A contribution to the
International Hydrological Decade

Ecology of water weeds in the neotropics

an ecological survey of the aquatic weeds *Eichhornia crassipedes* and *Salvinia* species, and their natural enemies in the neotropics

by D. S. Mitchell
and P. A. Thomas

Unesco Paris 1972

Technical papers in hydrology 12

In this series:

1 Perennial Ice and Snow Masses. A Guide for Compilation and Assemblage of Data for a World Inventory.
2 Seasonal Snow Cover. A Guide for Measurement, Compilation and Assemblage of Data.
3 Variations of Existing Glaciers. A Guide to International Practices for their Measurement.
4 Antarctic Glaciology in the International Hydrological Decade.
5 Combined Heat, Ice and Water Balances at Selected Glacier Basins. A Guide for Compilation and Assemblage of Data for Glacier Mass Balance Measurements.
6 Textbooks on hydrology - Analyses and Synoptic Tables of Contents of Selected Textbooks.
7 Scientific Framework of World Water Balance.
8 Flood Studies - an International Guide for Collection and Processing of Data.
9 Guide to World Inventory of Sea, Lake, and River Ice.
10 Curricula and Syllabi in Hydrology.
11 Teaching Aids in Hydrology.
12 Ecology of Water Weeds in the Neotropics.

1972 International
Book Year

LC No. 72-87508

Published in 1972 by the United Nations Educational,
Scientific and Cultural Organization,
Place de Fontenoy, 75 Paris-7e
Printed in the Workshops of Unesco

 Printed in France SC. 72/XXI.12/A

Preface

The International Hydrological Decade (IHD) 1965-74 was launched by the General Conference of Unesco at its thirteenth session to promote international co-operation in research and studies and the training of specialists and technicians in scientific hydrology. Its purpose is to enable all countries to make a fuller assessment of their water resources and a more rational use of them as man's demands for water constantly increase in face of developments in population, industry and agriculture. In 1972 National Committees for the Decade had been formed in 107 of Unesco's 127 Member States to carry out national activities and to contribute to regional and international activities within the programme of the Decade. The implementation of the programme is supervised by a Coordinating Council, composed of twenty-one Member States selected by the General Conference of Unesco, which studies proposals for developments of the programme, recommends projects of interest to all or a large number of countries, assists in the development of national and regional projects and co-ordinates international co-operation.

Promotion of collaboration in developing hydrological research techniques, diffusing hydrological data and planning hydrological installations is a major feature of the programme of the IHD which encompasses all aspects of hydrological studies and research. Hydrological investigations are encouraged at the national, regional and international level to strengthen and to improve the use of natural resources from a local and a global perspective. The programme provides a means for countries well advanced in hydrological research to exchange scientific views and for developing countries to benefit from this exchange of information in elaborating research projects and in implementing recent developments in the planning of hydrological installations.

As part of Unesco's contribution to the achievement of the objectives of the IHD, the General Conference authorized the Director-General to collect, exchange and disseminate information concerning research on scientific hydrology and to facilitate contacts between research workers in this field. To this end Unesco has initiated two collections of publications: 'Studies and Reports in Hydrology' and 'Technical Papers in Hydrology'.

The collection 'Technical Papers in Hydrology' is intended to provide a means for the exchange of information on hydrological techniques and for the co-ordination of research and data collection.

The acquisition, transmission and processing of data in a manner permitting the intercomparison of results is a prerequisite to efforts to co-ordinate scientific projects within the framework of the IHD. The exchange of information on data collected throughout the world requires standard instruments, techniques, units of measure and terminology in order that data from all areas will be comparable. Much work has been done already towards international standardization, but much remains to be done even for simple measurements of basic factors such as precipitation, snow cover, soil moisture, streamflow, sediment transport and ground-water phenomena.

It is hoped that the guides on data collection and compilation in specific areas of hydrology to be published in this collection will provide means whereby hydrologists may standardize their records of observations and thus facilitate the study of hydrology on a world-wide basis.

CONTENTS

FOREWORD

The present paper reproduces, with some minor changes, the report of a study tour undertaken by Messrs. D.S. Mitchell and P.A. Thomas, both from the United Kingdom. The countries visited were Argentina, Uruguay, Brazil, Guyana and Trinidad, from February to April 1970.

Eichhornia and Salvinia are native plants in the South American inland waters which were visited during the tour, the aims of which were to collect material for correct identification, and to study the extent of spreads in these waters, the biotic and environmental factors of existence, growth and limitation of these plants, and any existing biological control agents.

The problem of the control or eradication of aquatic nuisance plants has been studied by the Co-ordinating Council of the International Hydrological Decade since its first session, in view of the fact that a better understanding of the relation of plants and hydrology is essential for agriculture, irrigation, fisheries, wild life conservation, public health, recreation, flood control, drainage and inland navigation.

At its third session, the Council invited the International Biological Programme (IBP) to prepare an international programme, in collaboration with the IHD Secretariat. Accordingly, Unesco, advised by the International Biological Programme, set up an ad hoc panel of experts on ecology and control of aquatic vegetation which met in Paris in December 1968.

Taking into account the interest of hydrologists in man-made water bodies designed to reduce water losses through evapotranspiration, the Panel proposed the monitoring of these water bodies, including a study on the biological conditions and on the ecology of water plants. It was in response to this recommendation that Unesco arranged, with the help of the Freshwater Productivity Section of the IBP, for the study tour to be made.

Other activities of the Panel included listing the interferences of aquatic plants in man's use of fresh and brackish waters and non-oceanic water bodies, both advantageous and disadvantageous, as well as listing specific programmes for managing the growth of aquatic weeds according to man's needs. The Panel proposed that countries with a problem of excessive vegetation should analyse the problem, establish objectives and priorities on control and conservation and select appropriate methods of control. The Panel also proposed a manual for the identification of aquatic plants, particularly in tropical areas, and discussed the merits of the various control methods (chemical, biological, mechanical and physical) as well as the possibilities of utilization of controlled aquatic vegetation.

I. INTRODUCTION

Eichhornia crassipes (Water Hyacinth) and Salvinia auriculata (sens. lat.) (Water Fern, Kariba Weed, African Pyle) are notorious for their ability to colonise large areas of water in a short space of time. The explosive growth of these plants has caused difficulties in North America, Africa, Asia and Australasia. In particular they pose potential problems for the management of man-made lakes, canals and irrigation schemes in tropical areas. For example, Salvinia auriculata at one stage colonised 1000 km^2 (20%) of the water surface of Lake Kariba, in Central Africa, while the presence of Eichhornia crassipes in canals and other water bodies in Florida, Alabama, Mississipi and Lousiana (U.S.A.) was estimated to have caused an annual loss of $43,000,000 in 1956 (Holm, Weldon & Blackburn, 1969) and this is unlikely to have decreased.

There are many other examples of situations where these plants cause major problems following their invasion of waters outside their native environment. Within South America however, there are few reports of the utilisation of water bodies being interfered with by these plants. One noteworthy exception is the colonisation by E. crassipes of large areas of the Brokopondo reservoir, Surinam, soon after its formation.

The effects which the presence of these plants may have on water resource utilisation is varied. Penfoun & Earle, 1948; Little, 1967; Mitchell, 1970; Reis, pers comm., have demonstrated that both Salvinia and Eichhornia covering a water surface cause more water to be lost by evapotranspiration than would be lost by evaporation from an open water surface of the same size. In this respect Eichhornia has been shown to have a greater effect than Salvinia. This excess water loss is always likely to occur whenever floating or emergent vegetation is present in a water body. The problem may become more serious when populations of these plants occur where water is scarce, or when the contents of a reservoir are not rapidly replaced.

Permanent weed mats, especially when knit together by secondary colonising plants, can interfere with water transport and pose a hazard to navigation. On Lake Kariba large powerful boats 15m in length and equipped with two marine diesel engines are not able to penetrate into certain marginal areas of the lake because of the presence of such weed mats.

Where water is used for irrigation, the growth of aquatic plants always causes difficulties. Salvinia and Eichhornia pose a continual threat because of their potential for very rapid growth. However, if an irrigation canal is used fairly frequently, the intermittant water current may be sufficient to remove some of the infestation. This effect depends on the frequency of use and the construction and shape of the canal.

Canals and ditches in which there is little flow, as well as small water reservoirs and natural water bodies, may be completely covered by mats of Salvinia or Eichhornia in comparatively short periods of time. If the mats are then invaded by a growth of secondary colonising species, the accumulation of decaying debris from these large quantities of vegetation may lead to the rapid filling in of the water body. Rapid hydrological changes such as floods may prevent this outcome if they occur fairly early in this process, but are likely to have progressively less impact at later stages.

Large mats of floating vegetation can impede fishing operations. This could be significant in an area where economic or subsistence fishing was important. On Lake Kariba, for example, large numbers of the local indigenous population rely on fishing as a means of livelihood. Netting is carried out from small dugout canoes which often cannot penetrate weed mats; in addition the laying and lifting of nets is commonly hampered by the presence of Salvinia.

Considerable use is often made, particularly of man-made reservoirs, for recreational purposes. These activities, which are usually concentrated on the marginal areas of water bodies, may be restricted by the growth of aquatic weeds.

The types of interference listed above clearly indicate the need for an understanding of the factors which, in their native environment, maintain populations of these plants at such a level where they are rarely considered to constitute an economic nuisance. Several features of the environment could contribute to this. Hydrological factors, such as river flooding, fluctuations in water levels and water quality, could obviously limit populations of floating plants. Population growth would also be controlled by interspecific plant competition, the effects of natural enemies and other biotic factors. There were also strong indications that, in the case of Salvinia, the species causing problems in Africa and Asia did not occur, or was rare in South America, although it clearly originated from there. This survey was therefore undertaken to study the operation of these and any other factors on the limitation of aquatic weed populations in the neotropics, and to make comparisons between these situations and other tropical areas where these plants have been introduced. It was considered that this could increase our understanding of the phenomenon of explosive growth of which these plants were capable, and, perhaps also establish factors which could be used in control measures directed against them.

II. THE TAXONOMY AND DISTRIBUTION OF *SALVINIA* SPECIES IN THE NEOTROPICS

Recent studies have indicated that the plants being identified as *Salvinia auriculata* probably belong to a complex of related taxa. In view of the importance of the group, it is necessary that the different taxa be defined and their potential as aquatic weeds elucidated. It now appears that there are seven species of *Salvinia* in the neotropics:

- *S. oblongifolia* Martius
- *S. sprucei* Kuhn
- *S. minima* Bak. (*S. rotundifolia* Willd. sensu Herzog, 1935; de la Sota, 1963)
- *S. auriculata* Aubl.
- *S. herzogii* de la Sota
- *S. biloba* Raddi
- *S.* sp. nov. (weed in Kariba and Ceylon).

Herzog (1935) did not differentiate between the last four species but combined them in one taxon, *S. auriculata*. This was separated from the other species on the character of the hairs on the leaf papillae, which were joined at their distal end. The aggressive weed found on Lake Kariba and in Ceylon was identified as *S. auriculata* on this basis. In 1962, de la Sota described plants in Argentina, which had been named *S. auriculata*, as a new species, *S. herzogii*. Later, comparison of Trinidad and Kariba specimens of *S. auriculata* showed that these were also clearly different (Mitchell, 1970).

Investigations in South America were concentrated on plants in the *S. auriculata* complex and no serious attempt was made to collect material or make detailed examinations of other species. Consequently full descriptions will only be given of species belonging to this complex. de la Sota (1962, 1963, 1964) gives very detailed descriptions of the other species.

RESULTS

All members of the *Salvinia auriculata* complex are very similar in their vegetative morphology and, in all, the shape of the leaves is very variable so that it is impossible to distinguish between them on this character. Because of the uniformity in vegetative morphology, it is only necessary to describe this once and the general description given by Mitchell (1970) for the plants in Lake Kariba will suffice for all members of the complex.

"The stem of the plant is horizontal to, and just below, the surface of the water. Pairs of floating leaves arise at intervals along the stem and have been shown by Loyal & Grewal (1967) to be slightly alternate in origin. A third organ which is submerged in the water also arises at each node. This is rootlike in appearance and has been considered to be a 'wasserblatt' or wurzelblatt' (Herzog, 1934), a 'rootlike water leaf' (Arber, 1920) or 'un système d'axes' (Bonnett, 1955). When present, the reproductive structures, the sporocarps, are borne by the submerged organ. Aside from the upper leaf surface, the whole body of the plant bears wettable, uniseriate, multicellular hairs. The upper surfaces of the leaves bear rows of non-wettable multicellular papillae, on the tips of which are four fine uniseriate hairs which unite distally to form a 'birdcage-like' arrangement (the diagnostic character used by Herzog (1935) to distinguish S. auriculata from other species in the genus).

Generally, three forms of the plant may be distinguished in Lake Kariba and apparently in most other field situations. In the absence of competition for space and sometimes in poor light conditions or in rich nutrient conditions, Salvinia will produce small leaves up to 1.5cm in width that float flat on the water surface. Internodes are relatively long and the leaf area/dry weight ratio is often high. This form is often designated as a 'primary' form. The second type, 'secondary', also produced in favourable growth conditions and open water, generally on the edge of permanent mats, has leaves that are more than 2cm across. These become more or less deeply keeled and assume a boat shaped form with a rounded apex. The whole of the undersurface of the leaf is in contact with the water. In this type also the internodes are usually long in relation to the size of the plant. The third form of the plant, 'tertiary', developes when the plants become compressed together into a 'mat'. The floating leaves are usually large (up to 6cm in width), vary in shape from oblong to auriculate and are conduplicately folded along the midrib, so that most of the under side of the leaf is not in contact with the water. The internodes are relatively short and the leaves overlap one another".

The four species within the complex differ from one another mainly in the branching system and conformation of the sporocarps, and to a lesser extent in the morphology of the submerged organ. The distribution and distinguishing characteristics for each species are given below.

1. Salvinia auriculata Aubl. (Figure 1).

This species is widely distributed in tropical America. On this visit it was collected from Northern Argentina, Brazil, Guyana and Trinidad. The type specimen was collected from French Guyana (Aublet, 1775).

The main axis of the submerged organ divides into two or three, slightly reflexed, main branches immediately it emerges from the rhizome.

Each of these then gives rise to a number of secondary axes that are densely covered with uniseriate multicellular trichomes. The top of the submerged organ thus appears to be sessile and curved (see Figure 1a). There are usually two fertile axes on each submerged organ and these originate near the centre of the curved main axis. Each fertile axis has a scorpioid, cymose, branching system and bears a number of sporocarps up to a maximum of about 12, though three or four is the usual number. Each of these sporocarps is pedunculate and the length of the peduncle between the sporocarp and the origin of the preceding branch decreases with the production of the sporocarps, so that the longest peduncles are on the older sporocarps and the shorter on the youngest. As a consequence, all the sporocarps hang at about the same level below the plant. The first, and usually the second, of the sporocarps produced are smaller, more densely covered with trichomes and bear megasporangia. The rest are densely packed with smaller microsporangia. Both types of sporangia appear to contain fertile spores. The sporocarps are generally globose and not markedly apiculate.

Aublet's type for this species cannot be found and it is possible that it does not exist. However his illustration of the fertile axis (Aublet, 1775) is most like that of this taxon. Furthermore this is apparently the only species of Salvinia which occurs in the area of the type locality.

A particular form of this species, which could possibly be shown to be a distinct taxon, occurs in Northern Argentina and Uruguay. Specimens were collected from the Garupa River in Misiones Province, Argentina, and herbarium specimens from Uruguay were seen in Rio de Janeiro and Zürich. This form of the species is incompletely collected but may be distinguished by the production of long stalk-like main axes on the submerged organs in certain conditions. The older parts of the specimens from the Garupa River exhibited this character but the younger parts were typical of Salvinia auriculata (sens. strict.). The reason for this peculiar submerged organ is not known, but it may be postulated that it occurred in response to particular environmental conditions. However, the plants collected were not part of a permanent colony, but appeared to have been swept down the river and lodged in the marginal vegetation.

Living specimens of S. auriculata collected from Trinidad during the visit have been examined cytogenetically in Zürich by Schneller (Cook pers. comm.) and shown to have a chromosome number of 2n = 48.

2. Salvinia herzogii de la Sota (Figure 2).

S. herzogii is confined to Argentina and probably to the southern part of Brazil. The type locality is Gaudalupe lagoon, Santa Fé. In the northern part of its range its distribution overlaps with that of S. auriculata. Both species were collected between Corrientes and Resistencia in Northern Argentina. In the Middle Paraná Region around Santa Fé, S. herzogii appears to be the only member of the complex present.

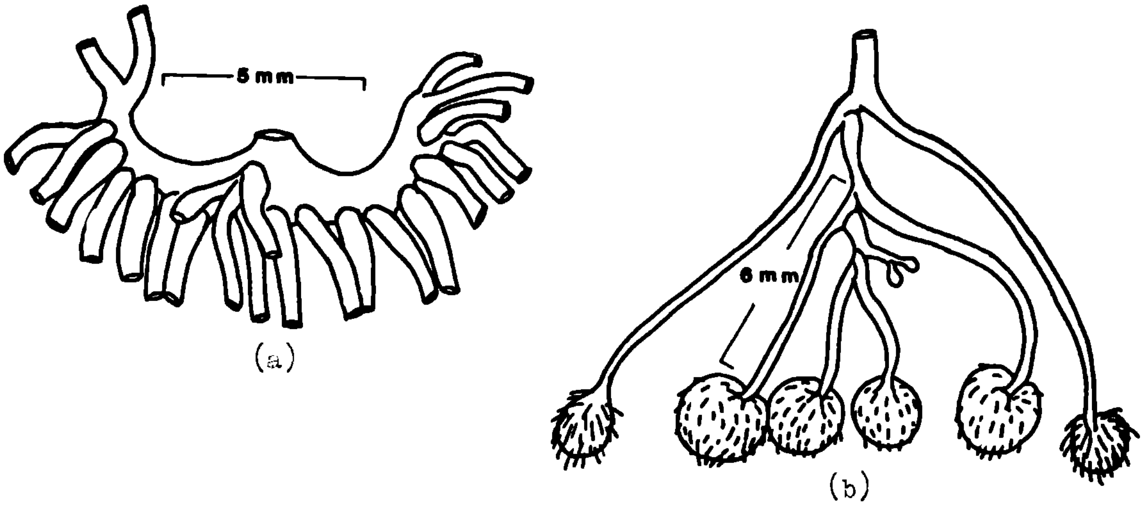


Figure 1. Salvinia auriculata Aubl. (a) lateral view of the top of the submerged organ; (b) lateral view of the fertile axis.

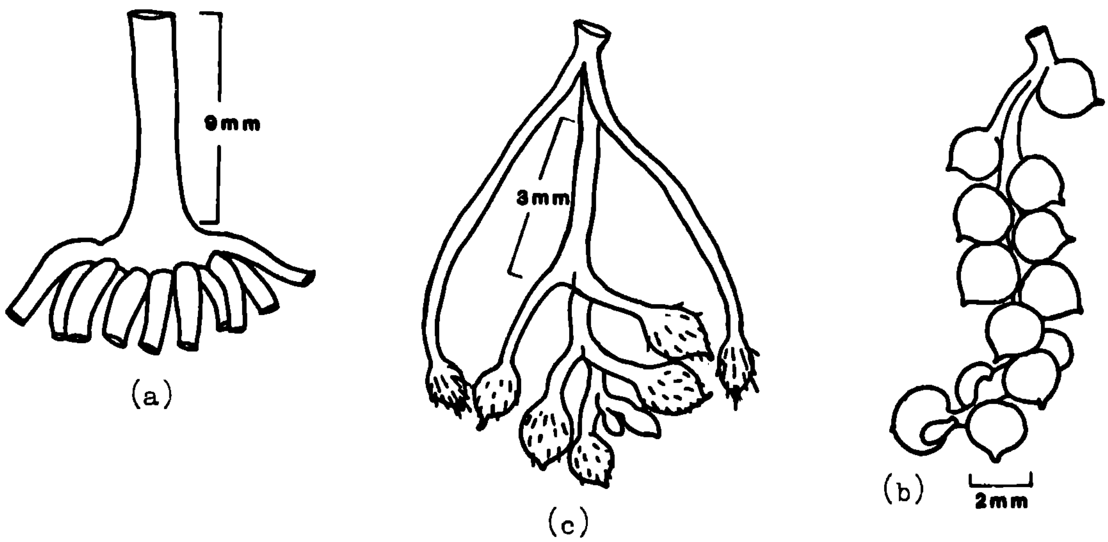


Figure 2. Salvinia herzogii de la Sota. (a) lateral view of the top of the submerged organ; (b) lateral view of the compact, reflexed form of the fertile axis; (c) lateral view of the lax form of fertile axis.

The submerged organ in S. herzogii has a well developed main axis which divides into secondary axes after about 2-5mm, though occasionally lengths of 14mm may be attained before the formation of secondary axes (see Fig.2a). The branching of the fertile axis is also scorpioid cymose, but its form is variable. At the one extreme it is very compact, slightly reflexed and markedly dorsiventral (Fig.2b), and at the other, it is lax with only little indication of dorsiventrality (Fig.2c). In both types the sporocarps are ovoid and apiculate with marked apical papillae. As in S. auriculata, the first two sporocarps are female, smaller, more densely covered with trichomes and have the longest peduncles. Fifty plants from three localities, in which there were representatives of each type, were examined and compared. It was found that there was a strong correlation between the form of the floating leaf and the form of the fertile axis. Plants, which were not compacted into mats at the time of the formation of the sporocarps, may be identified by the form of the leaf at the node concerned. These plants tended to produce the lax type of fertile axis with a small number of sporocarps, in which a high proportion of the sporangia appeared to be sterile. In contrast, the nodes with mat-form leaves had compact sporocarp chains, in which most sporangia contained spores. A number of transitory types were also observed in which both leaf form and fertile axis was intermediate between the two extremes. Thus it appears that the physiological factors which control leaf variability also affect the morphology of the fertile axis. Experiments with these plants in different conditions in culture solution would be useful in identifying these controlling factors, and in delimiting the extent of variation they bring about.

3. Salvinia biloba Raddi (Figure 3).

This species has a limited distribution and so far is only known from the vicinity of Rio de Janeiro, though it is possible that it might occur further south and de la Sota (pers. comm.) has examined a herbarium specimen collected in Santa Catarina Province, Brazil, which may belong to this taxon. On this visit, a population of these plants was found in Cabo Frio, 140km north east of Rio de Janeiro, but more populations need to be collected before the distribution of this species can be thoroughly known.

The type specimen of this species collected from Rio de Janeiro has been examined by de la Sota, who kindly allowed me access to his notes. Of three plants in the specimen, only one is fertile. On this plant the fertile axis is poorly developed, but shows the characters found in the specimens collected from Cabo Frio. Two further herbarium specimens were examined in the Rio de Janeiro Jardim Botanico. In all these, the fertile axis has a scorpioid cymose branching system without marked dorsiventrality (see Fig.3). The sporocarps are globose, not markedly apiculate, 2-3mm in diameter and contain a very high proportion of fertile sporangia. One of the most distinctive features was the length of the peduncle which is normally about 3mm but may reach 10mm in length.

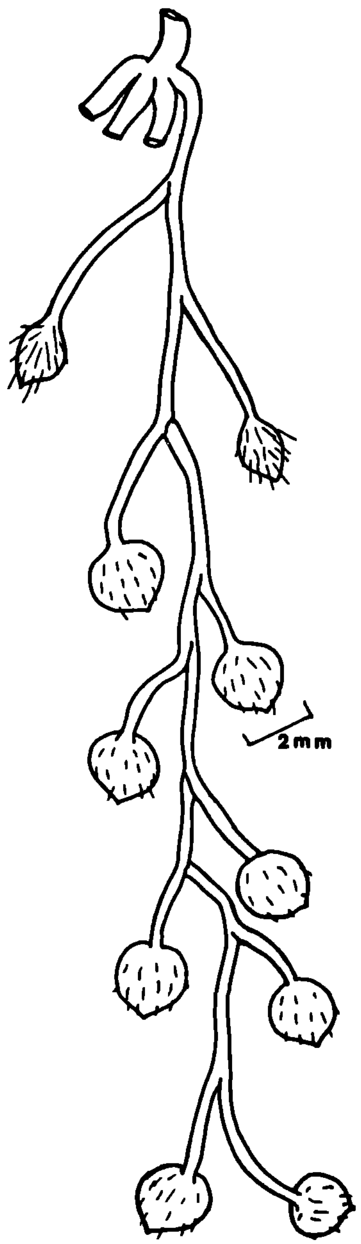
In all specimens the submerged organ has a well developed main axis which divides into secondary axes after 3-5mm.

4. *Salvinia sp.* nov. (Figure 4).

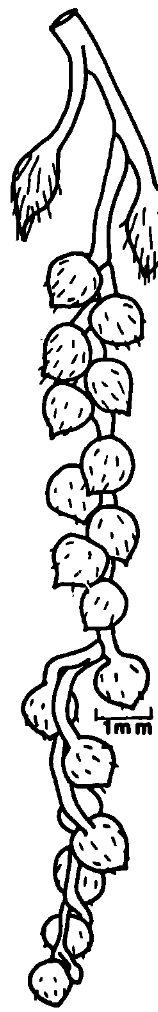
This species grows as an aggressive weed in Lake Kariba and Botswana. Specimens from Ceylon, which have been examined in the British Museum, clearly belong to the same taxon and the species probably has a wide distribution outside the neotropics. It is also probable that, identified as *S. auriculata*, it has been the subject of several previous studies, for example by Kopp (1936) and Bonnett (1955), (see also de la Sota). Only one specimen of this species was observed in South America. This was a pressed specimen in the herbarium of the Rio de Janeiro Jardim Botanico that had been collected in 1941 from the Botanic Garden (Kuhlman 06124). Kuhlman collected specimens of *S. biloba* and *S. auriculata* from the Garden at the same time and this raises the possibility that this aggressive weed species is a hybrid of horticultural origin. However, though the plant is robust (? hybrid vigour) and sterile, there is little indication of intermediate characters between *S. biloba* and *S. auriculata*, though in some respects the plant is intermediate between *S. biloba* and *S. herzogii.* Cytotaxonomic and chemotaxonomic studies of members of the genus may provide evidence which could support, or refute, this theory of hybrid origin for this species. In the meanwhile, consideration must be given to the possibility that this species may not occur naturally in S. America, though it is clearly of S. American origin.

In this species the submerged organ is similar to that of the preceding two species and has a well developed main axis which divides into many secondary axes after 5-8mms. The fertile axis bears a large number of sporocarps (up to 35) in a dorsiventral scorpioid cymose system (see Fig. 4). The sporocarps are small (less than 1mm in diameter), ovoid, apiculate, more or less sessile and contain a high proportion of empty sporangia. The first two sporocarps are more densely covered with trichomes, more or less penduncculate and contain megasporangia.

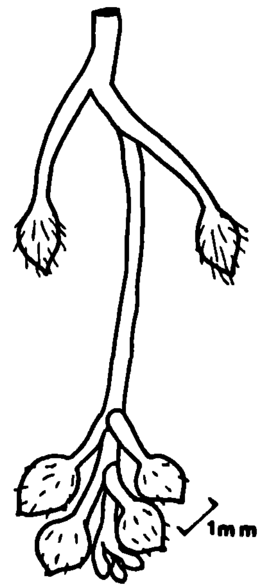
Specimens of this species from Lake Kariba and India (identified as *S. auriculata*) have been the subject of a cytogenetical study by Loyal & Grewal (1966). They have shown that a high proportion of the sporangia abort at the archesporial stage and, when meiosis does take place, the process is highly anomalous. They cite the number of chromosomes to be 45 and suggest that this species is a pentaploid. Competition experiments under greenhouse conditions have shown that this species is considerably more aggressive than *S. auriculata*. It is proposed to describe this taxon as a new species.



3.



4 (a).



4 (b).

Figure 3. *Salvinia biloba* Raddi. Lateral view of the fertile axis.

Figure 4. *Salvinia* sp. (a) and (b), lateral views of fertile axes.

KEY TO SPECIES OF *SALVINIA* IN SOUTH AMERICA

1. Four hairs on the tips of each leaf papilla joined at the distal end .... 2 (*S. auriculata* complex)

1. Hairs on tips of leaf papillae free 5

2. Main axis of submerged organ apparently curved and sessile, sporocarps usually few, globose, not markedly apiculate, pedunculate and in a sparsely branched scorpioid cymose branching system. Sporocarps with high proportion of fertile sporangia .... *S. auriculata* (1)

2. Main axis of submerged organ, stalk-like not curved, sporocarps apiculate and generally in a many branched scorpioid cyme 3

3. Sporocarps mostly subsessile with mainly fertile sporangia in a compact reflexed chain (mat form plants) or sporocarps few with mainly sterile sporangia, pedunculate in a sparsely branched scorpioid cyme (open water plants) .... *S. herzogii* (2)

3. Sporocarps in a long many branched chain 4

4. Sporocarps pedunculate, 2-3mm in diameter, and with fertile sporangia .... *S. biloba* (3)

4. Sporocarps less than 1mm in diameter. Female sporocarps briefly pedunculate, male sporocarps subsessile to sessile. Sporangia mostly empty .... *S. sp.* nov. (4)

5. Papillae on upper surface of the leaf confined to the margin.................................... *S. sprucei* (5)

5. Papillae over whole leaf surface 6

6. Leaves deeply carinate, main axis of submerged organ branched .... *S. oblongifolia*(6)

6. Leaves not deeply carinate, main axis of submerged organ unbranched .... *S. minima* (7)

CONCLUSIONS

The *S. auriculata* complex can thus be seen to consist of four taxa. However, the exact status of the form of *S. auriculata* from Northern Argentina and Uruguay is not clear and may constitute a fifth taxon. Furthermore the distribution of the species requires further amplification and the relationships between them is also obscure. More work is required on all these aspects. Nevertheless, because of the economic importance of the *Salvinia* species, which grows as an aggressive weed outside the neotropics, it is considered that the above information should be made available and this species described.

III. NOTES ON THE ECOLOGY OF SALVINIA SPECIES AND EICHHORNIA CRASSIPES IN SOUTH AMERICA

Examples of adventive growths of *E. crassipes* and *S. auriculata* (sens. lat.) are given by Sculthorpe (1967), Little (1966) and Mitchell (1968, 1969, 1970). The ecology of both species has been studied outside the neotropics. That of *E. crassipes* was described by Penfound & Earle (1948), Hitchcock, Zimmermen, Kirkpatrick & Earle (1949) and Gay (1960a, 1960b), while that of *Salvinia auriculata* (sens. lat.) was investigated by Mitchell (1968, 1970). However, very few ecological studies have been made of these plants in their native environment, though the explosive growth of *E. crassipes* on the Brokopondo Reservoir in Surinam has been described by van Donselaar (1968) and methods of measuring its productivity suggested by del Viso, Tur & Mantovani (1968). A major objective of this visit to South America was to attempt to fill part of this gap in our knowledge, though it was appreciated that a short visit would be insufficient for a proper study. Nevertheless, a survey of conditions in which the plants were growing and discussions with local scientists could bring together information and initiate co-ordinated programmes of ecological research which would then provide the necessary long term data.

METHODS OF STUDY

Because of the short length of time in each locality (with the exception of Santa Fé), many methods of ecological assessment were not possible and indeed even inappropriate. In most cases detailed observations were made on the composition of the aquatic flora, the size of the populations and the nature of the habitat. Discussions were held with local experts in botanical, entomological and hydrological fields, and literature was examined for environmental details. In Santa Fé it was possible to attempt some brief quantitative surveys. The results derived from all these approaches are described in the following paragraphs.

TYPES OF HABITATS

Aquatic plants were found growing successfully in every type of aquatic habitat encountered, except for densely shaded forest streams and swiftly running, steep banked rivers. However, *Salvinia* and *Eichhornia* were not present in every water body and, on a number of occasions, apparently ideal habitats were found to contain macrophyte floras of varying richness from which either *Salvinia*, or *Eichhornia crassipes*, or both, were absent. The habitats in which these species appeared to grow most successfully were calm ponds or sheltered backwaters where the water was not liable to much disturbance from wind or water currents.

THE COMPOSITION OF THE AQUATIC MACROPHYTE FLORA

Aquatic macrophyte plants may be free floating, such as *Salvinia* and *E. crassipes*, or attached to the substratum. In the latter case they may be completely, or partially, submerged. Examples of the former are *Cabomba* and *Potamogeton*. Partially submerged plants can vary from those with floating leaves, such as *Nymphaea*, to those with only rooting systems normally submerged, such as *Phragmites*. In certain circumstances the last type can become rooted in the substratum formed by a floating mat of plants. Tur (1965) described an intimate association of this type between the floating plant *Salvinia herzogii*, and the emergent macrophyte *Scirpus cubensis* var *paraguayensis*. In Lake Kariba a number of species have been recorded to grow on *Salvinia* mats and form floating islands (Boughey, 1963; Mitchell, 1969, 1970). Only those plants were noted that were considered to come into direct, substantial competition with *Salvinia* or *Eichhornia crassipes*.

Common free floating plants are:

Salvinia herzogii (Argentina)
S. auriculata (Brazil, Guyana, Trinidad)
S. minima
Eichhornia crassipes
Azolla spp.
Lemna spp.
Pistia stratiotes
Hydromistria stolonifera.

Important attached species with floating leaves are:

Nymphaea spp.
Nymphoides spp.
Victoria spp.

In shallow standing waters emergent species offer very considerable competition. Among the most common constituents of this life form are:

Ludwigia spp.
Thallia spp.
Panicum spp.
Echinocloea spp.
Paspalum spp.
Typha spp.
Cyperus spp.
Sagittaria spp.
Canna spp.
Eichhornia azurea
Pontederia spp.

Hydrocleys sp.
Reussia rotundifolia
Nelumbo sp.
Limnocharis sp.

Some of these species will also grow on the substratum provided by a weed mat, but *Scirpus cubensis* seems to be unusual in being limited to this habitat.

GROWTH RATE

Salvinia growing on Lake Kariba has been observed to increase in dry weight at a relative growth rate of 6.83% per day. The similar value for leaf number increase was 7.86% per day. This means the number of leaves was doubled every 12-13 days (Mitchell, 1970). It is possible that other members of the *S. auriculata* complex do not grow as rapidly as this, but no figures are available.

There are a number of estimations for the growth of *Eichhornia crassipes*. Penfound and Earle (1948) found that the rate of doubling in Louisiana, U.S.A., varied from 11 to 18 days during the growing season. Bock (1969) observed growth rates as increment in wet weight, averaging 5.7% per day and 3.7% per day during the summer growing season in temperate areas of California, U.S.A. Bock also quotes figures estimated by other authors for the growth of this species in various parts of the world. These vary from 12.5% per day in the Sudan to 4.8% in Florida. In Argentina, the productivity of *E. crassipes* has been investigated by del Viso, Tur & Mantovani (1968). They show that the annual growth cycle of this plant may be represented by a sigmoid curve, though the final biomass achieved depends on a number of variables. Productivity measurements have also been made by Alvim and Reitz (pers. comm.) near Itabuna, Bahia, Brazil. These were made on plants growing in culture containers designed to measure evapotranspiration and the results have not yet been published.

GROWTH FORM

The different growth forms produced by *Salvinia* are described on page 14. *Eichhornia crassipes* also exhibits a range of growth forms apparently in response to the same environmental conditions. When the plant is growing in crowded conditions in a mat, the leaves are tall and more or less erect with floatless petioles. In less crowded, open conditions, the leaves have a wide angle of insertion into the stem, are reclining rather than erect and have petioles with large floats of lacunate tissue. Our observations in South America appear to indicate that flowering is more frequent in this form. This was especially noticeable in Itabuna where a loose, mobile, mat had built up in a reservoir after plants had been mechanically cleared from it. All of these plants were in this form and most were in flower.

The size of the leaves is dependant on light conditions and on oxygenation and depth of the water (Sculthorpe, 1967).

REQUIREMENTS FOR THE FORMATION OF PERMANENT MATS

Factors which promote the formation of permanent Salvinia mats appear to be the same in the plant's native environment and in situations where it is a troublesome invading species. This important aspect of the ecology of the plant in the Middle Parana Region in Argentina was discussed with Tur and confirmatory observations were made in this area and in other parts of South America.

Generally speaking, Eichhornia and Salvinia require good light conditions. These are present in most tropical water bodies, the only exceptions being deeply shaded forest pools and streams. For these tropical plants, the optimum temperature for growth is fairly high (between 25°C and 30°C). Again, these temperatures are commonly manifested in tropical areas. The size of a population of these plants will ultimately depend on the availability of nutrients. There is evidence that they are tolerant of very dilute waters but are able to utilise nutrients for growth as they become available. If considerable quantities of nutrients, especially nitrogen, are supplied, growth can be very rapid and dense mats are soon formed.

An essential factor for the formation of permanent mats appears to be the presence of calm, still conditions. This is important for the development of many aquatic macrophyte communities, but is especially so for floating species such as Salvinia and E. crassipes. These are not fixed in position and are thus liable to wave damage in lentic environments, or to being swept away by river currents in lotic environments. This can be illustrated by the situation before and after the construction of Lake Kariba. Salvinia was present in the Middle Zambezi Valley before the construction of the Kariba Dam but did not form large colonies because of the continual effect of the river current. However, the formation of Lake Kariba created calm conditions, which were suitable for Salvinia, and the rapid explosive growth of the plant brought about the formation of large stable mats. Subsequent rises in lake level resulted in a larger lake surface area and greater wave action, so that the large mats hitherto common on the open water were eliminated. In the Middle Paraná River, there is no doubt that the river floods are annually responsible for the elimination of considerable quantities of Salvinia and the formation of large mats of a stable nature only occurs in sheltered calm water bodies at a time when these do not form part of the main river flow.

Another important factor is some form of "anchorage" to which a plant, or more frequently a group of plants, can become attached. This enables the plants to multiply in one place, so that crowded conditions develop and the plants become interlocked into a stable mat. In Lake Kariba, this "anchorage" is often provided by "woodlands" of partially submerged trees, which have been killed by their immersion in the waters of the new lake. In the Middle Paraná region a similar role is played by attached, emergent macrophytes.

When stable mats have developed, they form a suitable substratum for the growth of emergent aquatic macrophytes. Many of these are stoloniferous (e.g. Scirpus cubensis) and thus further serve to bind the plants into unwieldy masses of floating vegetation, so that the stability is enhanced.

The same factors undoubtedly contribute to the formation of stable communities of E. crassipes. This was clearly shown by differing conditions in the water bodies between Resistencia and Corrientes in Argentina. The Paraná River here was wide and swiftly flowing with steep banks and no floating plant vegetation was seen on it. On either side of the road between the Corrientes Ferry and Resistencia there were a number of deep, water filled depressions. These were mostly isolated, still ponds in which there was no water current. A contrast was provided by the Rio Tragedero which was crossed by the road about half way between the two cities. This river was small and appeared to have a relatively slow current at the time. The isolated water bodies were filled with aquatic vegetation, including some very extensive almost pure stands of Eichhornia crassipes. In contrast the Rio Tragedero contained only a few isolated patches of plants which had been retained against the river bank in some places by attached vegetation and riparian bushes.

REPRODUCTION

Vegetative reproduction is the most important method of multiplication of Salvinia and E. crassipes and their considerable efficiency in this regard is an important contributory factor to their ability for explosive population growth, and the consequent weed problems they cause. Sexual reproduction is far less important and also probably relatively uncommon. For example, E. crassipes reproduces by only vegetative means in California (Bock, 1969), and it has been reported that seeds are not set in north east Asia and Ceylon (Sculthorpe, 1967). The relative importance of vegetative and sexual reproduction in the spread of this species has been reviewed by Sculthorpe (1967), who concludes that propagation by seeds may be important in the right conditions (high enough temperature, light, shallow water) and could reinfest areas which had been cleared of the weed. In the Middle Paraná region, sexual reproduction appears to be unimportant in the spread and establishment of populations of E. crassipes (Tur pers.comm.).

Seedlings or young plants of this species were not observed in any of the localities visited in South America, even though the conditions described as being necessary for their development were frequently present. Whenever possible, ovaries were collected from flowering plants. Fully mature fruits or seeds were not found but all of the ovaries examined contained ovules.

The Salvinia species in Lake Kariba and India has been investigated by Loyal & Grewal (1966) who have shown that this taxon is a pentaploid incapable of sexual reproduction (see also Mitchell, 1970). This is not true for the other species in the S. auriculata complex, all of which appear to set normal spores, though the reproduction of this genus of ferns is complicated by its heterospory.

All the Salvinia plants collected in South America which were bearing sporocarps were found to produce normal spores. This contrasts very strongly with the plants from Lake Kariba, the sporocarps of which contain very few spores and most of these are mis-shapen, abnormal and almost certainly infertile.

Vegetative rates of growth for both species are given on page 24.

DISPERSAL

In the apparent absence of a high reproductive capacity through seeds and spores, these plants are mainly dispersed by vegetative propagules. Both wind and water current are responsible for distributing the plants within a water body, or system of connecting water bodies. Dispersal from one water body to another is carried out by animals. Birds probably transport small portions of plants and spores and seeds (Holm Weldon & Blackburn, 1969). However, man is probably the most effective agent for extending the plants' distribution through the tropics of the world.

HYDROLOGICAL EFFECTS ON PLANT POPULATIONS

South America is characterised by its large river systems. The Amazon carries the greatest volume of water of any river in the world and drains a catchment of 7,077,200km^2. The River Plate Basin which includes the Paraná, Paraguay and Uruguay Rivers, is also large with a drainage basin of 3,200,000km^2. These rivers are characterised by seasonal variations in level and river flow. At Santa Fé, about 400km above Buenos Aires, the maximum range between highest and lowest levels is nearly 9m while at the annual flood the water level rises 2.5 to 3.0m (Bonetto, Dioni & Pignalberi, 1969). The Amazon River system is subject to similar changes in water level and, even at the mouth of the river, the flood can produce a rise in level of 4m. Clearly these fluctuations in level bring about considerable flooding of the surrounding countryside. At Santa Fé in the

Middle Paraná the whole valley (30-35km wide) is flooded by exceptional floods (Bonetto, Dioni & Pignalberi, 1969).

The hydrological changes have considerable effects on the aquatic macrophyte vegetation in these systems. One obvious effect is to disperse the floating plants throughout the system. Another important effect is the flooding of the ponds and oxbow lakes which are isolated from the main river during most of the year. This has several consequences. Firstly, the enlargement of the surface area of a water body and the rise in water level serves to loosen stable mats of floating vegetation. These break-up into isolated plants which are more readily moved by wind and current. Secondly, the flooding often results in the direct connection of a pond with the main stream of the river so that water currents flow through the water body and sweep away unattached and unanchored plants. Thirdly, the change in water level and the different shape of the flooded pond may make it more exposed to winds which move the plants out of hitherto sheltered areas. If these plants are blown into the shallows, large quantities may be left stranded when the water level drops again.

The hydrological factors of the environment are dependant on the annual flooding of the rivers and any man-made interference with these are likely to alter their effects on the plant populations. The most usual method of controlling river floods is the construction of a dam across a river and the creation of a man-made lake in the flooded river valley behind the dam wall. As in the case of the Kariba Dam, this eliminates the flushing effect of the river floods and creates calm conditions in which explosive growths of aquatic macrophytes can occur. It is important to note that in most cases the water level of the man-made lake is subject to considerable fluctuation. This means that aquatic plants dependant upon attachment to the substratum are periodically subjected to too little, or too much, submergence. However, this limitation does not apply to floating species such as Salvinia and Eichhornia crassipes. The growth of Salvinia on Lake Kariba (Mitchell, 1968, 1969, 1970), of E. crassipes on the Brokopondo Reservoir, Surinam (van Donselaar, 1968), Lake Apanas, Nicaragua, and Lake Rio Lempa, El Salvador (Little, 1966) and of Pistia stratiotes on the Volta lake (Ewer, 1966; Holm, Weldon & Blackburn, 1969) are clear examples of this danger. Furthermore, these explosive growths can take place in the plants' native environments and are not limited to localities where they are invading species, though in these latter circumstances the situation is often aggravated. However, as the man-made lake matures, various factors may begin to exercise a controlling influence on the weed populations. Wave action often has an adverse effect and limits the plant to certain areas. Flooding in the tributary rivers could annualy damage large quantities of plants, as it does in Lake Kariba. Fluctuations in Lake level in shallow areas may cause high proportions of the weed population in those areas to be stranded. The break-down of partially submerged woody vegetation that may have been present initially can decrease the extent of anchorage for weed mats. The initial nutrient rich status of the water can decrease and thus support a smaller standing crop of weed plants. Finally, the morphology of the final lake basin may provide a considerable extent of inhospitable shoreline. It appears that steep shores are generally free of weed growth and, in this connection, it should be noted that the eroding effect of wave action may increase the proportion of steep shores.

Unfortunately our itinerary only allowed us to visit one major man-made lake in South America, the Reservoir Rio do Rio Grande outside São Paulo, Brazil. This had a very dendritic shoreline and generally steep banks. Salvinia was not observed though it is known to occur, but both Pistia stratiotes and E. crassipes were occasionally seen forming stable populations in sheltered inlets. We were informed that none of these plants had given evidence of becoming serious weed problems in this Reservoir. It would appear that the reasons for this are the lack of anchorage and the generally steep banks.

Industrial and agricultural development often depend on the construction of dams for hydro-electricity, irrigation and to provide water for domestic consumption. It is certain that the development of the countries of South America will include schemes of this sort. Thus it is necessary to state the importance of pre-impoundment and post-impoundment studies of these dams as they will undoubtedly interfere with the main factors at present controlling the extent of aquatic plants. These studies should include investigations of the flora, hydrology, physico-chemical limnology and morphology of the projected man-made lake, and should involve consultation between research workers and designers of the project, as well as attempt to predict the occurrence and possible course of weed growths in the proposed reservoir.

EFFECTS OF THE DISSOLVED CHEMICAL CONTENT OF THE WATER

The determination of the effects of dissolved chemicals in the water on the growth of Salvinia and E. crassipes is difficult and nearly impossible during short visits. However, it is clear that the chemical content of the water can have an effect. This was particularly evident in the contrast between the flora of the Amazon and Rio Negro. The former is characterised by the considerable growth of many aquatic plants, E. crassipes being prominent among the floating component. By contrast, very few large populations were seen in the Rio Negro water that had not been diluted by water from the Amazon and one population of E. crassipes in a lagoon off the Rio Negro exhibited symptoms of possible nutrient deficiencies. Further evidence of an effect was the poor growth of S. herzogii in certain river water in experimental tanks at Santa Fé (Tur, pers. comm.). A recent repeat of this experiment had the same result.

Experimental work with Salvinia sp. at Kariba has shown that this species is sensitive to low nitrogen values in the water. This may be important as it is possible that the supply of nitrogen may be limited in certain tropical areas (Brinckman, pers. comm.; Mitchell, 1970).

Definite detailed information on this aspect of the ecology of these plants will only be provided by further experimental work both in the field and in laboratory culture conditions.

THE EFFECTS OF BIOTIC FACTORS IN THE ENVIRONMENT

Excluding man's multitudinal effects on the environment, biotic factors are principally of three types: competition between plants in the community, disease, and the grazing of animals. The effect of insects feeding on Salvinia and E. crassipes was investigated by Thomas and is described later in this report. Cattle were observed to feed on E. crassipes on a number of occasions. In one instance, the growth of Pistia stratiotes was being favoured in one half of a pond, in which cattle that had waded into the pond to feed were observed to be selectively grazing E. crassipes. This pond, which was near Resistencia in Argentina, was bisected by a fence and the plant population on the ungrazed side was dominated by E. crassipes in contrast to that of the grazed side in which Pistia was more common.

The incidence of disease of Salvinia and Eichhornia, aside from that clearly initiated by insect damage, was apparently low.

The effect of interspecific competition among components of the aquatic macrophyte flora in South America was more difficult to assess. Communities were usually mixed but occasionally consisted of a mosaic of pure stands of different species. However, the consequence of competition between species is a change in the composition of the community, and it was clearly impossible to record this during visits of short duration.

Most descriptions of situations in which Salvinia and Eichhornia are providing weed problems are characterised by the dominance of the flora by the troublesome species. In Lake Kariba the species composition of the floating macrophyte flora is very poor. Only two species are widely encountered; namely Salvinia sp. and Pistia stratiotes and of these the former is by far the most common, usually forming pure stands. This situation is in very clear contrast with that in South America where the macrophyte flora is made up of a large number of species and pure stands of any one species are rare. Nevertheless, frequently the plant population tends to be dominated by one species. This was measured by randomly placed quarter square metre quadrats in which the composition of the plant population was ranked in terms of the estimated contribution of each species, or group of species, to the total biomass. Thus, plants ranked one made the greatest contribution, plants ranked two the second greatest, and so on. The exercise was carried out at two localities near Santa Fé and the following six components of the vegetation were assessed: S. herzogii, S. minima, Azolla caroliniana, E. crassipes, attached plants rooted in the floating vegetation ("sudd"), and attached vegetation rooted in the bottom. When a certain component was absent it was assessed at the lowest level. Fifty quadrats were placed in a stable mat and fifty in a mobile mat in "madregon" Don Filipe. The same number were placed in a pond adjacent to Los Espejos lagoon.

TABLE I.

Averages of biomass rankings on 50 randomly placed quarter square metre quadrats in three localities near Santa Fé, Argentina.

	DON FILIPE stable mat	DON FILIPE mobile mat	LOS ESPEJOS
S. herzogii	1.1	1.0	2.7
S. minima	3.9	2.1	4.2
A. caroliniana	3.5	3.4	4.5
E. crassipes	5.0	5.2	1.3
"sudd"	2.0	3.7	3.4
"attached"	5.0	4.8	4.8

The results, which can be seen in Table I, show that, not withstanding the greater complexity of the flora, there is still a tendency for a population to be dominated by one species. The reason for this domination is difficult to assess. The same species is not always dominant in the same habitat. It is probable that environmental changes may favour one species rather than another. It is also probable that the number of individuals of a species, which remain in a pond when it is reconstituted following flooding, may determine the rate at which it colonises the area once more and therefore the final extent of its domination of the eventual population. The problems of succession in aquatic plant communities and of compositional changes and interspecific antagonism is reviewed by Sculthorpe (1967), but most of the previous studies in these fields have been based on permanent or semi-permanent water bodies. Very few investigations appear to have been made of situations in which existing plant communities are annually drastically affected by environmental factors. However, it is clear that in these situations the plants with the most rapid rates of vegetative growth will be at an advantage and thus the frequent dominance of E. crassipes and Salvinia is further indication of their abilities in this respect.

Unfortunately there are very few instances in South America where the histories of the changes in plant populations are known. However, records have been kept of the fluctuations in macrophyte populations in some of the water bodies near Santa Fé, and it is interesting to review the data for two of these, Don Filipe and Los Espejos. I am grateful to Tur (pers. comm.) for permission to quote her unpublished information in the following paragraphs on these water bodies.

(a) Don Filipe

This oxbow lake or "madrejon" is situated about 8km N.E. of Santa Fé adjacent to the Rio Colastine. It is typical of many of the turbid water bodies in this area and its chemistry has been investigated by Stangenberg and Maglianesi (1968) for the years 1964 to 1966. These studies showed that the water was usually acid with relatively low conductivities and was of the bicarbonate-sodium-magnesium type. Turbidities ranged from 10 to 348 units with an overall average of 83 units during this period. The records of levels during these years showed a range of 6.5m, though the flood level reached in 1966 was the highest since 1905.

Records of the plant populations have been kept since 1963. At the commencement of this year there were considerable quantities of *Salvinia* (mainly *S. herzogii*) but, following the floods, this was reduced to less than 5% of the surface area. In the following year, 1964, the biomass of the rooted plants was greater than that of the floating species with *Ludwigia* and *Nymphoides* most common. During the exceptional floods in 1965 and 1966 the *Nymphoides* maintained its position and the floating plants were only present in small amounts. In 1967 the west arm of the oxbow was almost entirely cleared of vegetation by water currents. In the following year the *Nymphoides* decreased and there was a marked increase in the amount of *S. herzogii*. Growing at an exponential rate, this species succeeded in covering almost the entire water body by September. The resulting mat was very stable and supported many "sudd" plants. The floods in the following year swept most of the *Salvinia* away, but the quantities were beginning to increase again when the situation was observed in early 1970. This catalogue of events serves to illustrate the complexities of these successions of plant communities in which plant growth cycles, hydrological events and other environmental changes probably effect the composition of the community at any one time.

(b) Los Espejos

This lagoon is situated about 1.5km N.E. of Santa Fé near the Rio Santa Fé and is typical of clear water bodies in the Middle Paraná Region. It's chemical characteristics during 1965 and 1966 were studied by Stangenberg and Maglianesi (1969). Aside from the turbidities, which ranged from 6-71 units with an average of 18, there were no marked differences between the chemistry of this lagoon and Don Filipe, though its waters were often slightly alkaline. Generally, the plant populations were better developed, especially in respect of submerged plants. The floating plant population is dominated by *E. crassipes* and floating islands of vegetation ("embalsaldos") are commonly developed. During the winter months the *Eichhornia* is adversely affected by the cold temperatures and most of the plants turn brown and die. In 1967 and 1968, over 90% of the water surface was covered by the floating plant communities but, during the winter of 1969, large quantities of *Eichhornia* were killed and since then there has been an increased development of submerged plants and much less cover of *E. crassipes*. The changes in the plant populations in this lagoon are clearly due to a different set of environmental circumstances. The lagoon is fairly sheltered and isolated and flood effects are less marked, while the effect of seasonal temperature changes are clearly of considerable importance.

CONCLUSIONS

One of the main underlying objectives to this investigation of the ecology of these notorious aquatic weeds, *Salvinia* and *E. crassipes*, in their native environments was to ascertain why they were apparently normally less troublesome there than in situations where they are invading species. Mitchell (1970) reviewed the characteristics of *Salvinia* which facilitated its explosive spread. Four features were stated to be important:

(a) the plant is able to regenerate from relatively small pieces of tissue;

(b) vegetative propagation is the main means by which the population is increased;

(c) growth is manifested mainly as increment in photo-synthetic area;

(d) the plants are not limited by substrate requirements and water depth.

Most of these also apply to *E. crassipes* and all are relevant as much in the plants native environment as out of it. The differences between the situation in the neotropics and in Lake Kariba, for example, are the increased competition from other aquatic macrophytes and the presence of insects feeding off the plants in the former situation. However, these factors do not appear to exercise any major control of *Salvinia* and *E. crassipes* populations and it is clear that the main limiting factors are the periodic effect of river floods and fluctuating water levels.

IV. NATURAL ENEMIES OF EICHHORNIA CRASSIPES AND SALVINIA SPECIES IN SOUTH AMERICA

The possibility of biological control of Eichhornia crassipes and Salvinia has been under consideration for some time. Workers such as Bennett (1961, 1964, 1966, 1967, 1968a, 1968b); Bennett & Zwolfer (1968); Nag Raj (1965); Perkins (pers. comm.); Silveira Guido (pers. comm.); Seaman & Porterfield (1964); Thomas (1968) and Vogel (1968), have investigated the possibility of using various natural enemies for control of these plants. The investigations carried out by these workers have involved surveys for biological control agents over a very wide range, particularly in the neotropics. During the present survey, no new organisms were discovered which had any real potential for control of either Eichhornia or Salvinia and it seems unlikely that further surveys will reveal the presence of any more potential control agents of major importance.

Since time was very limited during the survey it was not possible to carry out extensive quantitative investigations at any of the places visited. Accordingly an attempt was made to make representative collections of the insects and other organisms associated with the plants and to supplement this, whenever possible, with field observations on their biology and the nature and extent of damage which they caused.

Biological control of weeds, and in particular of aquatic weeds, is a relatively new field when compared with biological control of insects. Nonetheless an impressive list of successful control programmes on terrestrial weeds exists; though the same cannot yet be said for plants which cause problems in aquatic ecosystems. The principals involved, however, are basically the same and there is no reason to suppose that biological control of aquatic weeds will not prove as successful as its terrestrial counterpart.

NATURAL ENEMIES OF EICHHORNIA CRASSIPES

The following organisms were found associated with E. crassipes during the survey and are considered to be the most important natural enemies of the plant.

(a) Neochotina spp. (Curculionidae: Bagoini)

The specific identity of the weevils attacking E. crassipes has not yet been fully resolved. Bennett & Zwolfer (1968) refer to one species, Neochotina bruchi Hulst, but Perkins (pers. comm.) considers that more than one species may be involved. The eggs are inserted singly at, or near, the base of the stems and on hatching the larvae mine and feed in the stems, particularly in the vicinity of the roots where they leave characteristic blackish tunnels. The larvae may move from one stem to another during the course of their feeding and eventually they pupate among the root hairs just below water level. The adults are almost entirely nocturnal; during the day they are found in the spaces where the new leaves are rolled around stem bases. They emerge at night to feed on the leaves where they cause squarish feeding punctures some 2-3mm across. In cases where there is a high level of infestation there is a concentrated feeding attack on the base of the leaf. This has the effect of girdling the stem at this point so that eventually the entire leaf collapses. Adult damage is mainly confined to a mechanical injury whereas larval damage is very often followed by a secondary invasion of pathogens, which further weaken the plant.

Although Neochotina was found over the entire survey area, the level of attack varied considerably from one place to another. Spectacular damage by this insect was found at a site near Manaus; some leaves had up to 300 feeding scars and an average of 6-7 adult Neochotina were found on each plant. No specific natural enemies of Neochotina were encountered, but Bennett & Zwolfer (1968) and Perkins (pers. comm.) have pointed out that the larvae would probably be susceptible to attack by predacious insects or fish when they leave the plant to pupate. Rao (pers. comm.) has had some difficulty in rearing the insect in the laboratory and considers that this may be due to attack by nematodes. Screening tests carried out by Perkins (pers. comm.) indicate that the insect is specific enough in its feeding habits to be safe to release.

(b) Acigona ignitalis Hmps. (Pyralidae: Crambinae)

This large lepidopterous stem borer seems to have a more restricted distribution than Neochotina. During the survey the insect was not encountered in Argentina or Uruguay. Silveira Guido (pers. comm.), who is working on this insect under contract to the United States Department of Agriculture considers that it is not important as a natural enemy in Uruguay or Southern Argentina. The eggs are laid in masses in crevices in the leaves, or stems, and the larvae initially mine in the leaf tissue. Later they enter a stem either directly from a leaf or by leaving it and burrowing into the stem lower down. The larvae often migrate to another stem but the damage which they leave is very characteristic because of the pinkish frass in the tunnels.

Bennett & Zwolfer (1968) record that small larvae frequently girdle stems, causing them to collapse. Pupation takes place inside the stem and the larva cuts a small hole to the outside leaving only the epidermis intact. After the adult emerges the pupal case is left protruding from the exit hole. Silveira Guido (pers. comm.) states that Acigona is parasitised by Apantales abditus Mues. Iphiaulax sp. and Basseus sp. The insect was found on Eichhornia azurea but Silveira Guido (pers. comm.) considers it unlikely that it can complete its life-cycle on plants other than the Pontederiaceae.

Acigona is capable of causing extensive damage to Eichhornia. At Cabo Frio in Brazil for example, a large stand of E. crassipes was found to be heavily attacked and an examination of 50 stems yielded 3 larvae and 2 pupae. In addition, 7 other stems showed damage characteristic of larval feeding, giving an overall level of attack of 17%. As with many other mining and tunneling insects, there is very often a secondary invasion of other organisms resulting in severe weakening or complete kill-off of quite large patches of Eichhornia.

(c) Epipagis abugutalis Hmps (Pyralidae: Pyraustinae)

As with Acigona this insect was encountered mainly in Brazil and Trinidad. Its biology is very similar to that of Acigona with the exception that often two or more Epipagis larvae are found in the same stem. Bennett & Zwolfer (1968) recorded two species of parasites, Bracon sp. and Spilochalcis sp., attacking the larvae and pupae. They further record that the rate of parasitism may become very high and give a figure of 66% parasitism from a site at Paramaribo in Surinam. Epipagis was found more commonly on small plants with inflated stems as opposed to Acigona which appears to have a preference for larger erect stems. Although the damage inflicted by Epipagis is essentially similar to that caused by Acigona, it did not appear to be so debilitating. This is probably in part due to its smaller size and possibly to some extent by the check kept on the populations by the high rate of parasitism. During the survey Epipagis was not found on any plant other than E. crassipes.

(d) Cornops longicorne Bruner. (Acrididae: Cyranthacridinae)

Cornops was encountered throughout the entire survey area. It was, however, less common in Argentina then elsewhere.

The female makes a chamber with her ovipositor in the stem and the eggs are inserted into this and covered with yellowish froth which rapidly hardens to form an ootheca. The young nymphs feed principally on the leaf epidermis causing typical elongated scars. Adults are capable of eating all the leaf tissue and will frequently feed on the stem. An elongated ragging of the leaves is characteristic of damage by this insect. On several occasions nymphs were observed to be attacked by the predatory grasshopper Phlugis teres De Geer, and Bennett & Zwolfer (1968) record that the eggs are attacked by the entomophagous weevil Ludovix fasciata Gyll, and by hymenopterous egg parasites.

Cornops was frequently found feeding on E. azurea as well as E. crassipes and it appears to have a preference for plants with upright stems. A secondary infestation often follows attack by Cornops which, in itself, by virtue of its large size, is capable of inflicting severe damage.

(e) Orthogalumna terebrantis Wallwerk. (Acarina. Oribatidae. Galumnidae)

With the exception of Guyana and Trinidad, this mite was found throughout the entire survey area. Small punctures and mines a few mm long in the leaves are characteristic of feeding damage by this mite and the leaves very often assume a brownish colour. Although the mites themselves are very small, they are capable of inflicting severe damage because of the high level of attack. At Manaus in Brazil for example, leaves of E. crassipes were found with up to 200 mines in them. Orthogalumna was not found on plants other than E. crassipes, but Silveira Guido (pers. comm.) considers that it may feed on other Pontederiaceae.

(f) Thrypticus sp. (Diptera: Dolichopodidae)

This insect was fairly common throughout the survey area. The larvae, which are only a few mm long, bore through the bases of the stem just above water level. Horizontal tunnels open at both ends and are typical of damage by Thrypticus. These tunnels are blackish in colour, due partly to the presence of frass and partly to the rotting caused by invasion of pathogens. The insect was found to cause considerable damage to a small patch of E. crassipes at Santos in Brazil. Nearly all the plants attacked had extensive rotting at the bases of the stems, and in many cases the stems had collapsed completely. It is felt that this insect warrants a much more detailed investigation particularly, initially, in terms of its host specificity.

OTHER ORGANISMS ASSOCIATED WITH EICHHORNIA

Many other organisms were found on, or associated with, Eichhornia and although some of them were definitely feeding on the plant they are considered to be of minor importance, or not specific enough to warrant further investigation. As has already been mentioned the predatory grasshopper Phlugis teres was found associated with the plant, as was another grasshopper Terantaenia phila Rehn, which was found feeding on both flowers and leaves of E. crassipes. Two other tettigonids and a cricket were also found associated with Eichhornia. Examination of E. crassipes at various sites in Uruguay revealed the presence of great numbers of Palustra spp. but only adults could be found and there seemed to be little evidence of larval damage. Several dynastid beetles, probably Dyscinetus spp. were found at several sites in Argentina and Uruguay. The damage inflicted by these insects to plants with bulbous stems were quite extensive, but it is almost certain that they have a wide host range. Silveira Guido (pers. comm.) considers that they are not specific even to the Pontederiaceae.

A weevil identified as Onichylus nigirostris was found feeding on E. crassipes in parts of Trinidad, but no details on this species are available. Pentatomids, aphids and tetranychid mites, were commonly found on Eichhornia but again these are almost certainly not specific.

Various hymenopterous parasites and coccinellids were also found on the plant; these were probably associated with the phytophagous insects described above.

NATURAL ENEMIES OF SALVINIA SPP.

As with Eichhornia, numerous organisms were found associated with Salvinia but the survey confirmed the findings of Bennett (1966), who considered only the following three species to be of major importance.

(a) Paulinia acuminata de Geer. (Orthoptera: Acrididae)

This insect was of considerable interest during the survey because of the interest already shown in it as a possible biological control agent for Salvinia, and also because of studies previously carried out on various aspects of its biology (Thomas, in prep.).

Eggs are deposited in oothecae on the undersurfaces of leaves. On hatching the nymphs climb out on to the upper leaf surface to feed. There are five or sometimes six moults before the nymphs become adult. The very small nymphs often feed initially on the leaf hairs; this is particularly the case on the large, robust, mat form plants. As the nymphs become larger their feeding may cause small holes in the leaf lamina. Eventually the large nymphs and adults are capable of destroying whole leaves.

Salvinia may exhibit three distinct growth forms which are described in detail on page 14. Feeding rate experiments with these various growth forms over a range of temperatures clearly show that Paulinia has a considerably greater feeding rate on primary than on secondary plants, and on secondary than on tertiary.

The maximum feeding rate occurred at a temperature in the range of 32°C to 36°C and a summary of the results obtained at 32°C is given in Table II.

TABLE II. Average amounts of Salvinia consumed by an adult Paulinia at 32°C in twenty-four hours

PRIMARY				SECONDARY				TERTIARY			
MALES		FEMALES		MALES		FEMALES		MALES		FEMALES	
Fresh Weight (g)	Leaf Area (cm^2)	Fresh Weight (g)	Leaf Area (cm^2)	Fresh Weight (g)	Leaf Area (cm^2)	Fresh Weight (g)	Leaf Area (cm^2)	Fresh Weight (g)	Leaf Area (cm^2)	Fresh Weight (g)	Leaf Area (cm^2)
0.259	17.8	0.544	36.4	0.240	9.6	0.496	19.9	0.128	4.2	0.327	10.8

It can be seen that, in terms of leaf area, the feeding rate on primary plants is more than three times that on tertiary plants.

Because of the more robust nature of tertiary plants, the difference in feeding rates is more obvious when expressed in terms of leaf area. The feeding rate on primary plants however, is still twice that on tertiary plants when expressed in terms of fresh weight. There is no significant difference in the moisture content of the three growth forms so this cannot account for the differences in feeding rate. Further, there is no difference in the gross chemical composition of the three growth forms (Mitchell, 1970). It is possible that the larger and more robust plants might be "tougher" and therefore less palatable. Chapman (1957) investigating the feeding of Nomadacris septemfasciata demonstrated that observed feeding preference on different grasses showed a close correlation with their hardness and moisture content. He showed however, that there was not necessarily a correlation between moisture and hardness, so it is possible that although the growth forms of Salvinia are not significantly different in terms of moisture content, there may be differences in their hardness. Plans have been made to investigate this point further. An interesting point is that the difference in feeding rates is manifested further in a definite preference for primary as opposed to tertiary plants. This was demonstrated by choice experiments in the laboratory, and by observations in the field which show that on tertiary plants it is the smaller and possibly "softer" apical growing points which are more often attacked. Other observations have further shown that the differences in feeding rate manifest themselves in a difference in the rates of nymphal development, i.e. the developmental rates of Paulinia on primary plants are always faster than on secondary or tertiary (Thomas, in prep.).

It is difficult to make predictions about the effects of Paulinia on Salvinia populations in the event of a release. This difficulty is enhanced by the absence of long term data on field populations. With one or two exceptions Paulinia was not observed to have any serious effect on the populations of Salvinia in South America. It is clear however that a combination of factors, including the effects of natural enemies, do limit populations of Salvinia. It is probable that at least in the case of permanent Salvinia mats there is a state of equilibrium between the plant, its natural enemies, and the other factors which effect both of these populations.

A disturbing feature about Paulinia is that no specific parasites or predators could be found. Nymphs and adults are preyed on by birds and frogs, and Paulinia which jumped into open water surfaces were observed to be quickly taken by fish. These organisms probably exist wherever there is Salvinia, and it seems likely that the same factors which control Paulinia populations in the natural habitat would operate anywhere where the insect was introduced. Paulinia was found throughout the entire survey area and it is probable that, in the neotropics, its distribution is closely tied to that of Salvinia. The insect was frequently found on Pistia stratiotes and Azolla spp. and it can certainly complete its life cycle on these two plants. According to Bennett (1966) it can possibly do the same on Hydromistria stolonifera. In addition to these plants, Paulinia will also feed on *Spirodella intermedia*, *Lemma* spp. and *Nymphaea* spp. However, screening tests show that the insect will not damage any terrestrial plants. Further, it is tied to a semi-aquatic environment by virtue of its ovipositional habits and can be safely recommended for release.

(b) Cyrtobagous singularis Hulst. (Coleoptera: Curculionidae)

This weevil appears to have a very restricted distribution and it was only found in any numbers at Manaus in Brazil, and at Georgetown in Guyana. Populations of this insect may fluctuate seasonally as J. Bates (pers. comm.) reports having seen large patches of *Salvinia* in Georgetown completely destroyed by great numbers of *Cyrtobagous*.

According to Bennett (1966) the eggs are laid in stems and leaf veins below the water surface. Larvae were observed mining in the stems and leaves of *Salvinia*. Pupation is below water among the roots and after emergence the adults may feed on the upper or lower surfaces of the leaves. It appears that a secondary infestation often follows damage by this insect and this accelerates the destruction of the plant tissue. Bennett (1966) records that *Cyrtobagous* could not be induced to feed on any plant other than *Salvinia*.

(c) Samea multiplicalis Guenee (Lepidoptera: Pyralidae)

Samea was found at several sites in Northern Brazil and Guyana but was not common elsewhere in the survey area. The eggs are laid on the upper surfaces of leaves among the leaf hairs. Larvae mine through the epidermis of the leaves leaving silken galleries as they move about. As with *Cyrtobagous*, there is often a secondary infestation and the leaves quickly break down.

In addition to *Salvinia*, *Samea* was found on *Pistia* and Bennett (1966) records that it also feeds sparingly on *Lemna* spp. and *Eichhornia*. Some small patches of *Salvinia* were found to be heavily infested with *Samea* and damage was quite extensive, but where large areas of *Salvinia* were present the damage was not so noticeable. Bennett (1962) recorded three hymenopterous parasites attacking *Samea* and it is possible that adults and larvae are susceptible to attack by a number of general predators.

OTHER ORGANISMS ASSOCIATED WITH SALVINIA

In addition to these three insects, a number of other organisms were found in association with *Salvinia*, but these are considered to be of minor importance. An unidentified lepidopterous leaf miner was found in large numbers attacking *Salvinia* and *Pistia* near Manaus in Brazil. It did not appear to cause extensive damage to *Salvinia* but Bennett (pers. comm.) considers that it may warrant further investigation. A lygaeid bug, Lipostemmata purpurata was common in large numbers wherever Salvinia was found, as was an aphid Rhopalosiphum nymphaea, but the presence of these insects did not seem to have a significant effect on the plant. Furthermore, Rhopalosiphum is already present on Salvinia on Lake Kariba, and is apparently of almost world wide distribution. The larvae and adults of various aquatic beetles, and larvae of aquatic Diptera were commonly found among the roots of Salvinia, but their presence there cannot be said to have any significance as far as biological control is concerned. Phytophagous crickets and the curious semi-aquatic grasshopper Marellia remipes were found on Salvinia in Argentina and Uruguay, but neither of them are considered to be important or specific enough to warrant further investigation.

GENERAL OBSERVATIONS

During the survey collections of insects were made from 24 localities, and numerous other sites were examined although no collections were made from them. Details of the more important observations are given below.

The most extensive work in one place was carried out at Don Filipe a lagoon near Santa Fé, Argentina. Details of the botanical history of this water body are given on page 32. A more or less permanent mat of Salvinia herzogii and Salvinia minima was present around most of the margin of the lagoon. This was anchored by a belt of Salvinia matted together by Scirpus spp., Hydromistria stolonifera, and Eichhornia crassipes some 10 metres from the shore. Outside this zone was a narrow margin of largely errant Salvinia approximately one metre wide. This Salvinia consisted almost entirely of tertiary plants generally in rather poor condition. Paulinia occurred here rather sparsely and small groups of 10-20 insects were found at intervals of up to 50 metres along the mat. On the inner zone of Salvinia however, the plants did not cover the surface completely and were generally younger and in better condition. Paulinia were found here in much greater numbers. A quarter square metre quadrat was thrown 50 times and this revealed an average density of 9-10 Paulinia per square metre with peak densities of up to 25 per square metre. Damage to Salvinia in small patches where groups of Paulinia were concentrated was severe, but the presence of Paulinia did not appear to have any overall serious effect. At this site, jacanas (Jacana spinosa) were observed feeding on Paulinia, and the insect was found in the gut contents of frogs. Large nymphs were found in spider webs and spiders were seen eating Paulinia on several occasions.

An interesting feature of this site was the fact that mixed with the Salvinia was a small amount of Azolla sp. Although there was no indication of preferential feeding on the Azolla, there was, at one spot in a small backwater, a stand of almost pure Azolla and the density of Paulinia here was at least twice as high as anywhere on the Salvinia.

Near the Guadelupe lagoon only a few kilometres away from Don Felipe, there was a large area of pure Azolla and although the density of Paulinia was not high, (1-2 per square metre), there were a number of interesting features about the site. It was known from laboratory experiments that Paulinia is remarkably colour polymorphic and that its colour varies according to the background on which it is reared. Although individuals had been observed which were various shades of green and, in some cases brown or almost black, the insects at Guadelupe were a distinct red colour, imitating the Azolla on which they were living.

Bennett (1964) and Carbonell (1964) pointed out that Paulinia is normally brachypterous in the field. Experiments have shown that wing development is dependant on at least two factors, i.e. rearing density and temperature. At Guadelupe the entire population of Paulinia was macropterous whereas at Laguna del Sauce in Uruguay the entire population was brachypterous. At all other sites however, the populations of Paulinia were mixed brachypterous and macropterous. It is clear that some factor, or factors, other than those already mentioned must have an effect on the development of wings. There was not sufficient time to investigate this phenomenon in the field, but it is one which would warrant further study as the factors affecting the dispersal of the insect would be most important in determining its success as an agent for biological control of Salvinia.

At Don Flores, also near Don Felipe, there was a mature mat of Salvinia almost entirely covered by Scirpus sp. but a search of over an hour revealed the presence of only one third instar nymph of Paulinia. The very low incidence of Paulinia at this site is odd since on every other patch of Salvinia examined during the survey Paulinia was easily found. It is possible that the nature of the mat, i.e. all tertiary plants covered with Scirpus, discouraged Paulinia. Alternatively, it is possible that the scarcity of Paulinia was due to some other reason, and that this, in part at least, might have contributed towards the formation of what was stable permanent mat of Salvinia which would, if the water body was to be used, constitute a serious hazard.

On a small pond near Itabuna in Brazil a healthy mat of Salvinia was found covering the entire water surface. The history of this pond is interesting as it had been cleared completely of Juncus reeds two months previously and the Salvinia had covered the surface in that time. High concentrations of Paulinia were found on the edges of the pond where there was still some open water and the plants were mainly young. Very few insects were found on the main body of the mat.

Although Lepidopterous larvae and Hemiptera were encountered on Salvinia throughout the survey area, it was not until Belem that severe damage other than that caused by Paulinia was found. At a small dam in the grounds of IPEAN*, a patch of primary and secondary Salvinia was found which was very heavily attacked by Samea. A similar level of attack was

---

* Instituto de Pesquisas Agronomicas, Recife, Brazil.

found on ponds at the Museo Goeldi also in Belem. Although the signs of attack were very obvious the insect itself was difficult to find and only a few specimens were collected.

Mention has been made of the spectacular damage caused to Eichhornia by Acigona at Cabo Frio. This site was also interesting because of the very high level of attack by Cornops and nearly all the plants were found to be damaged. Further, Neochotina was found in very small numbers on this stand of Eichhornia, whereas a patch of very young plants only a few metres away was heavily attacked by the weevil.

At Laguna del Sauce a belt of Eichhornia azurea was found to be heavily damaged and in places totally destroyed by Cornops, whereas a zone of E. crassipes with bulbous stems a few metres away was completely untouched and the only damage to it was a slight attack by dynastid beetles. A few hundred metres away however was a stand of large, erect, E. crassipes which was severely damaged by Cornops.

DISCUSSION AND RECOMMENDATIONS

In the field both Eichhornia and Salvinia are attacked by a complex of insects. The effect which this attack has on the plants is dependant on a number of factors. Obviously the most important, as far as any one species of insect is concerned, is the level of attack, but the age or growth form of the plant is also of great importance, as this has a bearing on the feeding rate, in the case of Salvinia, and may determine the level of attack, in the case of Eichhornia.

Both plants were found to suffer severe damage in patches as a result of feeding , but there was no indication that this feeding had any great limiting effect on a large scale.

It seems that Eichhornia is considerably more affected by insect damage than Salvinia and the range of organisms attacking it is much greater. The feeding activities of insects which mine or tunnel in the tissue of both plants often result in more damage eventually, because of the invasion of pathogenic organisms which cause rotting and further destruction of the plant tissue. Of the insects found associated with Eichhornia, the most promising seem to be Neochotina, Acigona, Epipagis, Cornops and Orthogalumna. Neochotina has been under investigation for some time by Dr. D. Perkins of the United States Department of Agriculture. Acigona has been studied by Silveira Guido, who has also worked with Cornops. All of these insects have, at one time or another, been studied by the Commonwealth Institute of Biological Control.

Recently there have been several developments in the biological control of Eichhornia and Salvinia. Orthogalumna and Neochotina were released in 1971 against Eichhornia in Zambia, but no details of this release are yet available.

Releases of Paulinia on Lake Naivasha in Kenya have been unsuccessful, as have releases of Samea (Hiscock pers. comm.). Temperatures at Lake Naivasha do become very low at times, and it is possible that due to the small initial release which was carried out without bulking up the populations, the rate of reproduction may have not been fast enough to achieve permanent establishment.

Paulinia has been released on to Lake Kariba and the insect is well established there, but as yet no studies have been made of the overall effects of the release. In addition Cyrtobagous and Samea have been released on to Kariba, but again the initial populations were very small and as yet there is little evidence of establishment (Bennett pers. Comm.).

If an answer is to be found to the problem of Eichhornia and Salvinia it is likely to lie in releasing a complex of natural enemies under carefully chosen conditions. These should take into account the age and growth form of the plants, the climatic conditions and, if possible, the release should be made in a situation where its effects could be closely monitored.

The usefulness of these biological control agents will probably lie more in the realm of intergrated control as none of them seem likely to be able to destroy large, well established stands of the plants. Integrated control might be achieved by interspersing a system of strip spraying of herbicides with the establishment, on untreated plants, of natural enemies. Alternatively, a full scale herbicidal control programme is always likely to leave a few plants which may be a source of re-infestation, and it is possible that biological control agents could be used to contain these plants at a level where other control measures would be unnecessary. In the case of Salvinia in particular, Paulinia might serve as a useful means of controlling new infestations where there would tend to be a large number of primary and secondary plants on which the feeding rate would be greater.

In any event a final answer cannot be obtained by laboratory investigations, and the long-term effectiveness of any of the natural enemies described here can only be ascertained by initiating properly managed control programmes at sites outside the neotropics.

V. SUMMARY OF RESULTS AND RECOMMENDATIONS

Specimens from the Salvinia auriculata complex were collected over a wide distribution range. Investigations of these and other dried and preserved material indicated that the complex consists of at least four taxa. One of these, the group which occurs as an aggressive weed outside the neotropics, is undescribed. This species is not a problem in South America because it either does not occur there naturally or has a very restricted distribution.

Ecological observations indicated that the sizes of populations of Salvinia spp. and Eichhornia crassipes in South America are controlled by a complex of interacting factors. The most important limiting factors appeared to be hydrological. Flooding rivers and fluctuations in water level interacting with climatic factors cause substantial annual decreases in the sizes of many populations. When these hydrological factors are eliminated or decreased, large populations of these plants (especially Eichhornia crassipes) can develop.

Investigations of the fauna of populations of both Salvinia and Eichhornia showed that these plants are extensively attacked by a complex of insects in their natural habitat in South America. It is probable that some form of biological control of these plants outside the neotropics can be achieved.

Other observations indicated that interspecific competition between aquatic plants may also exercise a limiting effect on the size of the population of a particular plant species in a locality, though the total biomass of plants does not appear to be decreased.

Further research on the biological control of Salvinia is most important and would be likely to produce economically valuable results. This research should include more detailed, intensive studies of the physiology and biology of Paulinia in its native environment, and investigations of Samea and Cyrtobagus.

Detailed ecological studies of aquatic macrophytes and especially of Salvinia spp. and Eichhornia crassipes in relation to disturbance of the hydrological régime by man-made lakes and similar artificial water bodies, should be undertaken in South America.

Cytogenetical research of the Salvinia auriculata complex is required in order to ascertain the origin of the aggressive weed species in the complex.

Interspecific competition between aquatic macrophytes requires investigation both in field and in laboratory conditions. It is anticipated that further field observations should be made in the neotropics, as well as some laboratory experimental work with Salvinia spp., Eichhornia crassipes, Azolla spp. and Pistia stratiotes.

ACKNOWLEDGEMENTS

We wish to record our gratitude to UNESCO and the International Biological Programme for their sponsorship of this visit. We are especially grateful to Dr. J. Rzóska of the International Biological Programme who handled the complex negotiations leading to the organization of the study tour.

We were very appreciative of the hospitality and kind reception which we were given, and for the facilities and assistance we received from:

Instituto de Limnologia, Santa Tome, Argentina;
La Plata University, La Plata, Argentina;
Instituto Botanico, Sao Paulo, Brazil;
Jardim Botanico, Rio de Janeiro, Brazil;
Centro de Pesquisas do Cacau, Itabuna, Brazil;
Instituto de Pesquisas Agronomico, Recife, Brazil;
Museo Goeldi, Belem, Brazil;
Instituto Nacional de Pesquisas da Amazonia, Manaus, Brazil;
Bookers Sugar Estates, Georgetown, Guyana;
Botanischer Garten und Institut für Systematische Botanik, Zürich, Switzerland;
Commonwealth Institute of Biological Control, Trinidad;
Agricultural Research Council Weed Research Organization, Kidlington, Oxford, United Kingdom;
British Museum (Natural History), London, United Kingdom;
Anti-Locust Research Centre, London, United Kingdom;
International Biological Programme Central Office, London, United Kingdom;
State University of New York, Stony Brook, United States of America.

REFERENCES

Arber, A. 1920. Water plants: a study of aquatic antiosperms. Cambridge University Press.

Aublet, J.B.C.F. 1775. Histoire des plantes de la Guyane française...., vol. 2. Londres and Paris.

Bennett, F.D. 1961. Investigations on Salvinia in Trinidad, British Guiana and Brazil during October-December 1961. Commonwealth Inst. Biol. Control. Unpublished report.

Bennett, F.D. 1964. Feeding tests with insects attacking Salvinia auriculata undertaken at Belem during October-December 1964. Commonwealth Inst. Biol. Control. Unpublished report.

Bennett, F.D. 1966. Investigations on the insects attacking the aquatic ferns, Salvinia spp. in Trinidad and Northern South America. Proc. sth. Weed Control Conf. 19; 497-504.

Bennett, F.D. 1967. Notes on the possibility of biological control of the water hyacinth Eichhornia crassipes. Pestic. Abstr. 13; 304-309.

Bennett, F.D. 1968a. Insects and mites as potential controlling agents of water hyacinth (Eichhornia crassipes (Mart.) Solms. Proc. 9th Brit. Weed Control Conf.

Bennett, F.D. 1968b. Investigations on insects attacking water hyacinth in Florida, British Honduras and Jamaica, 1968. Commonwealth Inst. Biol. Control. Unpublished report.

Bennett, F.D. & Zwolfer, H. 1968. Exploration for natural enemies of the water hyacinth in Northern South America and Trinidad. Hyacinth Control Journ. 7; 44-52.

Bock, J.H. 1969. Productivity of the water hyacinth Eichhornia crassipes (Mart.) Solms. Ecology, 50; 460-464.

Bonetto, A., Dioni, W. & Pignalberi, C. 1969. Limnological investigations on biotic communities in the Middle Paraná River Valley. Verh. Internat. Verein. Limnol. 17; 1035-1050.

Bonnett, A.L.M. 1955. Contribution à l'étude des Hydropteridées: recherches sur Salvinia auriculata Aublet. Annls. Sci. nat. (bot.), 16; 529-600.

Boughey, A.S. 1963. The explosive development of a floating weed vegetation on Lake Kariba. Adansonia, 3; 49-61.

Carbonell, C.S. 1964. Habitat, Etologia y Ontogenia de Paulinia acuminata (De g.) (Acridoidea: Paulinidae) en el Uruguay. Rev. Soc. Uruguay Ent. Montivedeo. 6; 39-44.

Chapman, R.F. 1957. Observations on the feeding of adults of the red locust (Nomadacris septemfasciata (Serville)). Brit. J. Anim. Behav. 5; 60-75.

de la Sota, E.R. 1962. Contribucion al conocimiento de las Salviniaceae neotropicales. I. Salvinia oblongifolia Martius. II. Salvinia auriculata Aublet. III. Salvinia Herzogii nov. sp. Darwiniana, 12; 465-520.

de la Sota, E.R. 1963. Contribucion al conocimiento de las Salviniaceae neotropicales IV. Datos morfoanatomicos sobre Salvinia rotundifolia Willdenow y Salvinia herzogii de la Sota. Darwiniana, 12; 612-623.

de la Sota, E.R. 1964. Contribucion al conocimiento de las Salviniaceae neotropicales. V. Salvinia sprucei Kuhn. Darwiniana, 13; 529-536.

del Viso, R.P., Tur, N.M. & Mantovani, V. 1968. Estimacion de la biomasa de hidrofitos en cuencas islenae del Parana Medio. Physis, B. Aires, 28; 219-226.

Ewer, D.W. 1966. Biological investigations on the Volta Lake, May, 1964 to May, 1965. In Man-made Lakes (ed R.H. Lowe-McConnell), pp. 21-30. London, Academic Press.

Gay, P.A. 1960a. Ecological studies of Eichhornia crassipes Solms in the Sudan. I. Analysis of spread in the Nile. J. Ecol. 48; 183-191.

Gay, P.A. 1960b. In The biology of weeds (ed. J.L. Harper), pp. 184-188. Oxford, Blackwells.

Herzog, R. 1934. Anatomische und experimentell-morphologische Untersuchungen über die Gattung Salvinia. Planta, 22; 490-514.

Herzog, R. 1935. Ein Beitrag zur Systematik der Gattung Salvinia. Hedwigia, 74; 257-284.

Hitchcock, A.E., Zimmerman, P.W., Kirkpatrick, H.S. & Earle, T.T. 1949. Water Hyacinth: its growth, reproduction, and practical control by 2,4-D. Contr. Boyce Thomson Inst. Pl. Res. 15; 363-401.

Holm, L.G., Weldon, L.W. & Blackburn, R.D. 1969. Aquatic Weeds. Science, 166; 699-709.

Kopp, J. 1936. Über die Kulturbedingungen und die systematischen Merkmale der Salviniaarten. Inaugral-Dissertation, Münster.

Little, E.C.S. 1966. The invasion of man-made lakes by plants. In Man-made lakes (ed. R.H. Lowe-McConnell), pp. 75-86. London, Academic Press.

Loyal, D.S. & Grewel, R.K. 1966. Cytological study on sterility in Salvinia auriculata Aublet with a bearing on its reproductive mechanism. Cytologia, 31; 330-338.

Loyal, D.S. & Grewal, R.K. 1967. Some observations on the morphology and anatomy of Salvinia with particular reference to S. auriculata Aubl. and S. natans All. Res. Bull. Panjab Univ. Sci. 18; 13-28.

Mitchell, D.S. 1968. Ecological studies of Salvinia auriculata with particular reference to Lake Kariba (Rhodesia and Zambia) and the Chobe River (Botswana). Paper presented to IHD Meeting of Experts on Ecology and Control of Aquatic Vegetation at UNESCO, Paris, 16-18 December, 1968. (unpublished)

Mitchell, D.S. 1969. The ecology of vascular hydrophytes on Lake Kariba. Hydrobiologia, 34; 448-464.

Mitchell, D.S. 1970. Autecological studies of Salvinia auriculata Aubl. Ph.D. Thesis (unpublished), University of London.

Nag Raj, T.R. 1965. Thread blight of Water Hyacinth. Curr. Sci. 34; 618-619.

Penfound, W.T. & Earle, T.T. 1948. The biology of the water hyacinth. Ecol. Monogr. 18; 447-472.

Sculthorpe, C.D. 1967. The biology of aquatic vascular plants. London, Edward Arnold.

Seaman, D.E. & Porterfield, W.A. 1964. Control of aquatic weeds by the snail Marisa cornuarietis. Weeds, 12; 87-92.

Stangenberg, M. & Maglianesi, R.E. 1968. Composicion quimica de las aguas de la cuenca del Parana Medio. Primera parte: Madrejon Don Filipe. Physis, 27; 391-405.

Stangenberg, M. & Maglianesi, R.E. 1969. Composicion quimica de las aguas de la cuenca del Parana Medio. Tercera parte: Laguna Los Espejos. Physis, 28; 229-238.

Thomas, P.A. 1968. Biological control of Salvinia auriculata by Paulinia acuminata. De Geer (Orthoptera: Acrididae). Paper presented to the IHD Meeting of Experts on Ecology and Control of Aquatic Vegetation at UNESCO, Paris, 16-18 December, 1968.

Tur, N.M. 1965. Un caso de epifitismo acuatico. Bol. Soc. argent. Bot. 10; 323-327.

van Donselaar, J. 1968. Water and marsh plants in the artificial Brokopondo Lake (Surinam, S. America) during the first three years of its existence. Acta bot. neerl. 17; 183-196.

Vogel, E. 1968. Life history and evaluation of Arzama densa Walker for control of water hyacinth, Eichhornia crassipes (Mart.) Solms. Unpublished Ph.D. thesis. Louisiana State University.