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Plant Architecture and How Biological Control Agents Affect the Dynamics of Weeds

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Abstract

Plants are constructed of modules such as roots, shoots and leaves, which are produced in a genetically determined pattern or architecture. Plants respond to the environment more by changing the number and distribution of these modules rather than the size of modules. The importance of damage by biological control agents for plant dynamics depends not only on the amount of tissue destroyed but also on the age and position of the modules damaged. Age and position determine the importance of a module to a plant and to its potential to grow and reproduce. It is suggested that the relative effectiveness of different control agents might be better understood by comparing their effects on plant architecture. Use of this architectural approach is illustrated for insects attacking the floating weed *Salvinia molesta*.

Configuration des Plantes et Effets des Agents de Lutte Biologique sur la Dynamique des Plantes Nuisibles

Les plantes sont constituées de modules, comme les racines, les pousses et les feuilles, qui se développent selon un modèle ou une configuration génétique déterminée. Elles réagissent davantage à leur milieu par la modification du nombre et de la distribution de leurs modules plutôt que par la modification de la taille des modules. Sur le plan de la dynamique des plantes, l'importance des dégâts dépend non seulement de la quantité de tissus détruits mais également de l'âge et de la position des modules endommagés. L'âge et la position déterminent dans quelle mesure un module est important pour le plant entier actuel et pour le potentiel de croissance et de reproduction de ce dernier. Des insectes qui attaquent la plant nuisible flottante *Salvinia molesta* sont utilisés pour illustrer comment l'étude de la configuration des plantes peut permettre de comprendre le rôle des agents biologiques.

Introduction

Though plants stay still to be counted, there are difficulties in studying their population dynamics which are not usually encountered in studies of animals. Levin (1976), for example, discussed the difficulty of defining a species when there is such a range of breeding systems among plants and Harper (1977), White (1979) and Whitham and Slobodchikoff (1981) discussed the difficulty of defining an individual when there is such a range of cloning and somatic mutation among plants. Harper (1976) made the distinction, followed here, between genets, or genetic individuals each derived from a single zygote, and ramets, or ecological individuals which can live independently even though a number may have originated from a single zygote. His restriction of the term reproduction to the production of new zygotes (Harper 1977) is also followed.

Ramets are themselves composed of populations of parts, or modules, such as leaves, shoots and branches. Ramets usually respond to their environment more by changing the number and arrangement of the modules they produce rather than changing the size or shape of individual modules (Bradshaw 1965; Harper 1977). Plants depend on diffuse resources and, unlike all animals except colonial ones such as hydroids, growth generally results in increased capture of resources as well as increased costs of maintenance. Most plants respond to shortages by shifting investment into growth of those parts which capture whatever resource is limiting. Shoot–root ratios, for example, can vary enormously depending on whether light or water and nutrients are in short supply. At any moment, particular modules of a plant are sources and other are sinks for particular resources. The source/sink role depends not only on type of module, but changes with a module's age and position within a plant. The effects of damage therefore depend on ages and positions of modules damaged as well as on their types.

Most herbivores and plant pathogens attack certain kinds of modules and not others, for example leaves but not roots or stems, and they usually prefer only those modules of particular ages in particular positions on the plant because of variations in toughness, nutrient content, defensive chemicals or microclimate (Denno and McClure 1983). This paper describes a way of relating attack on specific modules to growth of ramets and the dynamics of populations of ramets.

The Concept of Plant Architecture

Though it is unusual for two ramets to have an identical arrangement of modules, it is common experience that structural variation is within limits which allow fairly accurate identification of ramets to species based on general shape alone. Halle *et al.* (1978) have extended this observation into the concept of a genetically encoded 'architectural model', or arrangement of modules, which is expressed most fully under conditions optimal for growth. The architecture is expressed through genetic control of the angles and sequence of branching, and of whether indeterminate vegetative or determinate reproductive modules will be produced. Growth hormones and electrical and pressure gradients control when meristems will divide, the sequence in which the resultant parts will grow or remain dormant, and the types of modules produced (Leopold and Kriedemann 1975).

Under sub-optimal conditions the architectural model is expressed less completely, with the details of expression depending on the exact position and timing of environmental factors. For example, shading on one side of a tree commonly reduces the production of branches on that side. Ward (1964), Gill (1971), Fisher and Tomlinson (1973) and Maillette (1982*a*, *b*) have shown that the expression of architecture by a plant can be defined by the probabilities that meristems will develop into modules of particular types within certain intervals of time.

Architecture and Plant Population Dynamics

The architecture of a plant imposes constraints on the rate of increase of populations of each type of module, and in this way on the growth of individual ramets. For example, a plant which branches by apical bifurcation has the potential for much faster growth than a plant which produces lateral branches (Fig. 1). Through growth of individual ramets, the architecture imposes constraints on increase of populations of ramets (and genets) because faster-growing ramets become larger and can produce more offspring, whether by reproduction or vegetative proliferation.

Similarly, sexual reproduction requires that some meristems develop into reproductive modules, leaving fewer meristems to continue indeterminate growth. This reduces the size of a ramet, the number of reproductive modules and the number of vegetative propagules which can be produced later. Watson (1984), for example, found that vegetative production of new ramets in flowering compared with non-flowering clones of water hyacinth (*Eichhornia crassipes* [Mart.] Solms-Laubach; Pontederiaceae) was limited by the availability of meristems rather than availability of resources.

In environments varying in time, there will be a tradeoff between committing meristems to reproductive modules when conditions are good, and the risk of continued indeterminate growth which may be followed by production of greater numbers of reproductive modules if conditions remain favourable. For example, *Floerkea proserpinacoides* (Limnanthaceae), a short-lived ephemeral, commits meristems to reproductive modules at an earlier stage of growth when crowded than when less crowded (Smith 1984). Extreme examples are provided by palms such as *Corphya alata* in which the inflorescence is terminal and flowering ends the life of the tree (Halle *et al.* 1978). However, many plants retain the potential for phenotypic plasticity by holding a substantial proportion of their meristems dormant, only allowing them to develop after stimulation by damage or other changes in the environment.

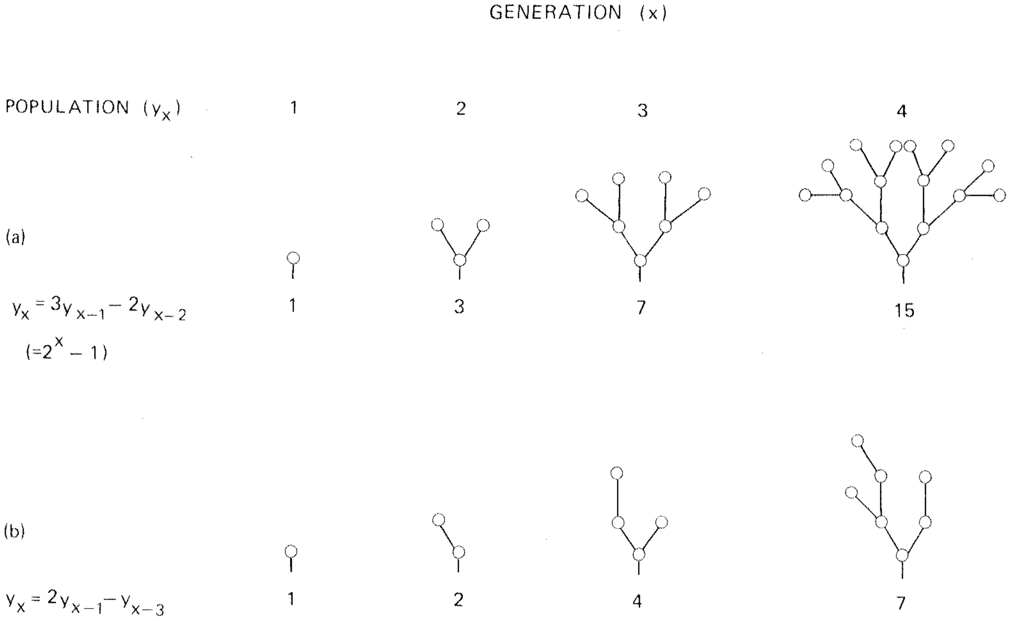

Fig. 1. Growth of populations of modules (y_x) in the first four module generations (x) compared for plants which branch by apical bifurcation (a) and by development of lateral buds one generation after apical buds (b). Relative growth rates stabilise 0.69 modules/mod./gen. for (a) and 0.49 mod./mod./gen. for (b).

In environments varying in space, there will be a similar tradeoff between committing currently available resources to reproduction allowing further vegetative extension which may encounter richer supplies of resources and allow greater reproductive effort later. The observed architectures of plants represent conservative, compromise, answers to these interlocking questions of action 'now or later' and 'here or elsewhere' facing all organisms in an uncertain world (Southwood 1977).

Architecture and Effects of Damage on Plant Populations

Herbivores and pathogens damage plants in a variety of ways but all probably affect the expression of architecture, either through direct removal of mature or developing modules or through removal of resources forcing plants to alter their priorities and timing for development of meristems. The changed expression of architecture can be used for comparing the effects of different kinds of attack in a way which relates numbers of herbivores to changes in a plant's potential for growth and reproduction.

The effects of damage can be assessed by measuring the proportions of meristems which develop into modules of particular types in particular intervals of time in the presence of the damaging factor acting at different intensities. The proportions, expressed as probabilities, can then be used to calculate effects on rates of change of populations of modules and ramets of the plant.

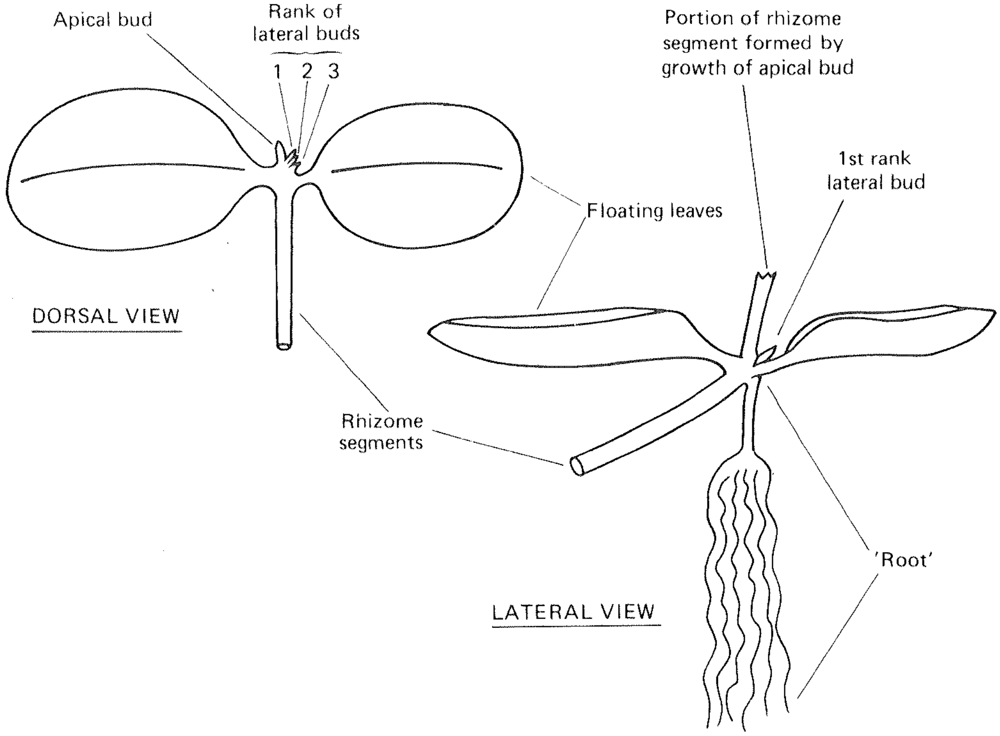

Fig. 2. Diagrammatic representations of ramets of *Salvinia molesta* D.S. Mitchell in which (dorsal view) the apical bud has yet to develop and (lateral view) the apical bud, but none of the lateral buds, has grown into a new ramet in continuation of the parent branch.

Salvinia molesta — A Simple Example

The floating fern *Salvinia molesta* D.S. Mitchell (Salviniaceae) has several characteristics which allow easy application of this architectural approach. There is no sexual reproduction and the entire species appears to be a single genet without variation due to genetic mutations. Having no gametophyte stage in the life cycle, population processes depend solely on growth and survival of vegetative parts. The rate of growth is very high under conditions close to optimal, allowing experiments to be conducted quickly. All parts of the plant are accessible without excavation, branching takes place in two rather than three dimensions and ramets are formed of a constant small number of parts.

Each ramet consists of a pair of leaves which float on the water surface, a dissected leaf which hangs below and functions as a root, and a horizontal segment of rhizome (Fig. 2). Each ramet initially bears an apical bud, which usually develops into a new ramet in continuation of the parent rhizome branch, and three lateral buds which can develop into the first ramets of new side-branches. The growth of buds gives rise to two-dimensional 'trees' of rhizomes which continue to grow distally while senescing and fragmenting proximally. The morphology and anatomy of ramets have been described by Bonnet (1955) and Croxdale (1978, 1979, 1981). In the present study, ramets were chosen as the modules of the plant's architecture because they are constructed of a constant number of parts.

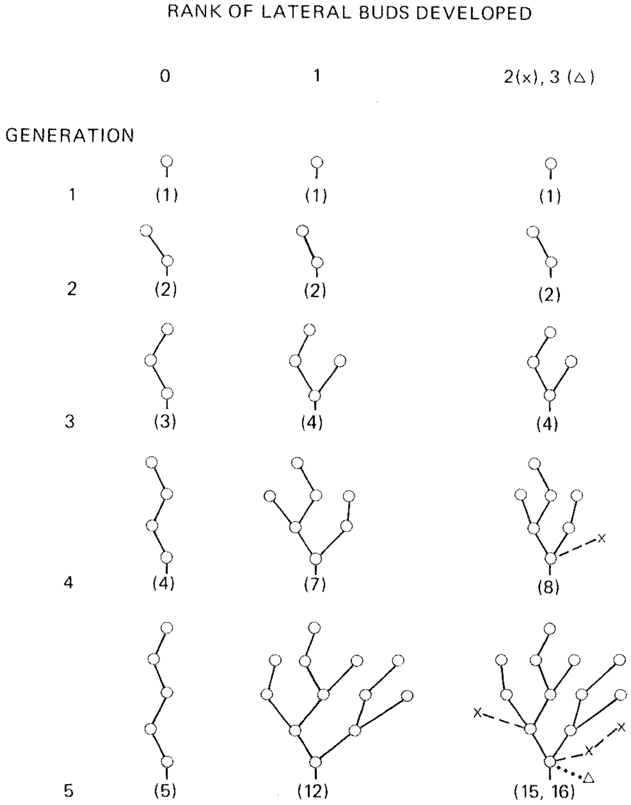

Fig. 3. Architecture of *Salvinia molesta* D.S. Mitchell: five ramet-generations of growth from a single ramet (○) with complete development of zero, first-, second- (x) and third- (△) rank lateral buds. Populations of ramets in each generation are shown in parentheses.

The rhizome architecture of *S. molesta* (Fig. 3) was investigated by mapping rhizomes connecting groups of ramets, referred to as colonies, collected from a range of conditions but having suffered no damage (Room 1983). Under conditions stimulating development of all lateral buds, there was a sequence of development in each ramet from apical to first- to second- to third-rank lateral buds, each separated in physiological time by one ramet generation. Second- and third-rank buds do not usually develop in natural waters and neither do all first-rank buds. Development of second- and third-rank buds occurred frequently in a sewage treatment lagoon and the branches which resulted followed the same rules of growth as branches arising from first-rank lateral buds. This appeared to be an example of adaptive reiteration (Bell and Tomlinson 1980) in which the basic architecture for first-rank branches was repeated under conditions 'better' than those which stimulate development of all first-rank buds.

A difference equation model was constructed (Appendix 1) which described growth in numbers of ramets for the cases of complete expression of first-, second- and third-rank branching (Fig. 3) (Room 1983). The model was extended to include loss of ramets due to senescence (Fig. 4), loss of ramets and individual buds due to damage, and the fission of colonies resulting from loss of ramets. The assumption of complete expression of any degree of branching was unrealistic, so a stochastic simulation model was also built which used age- and position-specific probabilities of bud development and a set of branching rules to generate intermediate degrees of branching. The simulation model included routines representing losses due to senescence and damage and compensation for damage. Its performance was checked for the special cases of complete first- and second-rank branching by comparison with the difference equation model. A graphics facility allowed maps of colonies grown and damaged by the simulation model to be displayed on a television monitor.

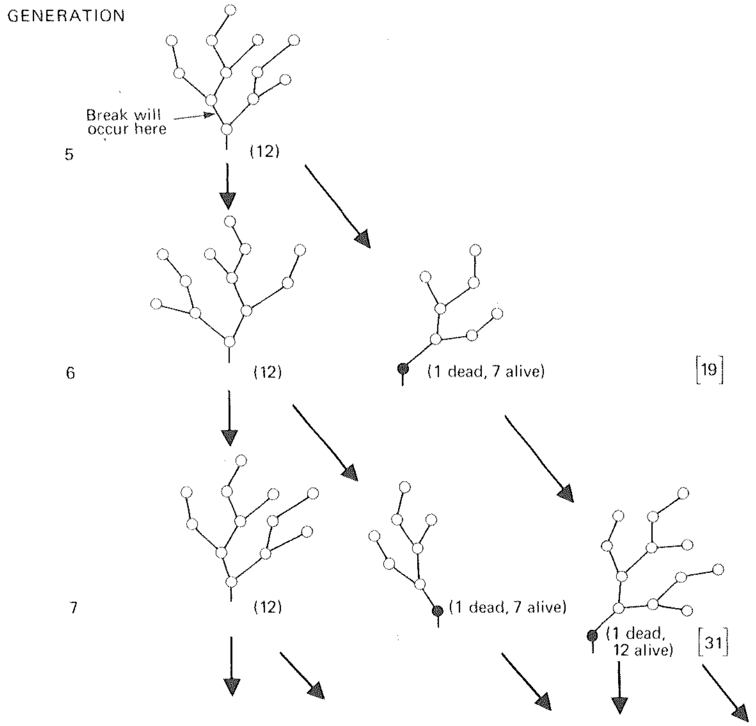

Fig. 4. Continued growth of the colony having complete development of first-rank lateral buds in Fig. 3 when ramets die at a constant age of five ramet-generations and colonies fragment as the dead rhizome segments break. Dead ramets are represented by solid circles, gross populations are shown in parentheses, and nett populations in square brackets.

The models were run with different percentages of buds alone being destroyed, and then with buds plus ramets being destroyed, and the effects on rates of change of populations of ramets and of colonies were calculated assuming no growth in compensation for damage (Fig. 5). During its lifetime, each ramet produces two new ramets for complete first-rank branching, or three new ramets for complete second-rank branching (Fig. 3). Ramets will simply replace themselves, rather than increasing their population, if 50% or 67% respectively of developing buds are destroyed as shown by curves c and a for $r = 0$ in Fig. 5. Probabilities of bud development in the field are usually less than 1.0 (Room 1983) and curves e and f show how destruction of buds alone depressed population increase for incomplete first-rank branching. The irregular shapes of curves e and f were due to the use of a random number generator which resulted in variation between the 50 colonies simulated for each point in the curves. Curve d shows that destruction in each generation of 44% of developing buds plus 22% of ramets less than three generations old should result in zero population growth under conditions otherwise stimulating complete first-rank branching.

The two biological control agents for *S. molesta* which have been released in Australia (Room *et al.* 1981, 1984) cause different kinds of damage to the plant. The weevil, *Cyrtobagous salviniae* Calder & Sands (Coleoptera: Curculionidae), causes most damage to buds and young sections of rhizomes, and larvae of the moth, *Samea multiplicalis* (Guenée) (Lepidoptera: Pyralidae), damage expanded leaves. Studies of the effects of the different kinds of damage are still in progress (Room *et al.* 1985) but preliminary results will be used below to show how numbers of insects can be related to reduced growth by the plant.

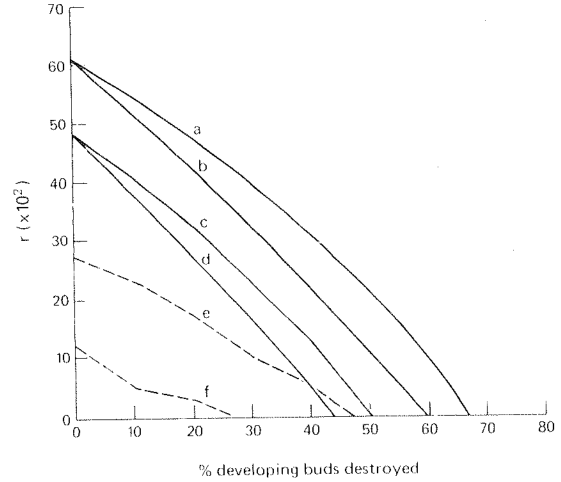

Fig. 5. Rates of ramet population increase (r) for *Salvinia molesta* D.S. Mitchell derived from the difference equation model (a to d) and simulation model (a to f): (a, c) complete first- and second-rank branching respectively, only buds destroyed; (b, d) as for (a, c) but with young ramets destroyed in addition to and at half the rate of, buds destroyed; (e, f) buds only destroyed when probabilities of development are 1.0 for apical buds and 0.2 and 0.03 respectively for first-rank lateral buds remaining.

Under conditions close to the optimum for the insects, it appears that *C. salviniae* adults each destroy about five buds (Forno and Bourne, pers. comm.) and their larvae each destroy about 1.2 rhizome segments (Sands *et al.* 1983) in one ramet generation of *S. molesta*. In the absence of compensation by the plant, 10 adults per 100 buds should result in destruction of 50% of buds and control of the weed in most conditions experienced in the field. Alternatively, 8.8 adults plus 18.3 larvae/100 buds should have the same effect by destroying 44% of buds plus 22% of young ramets.

In fact, the plant responds to destruction of buds, or ramets bearing buds, by increasing the probabilities of development of buds eligible to develop in the next ramet generation while keeping generation-time constant (M.H. Julien, pers. comm.). This seems to be a case of instantaneous compensation (Hearn and Room 1978) in which materials which would have been allocated to destroyed buds are redirected to remaining buds. The depression of ramet population increase by damage is reduced and the expression of architecture is changed, exhibited sometimes by the growth of second or higher rank branches where previously there were only first-rank branches. Making the simulation model compensate for damage by replacing each bud destroyed in one generation by a new bud in the next generation suggested that 67% of buds alone, or 60% of buds plus 30% of young ramets, should be destroyed to result in control of the weed. This level of damage should be caused by populations of 13.4 adults/100 developing buds in the case of buds only destroyed, or by 12 adults plus 25 larvae/100 developing buds in the case of buds and ramets destroyed. These estimates compare with maxima of *c.* 10 adults plus unknown numbers of larvae/100 buds observed just prior to rapid destruction of *S. molesta* mats in several lakes in Papua New Guinea (P.A. Thomas and P.M. Room, unpubl. data).

Preliminary studies of *S. multiplicalis* suggest that its damage increases the duration of each ramet-generation (L. Duivenvoorden, pers. comm.). The effect may be due to removal of photosynthetic area, or resources, and might result in the development of fewer buds than in undamaged plants. This could be simulated by reducing probabilities of bud development and increasing the duration of a ramet generation according to the population density of the insect and consequent severity of damage.

Discussion

The approach described here gives understanding of plant/herbivore interactions at a level intermediate between that given by physiological or chemical measurements and that given by measurements of weight, volume or area occupied by plants. Appropriate records can be made non-destructively, at least for above-ground parts, and the results allow the numbers of herbivores present at one time to be used to predict the numbers and types of plant modules present in the future.

By using probabilities of development in a series of time intervals, the technique can take into account the timing of damage and can be used to show how delays in growth caused by damage can reduce the competitiveness of individual plants. Unlike *S. molesta*, many plants have a seasonal cycle of reproduction which must be completed before physical conditions become unsuitable. For those plants, the timing of attack in relation to the time available for compensatory growth will be just as important as the ages, positions and numbers of modules damaged (Harris 1971; Hearn and Room 1978).

The architectures of plants are compromises resulting from past actions of sometimes opposing selective forces and architectures are unlikely to be expressed as optimal arrangements of modules for the exploitation of any particular circumstances. Further, the expression of architecture stimulated during early development might not be the most efficient for conditions experienced later. A common response to this situation is self-pruning, often seen for example in trees grown in dense plantations (Kozlowski 1973). It follows that damage of certain types at certain times could prune plants to give more efficient arrangements of modules, and hence more growth, of damaged compared with undamaged individuals (Harris 1974). However, such positive effects must have been small, or unpredictable, or there would have been selection for the architecture to be modified to give the same arrangement of modules without incurring the losses due to pruning.

Though the number and arrangement of modules is generally more plastic than their size, shape and chemical quality (Bradshaw 1965), there is variation among modules of the same type and this variation is suspected to be of great importance to plant–herbivore interactions (Denno and McClure 1983). The architectural approach outlined here could be used to place information on such variation, and associated patterns of damage, into the context of growth of whole ramets and populations of ramets. For example, modules containing higher concentrations of defensive chemicals might be less susceptible to attack but might also grow more slowly (Cates 1975; Whitham and Slobodchikoff 1981). The position, number and timing of appearance of such modules in relation to overall growth and the timing of attack should have significant effects on rates of change of plant populations which could be explored using architectural models.

Most plants have more complex morphologies and biologies than *S. molesta* and application to them of the architectural approach would require a greater investment of effort. However, Fisher and Honda (1979) and Maillette (1982*a*, *b*) have shown that even the structural dynamics of trees can be analysed and modelled in appropriate ways and there seems to be no alternative method for relating the position, nature and timing of damage, and effects of the environment, to growth and reproduction of plants. Could measuring probabilities of meristem development satisfy 'one of the most urgent needs in the biological control of weeds ... a method by which individual stresses on the target plant, whatever their origin, can be quantified in a common unit and summed' (Harris 1981)?

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Appendix 1

Computer Model of Biological Control of Salvinia

The following is a listing of a model which was demonstrated at the Symposium. The model is a simplified version of that described in this paper and it is written in BASIC for the Commodore 64 microcomputer. It uses the SCREEN-GRAPHICS-64 software package marketed by Abacus Software which must be wedged into the C-64 memory before the model is loaded.

The model grows branching rhizomes of salvinia on a TV screen, in colour, and shows old sections of rhizome being removed by senescence and younger sections and buds being removed by larvae and adults respectively of the biological control agent *Cyrtobagous salviniae*. Records of the input paramets being used and counts of the numbers of generations of growth, numbers of ramets and numbers of colonies present are shown in the corners of the screen. Sound effects are used to distinguish between birth and death of ramets and to indicate when biological control has been achieved. A menu enables initialisation with parameters such as the longevity of undamaged ramets and probabilities of attack by adults and larvae of *C. salviniae*. Note that special Commodore characters controlling spacing in PRINT and INPUT statements in lines 6 to 55 could not be shown in this listing and the menu will appear crowded unless those characters are added.

```
0 REM:      SALVINIA
1 REM: RA(NO,V) V=1ANGLE, 2X, 3Y, 4AGE, 5FROM, 6TOMAIN, 7TO1ST, 8RIGHT/LEFT
2 REM:
5 M=100:DIMRAM(M,8):S=54272:S1=S+1:S2=S+4:S3=S+5:S4=S+15:S5=S+24
6 PRINT"         SALVINIA RHIZOME MODEL":PRINT"  PRESS RETURN FOR DEFAULT OPTIONS"
7 INPUT"RAMET LIFESPAN (RAMET GENERATIONS)  4";MA:MA=MA+2
8 INPUT"LATERAL BUD DELAY (RAMET GENS.)  1";AB
9 INPUT"APICAL & LATERAL ANGLES(RADIANS)  .6,.7";T,TB
10 SA$="L.ANGLE"+STR$(TB):SM$="A.ANGLE"+STR$(T):OA$="R. LIFE"+STR$(MA-2)
11 BG$="L.DELAY"+STR$(AB):LPOP=0
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12 INPUT"APICAL & LAT. PROBABILITIES  1,1";PM,PB:PM$="A.PROB"+STR$(PM)
13 INPUT"% BUDS & RAMETS DESTROYED  0,0";B%,R%:BD$="%BUD D"+STR$(B%)
14 PB$="L.PROB"+STR$(PB):R$="%RAM D"+STR$(R%)
18 INPUT"LENGTH OF RHIZOME SEGMENT(00;10-35)  35";R
19 IFR=0THEN6
20 Q=R/7:NX=2:CL=0:ZZ=0:DD=0:LPOP=0
40 PRINT"          RUN CONTROLS":PRINT"         * FOR CONTINUOUS RUN"
42 PRINT"        A TO ABORT RUN"
45 PRINT"        R TO RESET":PRINT"         F5 MEANS PRESS FUNCTION 5"
50 FORI=0TO500:NEXTI:FORI=1TONR+5:FORJ=1TO8:RA(I,J)=0:NEXT:NEXT:RA(0,4)=99
55 PRINT"          PRESS BAR TO START":C$=""
60 GETA$:IFA$=""THEN60
75 PRINT"":NR=1:NW=1:HIRES6,10
77 CHAR1,1,198,7,"GENERATION":CHAR1,1,190,7,"NO RAMETS"
80 CHAR1,1,182,7,"NO COLONIES":CHAR1,1,174,7,"RGR RAMETS"
82 CHAR1,1,8,1,SA$:CHAR1,1,16,1,SM$:CHAR1,1,24,1,BG$:CHAR1,1,32,1,OA$
85 CHAR1,245,8,1,R$:CHAR1,245,16,1,BD$:CHAR1,245,24,1,PB$:CHAR1,245,32,1,PM$
88 RAM(1,1)=T/2:RAM(1,2)=160:RAM(1,3)=90-2*R:RAM(1,8)=1:RAM(1,4)=2:ZA=0
90 CIRCLERAM(1,2),RAM(1,3),Q,1:DRAWRAM(1,2),RAM(1,3),RAM(1,2),RAM(1,3)-R/3,1
95 COPY1,2000:COPY2,3000:COPY3,4000:SPRITE1,1,0,0,0,0,7:SPRITE3,3,0,0,0,0,2
96 IFB%<>0THEN:PLACE1,235,26
97 IFR%<>0THEN:PLACE3,235,20
130 REM:
131 REM:   GENERATION AND RAMET LOOPS
132 FORZ=1TO99:FORN=1TONW:IFN=1THEN140
134 REM:    DESTROYS NEW RAMETS
135 IFRAM(N,4)<3ANDR%>100*RND(1)THENRAM(N,7)=999:RAM(N,6)=999:GOTO180
140 IFRAM(N,4)>MATHEN180
141 IFRAM(N,6)=0THENTY=0:GOTO150
142 IFRAM(N,7)>0THEN180
143 IFRAM(N,4)<AB+2THEN180
145 TY=1:GOTO152
150 IFPM>RND(1)THEN160
151 GOTO180
152 IFPB>RND(1)THEN160
153 GOTO180
154 REM:    DESTROYS BUDS
160 IFRA(N,6+TY)=998THEN170
163 IFB%>100*RND(1)THENRA(N,6+TY)=998:PLACE1,RA(N,2)+12,RA(N,3)+19+Q:
    GOSUB1200:GOTO170
168 GOSUB500:IFZZ=1THEN14
170 IFAB=0ANDTY=0THEN145
180 NEXTN:NW=NR:GOSUB600:IFZA=1THEN18
185 POP=NR-DD:IFPOP=0ORLPOP=0THENRGR=0:GOTO189
187 RGR=INT(100*(LOG(POP)-LOG(LPOP)))/100
189 CHAR1,90,198,2,STR$(Z):CHAR1,90,190,2,STR$(POP):CHAR1,90,182,2,STR$(CL+1)
190 CHAR1,82,174,2,STR$(RGR):CHAR1,245,198,2,"PRESS BAR"
191 IFC$="*"THEN193
192 GETC$:IFC$=""THEN192
193 IFC$="A"THEN:NORM:GOTO14
194 IFC$="R"THEN:NORM:GOTO6
196 LPOP=POP:MODE1:CHAR1,245,198,2,"PRESS BAR"
197 CHAR1,90,198,2,STR$(Z):CHAR1,90,190,2,STR$(POP):CHAR1,90,182,2,STR$(CL+1)
198 CHAR1,82,174,2,STR$(RGR)
200 MODE0:NEXTZ:END
499 REM:
500 REM: FINDS NEW ANGLES AND POSITIONS
510 X=RAM(N,2):Y=RAM(N,3):IFTY=1THENRAM(N,1)=RAM(N,1)-2*RAM(N,8)*TB
520 C=RAM(N,8)*-1:X1=X+R*SIN(RAM(N,1)):Y1=Y+R*COS(RAM(N,1))
525 GOSUB1000:IFZZ=1THENRETURN
```

```
528 NR=NR+1:IFNR>MTHEN:CHAR1,170,190,2,"ARRAY EXCEEDED: F5":END
529 RAM(NR,4)=1:RAM(NR,5)=N
530 RAM(NR,1)=RAM(N,1)+(C*T):RAM(NR,2)=X1:RAM(NR,3)=Y1
535 IFTY=0THENRAM(N,6)=NR:RAM(NR,8)=C:GOTO550
540 RAM(N,7)=NR:RAM(NR,1)=RAM(N,1)+(-1*C*T):RAM(NR,8)=-1*C
550 RETURN
599 REM:
600 REM: INCREMENTS AGES
610 FORN=1TOM:IFRAM(N,4)=0THENRETURN
620 IFRAM(N,4)=99THEN800
625 IFR<30THEN631
630 MODE1:CHAR1,RAM(N,2),RAM(N,3),1,STR$(RAM(N,4)-2)
631 IFRAM(N,7)=999THEN:PLACE3,RA(N,2)+12,RA(N,3)+12:GOSUB1300:GOTO640
635 RAM(N,4)=RAM(N,4)+1:IFRAM(N,4)<MATHEN780
640 RA(N,4)=99:MODE1:CIRCLERA(N,2),RA(N,3),Q,1:DOTRA(N,2),RA(N,3),1
650 FORU=15TO5STEP-1:POKES5,U:POKES2,129:POKES3,15:POKES1,40:POKES,200:
    NEXT:POKES2,0:POKES3,0
660 IFN=1THEN675
670 TX=RAM(RAM(N,5),2):TY=RAM(RAM(N,5),3):DRAWRA(N,2),RA(N,3),TX,TY,1:GOTO680
675 DRAWRAM(1,2),RAM(1,3),RAM(1,2),RAM(1,3)-R/3,1
680 MODE0:DD=DD+1:T1=RAM(N,5):T2=RAM(N,6):T3=RAM(N,7):IFT2>996ORT3>996THEN750
682 IFRA(T1,4)=99ANDN<>1THEN700
683 IFT2=0ANDT3=0THENCL=CL-1:GOTO760
684 IFT2=0ORT3=0THEN800
685 IFRA(T2,4)=99ANDRA(T3,4)=99THENCL=CL-1:GOTO760
686 IFRA(T2,4)=99ORRA(T3,4)=99THEN800
688 CL=CL+1:GOTO800
692 IFRAM(T2,4)=99ANDRAM(T3,4)=99THENCL=CL-1:GOTO760
700 IFT2=0ANDT3=0THENCL=CL-1:GOTO760
710 IFT2=0ANDRA(T3,4)=99THENCL=CL-1:GOTO760
720 IFT3=0ANDRA(T2,4)=99THENCL=CL-1:GOTO760
725 IFRA(T2,4)=99ANDRA(T3,4)=99THENCL=CL-1:GOTO760
730 IFT2>0ANDRA(T2,4)<>99THEN:IFT3>0ANDRA(T3,4)<>99THENCL=CL+1
740 GOTO800
750 IFRA(T1,4)<>99THEN800
752 IFT2=999ORT3=999THENCL=CL-1:GOTO760
754 IFT2=998ANDT3=998THENCL=CL-1:GOTO760
756 IFT3<>998THEN:IFT2=998ANDRA(T3,4)=99THENCL=CL-1:GOTO760
758 IFT2<>998THEN:IFT3=998ANDRA(T2,4)=99THENCL=CL-1:GOTO760
759 GOTO800
760 IFCL<0THEN:CHAR1,120,110,3,"EXTINCT!   F5":ZA=1:GOSUB900:RETURN
770 GOTO800
780 MODE0:IFR<30THEN800
790 CHAR1,RAM(N,2),RAM(N,3),1,STR$(RAM(N,4)-2)
800 NEXTN
900 REM:     EXTINCTION SOUND
902 IFR%=0ANDB%=0THEN906
905 OFF1:OFF3:SPRITE2,2,0,0,0,0,7:PLACE2,160,100
906 FORV=54272TO54296:POKEV,0:NEXTV
910 POKES5,15:POKES3,15:POKES+6,16:POKES1,38:POKES,126:POKES2,17
920 FORI=50TO250STEP5:POKES1,I:POKES,I-50:NEXT
930 FORI=200TO50STEP-4:POKES1,I:POKES,I-50:NEXT
940 POKES1,34:POKES,75:FORI=0TO100:NEXT
950 POKES2,0:POKES3,0:POKES+6,0:POKES5,0:RETURN
999 REM:
1000 REM: CREATES NEW RAMET
1010 IFX1>320-QTHEN1030
1011 IFX1<QTHEN1030
1012 IFY1>200-QTHEN1030
1013 IFY1<QTHEN1030
```

```
1015 GOTO1050
1020 IFY1<190ANDY1>QTHEN1050
1030 CHAR1,190,190,2,"OUT OF SPACE: F5":ZZ=1:RETURN
1050 DRAWX,Y,X1,Y1,1:CIRCLEX1,Y1,Q,1
1060 POKES1,130:POKES3,9:POKES4,30:POKES5,15:POKES2,21:FORUQ=1TO70
1070 NEXT:POKES2,20:POKES5,0:RETURN
1199 REM: ADULT SOUND
1200 FORV=54272TO54296:POKEV,0:NEXTV
1210 POKES5,15:POKES3,15:POKES+6,16:POKES1,38:POKES,126:POKES2,17
1220 FORI=50TO250STEP5:POKES1,I:POKES,I-50:NEXT
1250 POKES2,0:POKES3,0:POKES+6,0:POKES5,0:RETURN
1299 REM: LARVA SOUND
1300 FORU=20TO5STEP-1:POKES5,U:POKES2,33:POKES3,15:POKES1,40:POKES,200:
     NEXT:POKES2,0:POKES3,0
1310 RETURN
1999 REM:    WEEVIL SPRITE
2000 BIT"000000000000000000000000"
2001 BIT"000000000000000000000000"
2002 BIT"000000000000000111100000"
2003 BIT"000000000000011111111000"
2004 BIT"111000110110111111111100"
2005 BIT"000100101111111111111110"
2006 BIT"000011110111111111111110"
2007 BIT"000011000101101111111111"
2008 BIT"000110001000010111111111"
2009 BIT"000000010000010000010011"
2010 BIT"000000100000010000100000"
2011 BIT"000000100000010001000000"
2012 BIT"000001100000011001110000"
2013 BIT"000000000000000000000000"
2014 BIT"000000000000000000000000"
2015 BIT"000000000000000000000000"
2016 BIT"000000000000000000000000"
2017 BIT"000000000000000000000000"
2018 BIT"000000000000000000000000"
2019 BIT"000000000000000000000000"
2020 BIT"000000000000000000000000"
2999 REM:    DEAD WEEVIL SPRITE
3000 BIT"000000000000000000000000"
3001 BIT"000000000000000000000000"
3002 BIT"001100110011011000000000"
3003 BIT"001100110001101100000000"
3004 BIT"001101100001100011000000"
3005 BIT"111101100000110001100000"
3006 BIT"111000110000011011000000"
3007 BIT"011100011001100110011100"
3008 BIT"001110011110011111111110"
3009 BIT"000011111111111111111111"
3010 BIT"000011111111111111111111"
3011 BIT"000001101100111111111110"
3012 BIT"000000000000011111111100"
3013 BIT"000000000000000111110000"
3014 BIT"000000000000000000000000"
3015 BIT"000000000000000000000000"
3016 BIT"000000000000000000000000"
3017 BIT"000000000000000000000000"
3018 BIT"000000000000000000000000"
3019 BIT"000000000000000000000000"
3020 BIT"000000000000000000000000"
3999 REM:    LARVA SPRITE
```

```
4000 BIT"000000000000000000000000"
4001 BIT"000000000000000000000000"
4002 BIT"000000000000000000000000"
4003 BIT"000000000000000000000000"
4004 BIT"000000000000000000000000"
4005 BIT"000000000000000000000000"
4006 BIT"000000000000000000000000"
4007 BIT"000000000000000000000000"
4008 BIT"000000000111111000000000"
4009 BIT"000000011111111110000000"
4010 BIT"000000111111111111110000"
4011 BIT"000001111111111111111100"
4012 BIT"000001111110000000001111"
4013 BIT"000001111000000000000011"
4014 BIT"000000000000000000000000"
4015 BIT"000000000000000000000000"
4016 BIT"000000000000000000000000"
4017 BIT"000000000000000000000000"
4018 BIT"000000000000000000000000"
4019 BIT"000000000000000000000000"
4020 BIT"000000000000000000000000"
```