INTERNATIONAL ATOMIC ENERGY AGENCY
UNITED NATIONS EDUCATIONAL, SCIENTIFIC AND CULTURAL ORGANIZATION
INTERNATIONAL CENTRE FOR THEORETICAL PHYSICS
I.C.T.P., P.O. BOX 586, 34100 TRIESTE, ITALY, CABLE: CENTRATOM TRIESTE

UNITED NATIONS INDUSTRIAL DEVELOPMENT ORGANIZATION

INTERNATIONAL CENTRE FOR SCIENCE AND HIGH TECHNOLOGY
c/o INTERNATIONAL CENTRE FOR THEORETICAL PHYSICS 34100 TRIESTE (ITALY) VIA GRIGNANO, 9 (ADRIATICO PALACE) P.O. BOX 586 TELEPHONE 040-224572 TELEFAX 040-224575 TELEX 460449 APH I

SMR.648 - 54

SECOND AUTUMN WORKSHOP ON MATHEMATICAL ECOLOGY

(2 - 20 November 1992)

"Energy Partitioning Models and Conservation"

P. Kindlmann
Department of Biomathematics
South Bohemian Biological Research Centre
Czechoslovak Academy of Sciences
37005 Ceske Budejovice
Czechoslovakia

These are preliminary lecture notes, intended only for distribution to participants.

MAIN BUILDING Strada Costiera, 11 Tel. 22401 Telefax 224163 / 224559 Telex 460392 ADRIATICO GUEST HOUSE Via Grignano, 9 Tel. 224241 Telefax 224531 Telex 460449
MICROPROCESSOR LAB. Via Beirut, 31 Tel. 224471 Telefax 224600 GALILEO GUEST HOUSE Via Beirut, 7 Tel. 22401

ENERGY PARTITIONING MODELS AND CONSERVATION

- **review of the state-of-the-art** *(energy partitioning models)*.

- **need of this** approach **in conservation** biology *(case of orchids and other rare plants)*

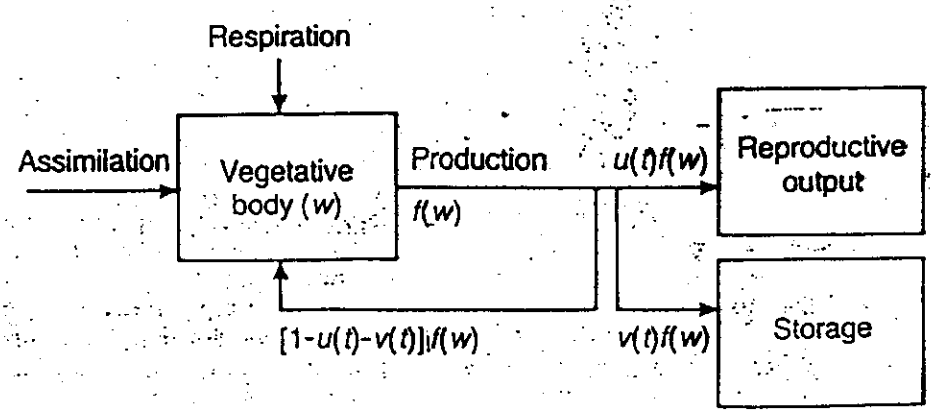
- the **orchid** model *(problems to be solved and some thoughts of how to do it)*

- **preliminary** results from the **empirical** data

- **suggestions** for the future *(model predictions and their validation, application to other problems)*

ENERGY PARTITIONING MODELS

Box 1. Schematic representation of energy allocation



An organism assimilates and dissipates energy at size-dependent rates, and at each moment t allocates the fraction $u(t)$ of surplus energy to reproduction, the fraction $v(t)$ to storage and the remaining part to increase its size w, at a production rate $f(w)$. Control variables $u(t)$ and $v(t)$ are optimized in order to maximize lifetime reproductive output. An additional assumption is that maintenance costs are not optimized, and that they always have priority.

General features:

- nice maths
- empirical data for validation: missing or very few
- predictions: general, vague

Predictions (some examples):

- The best strategy is to continue growth until the change of production rate with respect to increasing body size, multiplied by life expectancy for those attaining adulthood and reproducing successfully, is greater than one. *(Kozlowski & Wiegert, Theor. Pop. Biol. 29:16 (1986))*

- When temporary storage of energy is impossible or too costly, a gradual switch from vegetative to reproductive growth will be optimal. *(Kozlowski & Ziolko, Theor. Pop. Biol. 34:118 (1988))*

- High chances of survival in winter lead to much greater body size. *(Kozlowski, Acta Oecol. 12:11 (1991))*

- When the growth function is concave and the probability of survival is constant, there exists an optimal body size R and the optimal strategy is to grow without reproducing to size R. *(Pugliese, J. Theor. Biol. 126:33 (1987))*

- If the plant is adapted to a slowly changing environment, it should continue to grow until late in a favorable environment but should start reproduction earlier in an unfavorable one, showing large phenotypic plasticity. *(Iwasa, Theor. Pop. Biol. 40:246 (1991))*

RARE PLANTS - CONSERVATION

- need to learn a lot about their bionomy

- use non-destructive methods

Example:

- **plants with** persisting storage orans (e.g., pseudobulbs, tubers)

- tubers condition may influence flowering in **the next season**

- flowering seems to be erratic

Question:

How to describe and **predict flowering patterns without** using destructive methods?

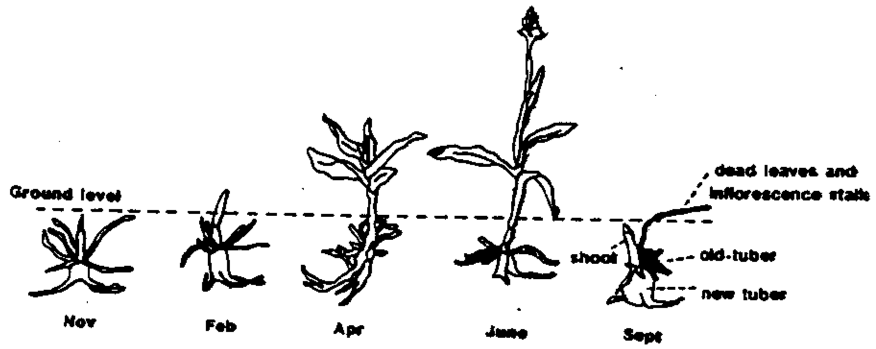


Fig. 4. Generalised phenology of *Dactylorhiza fuchsii*, illustrating tuber formation and annual production of leaves, roots and inflorescence.

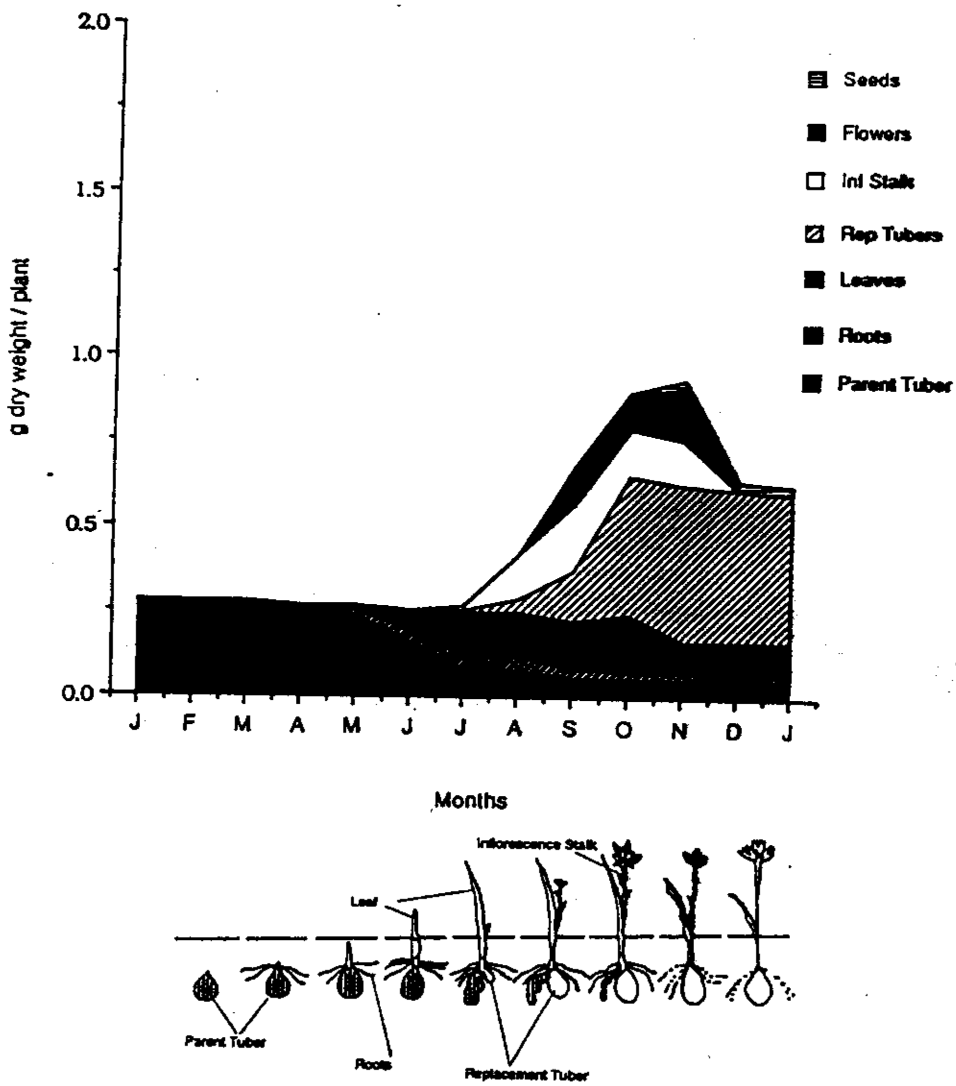


Fig. 2. Phenology of growth and dry matter partitioning in the south west Western Australian terrestrial orchid *Thelymitra fuscolutea*.

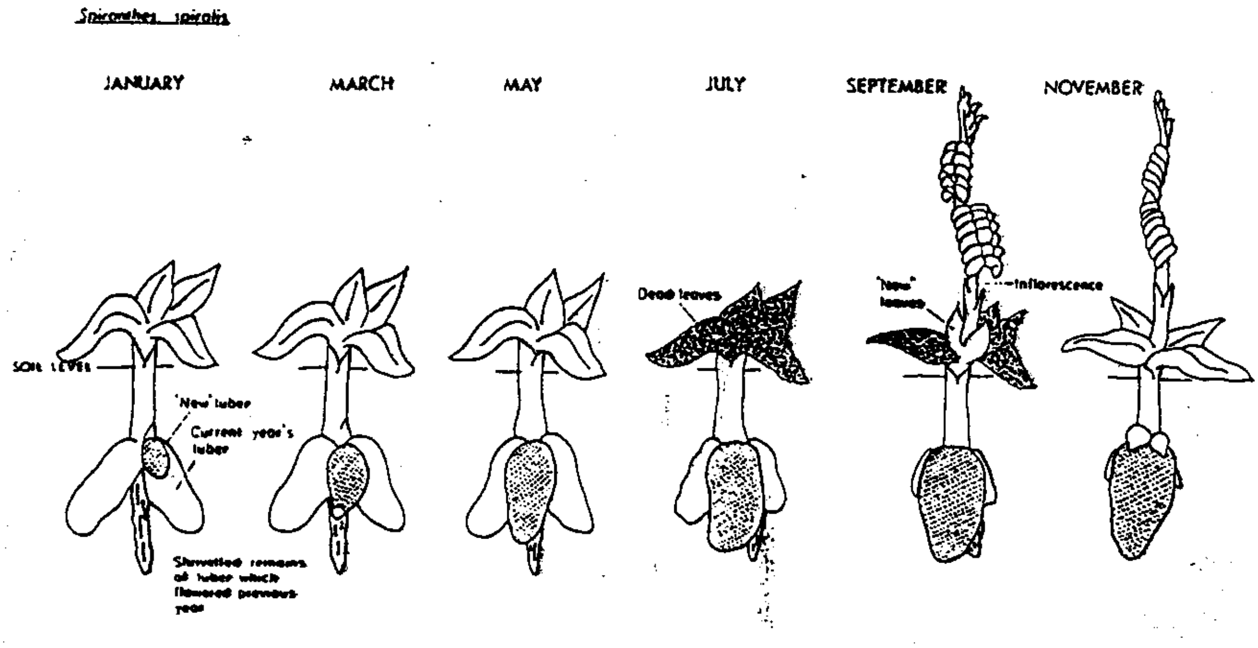


Figure 1 Generalized phenology of *Spiranthes spiralis*, showing formation of tubers and production of leaves and inflorescence

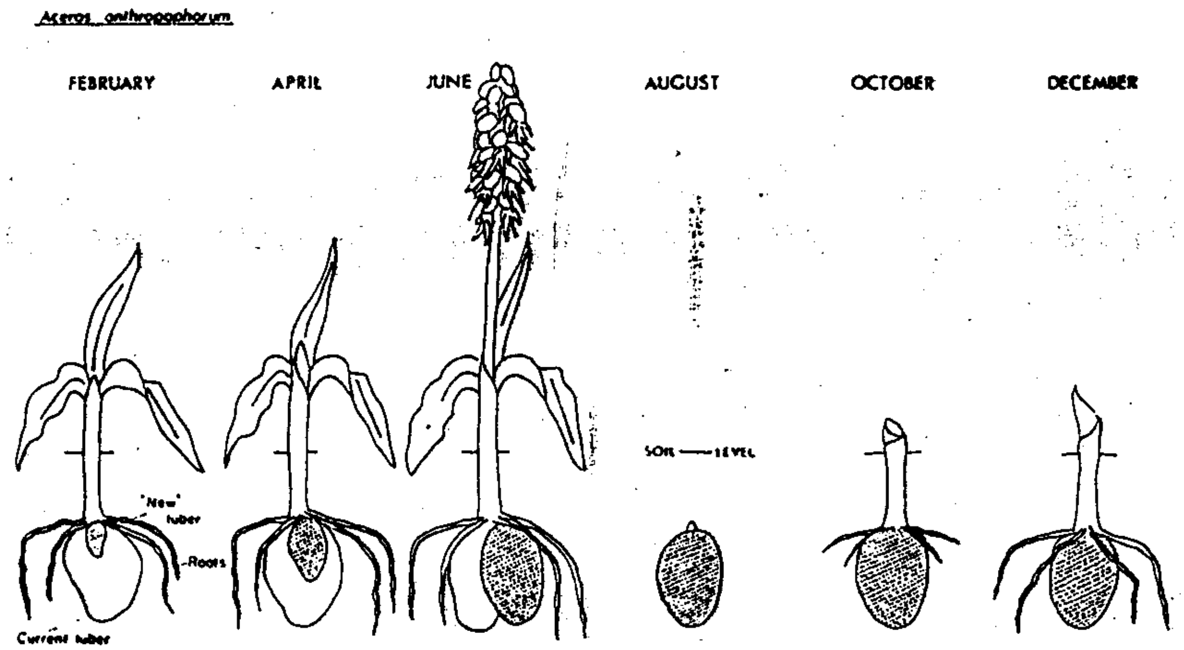


Figure 2 Generalized phenology of *Aceras anthropophorum*, illustrating tuber formation and annual production of leaves and inflorescence

6

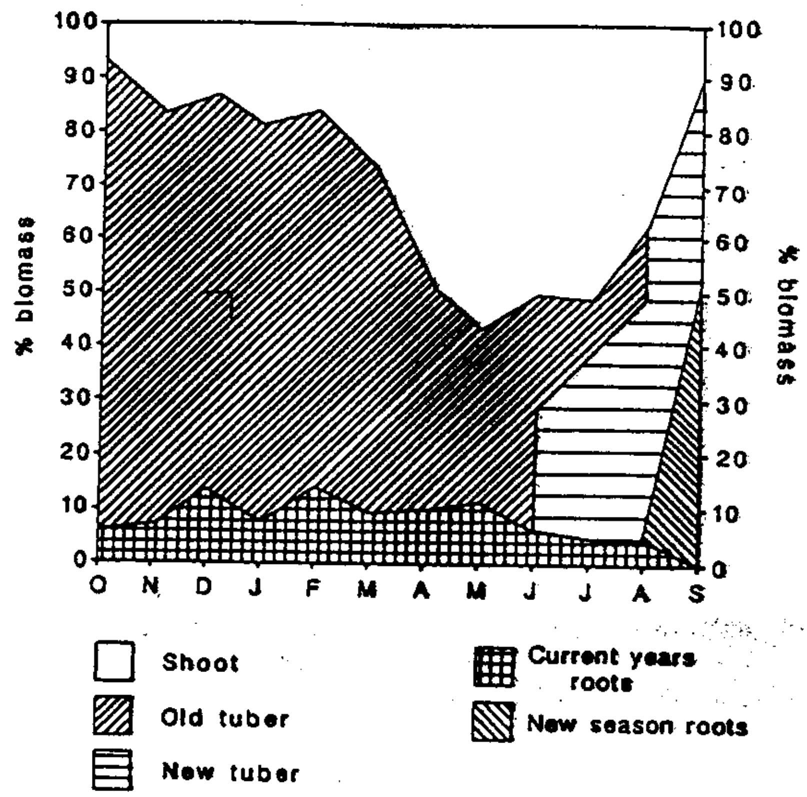


Fig. 5. The distribution of biomass of *D. fuchsii* throughout the study period.

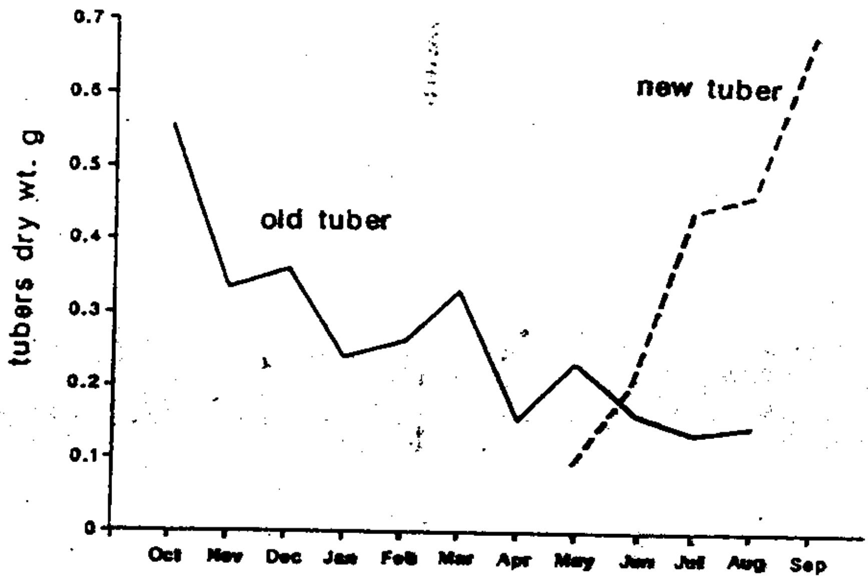


Fig. 3. Changes in the dry weight of old and new tubers of plants of *D. fuchsii* from Oct. 1988 to Sept. 1989.

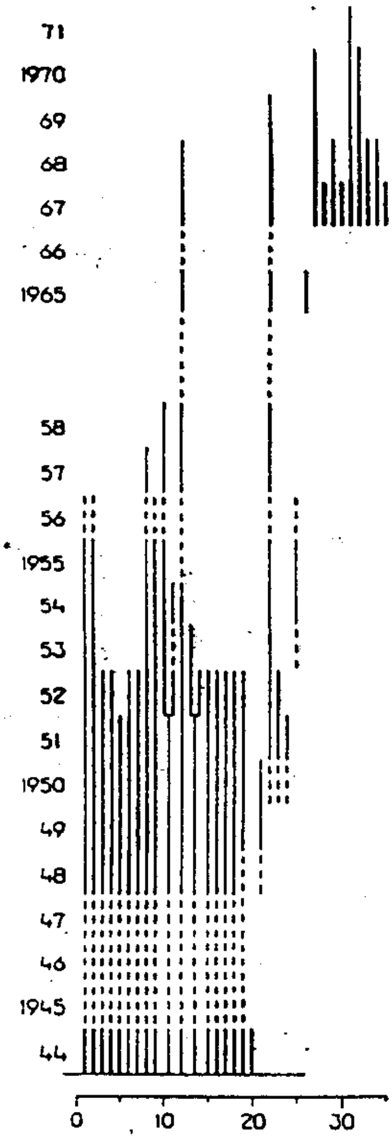


Fig. 1. The behaviour of *Dactylorchis incarnata* on plot 46 (wet meadow). Each vertical line represents one individual, straight for unramified ones, and branched where the plants appear to have branched. Heavy lines mark years when the plants have flowered, and broken lines indicate that the plant was not observed in that year.

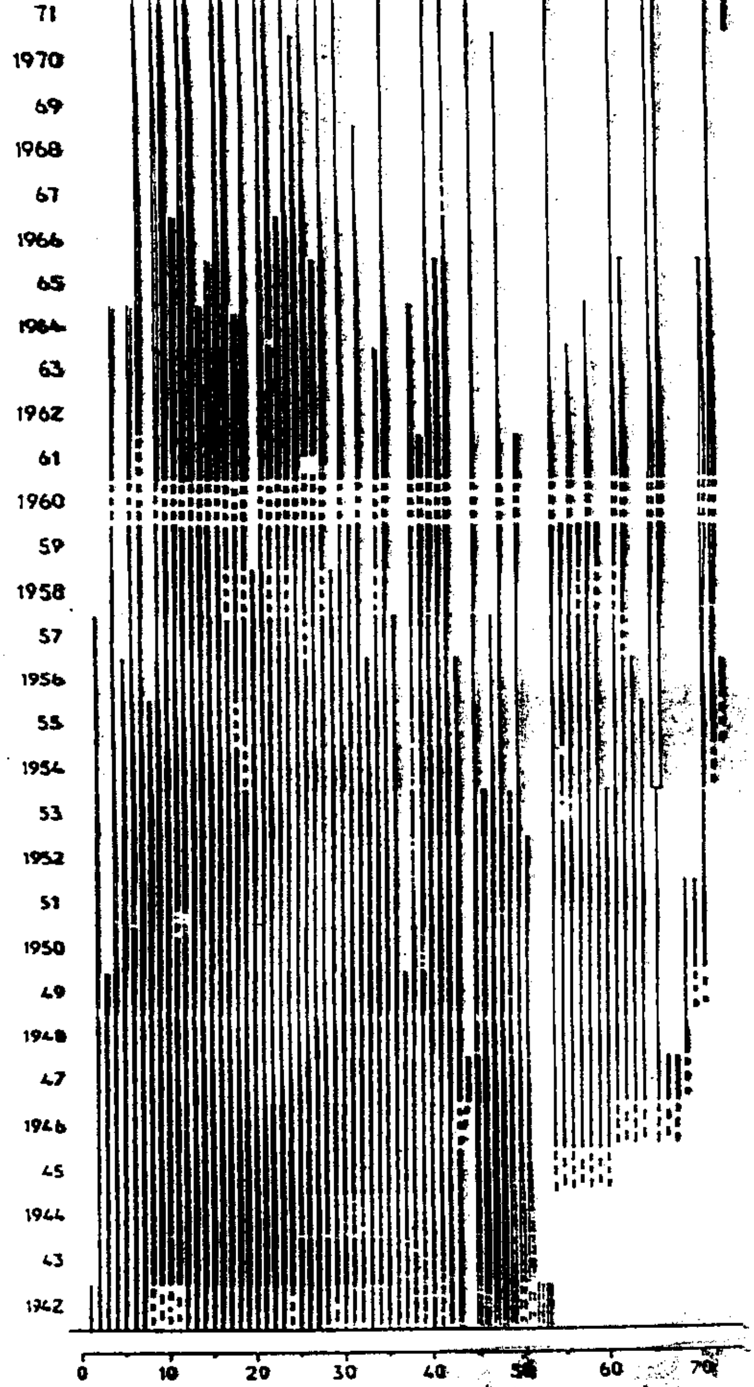


Fig. 2. The behaviour of *Dactylorchis sambucina* on plot 17 (dry wooded meadow). Symbols as in Fig. 1.

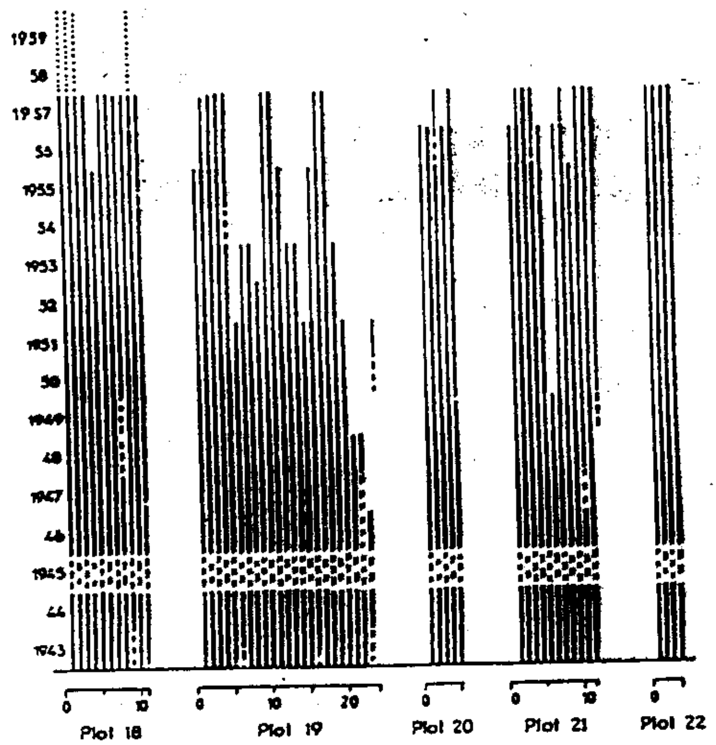
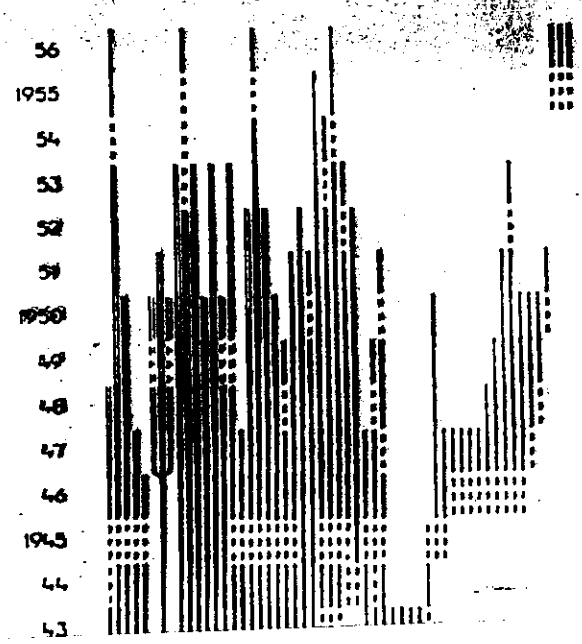


Fig. 3. The behaviour of *Dactylorchis sambucina* on plots 18–22 (mesic wooded meadow). Symbols as in Fig. 1.



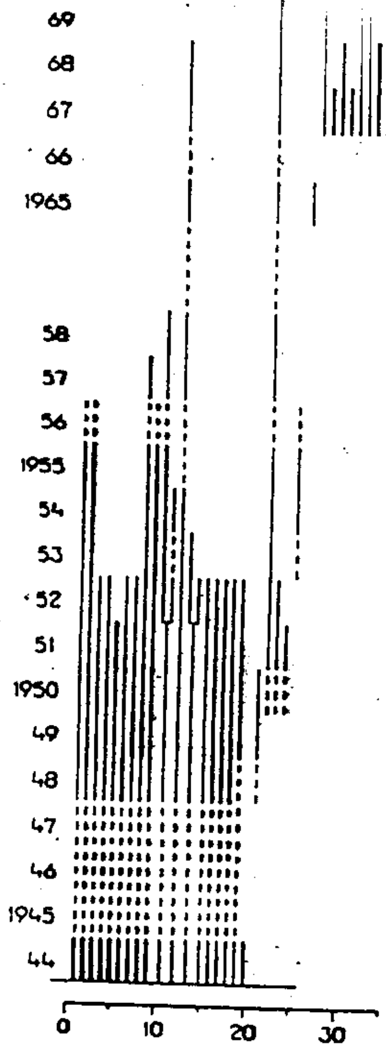


Fig. 1. The behaviour of *Dactylorchis incarnata* on plot 46 (wet meadow). Each vertical line represents one individual, straight for unramified ones, and branched where the plants appear to have branched. Heavy lines mark years when the plants have flowered, and broken lines indicate that the plant was not observed in that year.

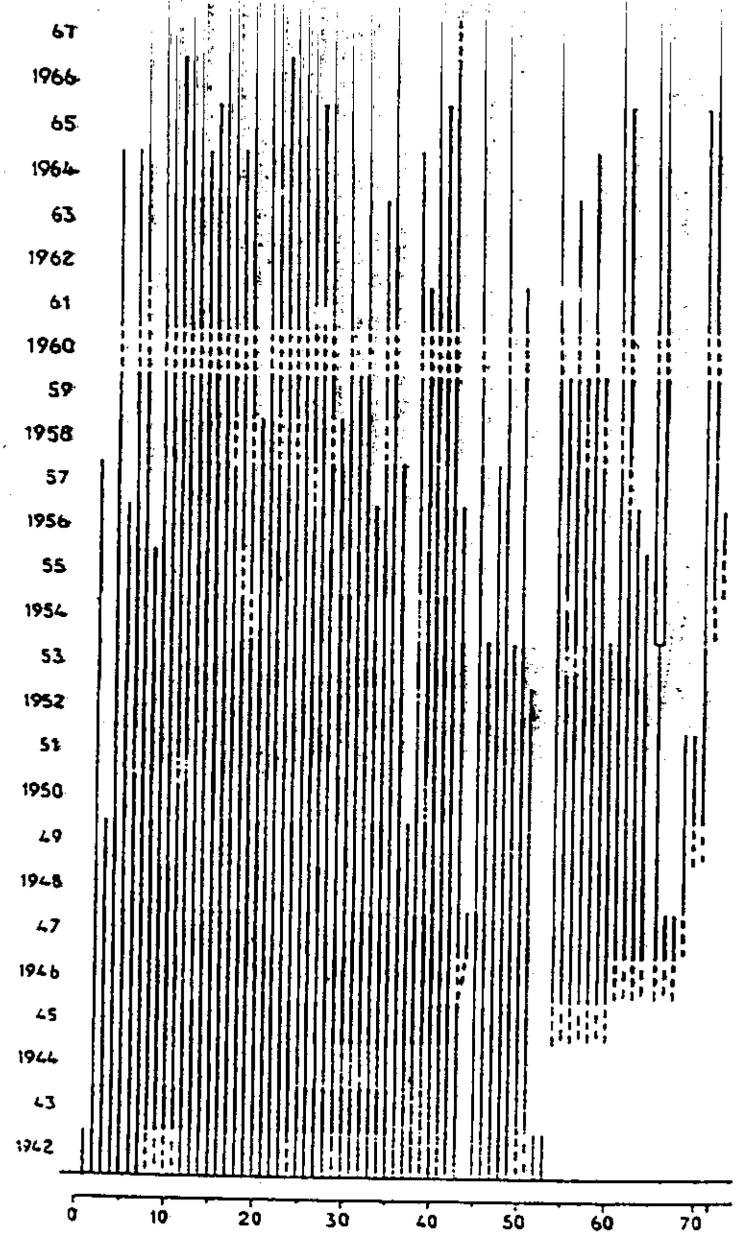


Fig. 2. The behaviour of *Dactylorchis sambucina* on plot 17 (dry wooded meadow). Symbols as in Fig. 1.

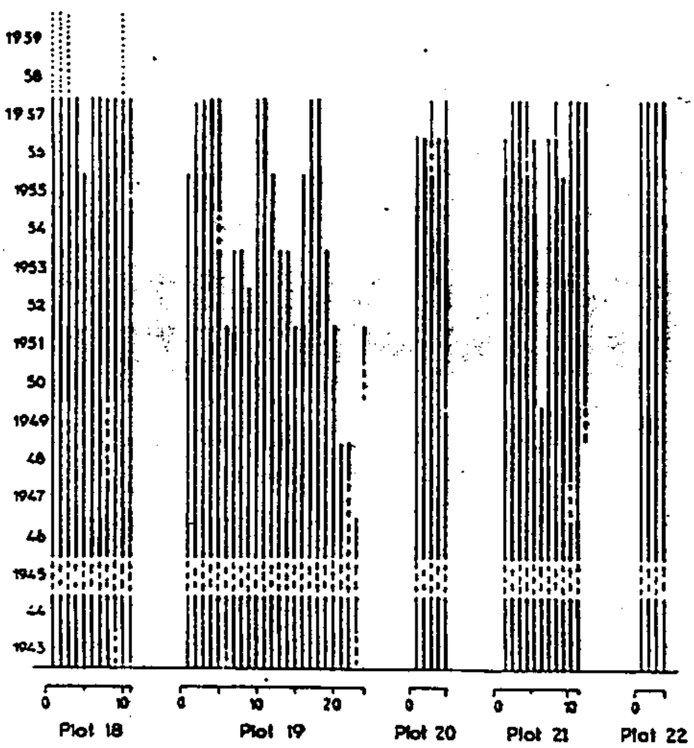


Fig. 3. The behaviour of *Dactylorchis sambucina* on plots 18–22 (mesic wooded meadow). Symbols as in Fig. 1. Plots 21 and 22 were damaged and not studied after 1957.

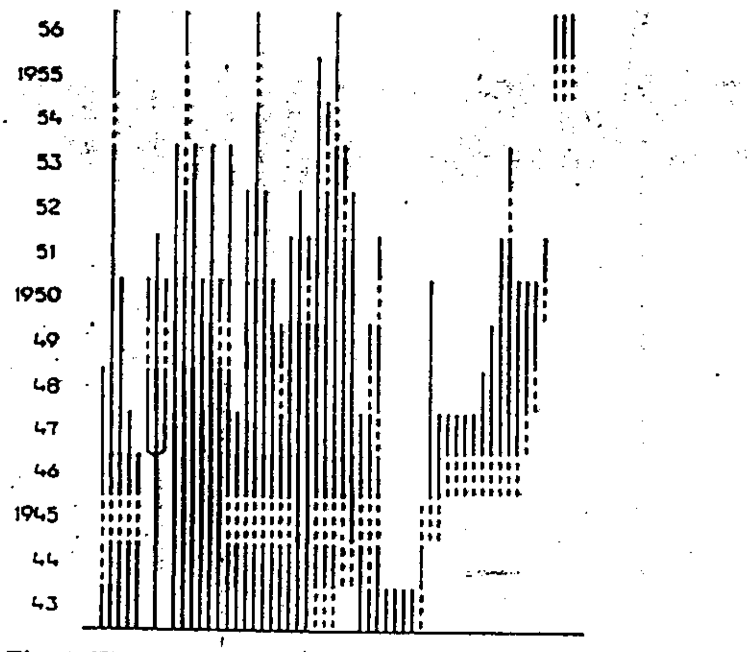


Fig. 4. The behaviour of *Orchis mascula* on plot 24 (mesic wooded meadow). Symbols as in Fig. 1.

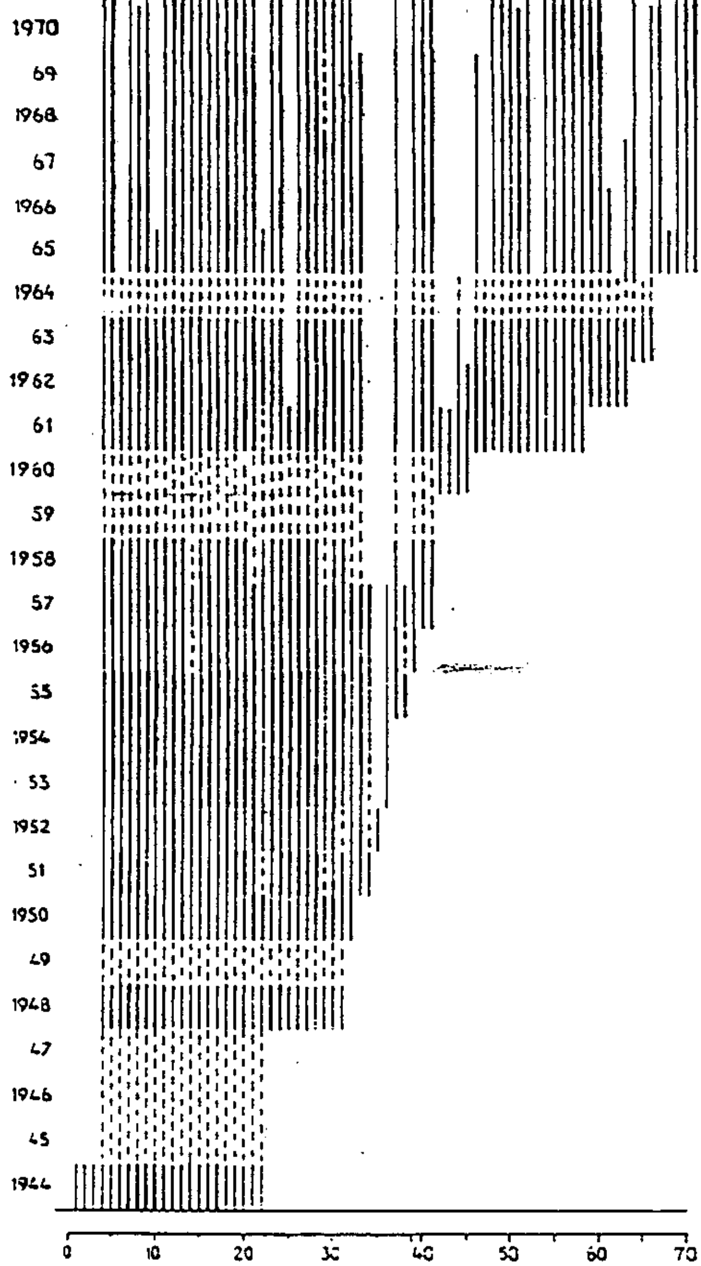


Fig. 5. The behaviour of *Listera ovata* on plot 48 (0.5 m × 0.5 m, mesic wooded meadow with almost closed canopy). Symbols as in Fig. 1.

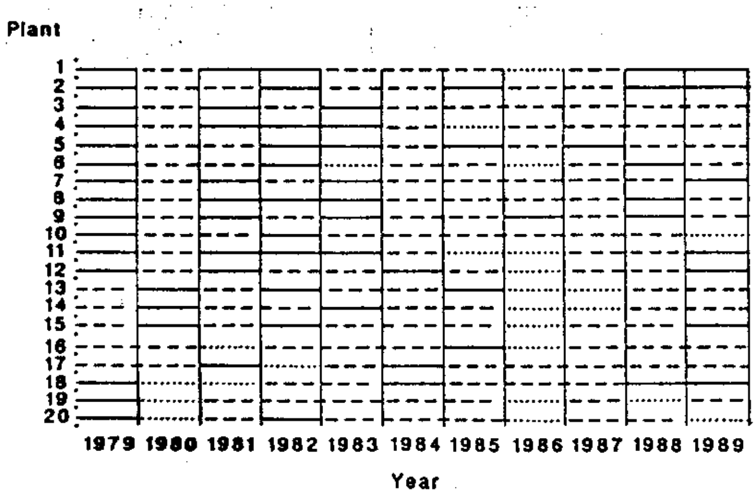


Fig. 7. The flowering behaviour, 1979–89, of 20 plants of the 1979 cohort which survived until 1989. ——— flowering, ––– vegetative, . . . 'missing' at the time of recording.

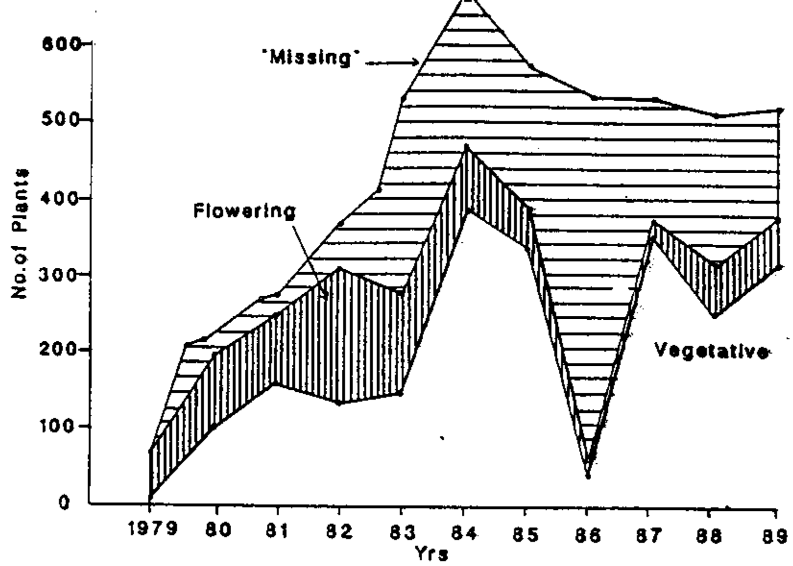


Fig. 1. Population dynamics of *Ophrys apifera* in a 10 × 10 m area, Monks Wood, Cambridgeshire, 1979–89, recorded in July each year. 'Missing' plants are those with no above-ground organs, but are present as tubers and which reappear above ground in succeeding years.

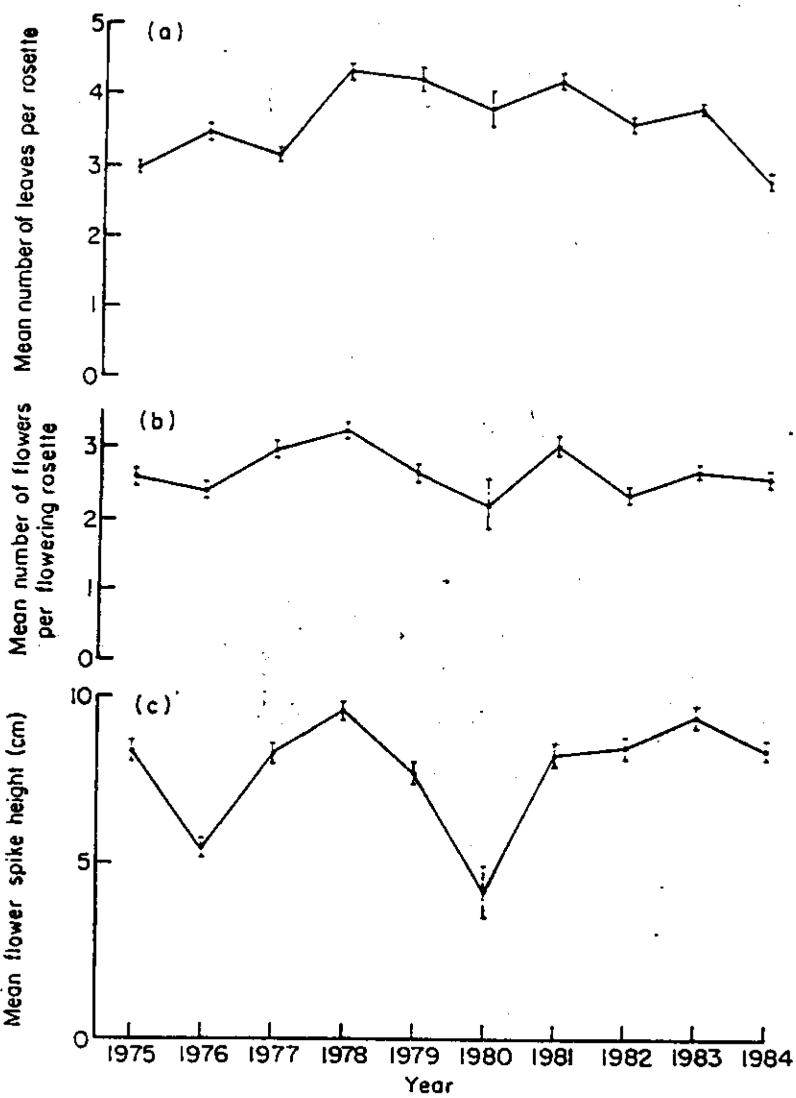


FIG. 4. Mean performance (±S.E.) of *O. sphegodes* at a site in Sussex, 1975–1984. **(a) Mean** number of leaves per rosette. (b) Mean number of flowers per flowering rosette. (c) **Mean flower** spike height.

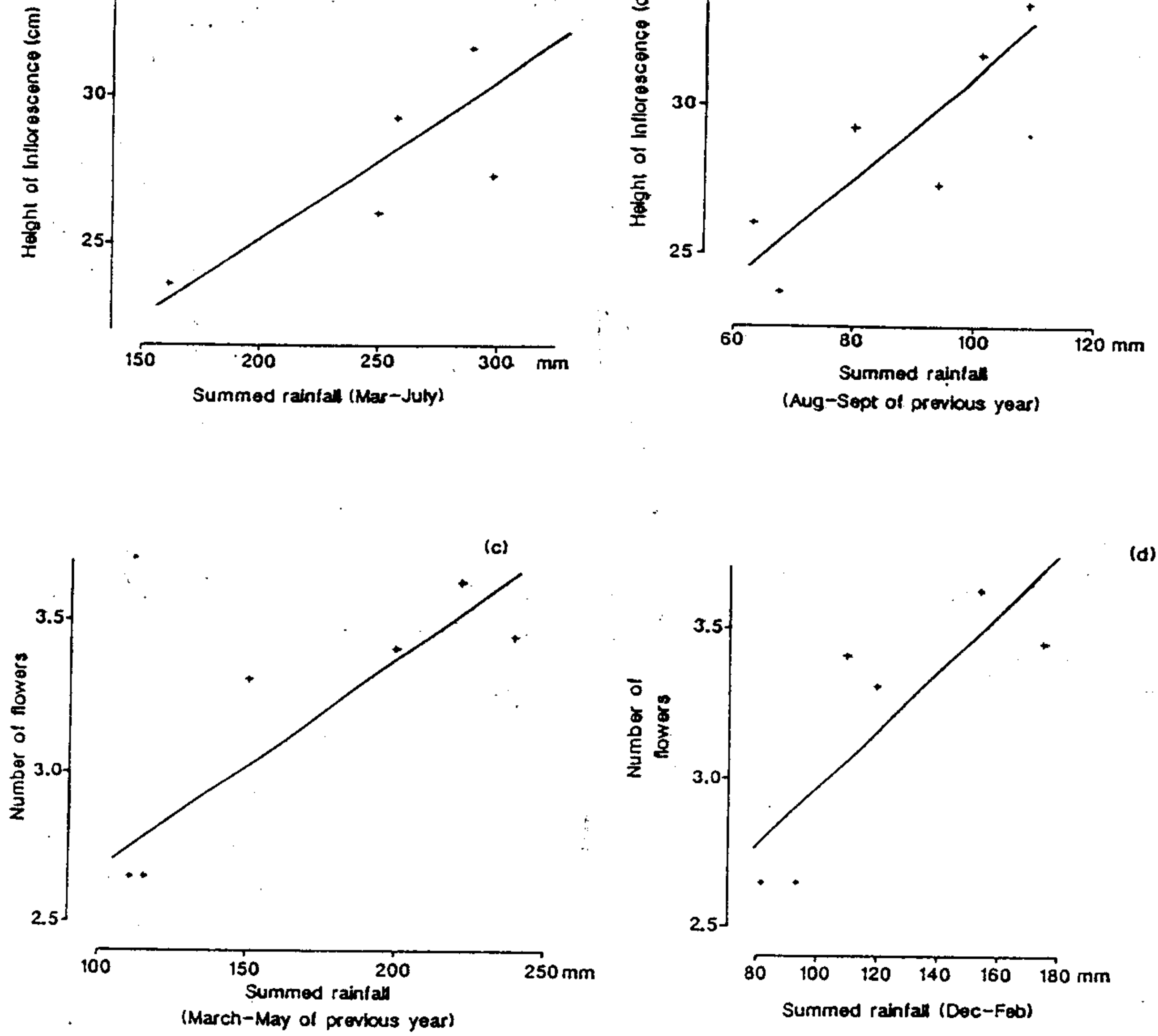


Fig. 6. Relationships between mean flower spike height in July and (a) summed rainfall in the period March–July of the current year, (b) summed rainfall in the period August–September of the previous year and between mean number of flowers per spike and (c) summed rainfall in the period March–May of the previous year and (d) summed rainfall in the period December–February of the current year.

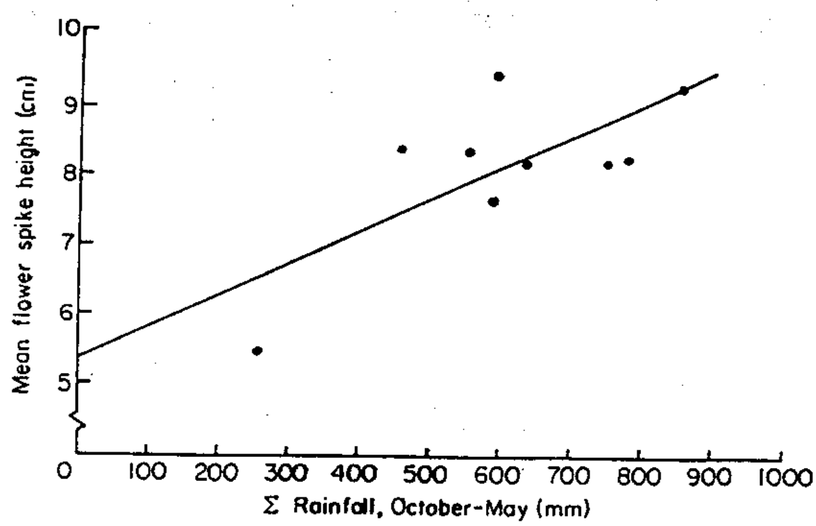


FIG. 5. Relationship between mean flower spike height of *O. sphegodes* and summed rainfall in the previous October–May. $r = +0{\cdot}72$, $P < 0{\cdot}05$

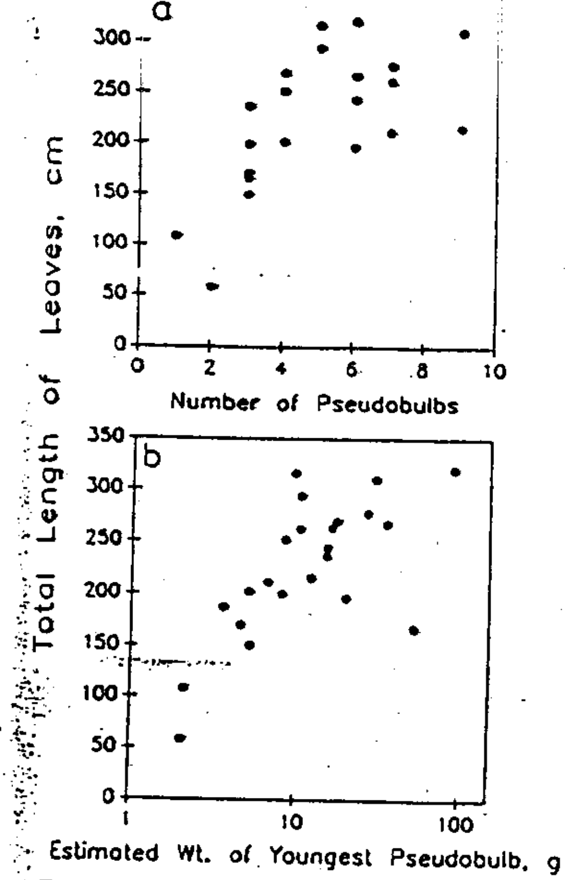


Fig. 2. Scatterplots of growth relationships in *C. viridiflavum* from a single site. a. Total length of leaves on shoots in the wet season (July 1985) vs. pseudobulb number in the previous dry season (Feb. 1985). b. Total length of leaves in the wet season vs. estimated weight of the youngest pseudobulb from previous dry season. Pseudobulb weights were ln transformed to provide a normal distribution.

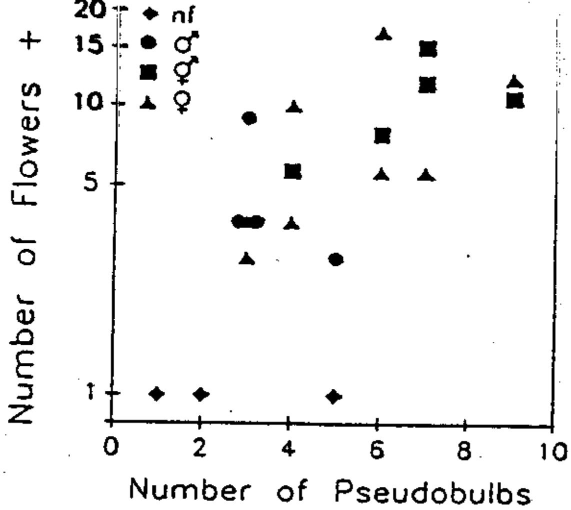


Fig. 3. Relationship between total flower production and sex expression (June–Nov. 1985), and pseudobulb number (Feb. 1985) at a single site. Prior to ln transformation, values of flower production were increased by 1 to include nonflowering plants ("nf") in the plot.

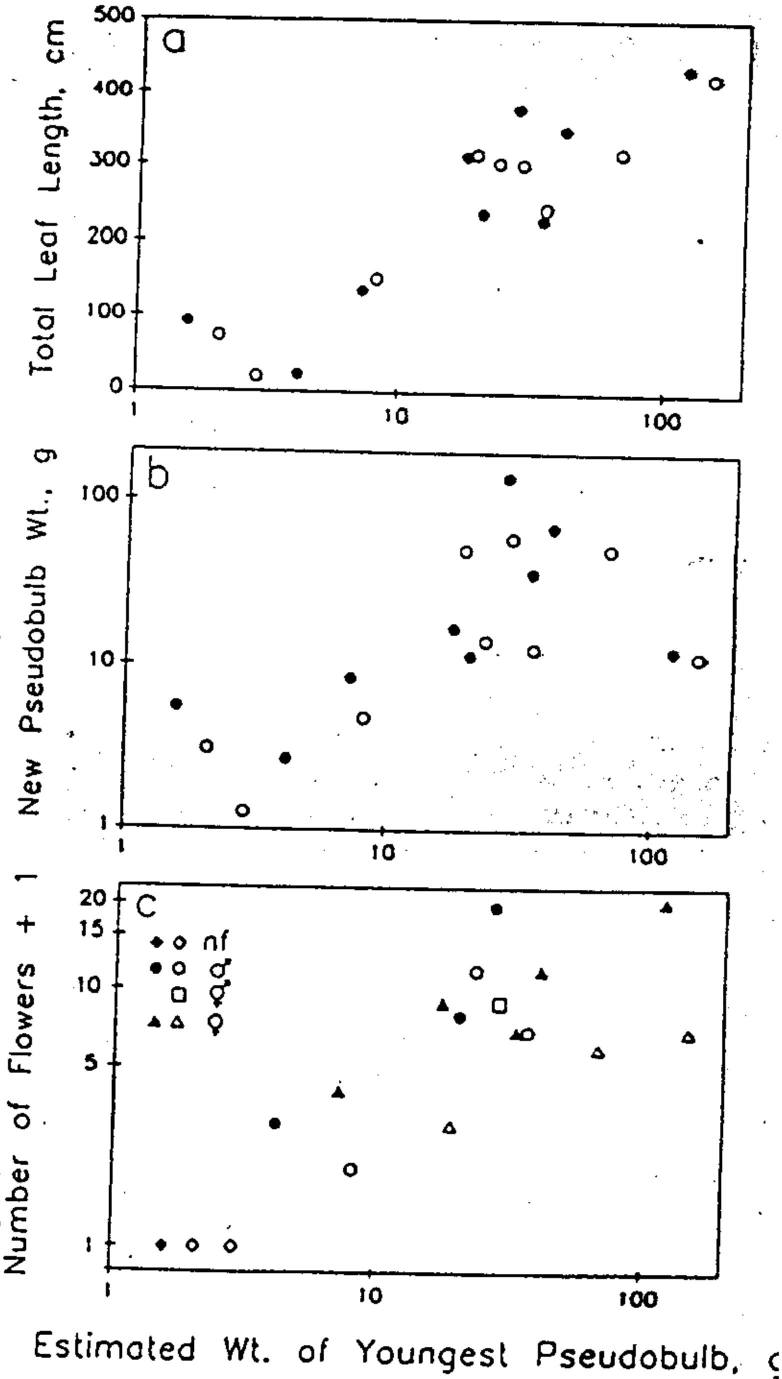


Fig. 4. Effects of the separation of youngest pseudobulbs from back bulbs on vegetative growth and flowering. Closed symbols represent control plants and open symbols represent plants in which connections were severed between the youngest and older pseudobulbs. All variables are shown in relation to weight of the youngest pseudobulb (estimated) in the dry season (Feb. 1985). a. Total length of leaves per shoot (Aug. 1985). b. Estimated weight of new pseudobulb (Feb. 1986). c. Flower production and sex expression (June–Nov. 1985).

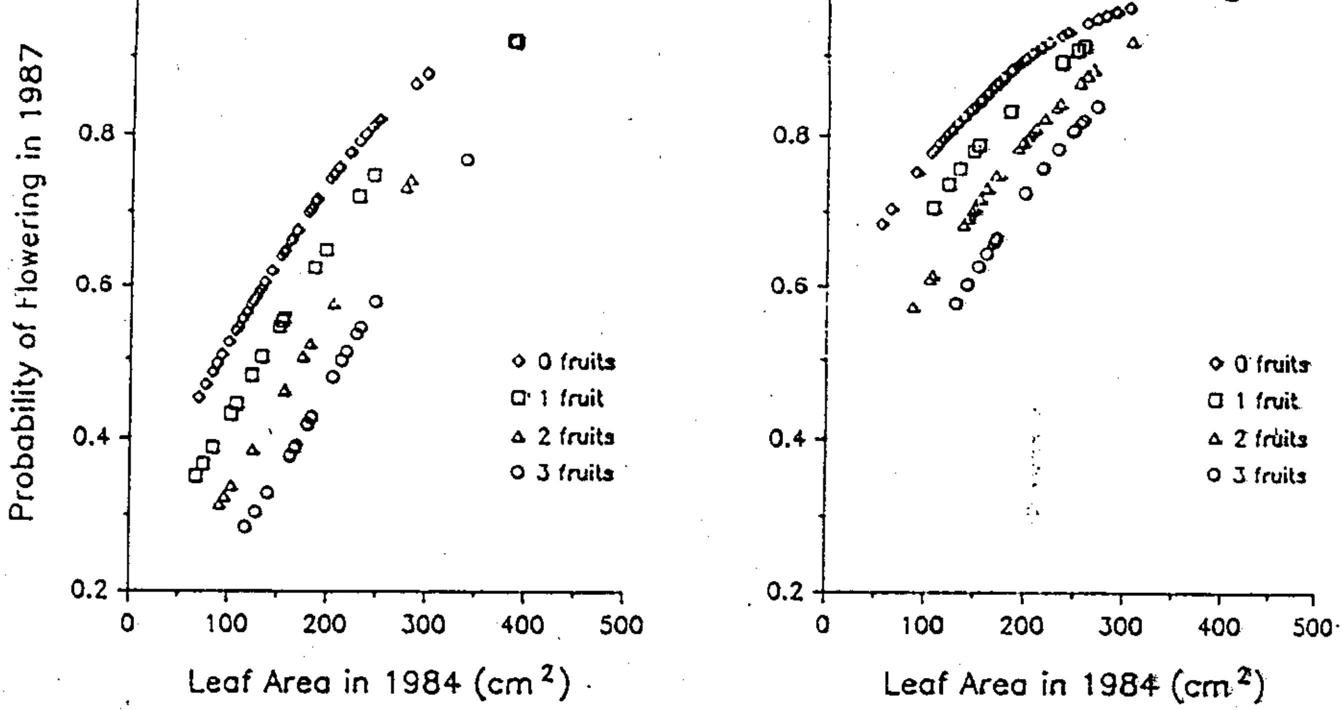


FIG. 1.—The calculated probability of a plant's flowering (p) in 1987 based on its initial leaf area in square centimeters (L) in 1984 and the number of fruits produced from 1984 through 1986 (F). S is a coded variable for site with Hammond Woods equaling -1 and Case Estates equaling 1. The estimated parameters of the logistic model are:

$$p = 1/(1 + e^{0.30 - 0.0095L + 0.40F - 0.56S}.$$

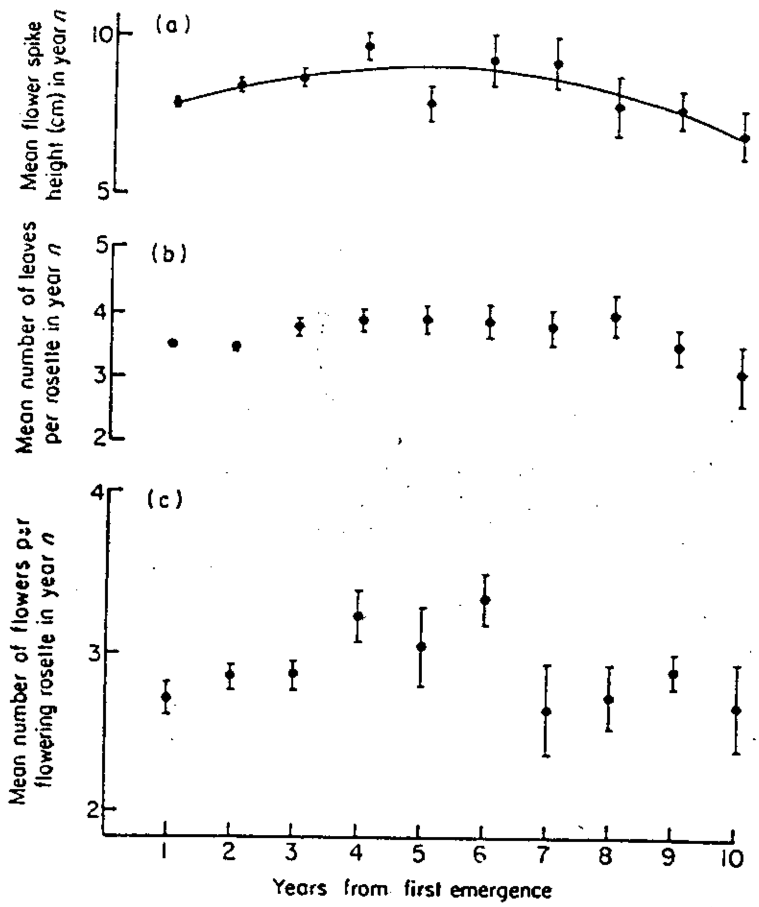
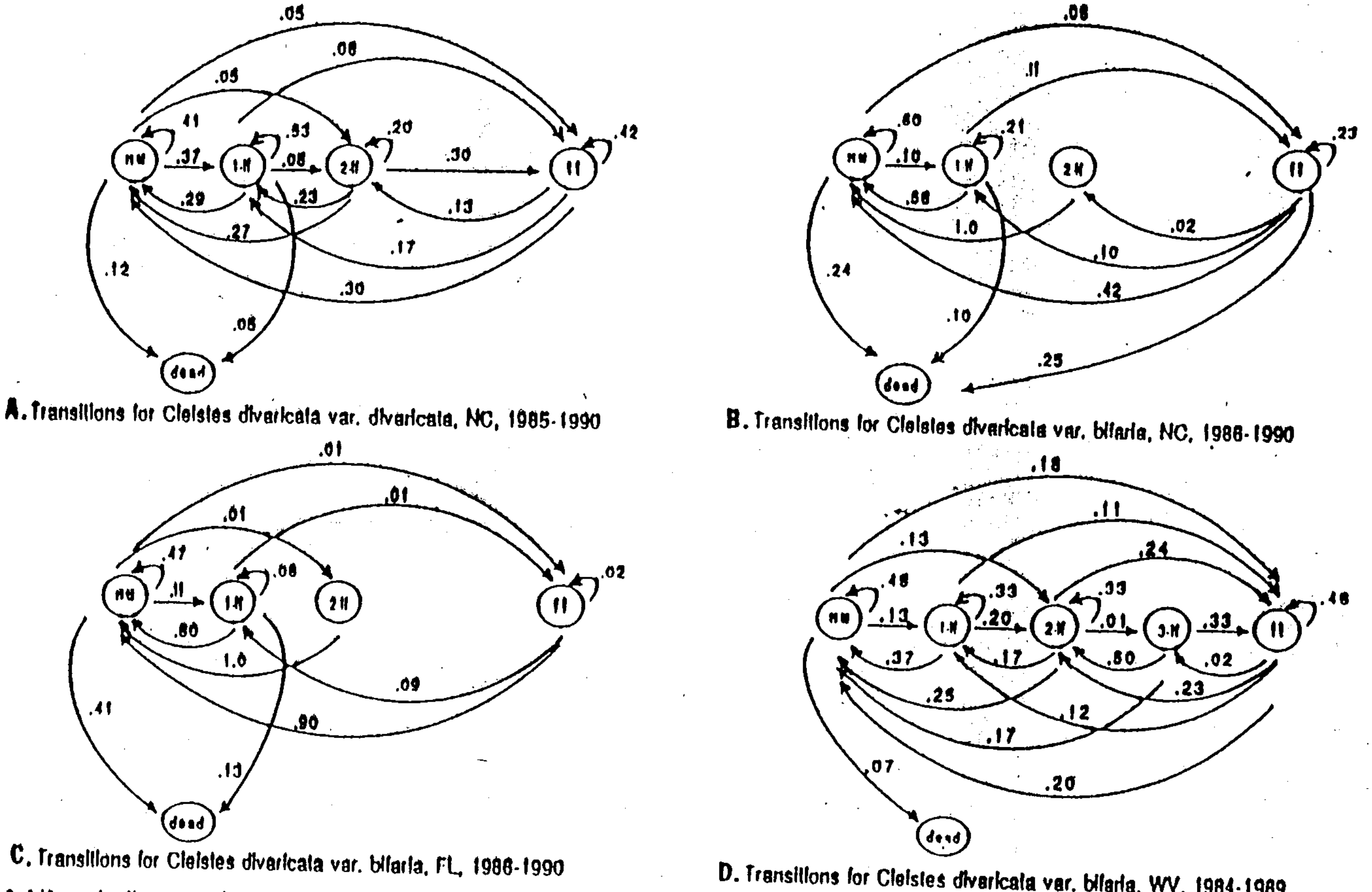


FIG. 2. Relationships between mean (±S.E.) measures of performance in *O. sphegodes* and number of years from first recording above ground. The precise age of orchids which were first recorded eight or more years ago is not known with certainty. (a) Mean height of flower spikes. (b) Mean number of leaves per rosette. (c) Mean number of flowers per spike.



3. Life cycle diagrams of four populations of *C. divaricata*. A, var. *divaricata*, Brunswick County, North Carolina. B, var. *bifaria*, Brunswick County, No
olina. C, var. *bifaria*, Alachua County, Florida. D, var. *bifaria*, Barbour County, West Virginia. Numbers above the arrows represent average transit
portions for the periods indicated; nu = not up; 1-lf, 2-lf, 3-lf = one, two, or three leaf ramets; fl = flowering ramet. The seed stage was intentionally omitted fr
diagrams.

Explanations:

- MATRIX MODELS: prediction of the behavior of an average population; no predictions on individual level

- CHAOTIC DIFFERENCE EQUATION MODELS *(Inghe, J. Theor. Biol. 147:449 (1990))*: prediction of chaotic flowering behavior, but:

  1. constant parameters,

  2. assumptions descriptive, no optimization (e.g., $R = a + bV$)

- OPTIMUM ENERGY PARTITIONING MODELS

WHICH MODEL IS APPROPRIATE?

Starting point: *Pugliese & Kozlowski, Evol. Ecol. 4:75 (1990)*

$V_i(t)$ - size of the vegetative part at time t of season i,
$R_i(t)$ - size of the reproductive part at time t of season i,
$S_i(t)$ - size of the storage at time t of season i,
T - length of the growing season.

$$\frac{d}{dt}V_i = (1 - u_i - v_i)f(V_i),$$
$$\frac{d}{dt}R_i = u_i f(V_i),$$
$$\frac{d}{dt}S_i = v_i f(V_i).$$

$$V_{i+1}(0) = q_i V_i(T),$$
$$S_{i+1}(0) = S_i(T) + q_2 V_i(T),$$
$$R_{i+1}(0) = 0.$$

u_i, v_i - control functions, optimized w.r.t. the maximization of the expected (at birth) offspring number.

Qualitative results:

- $u_i(t)$ and $v_i(t)$ are bang-bang,

- there exists a critical proportion of persistent organs, q, which determines the optimal strategy.

The orchid case:

- Usually: $q_1 = 0$ and maybe also $q_2 = 0$,

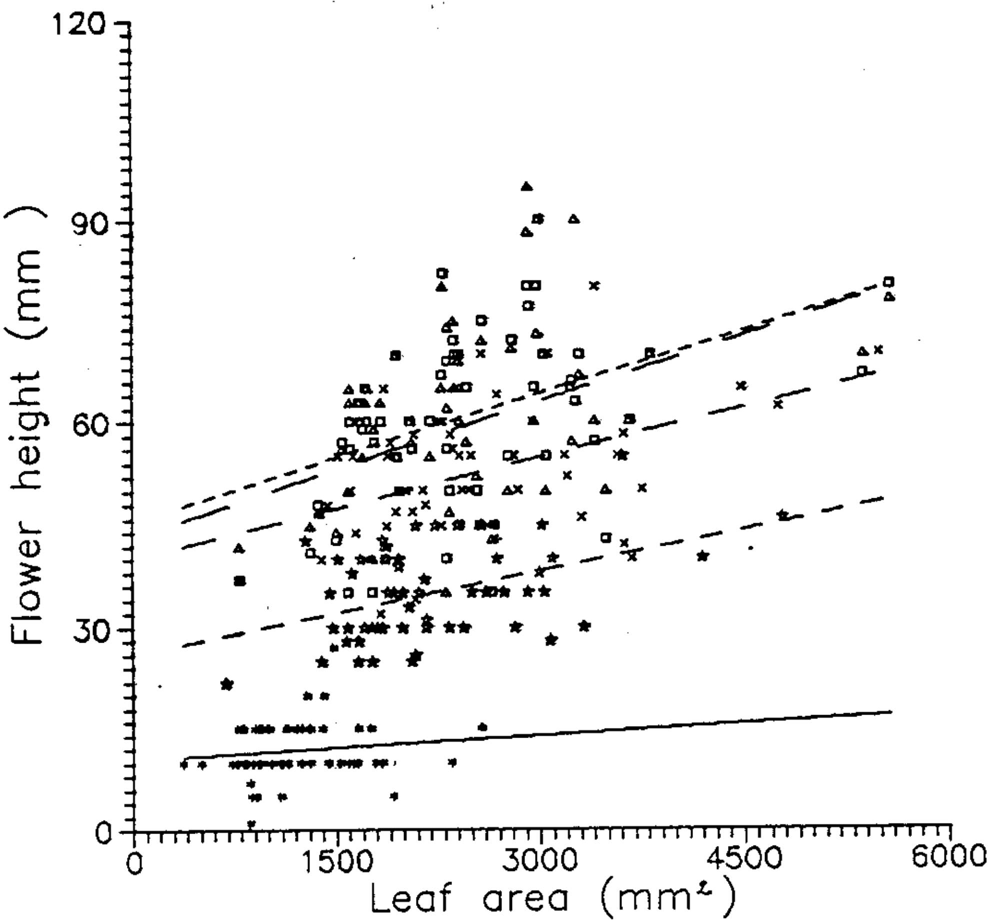
- $u_i(t)$ and $v_i(t)$ are not bang-bang.

Experiments

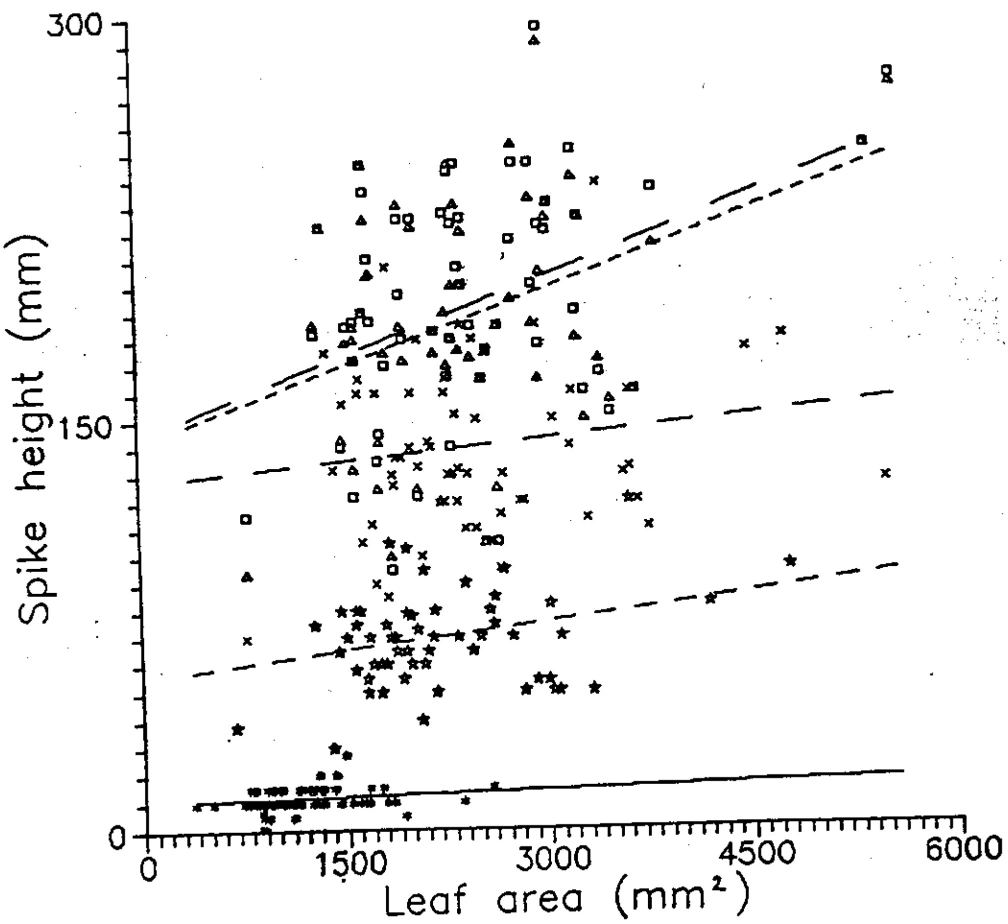
and preliminary analysis

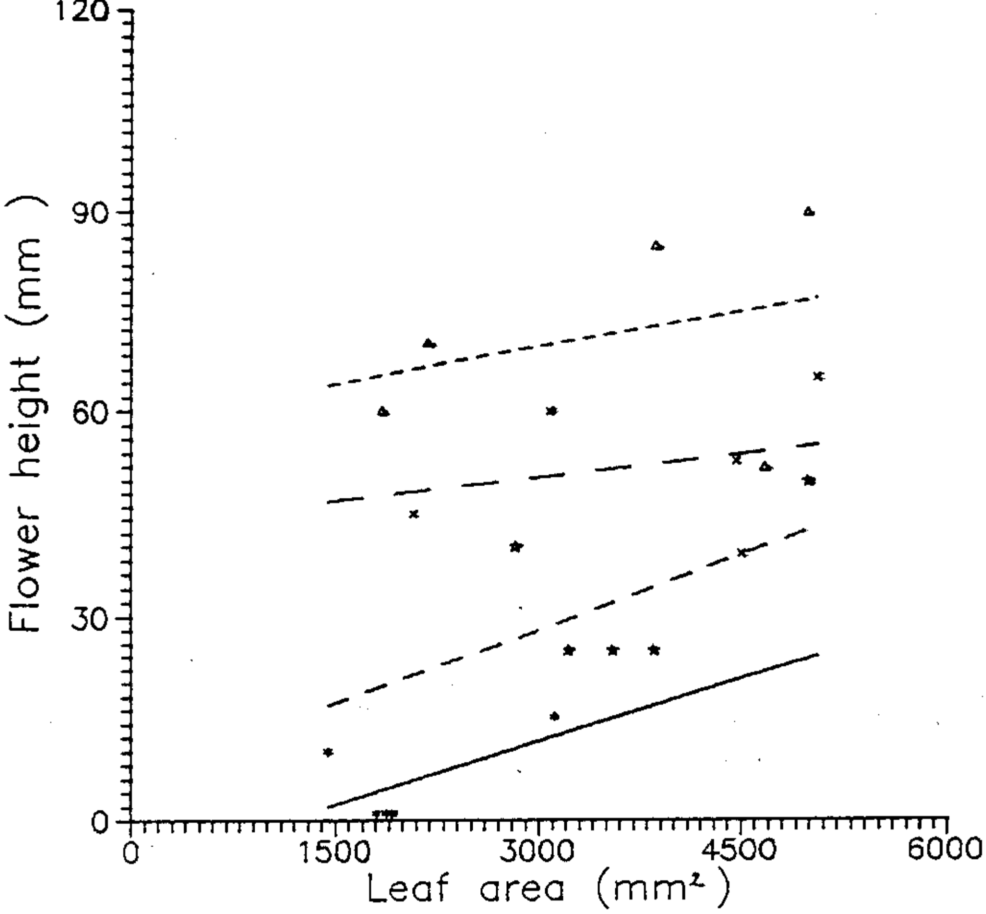
- Two localities with Dactylorhiza majalis: Milíkovice (M) - mown regularly; Vrbenské rybníky (V) - no management.

- Total leaf area, flower spike height and inflorescence height measured in regular intervals throughout the growing season in both localities in 1992.

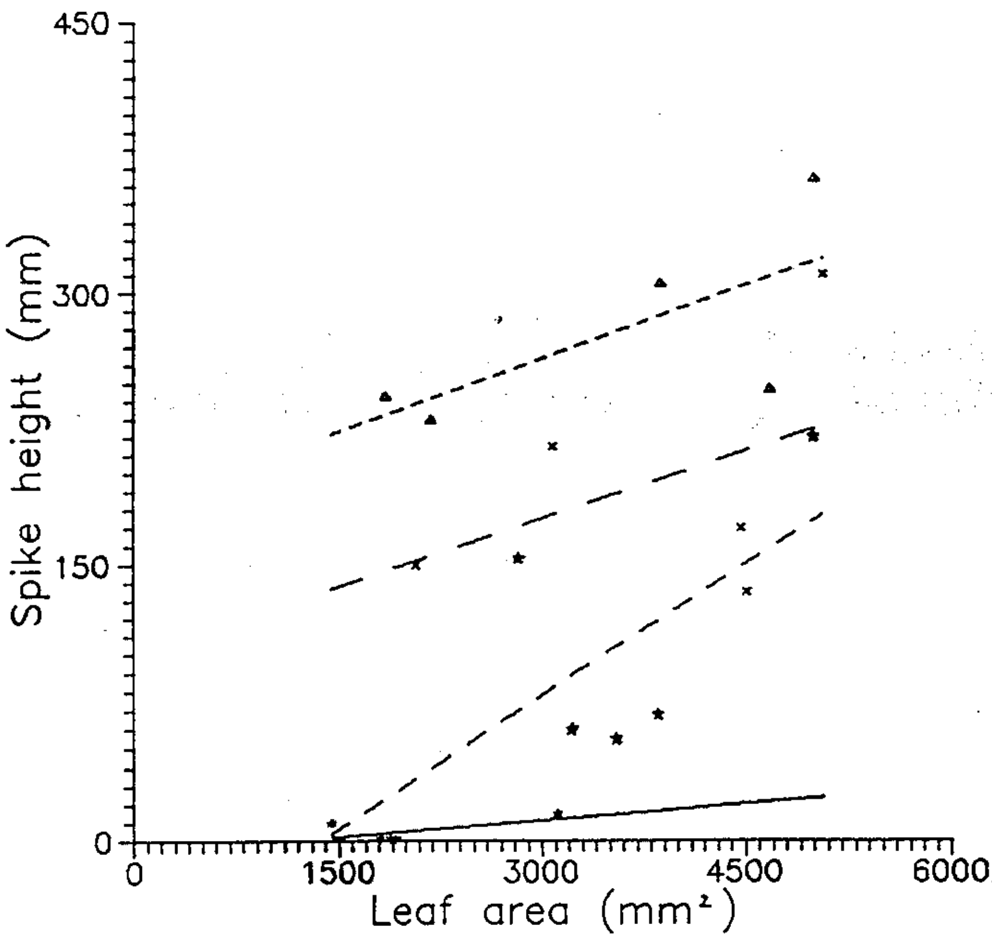

120
90
60
30
0
Flower height (mm)
0
1500
3000
4500
6000
Leaf area (mm²)

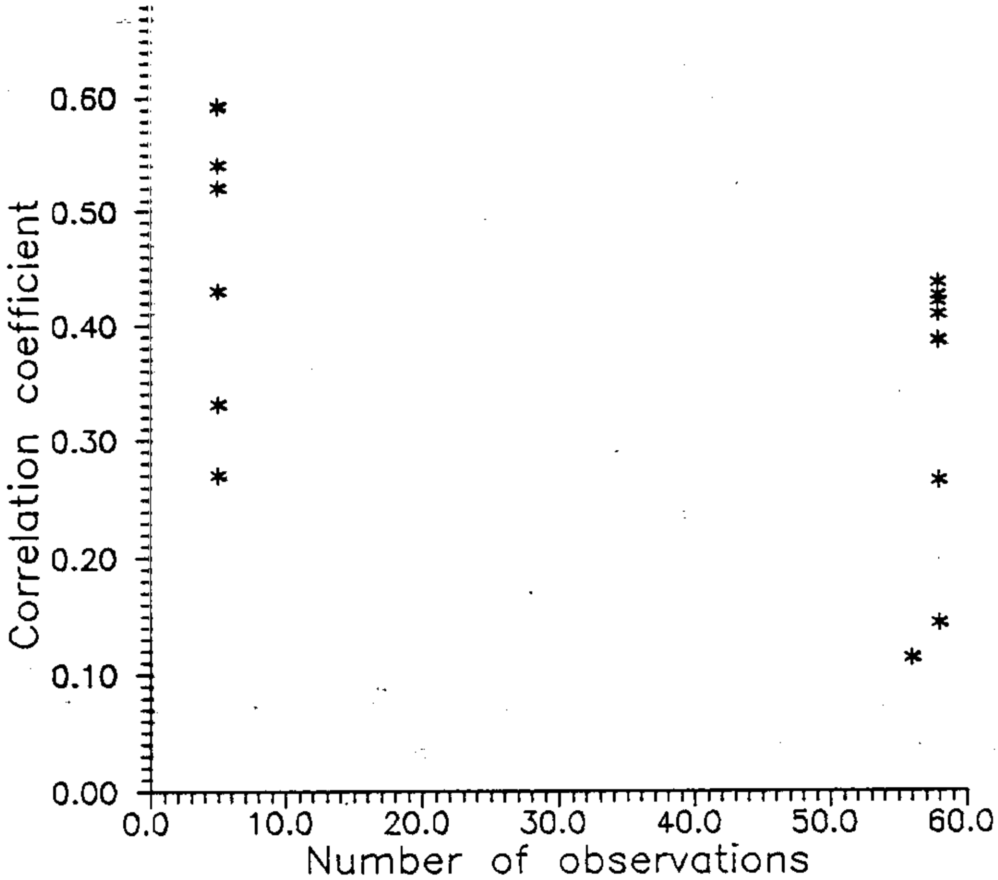
Milíkovice


300
150
0
Spike height (mm)
0
1500
3000
4500
6000
Leaf area (mm²)

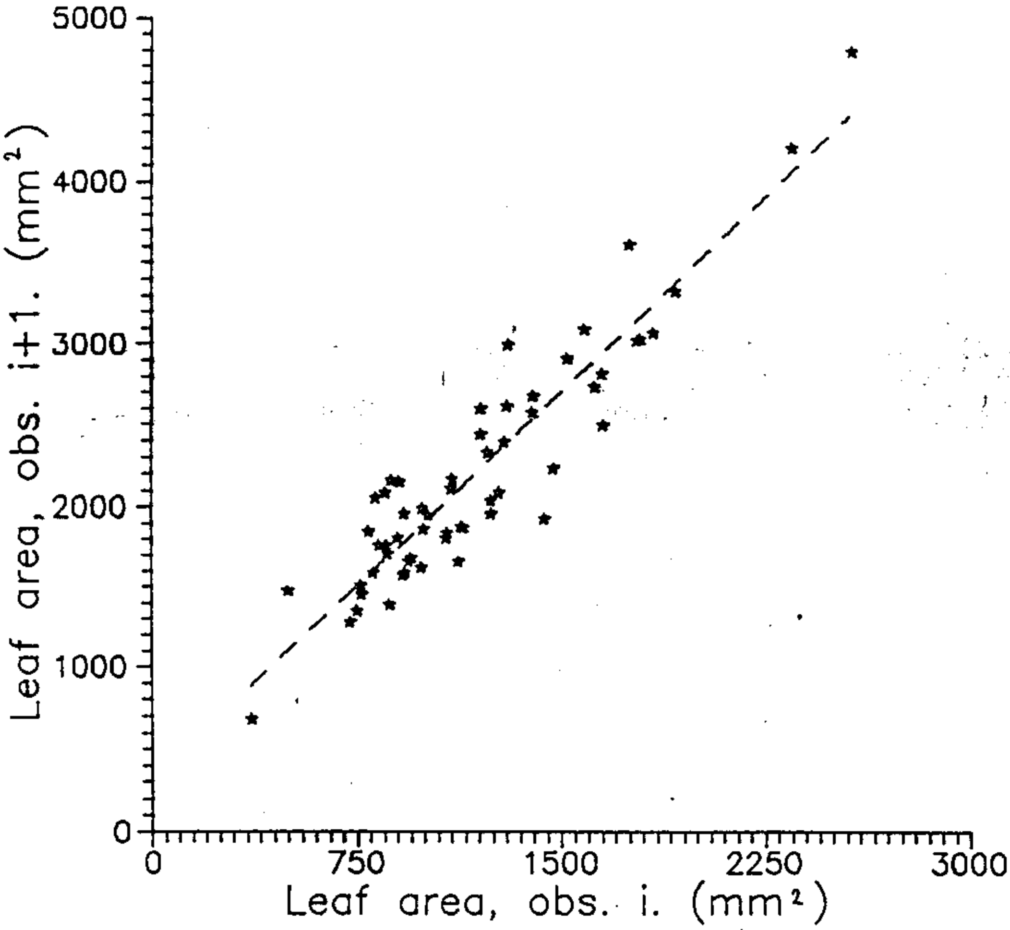


Vrbenské rybníky

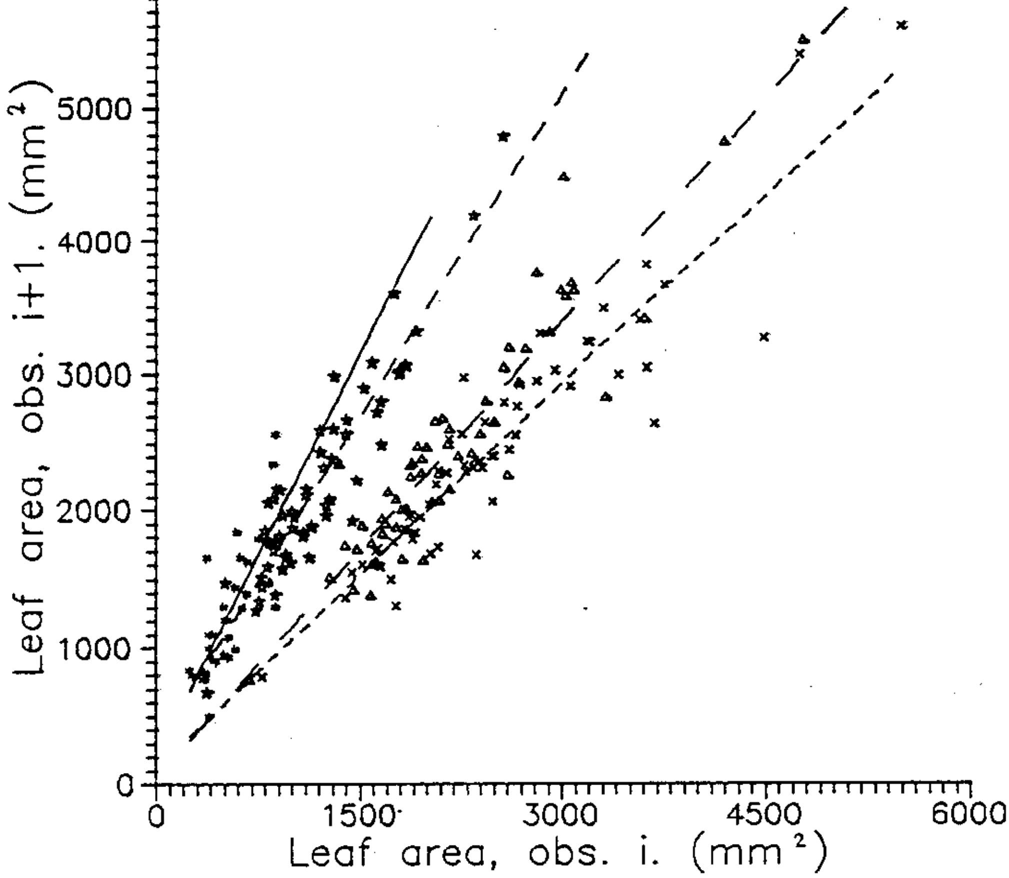




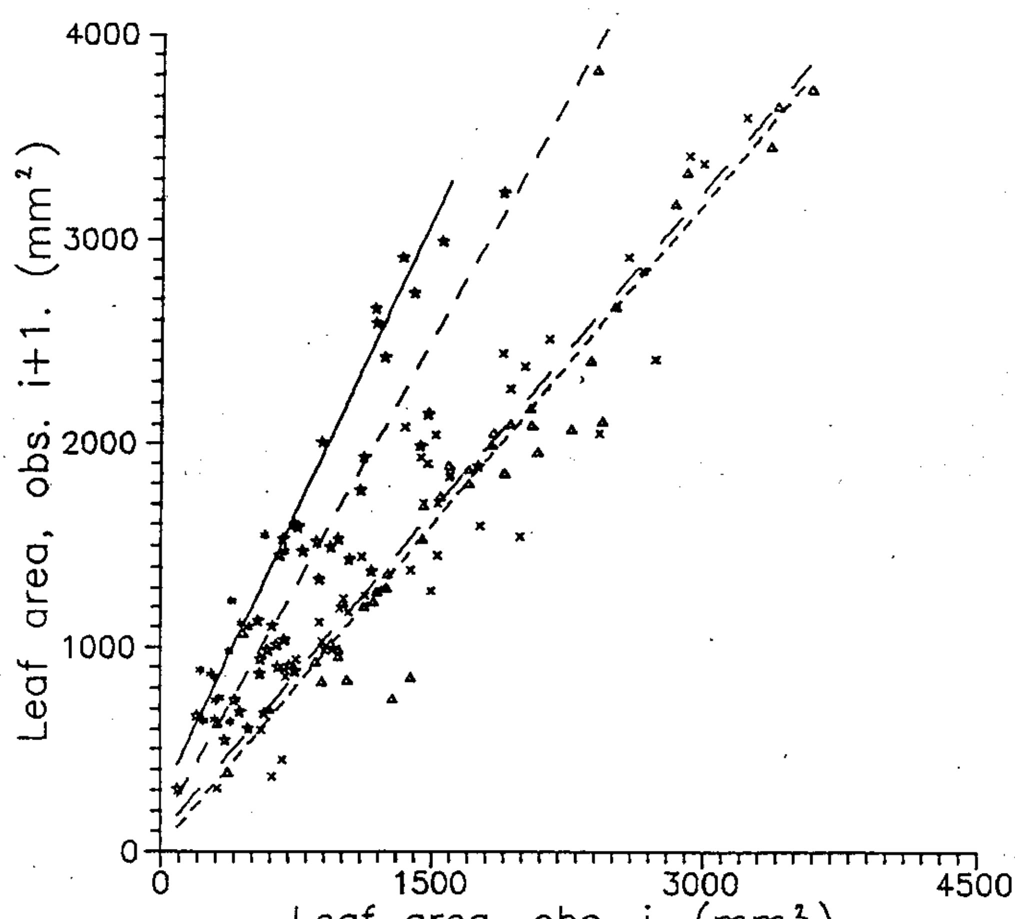
Correlation coefficient
0.60
0.50
0.40
0.30
0.20
0.10
0.00
0.0
10.0
20.0
30.0
40.0
50.0
60.0
Number of observations



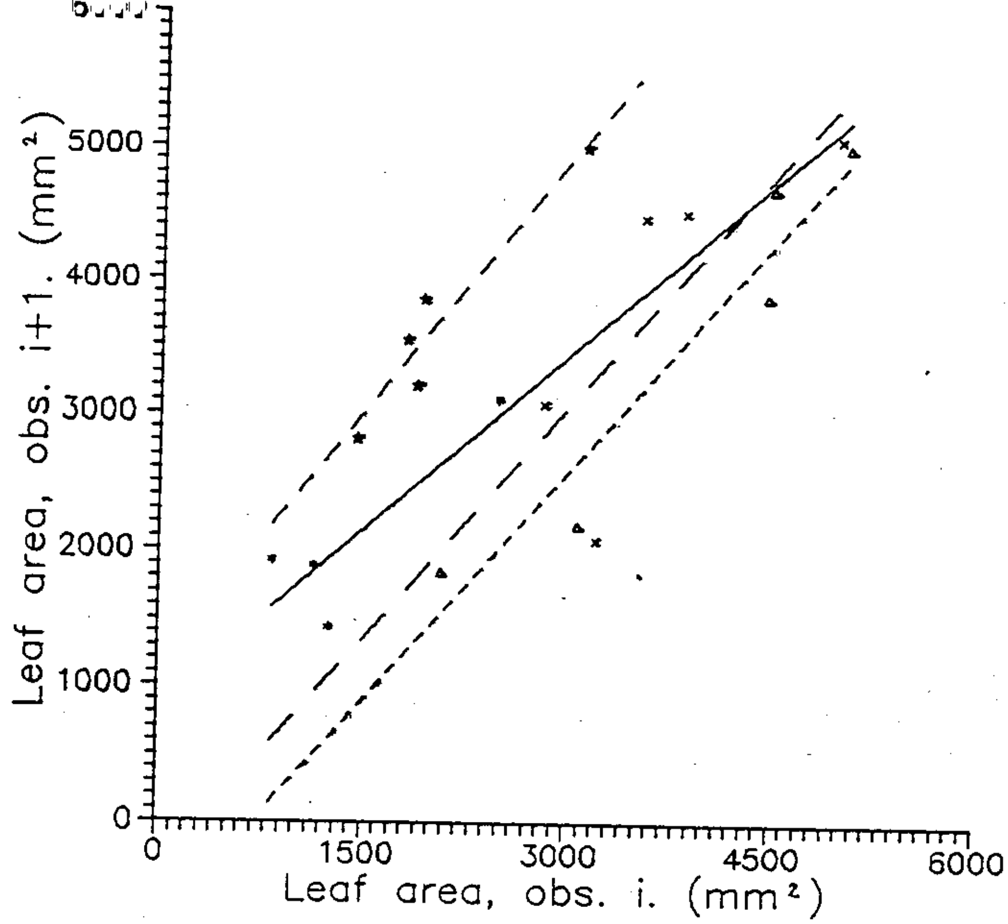
Leaf area, obs. i+1. (mm²)
5000
4000
3000
2000
1000
0
750
1500
2250
3000
Leaf area, obs. i. (mm²)



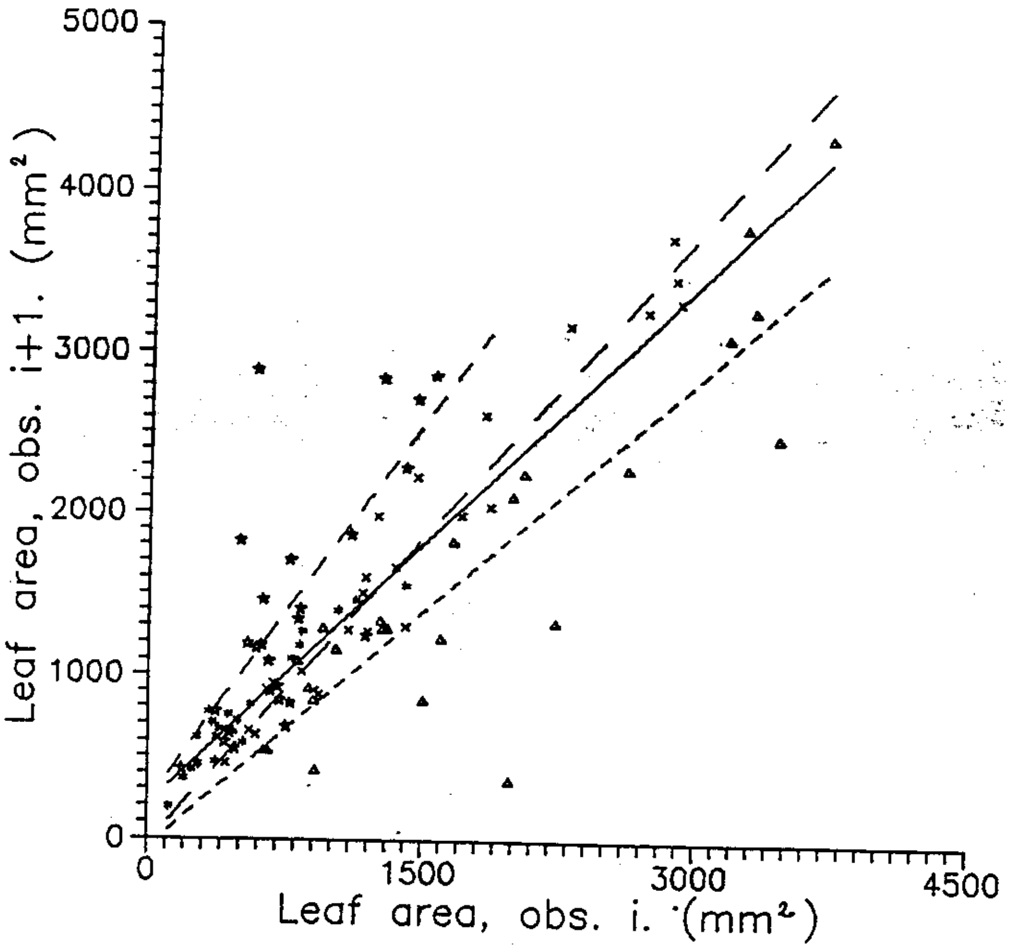
Milíkovice - flowering plants



Milíkovice - sterile plants



Vrbenské rybníky - flowering plants



Vrbenské rybníky - sterile plants

If $x(t+h) = ax(t) + b$ for any h, then $x' = kx + q$.

$$x(t) = \frac{e^{k(t+c)} - q}{k}$$

$$x(t+h) = \frac{e^{kt+kc+kh} - q}{k} = \frac{(kx(t)+q).e^{kh} - q}{k}$$

$$x(t+h) = e^{kh}.x(t) + \frac{q(e^{kh}-1)}{k}$$

Therefore:

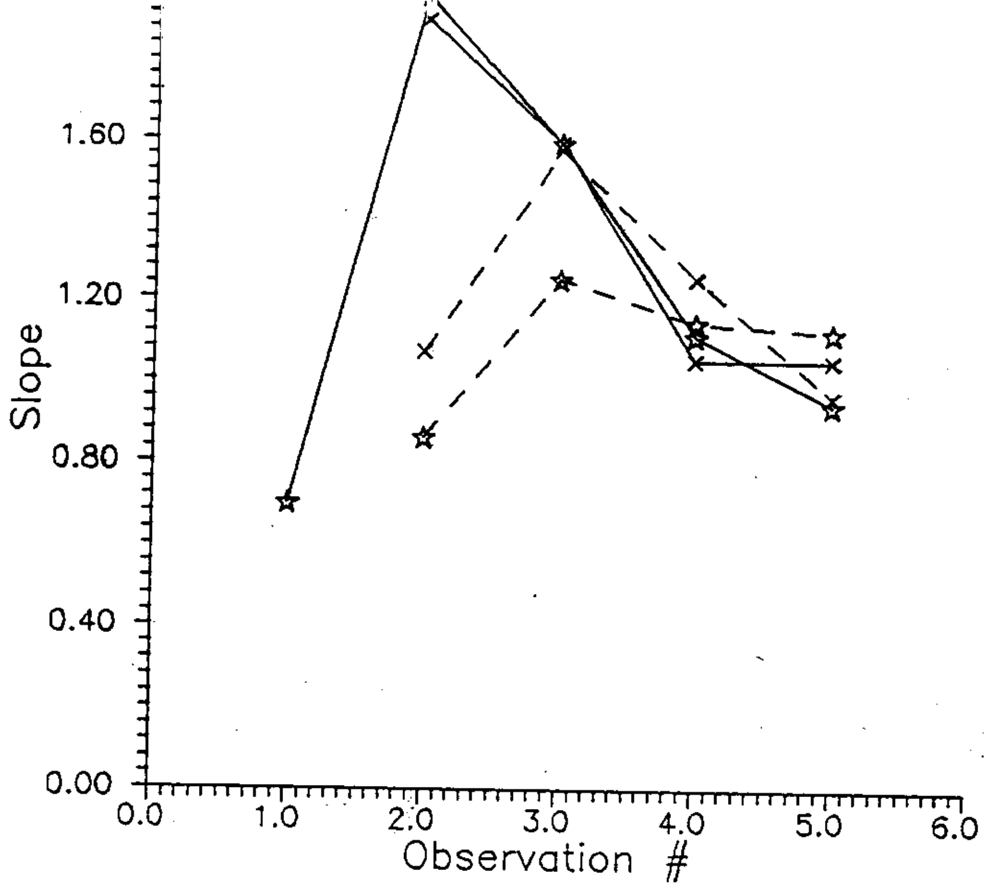
$k = \frac{ln(a)}{h}$ **and** $q = \frac{kb}{a-1}$ (if $a \neq 1$)

$k = 0$, $b = qh$ (if $a = 1$)

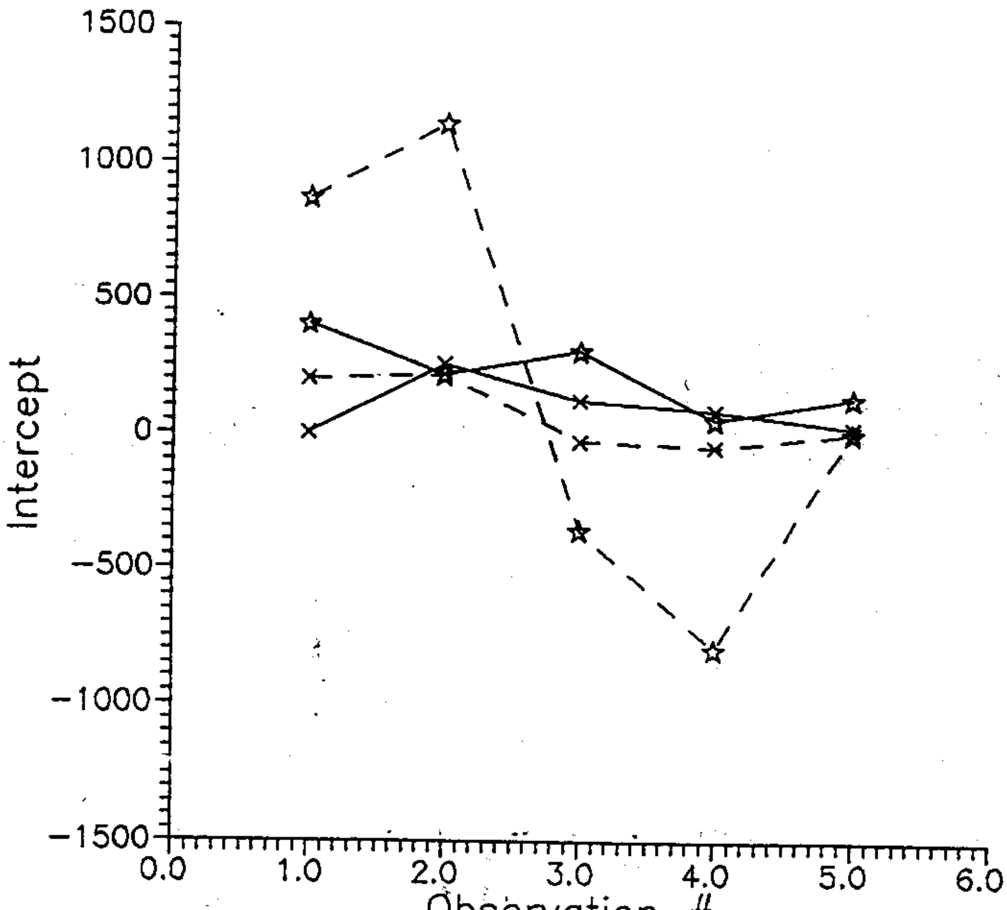
Biologically:

k **- assimilation**

q **- supply from tuber**



solid line - Vrbenské rybníky, dashed line - Milíkovice
x- sterile plants, asterisks - flowering plants



Preliminary results:

- model of energy flow in the initial stages
- simultaneous energy partitioning later on
- differences in assimilation between V and M

What next:

- energy partitioning model
- validation on empirical data from 1993
- suggestions for management strategies

Use of EPM in conservation

EPM enable to use non-destructive methods for:

- determination of bionomy in rare species

- locality assessment

- suggestion of management strategies

etc.