**Survival, Fecundity and Growth of Wild Cucumber, Echinocystis Lobata**

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# SURVIVAL, FECUNDITY AND GROWTH OF WILD CUCUMBER, *ECHINOCYSTIS LOBATA*

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## SUMMARY

(1) Survival, fecundity and growth of *Echinocystis lobata* (Cucurbitaceae) were studied in two populations in New York State, U.S.A. The plant is a climbing, monoecious annual of damp places which rarely occurs in the dense stands typical of other annuals.

(2) Disease eradicated the plant entirely from one study site and removed much of the population from the other site before flowering occurred.

(3) A life table and an age-specific fecundity schedule for the surviving population are presented. Plants are protandrous, and flower late in the life cycle. An evolutionary explanation is offered for late flowering in terms of the relationship between plant size and fecundity and the vegetative costs of fruit production.

(4) The size–frequency distribution of plants developed a right-handed skew with time and showed similarities with distributions observed in populations of other species growing in quite different ecological conditions.

## INTRODUCTION

Annual plants have frequently been chosen as subjects of demographic study because of their conveniently brief life cycles (Watkinson 1981; Silvertown 1982). They also occur usually as dense monocultures which provide large sample sizes within plots of limited size. In contrast, wild cucumber, *Echinocystis lobata* (Michx) T. & G. (Cucurbitaceae), is a monoecious annual found in local populations of scattered individuals. It occurs in riverine situations in deciduous forests of eastern North America and climbs 10–12 m into the canopy of trees and shrubs growing in tree-fall gaps or at the edge of rivers.

A study of this plant was undertaken in New York State, U.S.A., to provide information on the survival, fecundity and growth of a species which has an ecological habit quite unlike any other annual whose demography has hitherto been reported.

## STUDY SITES AND METHODS

Two study sites were chosen on Fall Creek, Ithaca (42°27'N, 76°29'W). The first site, on the northern margin of Beebe Lake, was on the campus of Cornell University. The second was 4·5 km upstream of the first on the southern bank of Fall Creek at Monkey Run. At both sites *E. lobata* occurred in tree-fall gaps.

One hundred and one plants of *E. lobata* were found scattered over about 100 × 200 m at Beebe Lake and eighty-three plants in a similar area at Monkey Run. In general, no more than three or four plants occurred within 100 cm of each other, loose clumps of this size typically being one to several metres apart. Isolated individuals several metres from the nearest *E. lobata* were common. A single dense clump of fourteen seedlings growing within an area about 100 cm² was found at Monkey Run. This was most probably derived from an abandoned rodent-cache of seeds. Seeds of this species are large (0·35 g) and are

*Demography of wild cucumber*

likely to be choice items of diet. All *E. lobata* plants at the two sites were marked individually and numbered between 30 May and 10 June 1983 when the stems were between one and ten nodes in length.

Censuses of the two populations were made at approximately 14-day intervals until 30 September 1983. At each census a loose-fitting coloured elastic band was placed over the apex of each plant and each branch. The number and positions of new branches, new nodes, flowers and fruit were also recorded.

The census observations provided three types of information: (i) life-table data; (ii) fecundity-schedule data; and (iii) data on the size (measured in numbers of nodes), growth and branching structure of each plant during the study.

## RESULTS

### *Life tables and causes of mortality*

Survivorship curves for the two populations are shown in Fig. 1. The Monkey Run population was almost eliminated by epidemic disease between the visits on days 65 and 83. Two of the three plants still alive on day 83 were over 50 m from the other plants, and none survived until the end of the study or produced any flowers. The agent of this mortality was not identified but the wilted appearance of the plants, feeding damage and presence of the striped cucumber beetle, *Acalymma vittata* (Fab), which is known to transmit cucumber-wilt bacteria suggest the latter as the cause. When the epidemic was discovered, unmarked plants of *Echinocystis lobata* were sought near the study site and several dead plants were found. Twelve living plants were also located nearby and marked. Seven of these were relocated 40 days later and all were found to have died
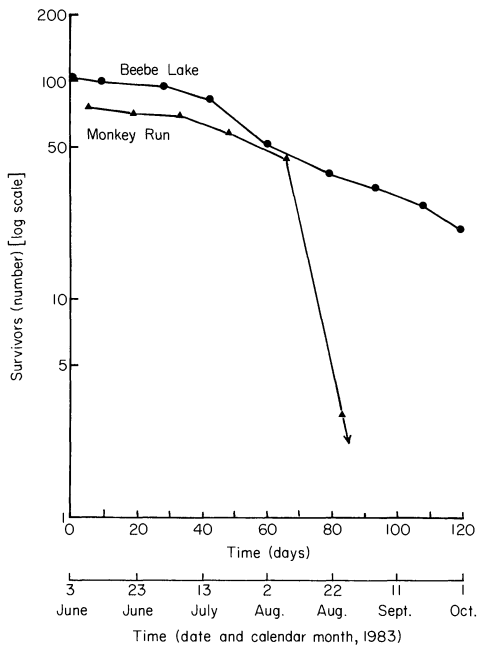


FIG. 1. Survivorship curves for populations of *Echinocystis lobata* at Beebe Lake (●) and Monkey Run (▲) in N.Y., U.S.A.

without setting fruit. Living plants with fruit were, however, found at this time in an area several hundred metres away from the study site.

A life table for the Beebe Lake population is given in Table 1. Mortality was less dramatic in this population though most occurred between days 28 and 60 amongst plants in one corner of the study site, completely removing the plant from it. Cucumber beetles were first recorded at Beebe Lake on July 1 (day 28). Wilting and stunted growth were observed amongst the plants which died.

Plants in the Beebe Lake population were occasionally killed after heavy rain when flash floods severed the stems (which are slender and fragile) or buried them in debris. The herbivore *Anasa armigera* Say (Hemiptera, Heteroptera) was recorded on many plants at both sites. Individual leaves, where the nymph of this animal fed in groups, wilted and died but overall plant growth and survival were not noticeably affected.

### Flower and fruit production

The phenology of flower and fruit production is shown in Fig. 2. Plants were strongly protandrous with some individuals producing many male flowers before any significant number of female flowers had appeared in the population. Male flowers (20–100) are borne on inflorescences which appear singly, or sometimes in pairs, at nodes. Inflorescence development occurs first at apical nodes and proceeds basipetally along the stem and branches. An inflorescence carries open flowers for 2–3 weeks though the life of individual flowers is shorter than this.

The development of female flowers is also basipetal, with only one or sometimes two individual flowers appearing at each node at any one time. Occasionally a third female flower will appear at a node where earlier ones have died. Individual plants are almost exclusively male at the beginning of the flowering season but there are nearly equal
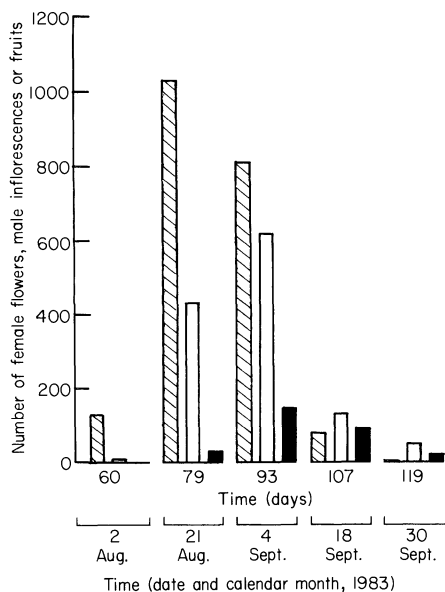
FIG. 2. The number of new male inflorescences (▨), female flowers (□) and new fruit (■) present in a population of *Echinocystis lobata* at Beebe Lake, N.Y., U.S.A., on five census dates during the reproductive phase of the life cycle.

TABLE 1. Combined life table and fecundity schedule for *Echinocystis lobata*, at Beebe Lake, Ithaca, N.Y., U.S.A.

| Date | $x$ | $D_x$ | $N_x$ | $l_x$ | $d_x$ | $q_x$ | $N_x^{\male}$ | $b_x^{\male}$ | $V_x^{\male}$ | $b_x^{\female}$ | $N_x^{\female}$ | $N_x^{frt}$ | $b_x^{frt}$ | $V_x^{frt}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 3 June | 0 | 0 | 101 | 1·00 | — | — | — | — | 3·18 | — | — | — | — | 3·17 |
| 17 June | 14 | 14 | 98 | 0·97 | 3 | 0·21 | — | — | 3·28 | — | — | — | — | 3·27 |
| 1 July | 28 | 14 | 93 | 0·92 | 5 | 0·36 | — | — | 3·46 | — | — | — | — | 3·45 |
| 15 July | 42 | 14 | 80 | 0·79 | 13 | 0·93 | — | — | 4·02 | — | — | — | — | 4·01 |
| 2 August | 60 | 18 | 54 | 0·54 | 26 | 1·44 | 130 | 2·45 | 5·94 | 0·02 | 1 | 0 | 0 | 5·93 |
| 21 August | 79 | 19 | 38 | 0·38 | 16 | 0·84 | 926 | 26·5 | 7·93 | 12·46 | 436 | 27 | 0·77 | 8·43 |
| 4 September | 93 | 14 | 33 | 0·33 | 5 | 0·36 | 813 | 28·0 | 4·58 | 21·30 | 618 | 151 | 5·21 | 8·80 |
| 18 September | 107 | 14 | 27 | 0·27 | 6 | 0·43 | 80 | 3·08 | 0·49 | 5·08 | 132 | 95 | 3·65 | 4·39 |
| 30 September | 119 | 12 | 21 | 0·21 | 6 | 0·50 | 6 | 0·30 | 0·04 | 2·35 | 47 | 19 | 0·95 | 0·95 |

$x$    day of census;
$D_x$    interval between censuses;
$N_x$    number of survivors on day $x$;
$l_x$    proportion of cohort surviving to day $x$;
$d_x$    number dying in interval;
$q_x$    daily mortality rate;
$N_x^{\male}$    total number of male inflorescences in the population at day $x$;
$b_x^{\male}$    number of male inflorescences per survivor at day $x$;
$V_x^{\male}$    reproductive value of plants, calculated for male component of reproduction only, $V_x^{\male} = [b_x^{\male} + l_{x+1}/l_x(V_{x+1}^{\male})]\, 0.149$; (multiplied by 0.149 to achieve a figure relative to the $\female$ component);

$N_x^{\female}$    total number of female flowers at day $x$;
$b_x^{\female}$    number of female flowers per survivor at day $x$;
$N_x^{frt}$    total number of fruit at day $x$;
$b_x^{frt}$    number of fruit per survivor at day $x$;
$V_x^{frt}$    reproductive value of plants, calculated for female component of reproduction only $V_x^{frt} = b_x^{frt} + l_{x+1}/l_x(V_{x+1}^{frt})$.

numbers of male and female flowers at the end. Male inflorescences present at the last two censuses were often very small with only 1–10 flowers.

Some female flowers produced a full-sized fruit in as little as 14 days, though seeds did not mature and were not shed until 4–6 weeks after flowering. Fruits at Beebe Lake contained from one to six seeds each, four being commonest (39% of fruits examined). Seeds are shed when the fruit dries out and the pericarp at the distal end splits and peels back to reveal the open mouths of two locules.

Nineteen plants of the original cohort at Beebe Lake survived to the end of the study. These were used to analyse the relationship between plant size and fecundity and the sources of fruit loss. Figure 3 shows the relationship between plant size (number of nodes) at the end of the study and the cumulative numbers of male inflorescences, female flowers and fruit. The numbers of flowers of both sexes are closely related to plant size but the number of fruits is less clearly so.

Every node on a plant may potentially produce a female flower although not every node does so. Likewise, every female flower may produce a fruit though not all do so. Hence, the number of potential fruits is approximately one per node and the numbers lost are the result of some nodes failing to produce a female flower and some female flowers failing to mature a fruit. These two components of fruit loss and their logarithmic sum are plotted against plant size (potential number of fruit) for the nineteen plants, in Fig. 4. Total fruit loss is highly variable but is, nevertheless, negatively correlated with plant size ($r = 0.62$, $P < 0.01$). Numerically the greatest source of fruit loss was flowers that failed to produce a fruit rather than nodes which failed to flower. However, the latter source of loss was more strongly correlated with overall loss than the former ($r = 0.66$, $P < 0.01$; $r = 0.78$, $P < 0.01$, respectively).

A fecundity schedule for the Beebe Lake population is given in Table 1. Reproductive value in units of fruit production ($V_x^{frt}$) was defined as:

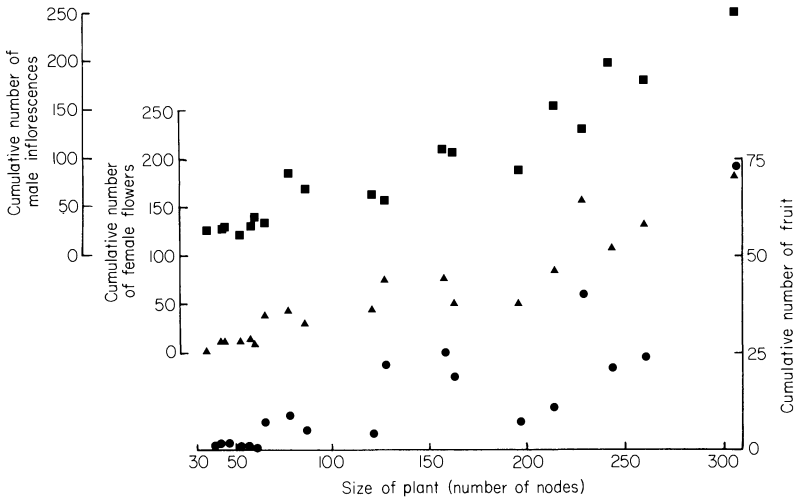$$V_x^{frt} = b_x^{frt} + \sum_{i=1}^{i=n} (l_{x+i}/l_x)\, b_{x+i}^{frt}$$



FIG. 3. The relationship between plant size (number of nodes) at the final census (30 September 1983) and the cumulative number of male inflorescences (■), female flowers (▲) and fruit (●) in the Beebe Lake, N.Y., U.S.A., population of *Echinocystis lobata*.
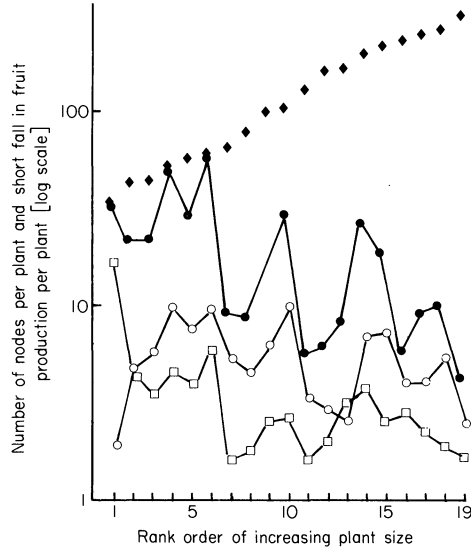
FIG. 4. Plant size (number of nodes) (♦) (equivalent to the potential fruit production) of the nineteen survivors to the last census (30 September 1983) of the Beebe Lake, N.Y., U.S.A., population of *Echinocystis lobata*. Numbers of fruit lost by each plant (●) and the components of that loss due to nodes not flowering (□) and flowers not producing fruit (○) are also shown.
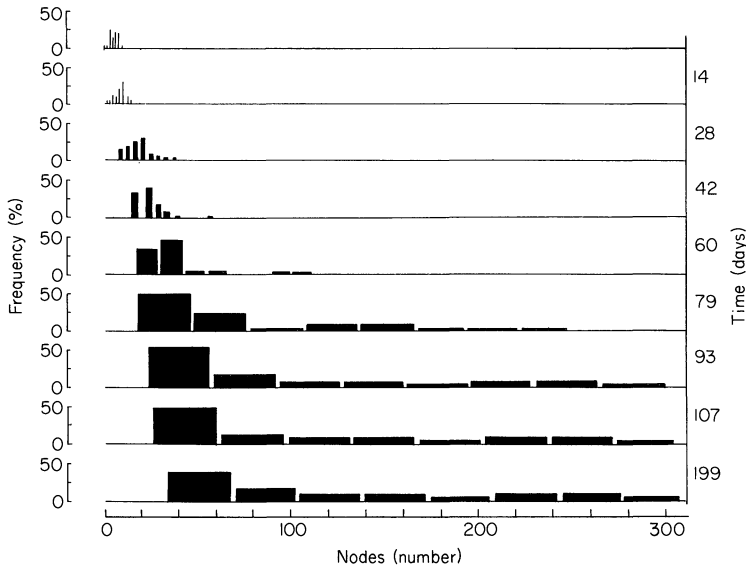


FIG. 5. Frequency distributions of plant size (number of nodes) at each census of the Beebe Lake, N.Y., U.S.A. population of *Echinocystis lobata*.

Where $b_x^{frt}$ is the average number of new fruit per plant recorded on day $x$, $l_x$ is the proportion of individuals surviving to day $x$ and $n$ is the last census. For calculation the equation was used in the form:

$$V_x^{frt} = b_x^{frt} + l_{x+1}/l_x(V_{x+1}^{frt})$$

It was not possible to estimate the reproductive success of male flowers. Reproductive

value in units of male inflorescence production ($V_x^{\circlearrowleft}$) was thus calculated by an equivalent formula, substituting $b_x^{\circlearrowleft}$ for $b_x^{frt}$. Since *Echinocystis lobata* is an annual, a new population appears almost synchronously each year from the seed pool and it is not appropriate to discount reproductive value by the finite rate of population increase when comparing progeny produced at different times within the same generation.

## Growth

The change in plant size distribution with time is shown in Fig. 5. The size distribution at each census was obtained by dividing the range of plant size present (size of largest plant minus the size of the smallest plant) into eight equal intervals.

The larger surviving plants at Beebe Lake showed a sigmoid pattern of growth with an exponential phase commencing at about day 60 when the plants began to branch profusely. The growth and structure of these plants is demonstrated by the branching diagram and growth curve for one of them shown in Fig. 6.
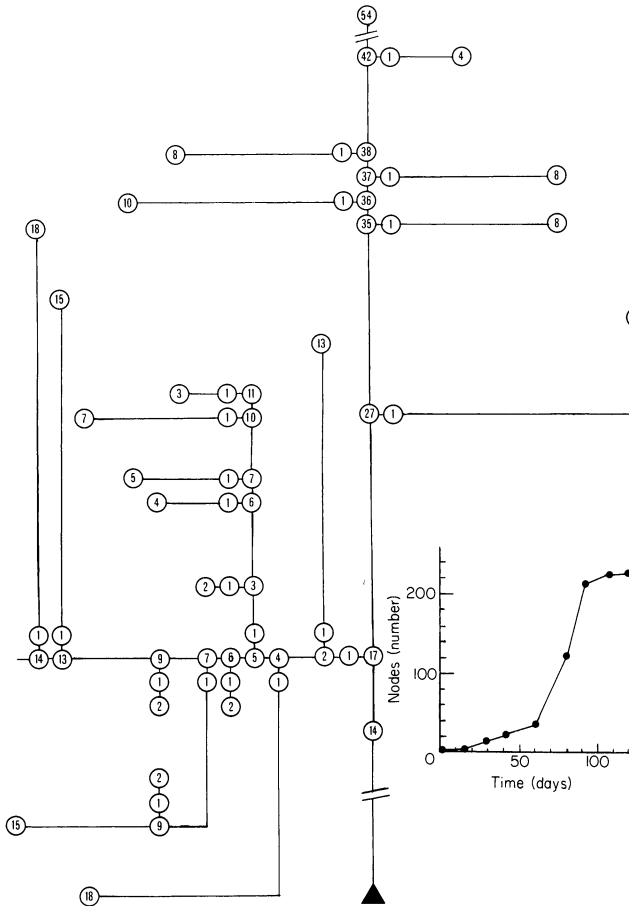


FIG. 6. (a) The branching pattern (drawn to scale) of a typical large plant of *Echinocystis lobata* at the last census in a study of a population at Beebe Lake, N.Y., U.S.A. The base of the main stem is marked (▲); it had fifty-four nodes. The position of each node on the main stem which bears a branch is indicated by its number. Each branch is numbered (1) at its proximal end and with the number of nodes it produced at its distal end. (b) The growth of this plant during the study, measured in cumulative numbers of nodes.

## DISCUSSION

### Mortality

Although the causes of death could not be precisely identified it is clear that *Echinocystis lobata* can be entirely removed locally by sudden death. The patchy distribution of this species is therefore likely to be the result of epidemic mortality as well as environmental patchiness and perhaps limited seed-dispersal.

### Fecundity

Flowering began relatively late in the lifespan of the plants. Since growth (Fig. 6) and fruit production (Fig. 2) had both virtually ceased by the last census, reproductive value was then negligible (Table 1). One hundred and thirty days may therefore be regarded as a good estimate of lifespan. Peak male-flowering occurred on day 79, 61% of the way through the lifespan and peak female flowering occurred on day 93, 73% of the way through the lifespan. Since fruit production reached a peak on day 93 also and exponential growth ceased about then (Fig. 6) there appears to have been a dramatic switch from vegetative growth to reproduction at this point in the life cycle. Theoretical models of reproductive allocation predict that such a switch should be abrupt in annuals living in a habitat where the growing season is relatively fixed (see King & Roughgarden (1983) for a review).

The abrupt switch from growth to reproduction late in the season may be explained in evolutionary terms as a means by which individuals maximize fruit production if (i) numbers of nodes (plant size) limit fruit production and (ii) fruit production carries a physiological cost to plants which has to be met at the expense of node production. The delay in the initiation of flowers and fruit till 60–85% of the way through the lifespan would allow node production to proceed at a maximum rate until the last possible moment, allowing just enough time for fruit to mature before plants are killed by the first frosts which generally occur in early October in the study area.

Fruit production (Fig. 3) increases with plant size and therefore the number of nodes does limit fruit production. Furthermore, the failure of nodes to flower is a significant contributing factor to overall fruit loss which declines in importance with plant size (Fig. 4). By comparison, fruit loss caused by unproductive flowers is numerically more important to overall loss, but this is relatively constant and less related to plant size.

The evidence that fruit production carries a cost in terms of node production is bound to be weak without experimentation. However, some evidence can be obtained by comparing vegetative growth between censuses on days 93 and 107 for branches bearing fruit and those not bearing fruit on day 93. Although many fruitless branches did not grow and many fruit-bearing ones did produce a single extra node, there was a tendency for greater amounts of growth (>1 node) to occur in fruitless growing branches (25% of the total) than fruit-bearing ones (10% of the total).

Many factors such as disease, differences in branch length, number of fruit per branch and possible physiological interdependence between branches may confound these data.

### Growth

The size–frequency distribution for the Beebe lake population (Fig. 5) show similarities with distributions which have been observed in monocultures of annual and perennial plants (e.g. *Tagetes patula* by Ford (1975) and *Festuca paradoxa* by Turner & Rabinowitz (1983). A distribution which is initially fairly symmetrical develops a

right-handed skew as a few plants grow much more rapidly than the rest. This type of pattern has been interpreted as evidence that small plants are suppressed by large ones (White & Harper 1970) though it has also been observed amongst plants grown spaced widely apart where this cannot be the explanation (Turner & Rabinowitz 1983). In *Echinocystis lobata* the development of the same pattern is observed in a natural population of an annual, which is in intimate mixture with woody perennials and for which within-species contact is negligible or absent.

Given that similar size–frequency distributions may be observed in such different populations under such a wide variety of conditions it seems likely that they are the product of exponential growth and it is unwise to interpret them as evidence one way or the other about the action of within-species competition, suppression and dominance.

## ACKNOWLEDGMENTS

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