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A Summary of Research into Biological Control of Salvinia in Australia

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Abstract

A weevil (*Cyrtobagous salviniae*) is controlling *Salvinia molesta* at an increasing number of sites in Australia, but a moth (*Samea multiplicalis*), though breeding and dispersing more rapidly than the weevil, is not. Temperature and availability of nitrogen are usually the most important factors controlling population growth rates of both the weed and the control agents. Experiments, field monitoring and modelling are being used to investigate how different conditions of climate and nutrition affect the dynamic equilibrium reached by the weed and insects. Prospects are good for being able to predict the effects of agents under different conditions in this comparatively simple system and, in the process, gain further insights into plant-herbivore dynamics.

Résumé des Recherches Relatives à la Lutte Biologique Contre *Salvinia molesta* en Australie

En Australie, le charançon *Cyrtobagous salviniae* est un agent de lutte biologique efficace contre *Salvinia molesta* dans un nombre croissant d'emplacements, contrairement au lépidoptère *Samea multiplicalis* bien qu'il se reproduise et se disperse plus rapidement que le charançon. La température et la présence d'azote sont habituellement les plus importants facteurs influant sur le taux de croissance des populations de *Salvinia* et d'agents biologiques. Au moyen d'essais, de surveillance sur le terrain et de modélisation, les chercheurs tentent de déterminer l'influence de divers paramètres climatiques et nutritifs sur l'équilibre dynamique des plantes nuisibles et des insectes. Cette méthode relativement simple semble offrir de bonnes possibilités pour la prévision des effets des agents biologiques dans diverses conditions et permettra également de rassembler d'autres données sur la dynamique plante-herbivore.

Introduction

Since the 1930s *Salvinia molesta* Mitchell (Salviniaceae) has been spread by man to Africa (Hattingh 1961; Gaudet 1976; Edwards and Thomas 1977), India (Cook and Gut 1971; Thomas 1979), Sri Lanka (Senaratna 1943; Chow *et al.* 1955), S.E. Asia (Arumugam and Furtado 1974; Soelastri and Tjitrosoepomo 1974), the Pacific (Johnstone 1969; Sundaresan and Reddy 1979; Mitchell *et al.* 1980) and Australia (Mitchell 1978). The weed is free-floating and causes problems by forming thick mats covering the surfaces of lakes, canals, paddy fields and slow-moving rivers.

S. molesta was recognised as being distinct from *S. auriculata* Aublet in 1972 (Mitchell 1972). Prior to this, attempts at biological control of *S. molesta* by the CIBC using insects collected from *S. auriculata* in Trinidad either failed or gave equivocal results (Bennett 1975; Kamath 1979; Mitchell and Rose 1979). CSIRO Australia started work on *S. molesta* in 1978 in South America and the previously unknown native range of the plant was discovered in S.E. Brazil (Forno and Harley 1979; Forno 1983). Three potentially useful insects were found and imported into quarantine in Australia: *Cyrtobagous salviniae* Calder & Sands (Coleoptera: Curculionidae); *Samea multiplicalis* (Guenée) (Lepidoptera: Pyralidae); and *Paulinia acuminata* (De Geer) (Orthoptera: Pauliniidae). After testing to ensure adequate host-specificity and freedom from their own natural enemies, *C. salviniae* and *S. multiplicalis* were released, but *P. acuminata* will not be released unless evaluation of the other two species suggest that it could improve the degree of control achieved.

Compared with other attempts at biological control of weeds, particularly those involving terrestrial weeds, the system containing *S. molesta* and its control agents in Australia is remarkably simple. The plant is a sterile pentaploid (Loyal and Grewal 1966) in which the entire species appears to be a single genet, it occupies a highly uniform two-dimensional habitat (the water surface), it suffers no water stress, in many waterbodies there are no other plants competing with it for space, and it is not attacked significantly by any natural enemies other than the introduced control agents. In addition, study of the system is comparatively easy because all parts of the plant are accessible without excavation and because the high rate of growth in good conditions allows experiments to be carried out quickly. It was recognised that this situation offered a unique opportunity to make a complete system study at minimal cost and it was decided to attempt to measure all of the most important interactions which ultimately determine the degree of control achieved.

Fig. 1 presents a conceptual model of what are thought to be the most important interactions and it is being used as a framework for integrating individual studies. It is hoped this approach will give some insight into such practical questions as what determines whether a given control agent will be effective or ineffective, whether different agents acting together are synergistic or interfere, and how the environment and insect damage interact to determine plant productivity. As Crawley (1983) has pointed out, there does not appear to be a single system for which the main determinants of abundance have been elucidated for both a plant and its herbivores and theory will continue to outstrip empirical understanding to an embarrassing extent until a body of such studies is accumulated.

Components of the Research Programme

Studies of the Plant

Temperature was expected to be an important variable affecting both plant and insects and it was suspected that temperature records from weather stations, which could be used in predicting the outcome of biological control in different climates, would differ from temperatures actually experienced by *S. molesta*. Consequently, a study was conducted to allow temperatures experienced by the plant to be predicted from standard meteorological data. It was found for one site that the plant was warmer than the air in a nearby Stevenson's screen most of the time and that good predictions of hourly temperatures experienced by the plant could be made from daily air maximum and minimum temperatures and a term representing inertia in seasonal changes of water temperature (Room and Kerr 1983). The generality of these findings has yet to be validated for other sites.

The studies of effects of temperature and nutrients on growth by *S. molesta* by Mitchell and Tur (1975) and Cary and Weerts (1981) are being extended, particularly in the field. It has been found that growth rate can be predicted with some accuracy using corrected weather station temperatures and the concentration of nitrogen in the plant. Flushes of nutrients in water, as occur in runoff after heavy rain, resulted in peaks of nitrogen and phosphorus concentrations in plant tissues several days later, followed by peaks in growth rate after another week. The critical concentration of nitrogen in plant tissues for growth was found to be near 0.9% dry weight and there was a rapid drop in tissue concentrations of nitrogen and phosphorus as buds developed into mature ramets.

Being sterile, population growth in *S. molesta* is entirely dependent on survival and development of meristems. Studies have been made of the spatial arrangement and dynamics of meristems (Room 1983) and computer models have been built to simulate population change under different conditions of insect and nutrient supply (Room 1985).

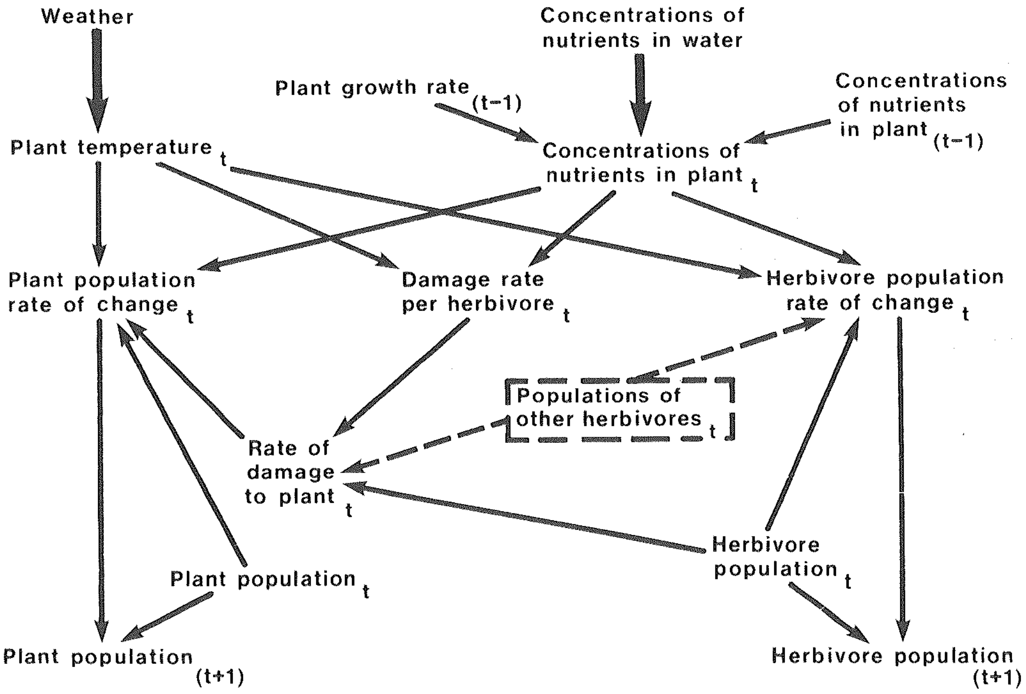

Fig. 1. Conceptual model of the most important interactions expected to take place between *Salvinia molesta* Mitchell and a biological control agent. This model is used to plan and integrate studies of particular interactions. Arrows go from independent to dependent variables and complexities due to the presence of a second control agent are indicated by dashed lines. t = time interval.

The models showed, for example, that growth of a typical population of the weed should be stopped by destruction of 50% of all buds which start to develop. Experiments are underway to examine the effects of insect damage and manual clipping on plant growth. Field experiments investigating the relationships between temperature, nutrients, insect damage and plant growth have shown a range of effects from reduced plant growth, to compensation, and even stimulated growth.

Laboratory Studies of Cyrtobagous salviniae

It was initially thought that the *Cyrtobagous* sp. found on *S. molesta* in Brazil was *C. singularis* (Forno 1981; Forno *et al.* 1983) and it was hoped that a biotype had been obtained which would be more effective against *S. molesta* than that collected from *S. auriculata* in Trinidad by Bennett (1975). However, comparison of the morphology and biology of insects from the two sources showed that those from *S. molesta* were a different, then undescribed species of *Cyrtobagous* (Sands 1983; Sands and Schotz 1985). The new species was subsequently named *C. salviniae* (Calder and Sands 1985).

The biology of *C. salviniae* was described by Forno *et al.* (1983) and Sands *et al.* (1983). The insect can only breed on species in the genus *Salvinia* (Forno and Bourne 1984). In laboratory tests adults fed actively on *Pistia stratiotes* L. (Araceae) and produced a single feeding scar on *Ipomoea batatas* (L.) Lam. (Convolvulaceae), but no breeding took place and none of a further 44 plant species was attacked. Laboratory studies have suggested minimum temperatures for various activities as follows: oviposition 21°C; egg hatch 19°C; larval development 16.3°C; pupal development 19.6°C; adult feeding 13°C; and have determined the effects of different constant temperatures on rates of development. The optimum temperature was 30°C, at which the complete life-cycle occupied 6 wks. An increase of 0.5% in the dry weight concentration of nitrogen in *S. molesta* decreased larval development time by 4.1 days at all temperatures and more than doubled the fecundity of adult females (Sands and Schotz, pers. comm.). Adults preferentially attacked buds, known to contain more nitrogen than other tissues, but varying the concentration of nitrogen had no effect on feeding activity.

Adult *C. salviniae* each destroyed about five buds of *S. molesta*/wk and live for 8 wks at 26°C. During their development, larvae each tunnelled through 2.4 sections of rhizome containing $< 1.5\%$ N or 1.2 sections containing $> 1.5\%$ N. Feeding by adults alone and by larvae alone has been observed to reduce growth by *S. molesta* significantly and experiments are in progress to relate the effects on growth to population densities of the insect, temperatures and availability of nitrogen.

Laboratory Studies of Samea multiplicalis

Information on the biology of *S. multiplicalis* additional to that recorded by Bennett (1966), Sankaran and Ramaseshiah (1973), Knopf and Habek (1976) and DeLoach *et al.* (1979) has been presented by Sands and Kassulke (1984) and Forno and Bourne (1984). In addition to *Salvinia* spp. the species breeds on *P. stratiotes* and *Azolla pinnata* R. Br. (Salviniaceae). It produced feeding scars on 13 of a further 50 species of plants, none of which supported complete larval development. Prior to release in Australia, much effort was expended in eliminating a *Nosema* microsporidian disease from the colony imported from Brazil.

Experiments in progress suggest that the optimum temperature for development is close to 30°C, at which the life-cycle takes about 24 days to complete. The minimum temperature for development is close to 11°C and all larvae held at constant 36°C died. Taylor (1984) showed that larvae fed *S. molesta* containing $< 1.35\%$ nitrogen in their first two instars pass through a supernumerary moult and spent up to 70% more time developing to pupation. In addition, larval mortality was higher when larvae were fed low-nitrogen tissues, and adult females which developed from larvae fed on plant tissues containing 2% nitrogen matured twice as many eggs as females from larvae fed on tissues containing 1% nitrogen.

Larvae of *S. multiplicalis* chew holes through the expanded leaves of *S. molesta*, consuming the equivalent of four mature leaves during development. Experiments are in progress to measure the effects of this damage on growth by the plant. Initial results indicate that the plant can sustain very high levels of leaf destruction without losing the ability to regrow.

Field Monitoring of Releases

The first release of *C. salviniae* was spectacularly successful, with the insect destroying the largest infestation of *S. molesta* in Australia, of some 10,000 tonnes, in less than 1 yr (Room *et al.* 1981). This insect has become established at sites from Brisbane to Cairns along the east coast, at Darwin and Mt. Isa (Room *et al.* 1984) and in Papua New Guinea (Thomas and Room 1985). Air temperatures at these sites have ranged from < 0°C to > 45°C and the weed has been, or appears to be in the process of being controlled at all of them. In all cases, *C. salviniae* has dispersed initially at rates of only a few metres/month. Berlese funnels have been found to give accurate estimates of adult population densities (Boland and Room 1983).

S. multiplicalis has been released, and become established at several sites in north-eastern Australia and spread at least 170 km north and south in 20 months (Room *et al.* 1984). Air temperatures at the sites colonised ranged from < 0°C to > 45°C. Populations of the insect have repeatedly caused extensive damage to *S. molesta* but the weed has regrown following decline in the insect populations and is not considered to be under control. Population crashes of the insect have coincided with periods of high temperature and native Australian parasites have been reared from field-collected larvae.

An experiment is in progress in which *C. salviniae* and *S. multiplicalis* are being released separately, into two cages each, at each of three sites separated by 600 km on a north–south transect. The *S. molesta* in one of each pair of cages is being fertilised with urea and it is hoped to gain useful information on the effects of climate and nutrition on interactions between the plant and its herbivores. The results to date show that application of urea can greatly increase the rates of population increase of the plant and of both insects.

S. multiplicalis breeds faster and disperses faster than *C. salviniae* and it would be reasonable to expect the former to be the more effective control agent. At this stage there seem to be five possible explanations why this is not the case. Compared with *C. salviniae*: (1) *S. multiplicalis* causes damage which has less effect/unit of tissue removed; (2) it suffers mortality from native Australian parasites; (3) it is more sensitive to high temperatures; (4) intra-specific competition may stop population densities from being maintained at levels sufficient to destroy the ability of the plant to regrow; and (5) it may be more susceptible to damage-induced defences (Rhoades 1983) produced by the plant. These effects are not necessarily mutually exclusive and may not apply to the same extent once *S. multiplicalis* becomes established in cooler, more southerly parts of Australia.

The Future

Populations of the plant and insects in the field will continue to be monitored to observe the dynamic equilibria and geographical limits attained and to evaluate possible effects of native Australian predators, parasites and pathogens on the insects.

Feeding by *C. salviniae* which damages buds and rhizomes, and by *S. multiplicalis*, which damages leaves, is likely to have different effects on the quality of undamaged tissues remaining, and experiments are planned to investigate this and other aspects of interference or synergism between the two insects. The results, and those of the other studies described above, will be used to extend the models of plant growth to include insect dynamics and their effects. A model of the plant–herbivore system, driven by weather and nutrients, will then be used to make predictions about the geographical limits of the component species and the degree of control to be expected in contrasting environments. It is hoped to test the model, and the understanding of the system that it represents, by creating new, isolated, infestations of *S. molesta* in different parts of Australia and then releasing the insects on them.

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