

# THE REPRODUCTIVE STRATEGY OF HIGHER PLANTS

## I. THE CONCEPT OF STRATEGY WITH SPECIAL REFERENCE TO *SENECIO VULGARIS* L.

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### INTRODUCTION

This paper is the first of a series in which the partitioning of dry matter and energy throughout the life cycles of different plant species will be described. In this paper the concepts of energy allocation (Cody 1966), strategy and tactics (Harper 1967), and the measurement of 'reproductive effort' (Ogden 1968) are discussed primarily in relation to annual plants. An experimental application of these concepts to the life cycle of *Senecio vulgaris* is described.

Consideration of the phenomenon of seed production in terms of a plant's energy budget leads one to ask such questions as: (i) what proportion of the energy fixed by a plant during its life cycle does a plant allocate to seed production? (ii) is the proportion allocated in this way fixed and characteristic of a species or group of species or is it plastic, being subject to change in response to environmental stress (Harper 1967).

Striking variation in plant size, number of inflorescences and 'reproductive capacity' (Salisbury 1942) can be easily observed by comparing annual weeds growing in fertile and less fertile soil. Individuals growing in unfavourable conditions frequently produce many fewer seeds, but it is not immediately obvious whether they allocate more or less of their gross energy budget to seeds than plants of the same species in favourable conditions.

### STRATEGY AND TACTICS

The life history of an organism is to some extent pre-determined; it is a function of the organism's genotype. The genotypic programme may include a range of possible developmental pathways, and the one followed will depend upon the environmental conditions to which the organism is exposed. Modification of the basic genotypic programme, or strategy, may be expressed in a range of phenotypes representing varied tactics. The strategy itself determines the possible range of tactics (Bradshaw 1965). The expression of the life cycle, the ontogeny of the phenotype, is the outcome both of the genotypic strategy, and the particular tactics followed in response to the environment in which the organism develops.

Growth is dependent upon the availability of supplies to the growing organs, and correlations between the growth of different structures seem to be at least in part a function of competition for such essentials (Brouwer 1962a). Consequently a change in the environment affecting the availability of some essential (e.g. light or water) may change the growth rates of different organs to different extents so that the overall pattern of dry matter distribution becomes altered; the root:shoot ratio is well known to be a sensitive

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indicator of such disturbance (Brouwer 1962a, b; Leonard 1962; Monk 1966). The duration of the rosette phase in biennials and winter annuals is similarly known to be sensitive to photoperiod, temperature and soil conditions (Owen, Carsner & Stout 1940). Such developmental plasticity represents a change in tactics by the plant. However, the strategy itself may change from generation to generation in response to selective pressures on the population. Van Dobben (1962, 1966) has presented data which indicate that breeding of cereals for increased yield and shorter straw has significantly increased the grain:straw ratio. The wild oat (*Avena fatua* L.) is the presumed ancestor of the two cultivated species *A. sativa* L., cultivated for grain production, and *A. strigosa* Schreb., cultivated as a fodder plant. The divergent pattern of evolution of these species has involved changes in the proportion of dry matter devoted to grain and vegetative growth (Table 1) which are of greater magnitude than the phenotypic changes which can be brought about by interspecific competition; for example *A. sativa* and *A. strigosa* devote

Table 1. *Components of yield of three species of Avena growing in different combinations*

Species	Growing in mixture with	Total yield (g)	Grain yield (g)	Kernel yield (g)	Grain/total (%)	Kernel/total (%)
<i>A. sativa</i>	<i>A. fatua</i>	12.1	4.9	3.9	40.9	32.4±2.1
<i>A. sativa</i>	<i>A. strigosa</i>	20.9	8.8	7.0	42.1	33.3±2.3
<i>A. fatua</i>	<i>A. sativa</i>	29.1	12.2	7.4	41.9	26.0±2.9
<i>A. fatua</i>	<i>A. strigosa</i>	29.3	13.3	8.1	45.3	27.2±1.4
<i>A. strigosa</i>	<i>A. fatua</i>	14.7	5.2	3.4	35.0	22.9±0.4
<i>A. strigosa</i>	<i>A. sativa</i>	27.9	9.3	6.1	33.5	22.1±1.0

The plants were grown in pairs in shallow trays. Total yield includes roots, dead leaves, and chaff. The grain yield is the shed, or threshed, propagule weight and the kernel yield is that weight after removal of lemmas, paleas and awns. Grain yield of *A. fatua* was estimated from (mean grain weight) × (twice the number of spikelets on the plant). Each figure is the mean of four plants. Data given as dry weights (g) per plant, originally weighed to nearest milligram (from Ogden 1968).

approximately 33 and 22% of their dry weight to kernels but the effect of interspecific competition, while having a profound effect on total yield, scarcely affects the proportion devoted to kernels. Linseed and flax, forms of *Linum usitatissimum* L. selected for seed yield and 'straw' production respectively, show a similar trend in the allocation of dry matter to reproduction, the seed forming c. 36% of the dry weight of linseed at harvest and c. 20% in flax (Khan 1967, analysed in Ogden 1968).

#### *Strategy and the principle of allocation*

It is possible to think of organisms as having a certain limited quantity of time or energy available for expenditure, so that each developmental response, each strategic or tactical solution, represents an allocation, or partitioning, of this time or energy (Cody 1966—following Levins & MacArthur, unpublished). Cody, considering clutch size in birds, argues that the way in which an organism allocates its energy to such ends as reproduction, competition and predator avoidance is a characteristic of ecological and evolutionary importance, and he uses the term 'principle of allocation' to express this idea. In this context the organism's quantitative programme of energy allocation is an essential feature of its strategy. 'Life cycle strategy' is used to express the whole complex

time and space pattern of energy allocation by the organism; 'reproductive strategy' is reserved to describe the energy allocation particularly associated with reproduction.

#### *Types of strategy*

Certain major patterns of energy allocation, which may be grouped at different levels of similarity, can be recognized. For example, in plants, the annual and biennial habits are both monocarpic, their time and energy allocation programme differ quantitatively rather than qualitatively. This introduces the problem of the relative size and time scale of the phenomena under investigation. The monocarpic higher plants, frequently colonizers of open areas, have life cycles which vary from a few weeks (e.g. *Senecio vulgaris* L., *Matricaria matricarioides* (Less.) Porter) to many years (e.g. *Agave* spp.).

In perennial polycarpic plants a wide range of life cycle and reproductive strategies is found. Reproductive behaviour may be sexual or vegetative or both. Frequently there is a juvenile phase, which may last many years in woody plants during which the plant increases its size, but no reproduction occurs.

Survival of the adverse period, which most perennial non-tropical plants must encounter, may be referred to as the perennation strategy. The significance of the adverse period in the life cycle was stressed by Raunkiaer (1934). One of the most conspicuous differences between the ecological races of *Potentilla glandulosa* Lindl. and *Achillea millefolium* L. studied by Clausen, Keck & Hiesey (1940, 1948) was in the occurrence of vegetative dormancy. The high altitude populations were all winter dormant, while the low altitude populations from dry areas were summer dormant, and those from moist coastal areas had no dormant period. Perennation is achieved by a variety of means, often involving organs of energy storage which may or may not serve also to reproduce the individual vegetatively. The stored assimilate may be variously 'packaged', to produce many new individuals in the following season, or to give to one or a few offspring a burst of early growth, as in plants of the vernal phase in woodland (e.g. *Anemone nemorosa* L.) or alpine plants with a short growing season (e.g. *Polygonum bistortoides* Pursh. or *Geum turbinatum* (Mooney & Billings 1961)).

The concept of strategy unites the common classifications of reproductive behaviour into sexual or vegetative, annual, biennial or perennial, with the life form classification of Raunkiaer (1934). It relates the reproductive and survival aspects of plant growth on a common scale, in terms of the relative quantities of energy expended on them. Moreover it may allow some form of 'value' judgement; the quantity of energy expended on a particular function or structure, relative to the total quantity of energy available for expenditure, may be some measure of the relative value which natural selection has placed upon that function or structure.

#### *Reproductive effort*

Energy allocation to seeds may be shared between a few large seeds representing few large capital investments or many small seeds each with small capital invested (Harper, Lovell & Moore 1970). As the size of a seedling represents the product of the embryonic capital, the growth rate and the time elapsed since germination, both seed size and dormancy constitute important quantitative features of reproductive strategy.

Just as a large production of small seeds might involve no more effort than a low production of large seeds, so vigorous seed production in 1 year of a long-lived monocarpic species may involve no more total output of energy than the small annual recurrent expenditure of an iteroparous species. Salisbury (1942) drew attention to the

broad correlations between the 'reproductive capacity', the seed characteristics of a species and its ecological status. However, 'reproductive capacity' has not itself proved very successful as a criterion for making ecological comparisons, presumably mainly because quantity of seed is highly correlated with vegetative vigour.

If the plant is regarded as a seed producing machine—the means whereby one seed produces more seeds—its energy *input* is the assimilated carbon (gross production), plus the starting capital of energy stored in the seed from which it originated. (Although starting capital may be ecologically extremely important, it is normally an insignificant item in the overall energy budget of the individual to which it gives rise.) The machine *output*, in this context, is the energy contained in the seeds or vegetative propagules, and the efficiency of the machine, as a propagule producer, is simply measured by the ratio of input energy: output energy.

Ideally a measure of reproductive effort would involve the determination of starting capital, gross production and that fraction which is output in the form of propagules. Although detailed energy budget studies of this type have been made for certain animal species, e.g. *Daphnia* (Richman 1958), *Operophtera brumata* (Varley 1967) and *Oniscus asellus* (Phillipson 1967), no similar analyses of complete plants grown over their whole life cycles appear to have been made. Transeau (1926) complained that 'there is no probability that we shall have in the near future an experimental determination of the energy budget for a complete plant, such as we have for a great variety of animals'. More recently Kieckhefer (1962) observed that 'little or no research is being done on the energy dynamics of individual species of plants'.

The ideal measurement of reproductive effort may be stated as:

$$(a) \text{ Gross reproductive effort} = \frac{\text{Total energy as propagules}}{\text{Total energy as starting capital plus gross assimilation}}$$

It is possible to simplify the practical problems implied in this equation by considering efficiency in relation to net, rather than gross, production:

$$(b) \text{ Net reproductive effort} = \frac{\text{Total energy as propagules}}{\text{Total energy as starting capital plus net production}}$$

Reproductive effort defined in equation (b) will be higher than in equation (a), by an amount dependent upon the respiratory energy loss. Ideal measurements of energy budgets are expressed in calories; in practice production figures are usually given as dry weights. 'Total energy' implies energy accumulated over the entire life cycle. Measurement in terms of dry weight rather than calories may have relatively small effects on the ratio where the per gram calorie values of propagules and vegetative structures are similar, as in the cereals where the seed food store is mainly carbohydrate. Where oils constitute any appreciable proportion of seed weight, as in the Compositae, reproductive effort estimated from weights will be lower than the estimate from calories.

If there is relatively little shedding of parts during the growth to maturity of an annual plant, net production might be approximated by biomass at maturity.

$$(c) \text{ Estimate of net reproductive effort} = \frac{\text{Total weight of propagules}}{\text{Total biomass weight at maturity (time } t)}$$

when:

- (1) Total weight is proportional to total calories (usually approximately true).
- (2) Starting capital is negligible (usually approximately true).

(3) Biomass at time  $T$  is equivalent to net production between germination and maturity ( $T_0-T_1$ ). In practice biomass at maturity will normally underestimate production.

It was thought that equation (c) might provide a simple means of comparing the order of magnitude of efficiency in different species, and a form of the equation was used for this purpose in a preliminary experiment. However, its satisfactory application was hindered by rather unexpected difficulties in estimating the time of maturity in different species. Size and maturity tend to be confounded; there is little difficulty deciding approximately when a small plant with a few seed heads is mature (i.e. when maximum net production has been achieved), but a large plant with many heads at different stages of development presents considerably more difficulty.

Various authors have presented data that allow some measure of equation (c) to be obtained for annual crop plants. Donald (1962), following Niciporovic (1954), realized the importance of this ratio as a characteristic of agricultural yield, and referred to it as the 'harvest index'. Harvest index was defined as the ratio of the economically important portion of the yield, usually grain, to the total biological yield of dry matter. The index has been used by subsequent workers (e.g. Stern and Beech 1965), but biological yield has been taken to mean the weight of above ground parts at the time of harvest. There is abundant literature on grain:straw weight ratios in cereals (e.g. Van Dobben 1962, 1966) but in very few instances has total root production been measured and included. Clearly, in order to compare reproductive efficiencies of different plants, and calculations from the works of different authors, the form of data must be taken into account.

Because the biomass of a perennial plant at any particular time gives a particularly biased estimate of net production up to that time (Mathews & Westlake 1969), any comparison of the reproductive efficiencies of annuals and perennials must be based on net production (equation b). In a harvesting system in which successive estimates of biomass are made, the major difficulty lies in estimating the loss of plant parts between harvests. Roots present an especial difficulty. The estimation of net reproductive effort in perennial plants will be dealt with in more detail in a later paper.

It seems realistic to include ovary and dispersal structure as part of the 'seed' for a discussion of energy expended on reproductive units. In the present studies of the Compositae the whole achene is taken to be the 'seed' (equation d).

$$(d) \frac{\text{Total production as achenes (+ pappus if present) (wt or cal)}}{\text{Total net production (wt or cal)}}$$

This ratio overestimates the true net reproductive effort (or 'efficiency') by an amount proportional to the pericarp (+pappus):seed ratio (in weight or calories). In species with a thin pericarp this overestimate will be small, especially when measured in terms of calories, and when making intraspecific comparisons it can probably be disregarded. When comparing different species with distinct achene morphologies it must be remembered that the energy represented by the shed propagules may overestimate the energy allocated to the next generation by different amounts. Allocation to reproduction can be sub-divided into that part of the investment which is allocated to the next generation (embryonic and endospermic capital), and that part which is allocated to the protection and dispersal of this investment.

We appreciate that there is some arbitrariness in selecting the net energy budget as the basis for describing the strategic allocation of a plant's resources. This may be justified in part by analogy with studies with animals (Cody 1966; Richman 1958; Phillipson 1967). It must be acknowledged that problems of energy allocation may be of less importance in

the evolution of strategies than the allocation of, for example, a limited nitrogen resource. Other budgetary descriptions will ultimately be needed before the best quantification of life cycle strategies can be selected.

#### THE REPRODUCTIVE EFFORT AND PROGRAMME OF ENERGY ALLOCATION IN *SENECIO VULGARIS* L. AND SOME OTHER ANNUAL COMPOSITES

*S. vulgaris* was chosen as the first species for detailed analysis of the programme of energy allocation. *S. vulgaris* possesses an ephemeral monocarpic strategy typical of many weedy species. A rosette phase of vegetative growth is followed by a more or less continuous period of seed production which eventually culminates in death. There is, however, considerable variation in the pattern and timing of development of the various organs. This study was designed to determine whether the 'reproductive effort' of the species was affected by gross variations in individual plant size brought about by differently available root volumes.

#### MATERIALS AND METHODS

Plants were grown in the temperate glasshouse of the School of Plant Biology experimental station, Pen-y-ffridd, Bangor, in 1966, in three replicate randomized blocks with twenty-five plants of each of three treatments in each block, giving 225 plants in all. The plants were all grown singly in pots of a 50:50 mixture of coarse sand and sterilized loam. Three 'stress' treatments were imposed by varying pot size. The smallest pots, giving the severest stress condition, were 3.75 cm diameter. Medium stress was given by using 7.5 cm pots and low stress by using 15 cm pots. The soil volumes in the pots were respectively 20, 300 and 1700 ml (1:15:85).

Decreasing soil volume treatments were suggested by the observation that *S. vulgaris* often grows, flowers and sets seeds under extremely harsh conditions, such as on stone walls, gravel pathways and sand dunes. In these circumstances the plants are often very depauperate with only one small capitulum and contrast strongly with plants from garden soil or agricultural land, which may bear more than 1000 capitula.

Seed of weed origin from a garden in Bangor was sown on 25 July 1966, and seedlings transplanted into pots on 8 August.

The experimental design provided for twenty-five harvests of three plants per treatment to be taken at random from the replicates every 3 or 4 days during the main flowering and seeding periods. Eighteen harvests were taken; the last, taken when the majority of plants in the experiment had died, consisted of the remainder. The plants were removed from the pots by immersing them in running water and working the roots loose from the soil by hand. At most harvests each plant was divided into roots, stems, leaves, receptacles and flowers, and these were weighed separately after drying to constant weight. The total area of leaf of each plant was measured with an electronic scanner before drying. At four harvests (20 August, 2, 10 and 22 September) the harvested plants were pressed whole, between sheets of blotting paper. These plants were not weighed, and served as a store of material for any observations subsequently required.

In addition to the main harvests, whole capitula were collected three times each week throughout the seeding period. Only those capitula which were in the 'clock' stage, had shed no achenes, and retained the dried remains of the floral structures, were taken. Each was cut below the receptacular disc leaving the recurved involucre bracts un-

damaged, dried to constant weight at 70° C and divided with forceps into (i) receptacle (with bracts), (ii) floral remains (dried corolla tubes) and (iii) achenes and pappus. Each fraction was weighed separately and the data were used to obtain the regression of achene and pappus weight on receptacle weight. This regression equation was subsequently used to estimate the shed achene weight of the harvested plants.

After weighing, the dried plant parts were ground to a fine powder using a Wiley mill, pelleted and the calorific values of hypocotyls, stems, roots, leaves, dead leaves, flower buds, complete flowers and floral parts, seeds with pappus and receptacles were determined with a Gallenkamp Adiabatic Bomb Calorimeter. Nitrogen and sulphur determinations were made on thirty test samples, and the calorific values corrected for heat liberated in the formation of nitric and sulphuric acids at combustion. This never accounted for more than 0.25% of the total heat release, and as the determinations took considerable time they were discontinued. Two or more replicate determinations were made on each sample where there was sufficient material.

## RESULTS

### *Net production and biomass*

The net production and biomass of each individual was related to the volume of soil in which it was grown (Table 2). The calorific values per gram of different plant parts dried at 70° C (containing an average  $3.9 \pm 0.1\%$  by weight of water) are given in Table

Table 2. *Pot size and productivity of Senecio vulgaris plants in the experiment*

Stress treatment	High	Medium	Low
Soil volumes (ml)	20 (1)	300 (15)	1700 (85)
Pot diameters (cm)	3.75 (1)	7.5 (2)	15 (4)
Maximum biomass per plant (g)	0.088 (1)	0.714 (8.1)	4.688 (53.3)
Maximum biomass per plant (cal)	359 (1)	3046 (8.5)	20333 (56.6)
Estimated total net production per plant (cal)	374 (1)	3282 (8.8) ± 492	22276 (59.6) ± 1293

Ratios are in parentheses; all figures are means of three plants.

Table 3. *Mean calorific values per gram of different plant parts\**

Plant part	No. of samples	Cal/g
Hypocotyl	1	4529
Stem	19	4084 ± 37
Root	17	4087 ± 45
Leaves	14	3976 ± 14
Dead leaves	6	3787 ± 96
Flower buds	1	4507
Floral parts (perianth)	1	4699
Whole flowers	2	4706 ± 44
Receptacles	3	3864 ± 34
'Seeds' (achenes + pappus)	3	5474 ± 125

\* Plant material dried at 70° C and containing on average  $3.9 \pm 1\%$  water. Separate determinations of calorific values were made for the different treatments where there was sufficient material but as no significant differences ( $P = 0.05$ ) were present the data were combined.

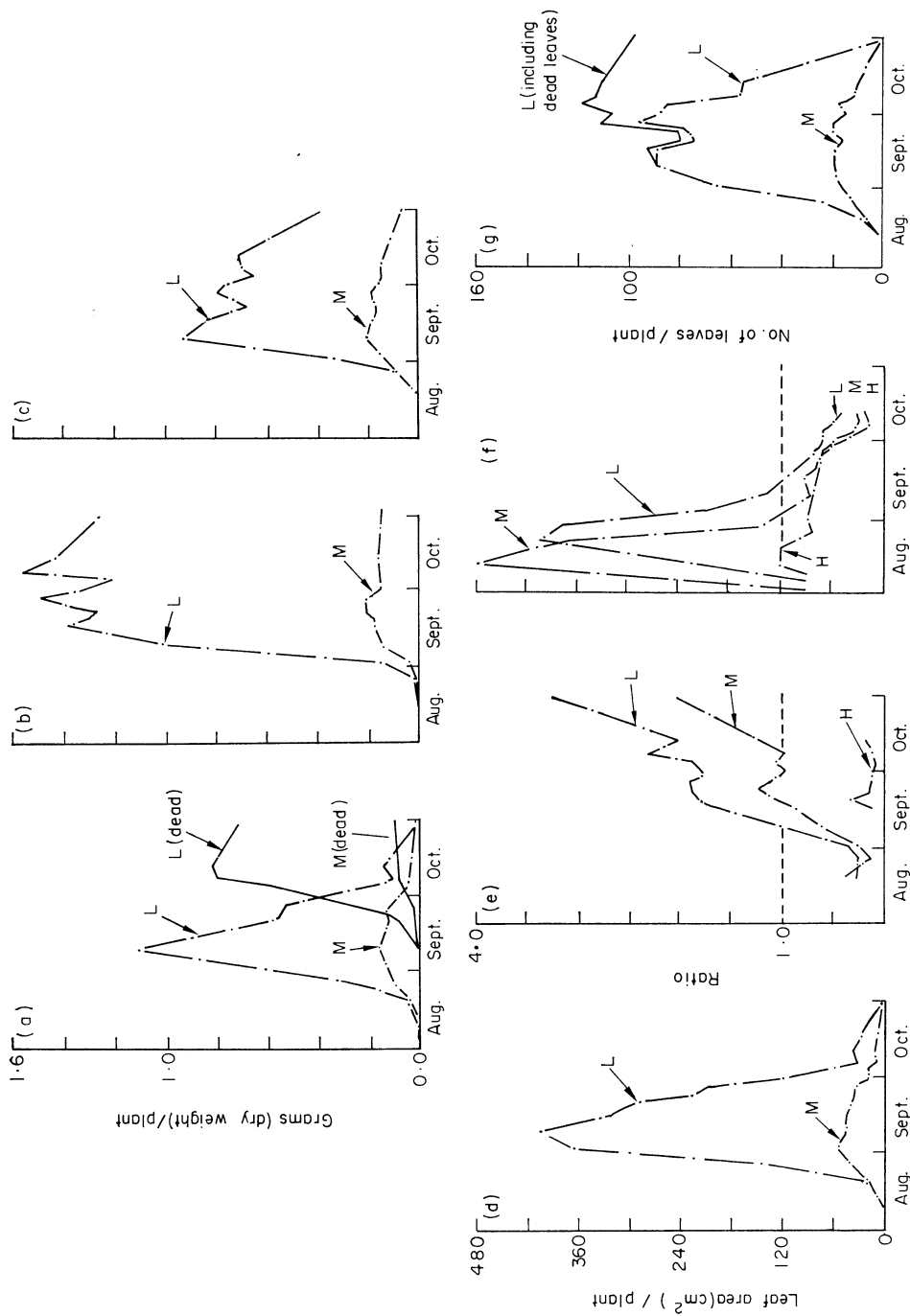


FIG. 1. Growth of vegetative parts of *Senecio vulgaris*. (a) Leaf weight (g); (b) stem weight (g); (c) root weight (g); (d) leaf area (cm<sup>2</sup>); (e) stem : root ratio (cal); (f) leaf number. L, 'Low stress' treatment (1700 ml soil/plant); M, 'medium stress' treatment (300 ml soil/plant); H, 'high stress' treatment (20 ml soil/plant).



No significant differences in calorific values per gram between treatments could be demonstrated, but the data are insufficient for any certainty on this point (see Long 1936).

#### *Precocity of development*

Maximum calorific values per plant were attained earlier under high and medium stress conditions than under low stress. The plants grown under medium stress attained

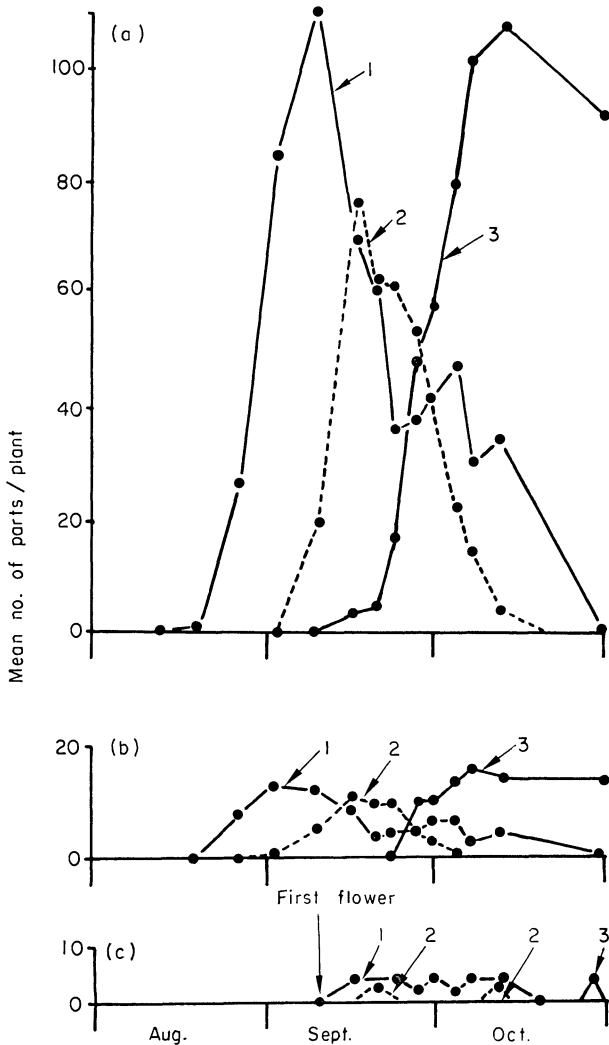


FIG. 2. The progress of flowering and seed shedding in *Senecio vulgaris*. (a) 'Low stress' treatment; (b) 'medium stress' treatment; (c) 'high stress' treatment. 1, Flower buds; 2, open flowers; 3, receptacles which have shed seed.

maximum leaf area, stem weight and numbers of reproductive parts a few days earlier than those under low stress (Figs. 1 and 2). This precocity was not shown by plants growing under high stress; on the contrary, these plants were very retarded. Many of them failed to flower and remained as 'seedling rosettes' throughout the experiment. The most

noticeable feature of the plants grown under high stress was their variability in time of stem elongation and flowering in comparison with plants under less severe conditions. Under low and medium stress all plants in the same-sized pots commenced stem elongation, flowering and seed setting synchronously. Under high stress the first individual to flower did so at the same time as the first individuals under other treatments, but individuals continued to elongate and produce one or two flowers in a haphazard way until the end of the experiment.

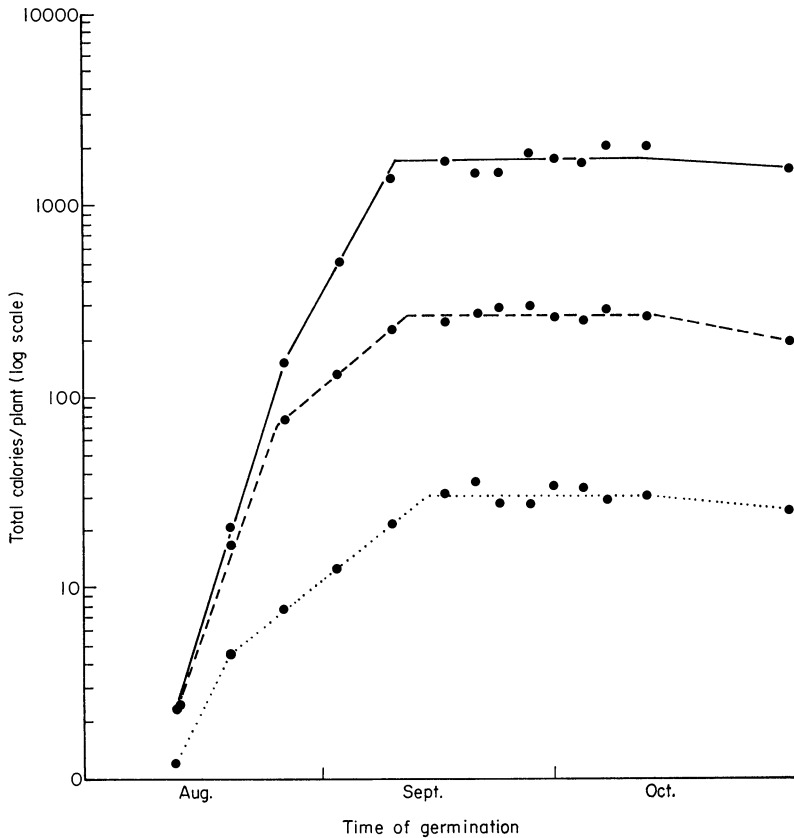


FIG. 3. Growth curves for *Senecio vulgaris*. —, 'Low stress' treatment; ---, 'medium stress' treatment; ···, 'high stress' treatment.

#### *Phases of development*

If a total dry matter growth curve is considered to be composed of a series of successive exponential growth curves, representing the growth of different plant organs, then successive stages can be represented as a series of straight lines on logarithmic plots (Williams 1964; Stern & Beech 1965). Logarithmic plots of the total biomass (cal) per plant at each treatment have been subjectively segmented in this way in Fig. 3.

Under low and medium stress, three fairly distinct growth phases can be recognized. These phases correspond approximately with overall changes in the morphology of the plant, and they presumably reflect alterations in the balance between assimilation and respiration. The first phase, from 31 July (germination) until 26 August was charac-

terized by a high growth rate, and the development of a leafy rosette. During the second phase, from 26 August until 9 September, growth rate declined, stem elongation and branching occurred, many buds developed and the first flowers opened. Under high stress conditions these two phases were not distinct, the plants remaining as little more than

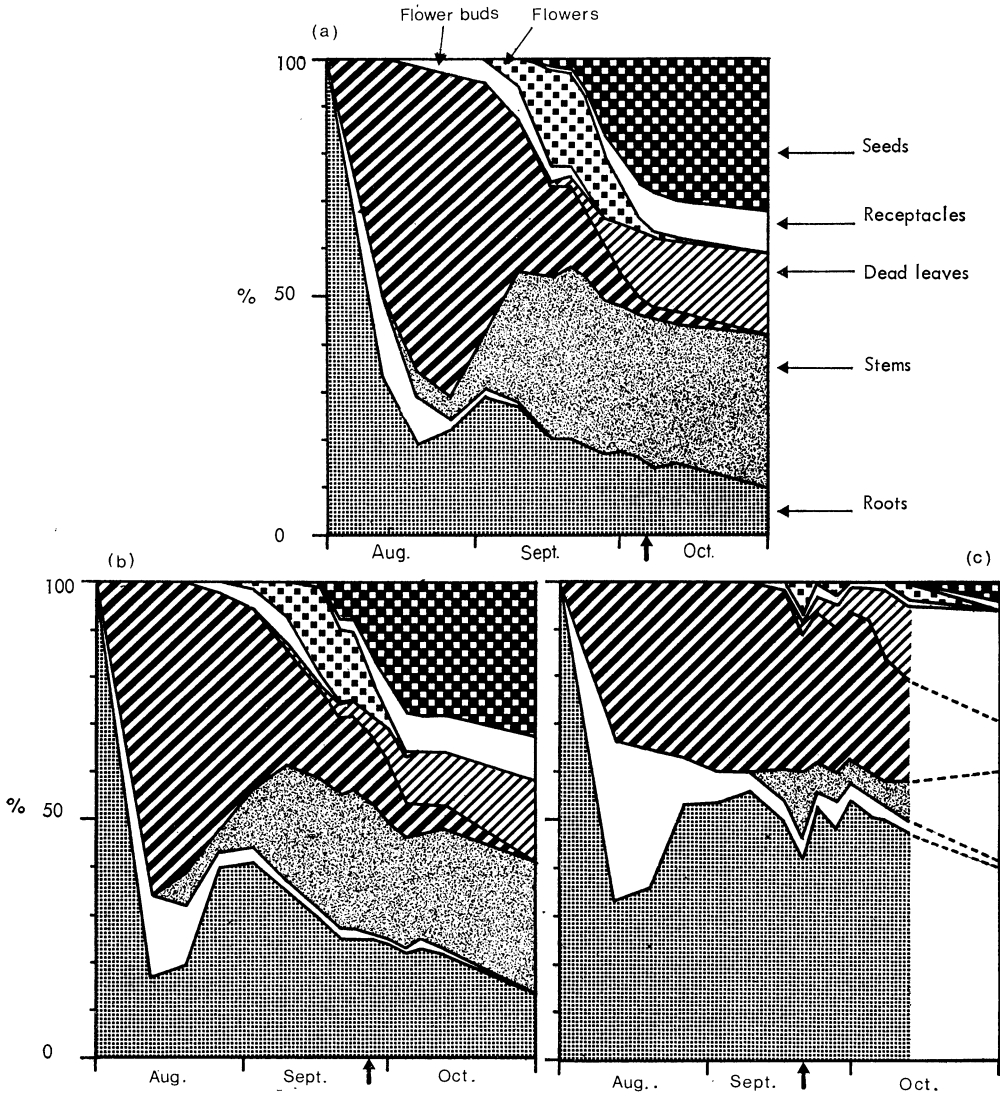


FIG. 4. Percentage allocation of total calories of biomass throughout the life cycle of *Senecio vulgaris*. (a) 'Low stress' treatment; (b) 'medium stress' treatment; (c) 'high stress' treatment. Vertical arrows mark dates at which maximum total calorific values were recorded.

seedlings, with seven or eight leaves, and with no stem elongation in most individuals ('seedling rosettes').

In all treatments the overall growth rate dropped to zero between 9 and 16 September. In low and medium stress treatments this corresponded with the peak of flower bud

development and the opening of the first seed heads. In these treatments the third growth phase corresponded to seed maturation and shedding, and was marked by root death, and a steep decline in leaf area due to death of leaves. While leaf area fell steadily, leaf number rose slightly (Fig. 1), due to continued production of a few small leaves on the branching inflorescence. In the severest stress treatment the sudden decline in growth rate was marked by the swelling of the flower buds, which had previously been too small to observe.

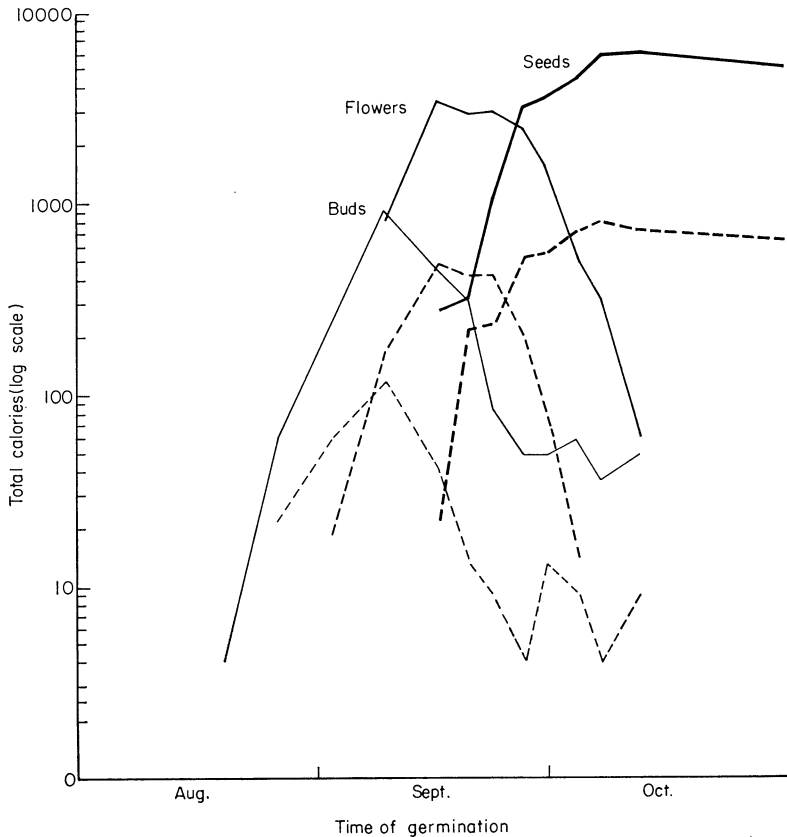


FIG. 5. Growth of reproductive structures of *Senecio vulgaris*. —, 'Low stress' plants; ---, 'medium stress' plants.

### *Yield components*

Plants growing at low and medium stress differed very significantly in the weights of all their component structures and in the extent of branching but at all stages during their life cycle the proportionate distribution of dry matter showed an overall similarity. In contrast, plants grown under high stress were quite distinct, mostly remaining in the 'seedling rosette' phase of development throughout the experiment. Under medium and low stress treatments, relative stability of the proportion of dry matter devoted to reproductive parts was achieved through plastic responses in other organs, particularly in the proportionate allocation to roots and stems. The proportion of total biomass in roots increased with increasing stress (decreasing soil volume) while the proportion in stems

declined. Fig. 4 shows the pattern of distribution of biomass at different times throughout the life cycle for mean plants at different treatments. It must be emphasized that, due to lack of synchrony between individuals, a 'mean' plant under high stress conditions is an abstraction from the data, rather than an approximation to the mean behaviour of the population. However, insofar as all the data were collected in the same way, they are comparable, and the high stress data are included for completeness.

#### *The reproductive phase*

The total calorific investment in reproduction gradually increases as buds become flowers, flowers are fertilized and seeds mature (Fig. 5). Buds persist throughout the whole flowering and seeding periods. The end of the main flowering phase is marked by the development of new flower buds, mainly on short branches arising in the axils of the main basal leaves. Usually the majority of these buds failed to flower or set seeds, but if the main axis was damaged, these branches elongated and a new flower phase was initiated. Consequently these short leafy axillary branches, with their flower buds, constitute a rejuvenation system which is normally inhibited, but ensures the rapid regrowth of a damaged plant.

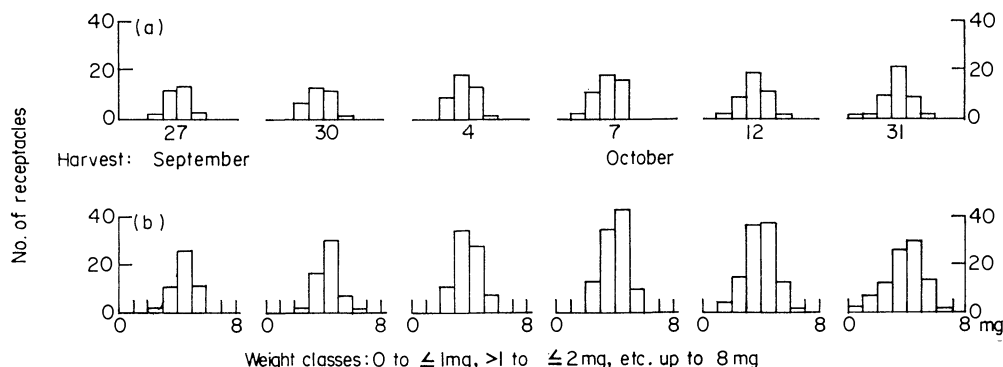


FIG. 6. Frequency distributions of receptacle weight in *Senecio vulgaris*. (a) 'Medium stress' treatment; (b) 'low stress' treatment.

The regression relationship between seed and receptacle weight was used to estimate the total weight of seed output by the plants, from the weight of receptacles which remained at final harvest. Mean capitulum size (weight) decreased with increasing stress. Every capitulum produced by low and medium stress plants at every harvest was weighed (Fig. 6). In both treatments and at all harvests receptacle weight was approximately normally distributed with a tendency to increased variance, due to a larger proportion of smaller receptacles, in the later harvests. This trend was shown most clearly under low stress, where the total number of receptacles per individual was about seven times the number under medium stress. Many of the smaller receptacles carried a large proportion of sterile seeds and little effective seed production occurred between 12 and 31 October when the plants were becoming senescent; due to the shedding of some capitula, the mean number per plant declined during this period. Although the range of receptacle weights was similar in low and medium stress treatments at most harvests, medium stress plants tended to have a lower modal weight class. This was true of most organs. Under low stress treatment the percentage of the (capitulum) population in the modal class (4-5 mg)

gradually fell as the number of capitula increased and the frequency distribution skewed to the left. Shortly after the commencement of seeding on 20 September, 63% of the (capitulum) population fell in the modal class. A week later only 53%, and by the end of the experiment (31 October 1966) only 33%, of the capitula belonged to the modal frequency class. These trends were less obvious under medium stress.

#### *Reproductive effort*

(a) *Medium and low stress.* In both low and medium stress treatments reproductive effort expressed as total calories in seed over total calories of biomass rose to a value of 26–28% by 4 October. Between 4 and 12 October (the main seed shedding period, Fig. 2) the reproductive effort remained almost unchanged. By the time of final harvest (31 October 1966) the plants were mostly dead, and values for reproductive effort estimated at this time were somewhat higher, probably due to some undetected decay of plant parts.

Data in Table 4 strongly suggest that there is no significant difference in the proportion of energy allocated to seeds under low and medium stress, even though the plants differed seven-fold in size (Table 2). However, the data in Table 4 are based on biomass rather than total net production. If it is assumed that the maximum total calorific content of leaves, stems and roots, represent energy fixed in them, which cannot be moved to other

Table 4. *Estimates of reproductive effort (as percentages)*

	Treatment 'stress'	Date (month indicated by second figure)								
		16/9	20/9	23/9	27/9	30/9	4/10	7/10	12/10	31/10
Seeds (cal)	Low	1.7	2.2	6.8	16.7	20.2	26.6	28.7	29.8	32.6
	Medium	0.9	8.2	8.1	17.1	20.6	28.2	28.8	27.7	33.3
Biomass (cal)	High	(8.0)								(4.3)

Percentages calculated from means of three plants/treatment at each harvest.

parts of the plant (i.e. once maximum weight is achieved in an organ it declines through respiration and decay, not through translocation), then the sum of the maxima for different vegetative structures, and the total accumulated weight of reproductive structures on 12 October, provides an approximation to the total net production by the plant over its life cycle.

Seed weight may be estimated from the sum of the calculated seed weights of all the individually weighed receptacles. This estimate of seed weight was taken along with the net production figures, to give the 'best estimates' of reproductive effort presented in Table 5. For low and medium stress plants the overall mean reproductive effort (energy allocated to seeds expressed as a proportion of the total net energy fixed) was calculated to be  $21.4 \pm 1.6\%$ .

(b) *High stress.* In estimating net production from changes in biomass between harvests it must be assumed that the development of all individuals in a treatment is approximately synchronous, so that 'mean plants' at different harvests may be taken to represent stages in the development of an individual. Due to the irregularity of flowering and seed setting under high stress, very few plants in this treatment were harvested while in the reproductive phase and those that were harvested were often included with non-reproductive individuals. As a result, harvest means for the high stress treatment relate to a 'mean plant' in an intermediate condition which has no basis in reality. These data are unsatisfactory for calculating reproductive effort unless certain assumptions can be made.

Under high stress many plants failed to flower, so that they had reproductive efforts of zero. Only at the final harvest were seeding plants included in the sample of this treatment, and they formed only a small proportion of the total. As a result the reproductive effort of 3.0% (4.3% expressed as calories) refers to the behaviour of the population, rather than the behaviour of those individuals within it which did produce seeds. One individual in the high stress treatment did set seeds between 16 and 20 September, when the first seeds were being shed in other treatments. Assuming that this individual had a similar stem and receptacle weight to the mean for high stress plants at that time, and a similar stem and receptacle weight to those plants which were setting seed at final harvest, its efficiency can be estimated as 6.0% (weight) or 8.0% (calories). These values are similar to those for medium stress plants at the same time. While these figures may be unreliable, taken along with the previous estimate, they do suggest that the plants under high stress had a very low 'reproductive effort' when compared to the plants in other treatments. The population as a whole was certainly less efficient in conversion of assimilates to seed, due to the inclusion within it of many non-flowering individuals. It would appear that plants grown under high stress have their reproductive development 'curtailed' after producing one to two receptacles and have at maturity efficiencies similar to less stressed plants in very early seeding stages, when they too have only one or two heads.

Table 5. *Best estimates of reproductive effort; (total seed weight produced)/(total net production up to 12 October) expressed as percentages in weight and calories*

Treatment 'stress'	% reproductive effort	
	Weight	Cal
Low	18.7 ± 2.3	23.8 ± 2.9
Medium	14.7 ± 0.5	18.9 ± 0.6
High	(6.0)	(8.0)

## DISCUSSION AND CONCLUSION

In *Senecio vulgaris* reproductive effort, expressed as the proportion of the total net energy budget allocated to seeds, was maintained at about 21% over a seven-fold difference in total plant weight, irrespective of alterations in the pattern of energy allocation to other structures. However, extreme conditions producing dwarf plants reduced reproductive effort and elicited great variation within the population. This response, resulting in great variation in the time at which individuals under the high stress treatment came into flower, rendered the 'mean plant' at each harvest unsatisfactory as a representative of the population as a whole, but it is nonetheless an interesting feature of the tactics under extreme stress. The irregular behaviour of these plants was remarkably similar to that of 'fertile soil biotypes' of *Capsella bursa-pastoris* grown in infertile sand in the experiments of Sørensen (1954) and to the exaggerated variation in heading response of *Lolium* sp. when exposed to alien photoperiods (Cooper 1954).

It must be emphasized that judging either efficiency or precocity on appearance alone can be very misleading; most of the flowering individuals at high stress at the end of the experiment appeared both precocious and efficient, they were small, had few (remaining) leaves, while the single capitulum appeared large in comparison with the (above ground) size of the plant.

Table 6. Crude reproductive efficiencies (harvest indices) of weed and cultivated composites; seed/biomass at final harvest (weight and calories) expressed as percentages

Species	Crude reproductive efficiency (%)	Sources (see notes)
<i>Helianthus annuus</i>	14, 28, 30(=32), 40*	(a), (b), (c)
<i>Carthamus tinctorius</i>	13-23*, 16-25*	(c), (d)
<i>Senecio vulgaris</i>	14, 14, 25-27(=32-34)	(a)
<i>Chrysanthemum segetum</i>	26-27	(e)
<i>Calendula officinalis</i>	27	(a)
<i>Matricaria matricarioides</i>	35	(a)

\* Excluding roots.

Figures in parentheses are based on calories. References: (a) Ogden (1968); (b) Long (1936); (c) Stern & Beech (1965); (d) Beech & Norman (1963); (e) Howarth & Williams (unpublished).

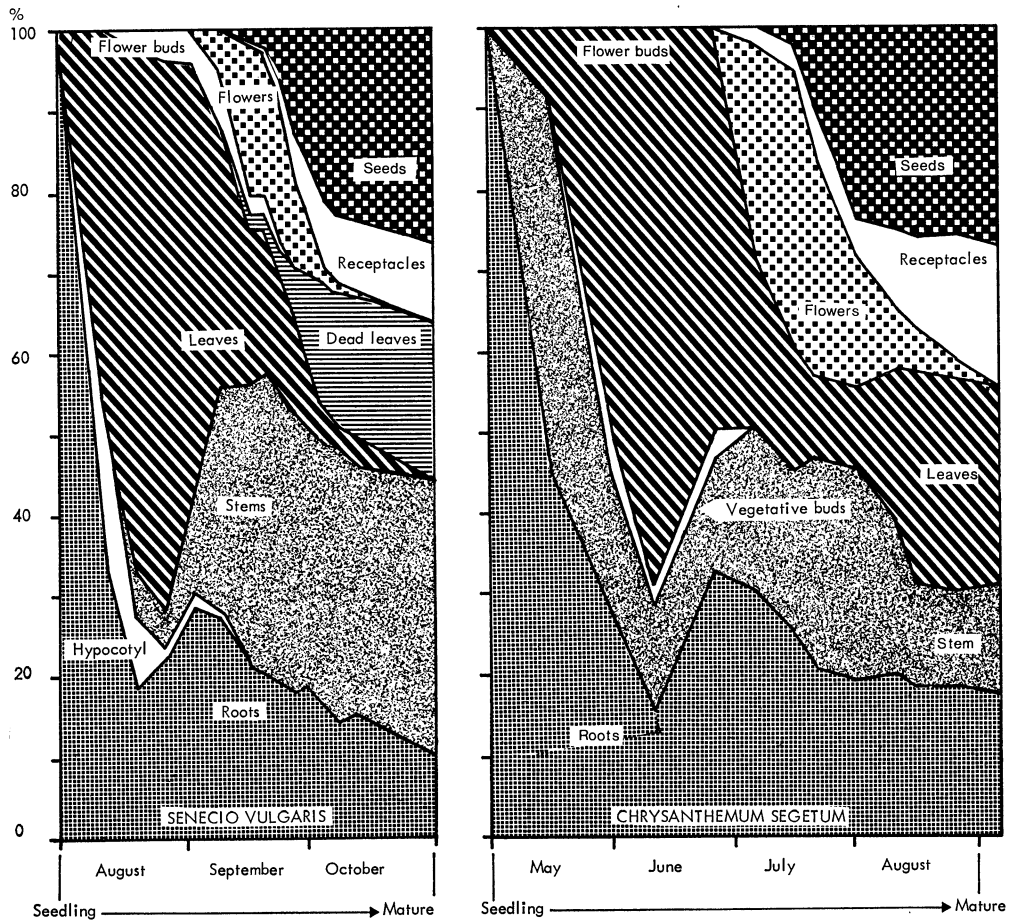


FIG. 7. Allocation of dry weight to different structures throughout the life cycles of *Senecio vulgaris* and *Chrysanthemum segetum*. (Data for *C. segetum* supplied by S. E. Howarth and J. T. Williams, reproduced with permission.)



'Harvest index' (Donald 1962) may be defined as: (seed weight)/(total weight) measured at final harvest. This index is a crude approximation to the net reproductive effort defined earlier. For *Senecio vulgaris* in this experiment the index was 26–27%. Measured as calories rather than weight it was 33–34%, considerably higher than the mean net reproductive effort of  $21.4 \pm 1.6\%$ . Harvest indices of 25–30% have also been recorded for *Helianthus annuus* L., *Carthamus tinctorius* L., *Chrysanthemum segetum* L. and *Calendula officinalis* L. (Table 6). Lower harvest indices (14%) were obtained for *Senecio vulgaris* in a preliminary experiment (Ogden 1968) in which the plants were relatively immature when harvested and for *C. tinctorius* in commercially grown stands (Stern & Beech 1965; Beech & Norman 1963). Safflower was grown under a wide range of density and fertilizer treatments in Stern & Beech's experiments; the authors consider that the lower values are not characteristic of the crop.

A critical consideration of the data, reviewed in Table 6, suggests that the net reproductive effort (weight) of the annual composites frequently lies between 20 and 30%. In this context, the quantitative similarities in the energy allocation programmes of *Senecio vulgaris* and *Chrysanthemum segetum* (Fig. 7) are particularly significant. It may be suggested, on the basis of the data reviewed, that these two weed species are no less efficient (as seed producing machines) than annual oil-seed crop plants in the same family.

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#### SUMMARY

This paper is the first of a series in which the partitioning of dry matter and energy throughout the life cycle of different plant species will be described. The concepts of energy allocation, strategy and tactics, and the measurement of 'reproductive effort' are considered, primarily in relation to annual composites. An experimental application of these concepts to the life cycle of *Senecio vulgaris* grown under different 'stress' conditions is described. Three 'stress' treatments were imposed by growing the plants from seed in pots of three different sizes, in a poor sandy soil. The smallest pots imposed the greatest 'stress'. The distribution of dry matter to the different parts of the plant was followed throughout the life cycle. Calorie conversion factors were obtained for the different organs, so that dry weights could be converted into calories, and the net energy budget described. 'Reproductive effort' defined as:

$$(\text{Total seed production})/(\text{total net production}) \times 100$$

(with production expressed as total calories) was found to lie between 18 and 24% for *S. vulgaris*, except under extreme stress conditions, when the plants were depauperate and flowering was erratic. The 'reproductive effort' estimated for *S. vulgaris* is very similar to estimates for other annual Compositae. Annual composites which have been cultivated as crop plants are apparently no more efficient (as seed producing machines) than weed species in the same family.

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