga control systems. The required material resources are not large compared with those already devoted to less potentially productive aid projects, but there is an over-riding need at the present time for a major international collaborative effort to support national R & D programmes with the basic information which they need to develop their own location control systems adapted to local farming systems. This would use all the available fundamental knowledge to increase food production immediately, and to give hope of the long term elimination of Striga spp. as an economic problem from most smallholdings. Ramaiah (1981) made a similar plea for a comprehensive international effort. Is it too much to hope that adequate resources will now be made available for a detailed applied research programme on the scale justified by the severity of the problem?

Table 1 : Available Striga spp. control techniques for smallholders

Method	Notes	Crop Protection	Eradication
Hand-pulling	Labour intensive	Yes	No
Resistant varieties	Research intensive	Yes	No
Genetic immunity	Location specific	Yes	Yes
Evasive immunity	Season dependent	Yes	Yes
Tolerant varieties	Little research input	No	No
Trap cropping	System dependent	No	Yes
Crop rotations	System dependent	Yes	Yes
Soil active herbicide	Season dependent	Yes	No
Strigol analogues	Still experimental	Yes	Yes
Ethylene injection	High technology	Yes	Yes
Ethepon application	Simple ethylene application	Yes	Yes
Extra fertilizer N	Standard crop input	Yes	No
Foliar active herbicide	Medium technology input	Yes	No
Biological control	Enhanced natural control	Yes	No

Table 2 : The effect of hand-pulling on Striga spp. emergence, host vigour and control effect. Samaru, 1969, Adapted from Ogborn (1970a)

Control technique	Grain yield kg/ha	Striga emergence 1,000s/ha	Control effort man hours/ha
Hand-pulling at emergence**	684	854	6,156
Hand-pulling after flowering*	299	93	510
No control	262	84	0
(Standard errors)	+214	+81	?

Notes :
* The practicable intensity of control used in most long-term experiments
** The impracticably intense effort recommended in most extension leaflets

REFERENCES

BABIKER, A.G. & HAMDOUN, M. (1983), "Factors affecting the activity of GR7 in stimulating germination of Striga hermonthica", Weed Research, 22(2) : 111-115

BUTLER, E.J. (1953-5), "Annual reports of the Northern Research Station", Northern Region, Department of Agriculture, Nigeria

CHANCELLOR, R.J., PARKER, C. & TEFEREDEGN, T. (1971), "Stimulation of dormant weed seed germination by 2-chloroethylphosphonic acid", Pest. C. Sci., 2 : 35-37

DOUGHTY, L.R. (1941), "East African research station annual report", Amani, 13 : 13-15

EPLEE, R.E., CARTER, E.M. & MOODY, A.V.Jr. (1976), "Back-pack ethylene applicator", US No. APHIS 81-25

GAMBIA (1981), "Annual Report (1979)", Crop Protection Division, Ministry of Agriculture and Natural Resources, the Gambia

GISBORNE, J.H. (1953), Unpublished manuscript in library of Institute for Agricultural Research, Ahmadu Bello University, Zaria, Nigeria

JOHNSON, A.W., ROSEBERY, G. & PARKER, C. (1976), "A novel approach to Striga and Orobanche control using synthetic germination stimulants", Weed Research, 16(4) : 223-227

KALIDAS, D. (1981), "Phytopathogens as weed control agents", Paper in Proceedings, 8th Asian Pacific Weed Conference, 1981

KASASIAN, S. & PARKER, C. (1971), "The effect of numerous herbicides on the germination of Orobanche aegyptiaca and Striga hermonthica", PANS, Vol. 17, No. 14

LANGSTON, M.A. & ENGLISH, T.J. (1981), "Corn varietal resistance or tolerance to witchweed (Striga asiatica)", Paper in Proceedings of 34th Annual Meeting, Southern Weed Science Society, USA

MANSFIELD, R. (1979), Unpublished internal report to the Weed Science Section, Institute for Agricultural Research, Zaria, Nigeria

McNALLY, S.F. & STEWART, G.R. (1982), "Modification in the N-metabolism of Striga associated with its parasitic habit", Plant Physiology, 69(4 supplement) : 110

OGBORN, J. (1970), "Studies in the chemical control of weeds not readily controlled by cultivation, Striga hermonthica", M.Sc. Thesis, Ahmadu Bello University, Zaria, Nigeria

OGBORN, J. (1972a), "The significance of the seasonal pattern of emergence of Striga hermonthica Benth.", Samaru Research Bulletin 239, Institute for Agricultural Research, Ahmadu Bello University, Zaria, Nigeria

OGBORN, J (1972b), "The control of Striga hermonthica in peasant farming", Proceedings of 11th British Weed Control Conference, Brighton, UK.

OGBORN, J. (1977a), "Integrated Striga control. Notes on the experimental cropping systems programme", Report to the Board of Governors, 1976-7, Institute for Agricultural Research, Ahmadu Bello University, Zaria, Nigeria

OGBORN, J. (1977b), "A genuine example of host immunity to Striga hermonthica attack", Letter to PANS, 11/10/1977

OGBORN, J. & MANSFIELD, R.A. (1979), "Responses to Striga germinators in the Nigerian Savanna", 2nd International Symposium on Parasitic Weeds, Raleigh, North Carolina, USA, July 1979

PESCH, C. & PIETERSEE, A.M. (1982), "Inhibition of germination in Striga by means of urea", Striga Workshop October 5-8, 1981, Ouagadougou, Upper Volta

RAMAIAH, K.V. (1981), "Striga research at ICRISAT/Upper Volta Centre", Paper at Striga Workshop, October 5-8, 1981, Ouagadougou, Upper Volta

VERNON, R. (1980), "Weed control in Zambia's maize", In proceedings of the 7th East African Weed Science Conference, 1979

WATSON, K.A. (1956-8), "Annual reports", Department of Agriculture, Northern Region, 1955-7, Nigeria

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