Acta Bot. Neerl. 38(2), June 1989, p. 183–201

Life history and plant architecture: size-dependent reproductive allocation in annual and biennial *Centaurium* species

H. SCHAT, J. OUBORG and R. DE WIT

Biologisch Laboratorium Vrije Universiteit, De Boelelaan 1087, 1081 HV Amsterdam, The Netherlands

SUMMARY

The frequency of annuals, monocarpic perennials and polycarpic perennials among the dicotyledonous, herbaceous representatives of the European plant families are compared and related to various characteristics of plant architecture. It is suggested that the evolution of life-history may be governed by plant architecture. A comparison between annual and biennial *Centaurium* species suggests that the selective advantage of bienniality could relate to the production of a large stem within a short period. The typical architecture of a monocarpic perennial does not automatically imply an allometric relation between seed production and plant size. Size-dependent seed allocation, when present, is due to disproportionality between the plant's size and the amount of resources available for reproductive allocation, and not to the size constraints imposed by the plant's architecture. The evolution of monocarpic perenniality is therefore not a simple allometric step. Interpopulation differences in seed allocation may arise from differences in the nature or the availability of that particular resource that limits the reproductive allocation of biomass, and do not necessarily reflect differences in partitioning strategies.

Key-words: Centaurium littorale, Centaurium pulchellum, life history, plant architecture, reproductive allocation.

INTRODUCTION

Biennials and monocarpic perennials are relatively rare within the plant kingdom (Hart 1977). Since Hart's study, emphasis has been placed on specifying the conditions under which bienniality or monocarpic perenniality is favoured over other life histories by natural selection.

Most of the so-called biennials may exhibit delayed flowering: only a fraction of the population flowers in the second year after germination, whereas the remaining fraction does not flower until the third or the fourth year or even later (Werner 1975; Harper 1977; Grime 1979; van der Meijden & Van der Waals-Kooi 1979; Gross 1981; van Baalen & Prins 1983; Klinkhamer & de Jong 1983; Schat *et al.* 1984). Rosette size appeared to be a better predictor of flowering than rosette age (Werner 1975; Gross 1981): beyond a certain size, the critical rosette size (Werner 1975) below which flowering cannot be induced, the probability of flowering in the next season increases with rosette size. This suggests that the selective advantage of delayed reproduction in monocarpic plants is associated with reproduction as a big plant. A delay in flowering will be an advantage as long as the associated increase in seed production is enough to compensate for the increase in mortality risk during the vegetative period (Hart 1977). In general, large plants have a greater amount of resources available for reproduction than small plants. Possible additional advantages of reproducing as a large plant have been proposed: (1) larger plants with taller inflorescences may attract disproportionally more pollinators (Schaffer & Schaffer 1977, 1979); (2) a taller inflorescence will increase seed dispersal (Klinkhamer & de Jong 1987); and (3) the seed production may increase more than proportionally with plant size. This could result from the fact that certain resources must be allocated to supportive structures, such as an inflorescence stalk, before any seed can be produced at all. The resource expenditure for supportive structures may increase less than proportionally with that for seed production, as the size of the inflorescence increases; in other words, the total resource expenditure needed to produce one seed may decrease with each additionally produced seed (Klinkhamer & de Jong, 1987). Silvertown (1983) argues that monocarpic perenniality has frequently evolved in families in which the seed production per plant is largely regulated by repeated vertical architectural units, i.e. an increase in seed production would be accomplished by increasing the number of branches per stem, capitula per branch, seeds per fruit, etc. This would lead to an allometric relationship between the seed number and stem size, which would explain the obvious tendency towards monocarpic perenniality within these families. On the other hand, families in which the seed production is largely regulated by repeated horizontal structures, such as rhizomes or stolons, are extremely poor in monocarpic perennials.

The literature provides only a limited number of data concerning the (dis)proportionality of plant size and seed production. The seed allocation (percentage of biomass allocated to seeds) of monocarpic annuals is often found to be independent of plant size (Harper & Ogden 1970; van Andel & Vera 1977; Harris & Lovell 1980; Ernst 1983a; Fenner 1986). However, positive (Snell & Burch 1975; Abul-Faith & Bazzaz 1979) as well as negative (Hickman 1975) correlations between seed allocation and plant size are also reported. In biennials the seed allocation may or may not be positively correlated with plant weight (Lovett Doust 1980; Reinartz 1984; Klinkhamer & de Jong 1987).

It is uncertain whether the above cited examples of size-correlated variation in seed allocation should be interpreted in terms of the size constraints governed by plant architecture. First, correlated changes do not necessarily imply a direct causal relationship. In the above studies, plant size variation was effected by the variation in environmental factors with a conceivably direct effect on seed allocation, such as competition, or soil fertility (see below). Second, pollination limitation, which may result in size-correlated changes in allocation patterns (Bierzychudek 1981; Klinkhamer & de Jong 1987), may have occurred in some cases. Third, the amount of resources available for the development of reproductive structures is not necessarily proportional to plant size. For example, mineral nutrient concentrations, particularly those of growth limiting nutrients, often vary consistently with plant size within natural populations (Ernst 1983b, for some examples). Moreover, the nature of the particular resource that restricts the reproductive allocation is unknown and may vary with environmental conditions and differ between species. In this respect it is of interest that seeds often show much higher concentrations of nitrogen, phosphorus and sulphur than vegetative tissues, particularly under conditions of low external availability levels. In addition, the concentrations of these elements in seeds are often found to be more or less independent of plant size and soil fertility (e.g. Ernst 1983a; Schat *et al.* 1984; Fenner 1986). The biomass allocation pattern is therefore not necessarily correlated with the pattern of phosphorus, nitrogen or sulphur allocation (van Andel & Vera 1977; Lovett Doust 1980; Ernst 1983a; Schat *et al.* 1984; Fenner 1986). Harper & Ogden (1970) have already stated that nutrient budgets might prove to be more important than energy budgets with regard to allocation strategies. The reproductive allocation may thus depend on the nature of the resource that limits the development of reproductive structures. Size-dependency of seed allocation may then result from size-dependent differences in the nature of the limiting resource (e.g. energy or a mineral nutrient), or from disproportionality between plant size and the amount of the limiting resource. The latter may be especially expected if the variation in plant size is imposed by environmental variation in the availability of that particular resource.

The above relates directly to a more general discussion on the quantification of reproductive efforts in plants. Thompson & Stewart (1981) suggest estimating reproductive efforts from nutrient allocation patterns, rather than from biomass allocation patterns, because reproductive structures are, to some extent, energetically self-supporting (Bazzaz & Carlson 1979; Bazzaz *et al.* 1979). Comparisons between species using biomass allocation patterns to measure energy allocation patterns may thus be misleading, due to the very pronounced interspecific differences in the degree of photoautotrophy of reproductive structures (Bazzaz *et al.* 1979).

Furthermore, there may be problems in applying the concept of reproductive effort in monocarpic plants. Many authors use the term reproductive effort as a synonym for final reproductive allocation, even while dealing with monocarpic species, whereas others (e.g. Bell 1980; Schaffer 1974) prefer to speak of a reproductive effort of 100% by definition, in the case of 'big bang reproduction' without any post-breeding survival. Monocarpic plants, however, are not always 'big bang' reproducers. Many of them produce leaves and reproductive structures at the same time during a period of their life, before they enter a purely reproductive phase. The allocation pattern throughout the former phase, and its time course, may be liable to quantitative changes, which may be considered as adaptive as long as they maximize the total seed production of the plant. In this way, the concept of reproductive effort may retain its usefulness in monocarpic plants (Hickman 1975).

The aim of the present study is threefold: (1) to relate the inhomogeneous distribution of life-history strategies over plant families to various aspects of plant architecture; (2) to compare the size-dependent seed allocation patterns of natural populations of three closely related monocarpic plant species, namely the summer annual *Centaurium pulchellum* (Sw.) Druce, the biennial *Centaurium littorale* (Turner) Gilmour and the biennial *Centaurium erythraea* Rafn. (nomenclature follows Heukels & van der Meijden 1983) and to comment on their possible relevancy with regard to the evolution of life-history; and (3) to discuss the above mentioned conceptual and practical problems associated with the measurement and meaning of reproductive allocation, and their relevance for evolutionary theory.

MATERIALS AND METHODS

Life-history and plant architecture

Data on the life-history and plant architecture of European plant species were collected from the *Flora Europaea* (Tutin *et al.* 1964), various local floras and other literature, as well as through inspection of the herbarium collection of the Vrije Universiteit, Amsterdam.

Size-dependent reproductive allocation in Centaurium

Centaurium plants were collected from various sites so that the whole range of plant size variation within the population was represented in the sample. The plants were sampled after termination of flowering, but before any significant leaf fall had taken place. In general, in the biennial species, at least 70% of the rosette leaves of the preceding season were still present as the leaves are very resistant to decay. Corrections for leaf fall were made by counting leaf marks on the rosette stem, when necessary. Plants damaged, either by treading, grazing or disease, were removed from the samples. *C. pulchellum* was sampled from two sites, namely a heavily eutrophicated site in a seagull nesting colony, located in a sandy beach plain on the Isle of Schiermonnikoog (The Netherlands) and an artificial sand flat, poor in organic matter and nutrients, particularly nitrogen and phosphorus, located in the Bijlmermeer, near Amsterdam (The Netherlands). At both sites, *C. pulchellum* behaved as a strict summer annual. *C. littorale* was sampled from the lower parts of dune slopes surrounding a primary dune slack in the Kobbeduinen at the Isle of Schiermonnikoog. The plants were collected from a narrow belt, just above the winter water level, which was heavily eutrophicated by ducks during the preceding winter. *Centaurium littorale* was also sampled from an artificial sand flat near Amsterdam, comparable to the one where *C. pulchellum* was sampled (see above). At this site, two strata were distinguished: first, almost bare sand with a sparse moss cover; second, a stratum with an appreciable cover of *Agrostis stolonifera,* where some profile development had taken place and where *C. littorale* was, on average, larger than on the bare sand. In the dune slack habitat, *C. littorale* behaved as an almost strict biennial: over 95% of the flowering individuals were only 2 years old, the rest no more than 3 years. A similar behaviour was found in the more fertile *Agrostis*-stratum of the Bijlmermeer site. In the bare sand stratum, however, an appreciable fraction (about 35%) of the flowering plants was at least 3 years old (these were invariably small plants). *C. erythraea* was collected from the same sand flat near Amsterdam as *C. pulchellum* (see above). About 15% of the flowering individuals appeared to be more than 2 years old here.

The capsules and vegetative parts were weighed separately after drying overnight in a stove at 80°C. Root systems were removed because it appeared impossible to collect them completely, partly due to the fact that they start to die off during the period of flowering. Reproductive allocation was either expressed as the number of seeds per milligram of vegetative dry weight (capsule walls excluded), or as capsule weight divided by the total plant weight, depending on the frequency of opened capsules. The number of seeds per capsule was calculated from the regression line $y = 40{\cdot}0x - 152$, where y represents the number of seeds and x the capsule length in millimetres, which accurately describes the relation between seed number and capsule length in all the species and populations under study (the maximal difference in slope between the populations was only 0·5). Although there was some variation between plants and individual capsules, a significant dependency on plant weight never occurred. The same holds true for individual seed weights.

The phosphorus contents of vegetative parts and capsules were measured following Chen *et al.* (1956) after wet ashing in a 7:1 mixture of HNO_3 and $HClO_4$. The nitrogen contents were measured using an elemental analyser (Carlo-Erba).

RESULTS

Life history and plant architecture

Table 1 gives the frequencies of polycarpic and monocarpic perennials and annuals within the largest European families of higher plants (only dicotyledonous, herbaceous species

Table 1. Numbers and frequencies of annuals, monocarpic perennials and polycarpic perennials among the herbaceous representatives of the European dicotyledonous plant families

Family	Annuals	Monocarpic perennials	Polycarpic perennials
Ranunculaceae	71 (0·23)*	0 (0·00)	233 (0·77)
Crassulaceae	26 (0·24)	3 (0·03)	77 (0·73)
Rosaceae	6 (0·03)	1 (0·01)	230 (0·97)
Papillionaceae	286 (0·45)	8 (0·01)	341 (0·54)
Saxifragaceae	5 (0·03)	4 (0·03)	141 (0·94)
Hypericaceae	2 (0·04)	0 (0·00)	46 (0·96)
Violaceae	9 (0·10)	0 (0·00)	83 (0·90)
Caryophyllaceae	194 (0·35)	6 (0·01)	357 (0·64)
Chenopodiaceae	114 (0·91)	0 (0·00)	11 (0·09)
Polygonaceae	35 (0·37)	0 (0·00)	59 (0·63)
Cruciferae	207 (0·33)	115 (0·18)	306 (0·49)
Papaveraceae	32 (0·34)	2 (0·02)	60 (0·64)
Resedaceae	11 (0·50)	4 (0·18)	7 (0·32)
Onagraceae	13 (0·28)	0 (0·00)	33 (0·72)
Umbelliferae	84 (0·19)	60 (0·14)	296 (0·67)
Valerianaceae	25 (0·48)	0 (0·00)	27 (0·52)
Gentianaceae	24 (0·34)	19 (0·27)	28 (0·39)
Rubiaceae	20 (0·09)	0 (0·00)	201 (0·91)
Campanulaceae	19 (0·09)	32 (0·16)	153 (0·75)
Compositae	276 (0·18)	158 (0·10)	1117 (0·72)
Geraniaceae	23 (0·31)	0 (0·00)	51 (0·69)
Linaceae	10 (0·28)	2 (0·05)	24 (0·67)
Polygalaceae	2 (0·07)	0 (0·00)	27 (0·93)
Malvaceae	20 (0·51)	1 (0·02)	18 (0·77)
Euphorbiaceae	31 (0·29)	1 (0·01)	76 (0·70)
Plumbaginaceae	4 (0·03)	0 (0·00)	120 (0·97)
Primulaceae	10 (0·10)	0 (0·00)	89 (0·90)
Boraginaceae	82 (0·32)	40 (0·16)	131 (0·52)
Convolvulaceae	28 (0·56)	0 (0·00)	22 (0·44)
Labiatae	49 (0·16)	1 (0·01)	261 (0·84)
Plantaginaceae	9 (0·29)	0 (0·00)	22 (0·71)
Scrophulariaceae	190 (0·38)	73 (0·15)	232 (0·47)
Solanaceae	22 (0·63)	1 (0·03)	12 (0·34)
Other families†	81 (0·24)	0 (0·00)	250 (0·76)
Total	2040 (0·26)	545 (0·07)	5235 (0·67)

*Frequency between brackets.

†About 40 families with less than 20 representatives.

have been recorded; monocotyledonous species were left out, because of the almost complete absence of the perennial monocarpic life history within this group). Table 1 clearly shows the extremely uneven distribution of the three life-history types over the plant families: all the families, except four, namely the Crassulaceae, Onagraceae, Linaceae and Plantaginaceae, show a distribution that differs significantly from that of the total European dicotyledonous herbaceous flora ($P<0·05$ in a Chi-square test). There are nine families in which monocarpic perenniality occurs relatively frequently, namely

Table 2. Distribution of various morphological characteristics over the strict summer annuals, the winter annuals (strict or facultative), the monocarpic perennials and the polycarpic perennials of the Dutch herbaceous, dicotyledonous flora (significant differences at $\alpha = 0{\cdot}05$ in a *G*-test are indicated by different letters)

	Summer annuals	Winter annuals	Monocarpic perennials	Polycarpic perennials
Total number of species	227	67	68	444
Percentage of species with a basal rosette of leaves	28^{a}	70^{c}	94^{d}	46^{b}
Percentage of species with a thick tap root (thicker than the main stem)	«40^{*a}	«40^{*a}	62^{b}	«40^{*a}
Percentage of species with either terminal inflorescenses, or more or less purely reproductive upper stem parts	76^{a}	79^{a}	94^{b}	73^{a}
Percentage of rosette species in which the terminal bud of the rosette axis develops into a stem	93^{a}	95^{a}	94^{a}	82^{b}

*Exact data have not been recorded.

Cruciferae, Resedaceae, Umbelliferae, Dipsacaceae, Gentianaceae, Campanulaceae, Compositae, Boraginaceae and Scrophulariaceae. In all the other families it is more or less a marginal phenomenon. It is remarkable that over-representation of monocarpic pereniality is certainly not consistently associated with over-representation of annuality: within the Campanulaceae, for example, annuals are relatively rare, whereas the Scrophulariaceae, Gentianaceae and Resedaceae are comparatively rich in annuals.

There are some remarkable correlations between life-history and plant architecture, as shown by the frequencies of various morphological characteristics within the polycarpic perennials, monocarpic perennials, strict summer and winter annuals (including facultative ones) of the Dutch herbaceous, dicotyledonous flora (Table 2). The typical architecture of monocarpic perennials includes: (1) a thick tap root; (2) a basal leaf rosette; (3) a robust erect leaf-bearing stem, which develops from the terminal bud of the rosette axis; and (4) either terminal or axillary inflorescences. The latter are concentrated in the upper parts of the stem, where leaves are absent, or at least much smaller than in the basal region. As much as 56% of the monocarpic perennials possesses the total character combination. Polycarpic perennials and annuals, on the other hand, usually lack one or more of these characteristics. Strict summer annuals usually do not have a basal leaf rosette, whereas (facultative) winter annuals usually do, though not as frequently as monocarpic perennials. Furthermore, the growth form of a rosette of which the terminal bud continues to produce rosette leaves throughout its entire life (i.e. flowers, inflorescences or fertile stems are exclusively developed from the axils of rosette leaves), is almost confined to the polycarpic perennials. Finally, the frequency of plants with either terminal inflorescences, or with axillary inflorescences concentrated in an upper, almost leafless reproductive part of the stem, is much less common among polycarpic perennials and annuals than among monocarpic perennials. Obviously the latter ones conform much more to the image of a 'big bang reproducer' than annuals, where there is more often a less clear-cut separation in time between the production of leaves and the development of reproductive structures.

If we consider the distribution of life-history types over the families (Table 1), it appears that over-representation of monocarpic perennials roughly coincides with over-representation of the character combination, typified above as the usual monocarpic perennial architecture. Remarkably, this architecture also seems over-represented among the polycarpic perennials and annuals within most of these families. There are a few exceptions, however. First, the Gentianaceae usually do not have a thickened tap root; the lack of a storage organ may be compensated for by the persistence of the rosette leaves, which often remain green throughout the winter and early spring. Secondly, the Scrophulariaceae usually lack a rosette and a thick tap root. The monocarpic perennials within this family, however, do possess a rosette; the thickened rosette axis serves as a storage organ. Moreover, the over-representation of the monocarpic perennial life history is due exclusively to the high number of *Verbascum* species (70 species including 60 monocarpic perennials); judged from its distribution over genera, monocarpic perenniality is not particularly over-represented: only 14% of the genera accommodates monocarpic perennials, whereas in the other families with over-representation of monocarpic perenniality, this figure is usually 25% or more. Thirdly, there are a few families in which the typical monocarpic perennial architecture occurs more or less frequently, but without a clear-cut over-representation of monocarpic perenniality, namely the Onagraceae and the Geraniaceae. These families, however, are rich in predominantly winter annual but facultatively biennial species (these species were not recorded under monocarpic perennials in Table 1).

Families that lack the architecture typical of monocarpic perennials, apart from the aforementioned exceptions, accommodate only a few monocarpic perennials, usually of a non-typical architecture (e.g. *Melilotus* species, which form an erect branched stem in the first season that dies off during the winter and in the second season one or more fertile erect stems from the axillary meristems just above the tap root). In general, families with an exceptional over-representation of strict summer annuals (e.g. Chenopodiaceae, Convolvulaceae, Solanaceae) are almost devoid of rosette plants.

Size-dependent reproductive allocation in Centaurium

Figure 1 shows the seed allocation, expressed as number of seeds per unit of above-ground vegetative dry weight, for two populations of the summer annual *C. pulchellum*, and one population of each of the 'biennial' species *C. littorale* and *C. erythraea*, as a function of vegetative above-ground dry weight. The figure shows three important phenomena. (1) The annual *C. pulchellum* exhibits a much higher seed allocation than the two biennial species. This is mainly due to the stem allocation, which is much higher in the biennials (about 60% of the total shoot weight in the biennials and 25% in *C. pulchellum*). (2) The seed allocation in the populations from the eutrophicated sites is higher than in the corresponding populations from the infertile sites. (3) The relative increase in seed allocation with plant size found at the infertile sites ($P<0{\cdot}01$ for *C. pulchellum*; $P<0{\cdot}001$ for *C. erythraea*) is absent or less pronounced at the eutrophicated sites.

Besides seed allocation, the ratio between leaf dry weight and stem dry weight may also vary with total vegetative dry weight. This variation, which is particularly considerable in the *C. erythraea* population, is almost exclusively accounted for by the variation in the ratio between rosette weight and the weight of the erect stems (including stem leaves). In the *C. erythraea* population this ratio increases from 1:2 in the lowest weight class up to 1:12 in the highest one. In the *C. litorale* population it varies between only 1:8 and 1:12. The leaf/stem ratio within the stems is approximately constant. The leaf/stem ratio in *C. pulchellum*, which has no basal leaf rosette, is also approximately constant.

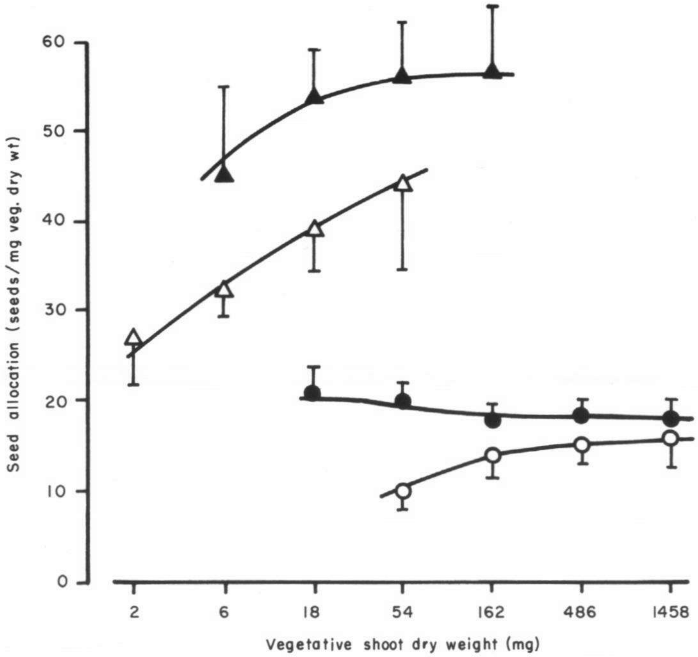

Fig. 1. Mean seed allocation, expressed as the number of seeds per milligram vegetative shoot dry weight in successive geometric classes of vegetative shoot dry weight (vertical bars indicate the 95% confidence limits for the means). (▲) *C. pulchellum*, Schiermonnikoog; (△) *C. pulchellum*, Bijlmermeer; (●) *C. littorale*, Schiermonnikoog; (○) *C. erythraea*, Bijlmermeer.

Further analysis shows that the difference in seed allocation between *C. pulchellum* on the one hand, and the biennials on the other, is explained exclusively by the number of capsules produced per unit of vegetative weight and not by capsule size (Figs 2 and 3). The mean capsule length increases with plant size in each of the populations under study. The populations from the eutrophicated sites produce longer capsules than those from the less fertile sites (Fig. 3). The number of capsules per unit of vegetative weight is less size-dependent than the mean capsule length. It is remarkable that *C. pulchellum* produces less capsules per unit of vegetative weight at the eutrophicated site than at the infertile site. Indeed, increasing capsule length seems a more efficient means of increasing the seed production per unit of plant weight than increasing the number of capsules, because the line that describes the number of seeds per capsule as a function of capsule length shows a positive abscissa-intercept (see the section on Size-dependent Reproductive Allocation). The high number of capsules per unit of above-ground vegetative weight in the lowest weight class of *C. pulchellum* (from the Bijlmermeer site) is due exclusively to the contribution of small one-flowered plants.

Figure 4 gives the reproductive allocation, in this case expressed as the total capsule dry weight divided by the total above-ground weight, for *C. littorale* in the two strata of the Bijlmermeer site. The plants from the *Agrostis*-stratum have a higher reproductive allocation than the plants from the bare sand. Moreover, the obvious increase in reproductive allocation with plant size ($P<0{\cdot}01$), apparent within the lower weight classes in the latter stratum, is absent in the *Agrostis*-stratum.

Within the whole population the above-ground plant weight was significantly positively

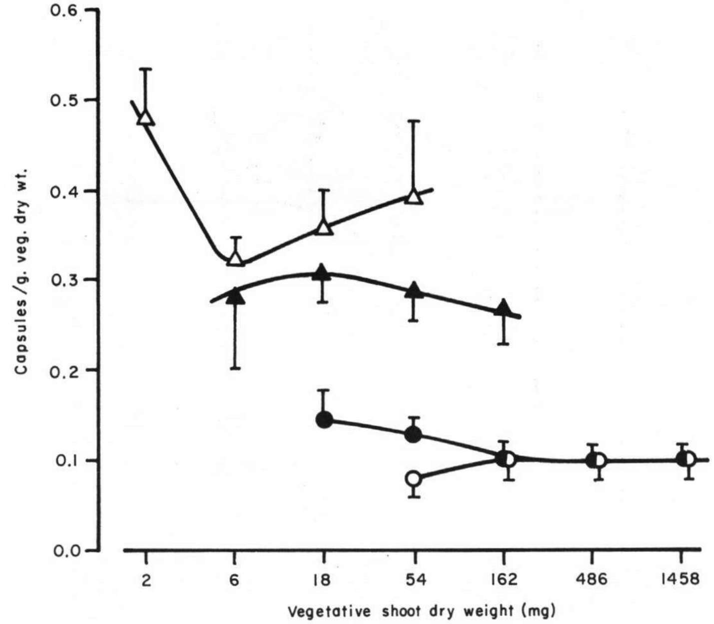

Fig. 2. Mean number of capsules per milligram vegetative shoot dry weight in successive geometric classes of vegetative shoot dry weight (vertical bars indicate the 95% confidence limits for the means). Legends as in Fig. 1.

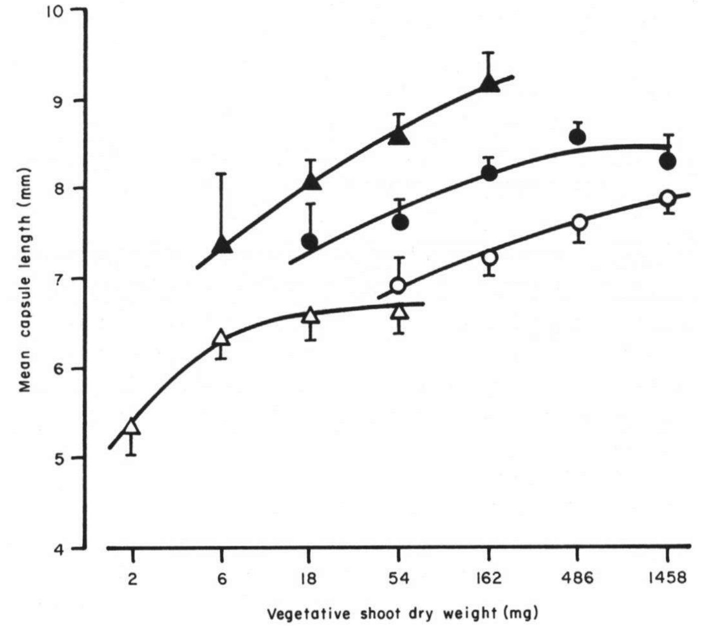

Fig. 3. Mean capsule length in successive geometric classes of vegetative shoot dry weight (vertical bars indicate the 95% confidence limits for the means). Legends as in Fig. 1.

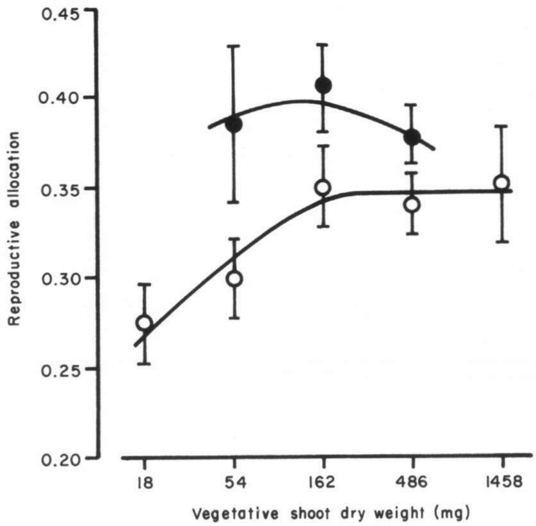

Fig. 4. Reproductive allocation, expressed as the fraction of shoot dry weight allocated to capsules in successive geometric weight classes, for *C. littorale* from the Bijlmermeer location (vertical bars indicate the 95% confidence limits for the means). (●) *Agrostis*-stratum, (○) bare sand stratum.

Table 3. Correlation coefficients (r) for vegetative shoot dry weight and phosphorus and nitrogen concentrations (expressed as the total amount of shoot phosphorus or shoot nitrogen, divided by the vegetative shoot dry weight) for *C. littorale* at the Bijlmermeer site ($n = 35$)

	[P]	[N]
Log vegetative shoot weight	0·434 (P<0·01)	0·151 (NS)

correlated with the phosphate concentration (= total amount of phosphorus in above-ground parts, including seeds and capsules, divided by the total vegetative above-ground plant weight) but not with the nitrogen concentration (Table 3), which may suggest phosphorus-limited growth. The reason for this particular expression of concentration lies in the fact that the nutrients in the seeds must have been largely reallocated from vegetative tissues, as the root system is already severely degenerated throughout the seed filling phase; the concentration measure chosen will thus more conveniently reflect the concentrations in the vegetative parts prior to flowering and nutrient reallocation. For the plants in the lower weight classes at the bare sand stratum, where the reproductive allocation is not yet maximal, the correlations between vegetative above-ground weight, reproductive allocation and either the phosphorus or the nitrogen concentration (again expressed as the total amount of phosphorus or nitrogen in the whole shoot divided by the total vegetative above-ground dry weight) are given in Tables 4 and 5, respectively. The partial correlation between plant size and reproductive biomass allocation, calculated

Table 4. Correlation coefficients (*r*) for vegetative shoot dry weight, reproductive allocation (percentage of shoot biomass in capsules), and the shoot phosphorus concentration, for *C. littorale* at the Bijlmermeer site (bare sand stratum) ($n = 25$)

	Vegetative shoot weight	Reproductive allocation	[P]
Log vegetative shoot weight	1	—	—
Reproductive allocation	0·3855 (NS)	1	—
[P]	0·4294 (NS)	0·8811 ($P < 0{\cdot}01$)	1

Table 5. Correlation coefficients (*r*) for vegetative shoot dry weight, reproductive allocation (percentage of shoot biomass in capsules), and the shoot nitrogen concentration, for *C. littorale* at the Bijlmermeer site (bare sand stratum) ($n = 16$)

	Vegetative shoot weight	Reproductive allocation	[N]
Vegetative shoot weight	1	—	—
Reproductive allocation	0·5751 ($P < 0{\cdot}05$)	1	—
[N]	0·2958 (NS)	0·8112 ($P < 0{\cdot}01$)	1

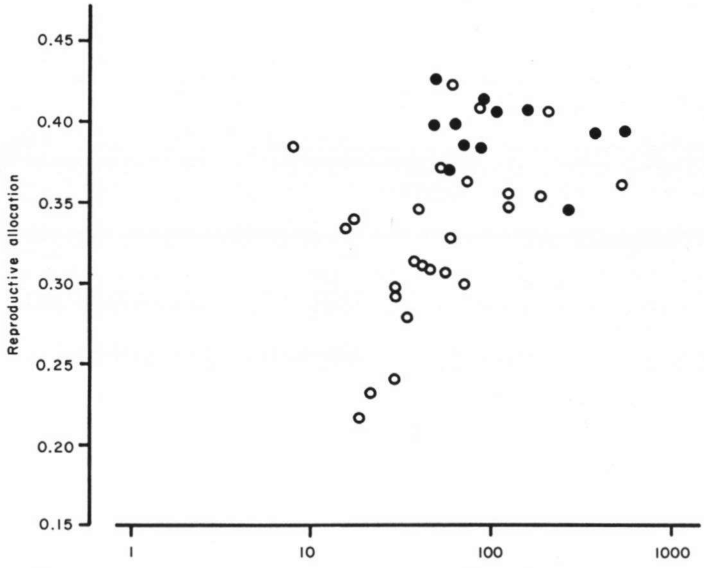

Fig. 5. Reproductive allocation, expressed as the fraction of shoot dry weight allocated to capsules plotted against vegetative shoot dry weight for *C. littorale* from the Bijlmermeer location. (●) *Agrostis*-stratum, (○) bare sand stratum.

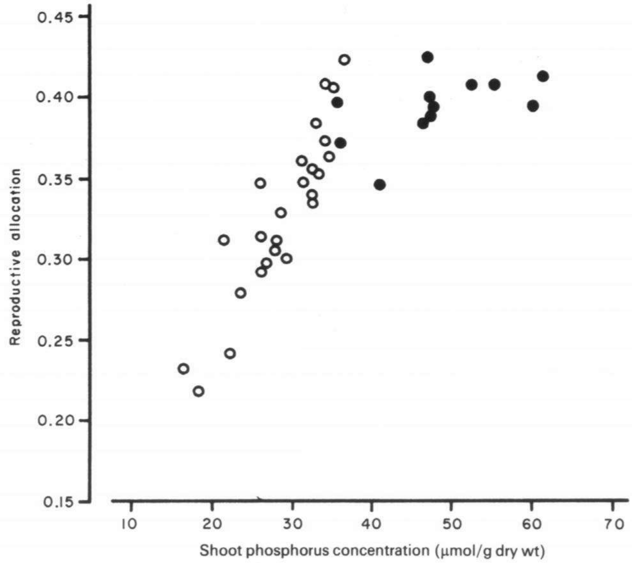

Fig. 6. Reproductive allocation, expressed as the fraction of shoot dry weight allocated to capsules, plotted against the shoot's phosphorus concentration (total shoot phosphorus per unit of vegetative shoot dry weight). (●) *Agrostis*-stratum, (○) bare sand stratum.

Table 6. Mean phosphorus concentrations of vegetative shoot parts and capsules, reproductive biomass allocation (percentage shoot dry weight in capsules) and reproductive phosphorus allocation (percentage shoot phosphorus in capsules) for *C. littorale* in the two strata of the Bijlmermeer site (standard deviation between brackets)

	Bare sand stratum	*Agrostis*-stratum	
Phosphorus concentration in vegetative shoot parts (μmol g^{-1} dry weight)	9·3 (1·56)	14·8 (4·44)	$P<0{\cdot}001$
Phosphorus concentration in capsules (μmol g^{-1} dry weight)	39·3 (3·71)	49·7 (6·45)	$P<0{\cdot}001$
Reproductive biomass allocation (%)	33·0 (5·36)	38·7 (2·84)	$P<0{\cdot}005$
Reproductive phosphorus allocation (%)	67·4 (4·93)	68·1 (8·57)	NS

from Table 4, is practically zero, i.e. $r=0{\cdot}0167$, which means that the statistically imposed constancy of the phosphorus concentration leads to a complete disappearance of the positive correlation between plant size and reproductive biomass allocation. On the other hand, the partial correlation between plant size and reproductive biomass allocation, calculated from Table 5, remains high ($r=0{\cdot}6020$).

Figures 5 and 6 show the individual data for the plants in both strata for which the phosphorus concentrations were measured. The phosphorus concentrations in the vegetative shoot parts and the capsules (expressed as micromoles of phosphorus per milligram dry weight), as well as the reproductive phosphorus allocation (amount of phosphorus in capsules, divided by the total amount of shoot phosphorus), are given in Table 6. In the bare sand stratum, the phosphorus concentrations in the vegetative shoot parts and the capsules are remarkably constant, as shown by the small standard deviations, and, moreover, uncorrelated with plant weight. In the *Agrostis*-stratum, the phosphorus concentrations of both vegetative and reproductive shoot parts are significantly higher and less constant. The phosphorus concentration of the capsules appears to be correlated significantly with vegetative shoot weight ($P<0{\cdot}05$), in contrast to the phosphorus concentration of the vegetative shoot parts, which is not correlated with vegetative shoot weight. The reproductive phosphorus allocation is equal in both strata.

DISCUSSION

Life history and plant architecture

The distribution of life history types over plant families is extremely uneven, particularly the distribution of the monocarpic perennial life-history, which was also noted by Silvertown (1983), who mentions the Umbelliferae and the Compositae as examples. Though the absolute numbers of monocarpic perennials within these families are extremely high indeed, there is a number of usually smaller families, in which the fraction of monocarpic perennials is as large or larger. Silvertown (1983) postulated several essential characteristics of the typical monocarpic perennial architecture, namely (1) the tap root, and (2) the regulation of seed production: the biennial architecture would allow an increase in seed production by simple repetition of 'vertical architectural units', which would lead to an allometrically increasing seed number with stem size.

It appears that other characteristics can be added, for example, (1) a basal leaf rosette, (2) a large vertical stem, which develops from the terminal rosette, though additional stems may be developed from the axils of the rosette leaves; and (3) flowers or inflorescences concentrated in the upper part of the stem, which is usually more or less leafless.

Silvertown (1983) argues that family-bound architectural patterns may constrain or favour the evolution of monocarpic perenniality. This study seems to confirm this point of view. The presence of a thick tap root, for example, is common in the majority of families with over-representation of monocarpic perennials. The tap root as a typical storage organ for monocarpic perennials is not surprising. Bulbs or rhizomes are part of the plant's horizontal structure. They ramify in a horizontal plane, thereby giving rise to new shoots, often becoming independent by adventitious root formation, which almost automatically leads to perennation of the 'genet' (Silvertown 1983), though the 'ramet' itself may be monocarpic (Harper 1977). A tap root is a vertical structure that is not capable of ramification in a horizontal plane. New shoots are exclusively developed from the axillary meristems of rosette leaves or lower stem leaves near the head of the tap root, which is not rejuvenated itself, in contrast to bulbs, rhizomes or corms. New shoots are thus forced to use the non-rejuvenating storage organ of the primary axis of the plant. It is conceivable that this may lead either to size constraints or limit the maximal age of the genet, which might in turn favour the evolution of monocarpy. It is interesting that many polycarpic perennial rosette plants with a tap root have only axillary inflorescences or fertile stems (e.g. many perennial Plantaginaceae) thus avoiding the need for ramification of the rosette axis.

The main difference between monocarpic perennials and monocarpic annuals lies in the storage organ (annuals usually do not possess a conspicuous storage organ) and the degree of separation between vegetative growth and reproduction. Whereas monocarpic perennials usually end their life with a purely reproductive phase ('big bang reproduction'), the annuals more often continue to produce normal-sized leaves throughout the flowering period. This may be interpreted as an opportunistic strategy that is convenient when the duration of period favourable for growth varies unpredictably from year to year. The most extreme example of the architecture associated with this strategy is that of indeterminately growing stems with equally sized and regularly spaced leaves and axillary single flowers. Such an architecture may prevent a possible allometric relation between seed production and stem size, which might reduce the chances for evolution of monocarpic perenniality, in line with Silvertown's argument (see above). The absence of a rosette in strict summer annuals, in contrast to (facultative) winter annuals and monocarpic perennials, is evidently associated with the lack of a need for hibernation. The more or less clear segregation of the stems of monocarpic perennials into an upper entirely reproductive part and a lower vegetative part may allow strong disproportionality between seed production and stem size. Reinartz (1984) refers to indeterminate growth of the upper reproductive part of the stem, whereas the size of the lower vegetative part and its number of leaves would be determined by the size of the stem primordium at the time of bolting.

Size-dependent reproductive allocation in Centaurium

With respect to plant architecture, there are marked differences between the summer annual *C. pulchellum* and the biennials *C. littorale* and *C. erythraea*. These differences are in line with the above-treated general differences between summer annuals and monocarpic perennials: (1) *C. pulchellum* has no basal leaf rosette, (2) though the main stem has typically four or five leaf pairs in all the species, it is much shorter and thinner in *C. pulchellum*, (3) the leaves on the branches of the inflorescence (a more or less regular dichasium) are much bigger in *C. pulchellum* than in the biennial species, (4) the development of the stem and the inflorescence occurs much faster in the biennials; the flowers are more simultaneously developed than in *C. pulchellum*, (5) in *C. pulchellum* the flowers are more or less diffusely dispersed over the plant, whereas in the biennials the inflorescences are more compact with the flowers closer together, sometimes more or less in one plane.

In all these respects the biennials conform more to the image of a 'big bang reproducer' than *C. pulchellum* does. With respect to the final pattern of biomass allocation, the most important difference is that the biennials produce much thicker and taller stems, with an associated decrease in final reproductive allocation, relative to the annual. With respect to the possible allometry between seed production and stem size, it is important that all the species eventually reach a purely reproductive phase with more or less indeterminate growth. The flowers of the highest branching orders have short stalks and no supporting leaflets. Flowers may even be developed when all the plant's leaves are completely yellow or dead. These flowers are typically small and produce few seeds. This phenomenon is also exhibited by *C. pulchellum*. Each of the species apparently has the possibility of indeterminate development of reproductive structures.

The present study suggests that size-dependent reproductive allocation may occur both in annual as well as in biennial *Centaurium* populations. However, plant size, as such, does not seem to constitute a major determinant of reproductive allocation. There are many arguments in favour of the absence of any size constraints within the whole range of plant sizes found in the populations under study. Even one-flowered plants that grow at fertile sites may achieve a seed allocation as high as or even higher than the maximal one recorded for the large plants, and exhibit a similar leaf and stem allocation. The lower reproductive allocation of smaller plants, which typically occurs at infertile sites, is probably due to the fact that the amount of resources available for reproductive allocation is not proportional to plant size. The availability of energy might be expected to increase proportionally with photosynthesizing leaf surface, which is in turn more or less proportional to vegetative shoot weight; at least in species without significant storage organs such as *Centaurium*. If energy is the limiting factor for reproductive allocation, a size-independent reproductive biomass allocation might be expected. This may have been the case at eutrophicated sites. The amount of available mineral nutrients, however, is usually not proportional to plant weight (e.g. Ernst 1983b; Reekie & Bazzaz 1987b; Ernst *et al.* 1987). If the reproductive biomass allocation is limited by one or another nutrient, of which the available amount varies disproportionately to plant weight, one might not necessarily expect a size-independent reproductive biomass allocation. The data for *C. littorale* (at the Bijlmermeer site) strongly suggest that phosphorus limits the reproductive biomass allocation of the smaller plants in the bare sand stratum. The strongest argument for this point of view is the total lack of correlation between plant weight and reproductive allocation after statistical correction for variations in phosphorus concentration. This can be compared with correction for variation in nitrogen content, which does not appreciably affect the correlation between plant weight and reproductive allocation.

The data may be best explained as follows. The plant size variation in the bare sand stratum is partly due to variation in phosphorus acquisition, as indicated by the positive correlation between plant weight and the shoot's internal phosphorus concentration. The seed biomass allocation increases with the shoot's phosphorus concentration until it reaches a maximum, possibly energetically determined, level as soon as a threshold phosphorus concentration has been reached (Fig. 6). Below this threshold concentration the plants obviously prefer to maintain a certain minimum phosphorus concentration in the seeds at the expense of the number of seeds produced. Only above the threshold concentration, where the seed biomass allocation is no longer phosphorus limited, does the seed's phosphorus concentration start to rise. The phosphorus concentration in the vegetative shoot parts after the seed filling increases as well, which indicates a decreased reallocation efficiency. The latter is confirmed by the fact that the reproductive phosphorus allocation of plants with a maximum seed biomass allocation is not higher than for plants with a low seed biomass allocation (Table 6). The correlation between plant size and reproductive biomass allocation is a consequence of the positive correlation between plant size and internal phosphorus concentration and the fact that maintenance of seed quality (weight, nutrient content) is preferred above the maintenance of seed quantity. In addition, the increased phosporus concentration in the plants from the *Agrostis* stratum may be due to mycorrhiza. McGee (1985) showed that *Centaurium* is exclusively infected by external hyphae that grow from roots of neighbouring species.

A comparison of the reproductive behaviour of *Centaurium* with that of other monocarpic species reveals a number of differences and similarities. Annual *Senecio* species, for example, maintain a constant seed allocation, even at low mineral nutrition levels. Remarkably, the phosphorus and nitrogen concentrations in the seeds are also kept constant. The strategy of these species probably involves a delay in flowering and growth retardation until the level of accumulated nutrients is high enough to avoid a decrease in reproductive allocation (van Andel & Vera 1977; Fenner 1986). The relative constancy of seed size, observed in *Centaurium*, was also found in *Senecio* (van Andel & Vera 1977; Fenner 1986) and a number of other species but is by no means a universal characteristic (e.g. Ernst 1983a). The same holds true for the relative constancy of the nitrogen and phosphorus concentrations of the seeds. These concentrations are also constant and independent of the external availability level in *Senecio* (Fenner 1986), however they can be increased by fertilizer application in a number of other species (e.g. Iwata & Eguchi 1958; Lipsett 1964; Austin 1966a,b; Schweizer & Ries 1969; Williams & Bell 1981). In the studies cited it would be interesting to know whether the reproductive biomass allocation was limited by one of the applied nutrients and by which. The present study suggests the possibility that an increase in the nutrient supply will only result in increased concentrations in the seeds, if the nutrient in question does not limit the reproductive biomass allocation.

With respect to its regulation of seed production, i.e. by varying the number of seeds per fruit, rather than by the number of fruits per unity of total plant weight, *Centaurium* is certainly not exceptional (e.g. Kelly 1984).

It is difficult to estimate the extent to which the results for *Centaurium* can be generalized. Nevertheless, we wish to draw a few concluding remarks concerning a possible wider applicability than the genus *Centaurium*. First, the typical architecture of monocarpic perennials may indeed allow a relatively pronounced size-dependency of the reproductive allocation, either through indeterminate growth of purely reproductive structures, or through varying the ratio between rosette and vegetative stem parts, or both. However, size-dependency of the reproductive allocation does not result from size constraints as such, but from disproportionality between plant size and the amount of the particular resource by which the development of reproductive structures is limited. There are no indications that the resource expenditure per seed decreases with each additionally produced seed. On the contrary, *Centaurium* maintains a strict proportionality between seeds, supportive reproductive structures and vegetative tissues, over an enormous range of plant sizes when grown on fertile soil. This is a firm argument against Silvertown's point of view, in which evolution of bienniality is no more than a simple allometric step. Though it seems unlikely that the biennial architecture automatically guarantees a positive size-dependency of the reproductive allocation, it may be important that it allows variation in reproductive allocation, which may guarantee that all the available resources, or at least the limiting ones, are completely depleted in the development of reproductive structures. This may be particularly advantageous for 'big bang reproducers'. This argument is essentially different from the one raised by Silvertown. Secondly, a comparison between *C. pulchellum* and the biennial *Centaurium* species suggests that the advantage of the biennial life history and architecture may be either associated with the rapid development of a robust stem, even at the expense of the final seed allocation, or with the more or less synchronous production of a large amount of flowers. A robust erect stem with many flowers may attract disproportionally more pollinators than a smaller one (Schaffer & Schaffer 1977, 1979), which may either increase female fitness through avoidance of pollination limitation, or male fitness. It is not clear, whether these possible advantages have played a significant role in life-history evolution in the genus *Centaurium*; all the species are capable of spontaneous self pollination (Hegi 1966). Hand pollination had no effect on the number of seeds per capsule in greenhouse experiments where no pollinators were available (H. Schat, unpublished). However, this does not rule out any significant effect of pollinators on fitness components, other than the mere number of seeds. Another possible advantage of a robust stem lies in the increased dispersal of seeds (Klinkhamer &

de Jong 1987). Furthermore, the faster development of stems and inflorescences, made possible by the depletion of stored resources, may have specific advantages that are not necessarily associated with pollinator attraction or seed dispersal capacity, such as avoidance of conditions unfavourable for seed ripening, or of predation or parasitism by organisms the populations of which are not capable of a rapid numerical response (cf. Janzen 1976). These factors are probably not important for *Centaurium* species, where grazing, seed predation and parasitism occur only rarely. In many other biennials, however, seed predation may cause heavy losses in seed production (e.g. Reinartz 1984).

The measurement and meaning of reproductive allocation and reproductive effort

With respect to the measurement of reproductive allocation patterns and their relevance to reproductive effort, it may be rewarding to distinguish between real 'big bang reproduction' and other strategies. Monocarpic perennials are typically 'big bang reproducers': once they enter the reproductive phase, they almost exclusively develop reproductive structures. In other words, their reproductive effort shifts suddenly from zero to 100%. Any variation in final reproductive allocation may be expected to result from variation in the amount of resources available throughout the reproductive phase per unit of plant weight, as there is no real choice between vegetative growth and reproduction once the reproductive phase has started. Polycarpic perennials, but also many annuals, have an architecture that allows synchronous or alternate-development of vegetative and reproductive structures. In this case, a real choice between vegetative growth and reproduction may persist throughout part of the reproductive phase. This implies that variation in final reproductive allocation may indeed reflect variation in reproductive effort, in the literal meaning of the word, though other sources of variation cannot be excluded. Moreover, quantifiable shifts in the reproductive allocation during part of the reproductive phase of the life cycle may have consequences for the remaining reproductive value, regardless of whether it concerns an annual or a polycarpic perennial.

This does not answer the questions concerning the correct expression of reproductive allocation as a measure of reproductive effort. Starting from the widely accepted point of view that life history evolution is governed by the nature of the trade-off between the number of offspring produced at any given age and the remaining reproductive value (Schaffer 1974), it is clear that reproductive allocation should be quantified by the partitioning of that particular resource that restricts the remaining reproductive value (Reekie & Bazzaz 1987a,c). The fact that reproductive structures are partly energetically self supporting is not a valid argument in favour of expressing reproductive allocation in terms of nutrient allocation patterns (Thompson & Stewart 1981). If energy is indeed the relevant currency, it is essential to correct for differences in the degree of photoautotrophy of reproductive structures in the case of interspecific comparisons. This study suggests that differences in reproductive allocation patterns may arise from differences in the nature or availability of the limiting resource. The marked differences between the biennial (sub)-populations, for example (Results: Size-dependent Reproductive Allocation), have nothing to do with differences in partitioning strategies. Comparative studies, aimed at describing and explaining evolutionary variation in partitioning strategies may be biased by these sources of variation. Fair comparisons require that the nature and the quantity (per unit of plant weight) of the limiting resource are similar.

REFERENCES

Abul-Faith, H.A. & Bazzaz F.A. (1979): The biology of *Ambrosia trifida* L. I. Influence of species removal on the organization of the plant community. *New Phytol.* **83:** 813–816.

Andel, J. van & Vera, F. (1977): Reproductive allocation in *Senecio sylvaticus* and *Chamaenerion angustifolium* in relation to mineral nutrition. *J. Ecol.* **65:** 747–758.

Austin, R.B. (1966a): The growth of watercress (*Rorippa nasturtium aquaticum* (L) Hayek) from seed as affected by the phosphorus nutrition of the parent plant. *Pl. Soil* **24:** 113–120.

— (1966b): The influence of phosphorus and nitrogen nutrition of pea plants on the growth of their progeny. *Pl. Soil* **24:** 359–368.

Baalen, J. van & Prins, E.G.M. (1983): Growth and reproduction of *Digitalis purpurea* in different stages of succession. *Oecologia (Berlin)* **58:** 84–91.

Bazzaz, F.A. & Carlson, R.W. (1979): Photosynthetic contribution of flowers and seeds to reproductive effort of an annual colonizer. *New Phytol.* **82:** 223–232.

—, — & Harper, J.L. (1979): Contribution to reproductive effort by photosynthesis of flowers and fruits. *Nature* **279:** 554–555.

Bell, G. (1980): The costs of reproduction and their consequences. *Am. Nat.* **166:** 45–76.

Bierzychudek, P. (1981): Pollinator limitation of plant reproductive effort. *Am. Nat.* **117:** 838–840.

Chen, P.S., Toribara, T.Y. & Warner, H. (1956): Microdetermination of phosphorus. *Anal. Chem.* **28:** 1756–1758.

Ernst, W.H.O. (1983a): Element nutrition of two contrasted dune annuals. *J. Ecol.* **71:** 197–209.

— (1983b): Ökologische Anpassungsstrategien an Bodenfactoren. *Ber. Deut. Bot. Ges.* **96:** 49–71.

—, Nelissen, H.J. & de Hullu, E. (1987): Size hierarchy and mineral status of *Rhinanthus angustifolius* populations under different grassland management regimes. *Vegetatio* **70:** 93–103.

Fenner, M. (1986): The allocation of minerals to seeds in *Senecio vulgaris* plants subjected to nutrient shortage. *J. Ecol.* **74:** 385–392.

Grime, P.J. (1979): *Plant Strategies and Vegetation Processes.* John Wiley, New York.

Gross, K.L. (1981): Predictions of fate from rosette size in four biennial species: *Verbascum thapsus, Oenothera biennis, Daucus carota* and *Tragopogon dubius. Oecologia (Berlin)* **48:** 209–213.

Harper, J.L. (1977): *Population Biology of Plants.* Academic Press, London.

— & Ogden, J. (1970): The reproductive strategy of higher plants. I. The concept of strategy with special reference to *Senecio vulgaris* L. *J. Ecol.* **58:** 681–698.

Harris, G.R. & Lovell, P.H. (1980): Growth and reproductive strategy in *Veronica* spp. *Ann. Bot.* **45:** 447–458.

Hart, R. (1977): Why are biennials so few? *Am. Nat.* **111:** 792–799.

Hegi, G. (1966): *Illustrierte Flora von Mittel-Europa,* Hanser Verlag, Stuttgart.

Heukels, H. & van der Meijden, R. (1983): *Flora van Nederland,* 20th edn. Wolters-Noordhoff, Groningen.

Hickman, J.C. (1975): Environmental unpredictability and plastic energy allocation strategies in the annual *Polygonum cascadense (Polygonaceae). J. Ecol.* **63:** 689–701.

Iwata, M. & Eguchi, Y. (1958): Effects of phosphorus and potassium supplied for the various stages of growth on the yield and quality of seeds of Chinese cabbage. *J. Hort. Assoc. Jpn.* **27:** 171–178.

Janzen, D.H. (1976): Why do bamboos wait so long to flower? *Ann. Rev. Ecol. Syst.* **7:** 347–391.

Kelly, D. (1984): Seeds per fruit as a function of fruits per plant in 'depauperate' annuals and biennials. *New Phytol.* **96:** 103–114.

Klinkhamer, P.G.L. & de Jong, T.J. (1983): Is it profitable for biennials to live longer than two years? *Ecol. Model.* **20:** 223–232.

— & de Jong, T.J. (1987): Plant size and seed production in the monocarpic perennial *Cynoglossum officinale* L. *New Phytol.* **106:** 773–783.

Lipsett, J. (1964): The phosphorus content and yield of grain of different wheat varieties in relation to phosphorus deficiency. *Austr. J. Agric. Res.* **15:** 1–8.

Lovett Doust, J. (1980): Experimental manipulation of patterns of resource allocation in the growth cycle and reproduction of *Smyrnium olusatrum. Biol. J. Linn. Soc.* **13:** 155–166.

McGee, P.A. (1985): Lack of spread of endomycorrhiza's of *Centaurium* (Gentianaceae). *New Phytol.* **101:** 451–458.

Meijden E. van der & van der Waals-Kooi, R.E. (1979): The population ecology of *Senecio jacobaea* in a sand dune system. I. Reproductive strategy and the biennial habit. *J. Ecol.* **67:** 131–153.

Reekie, E.G. & Bazzaz, F.A. (1987a): Reproductive effort in plants: 1. Carbon allocation at reproduction. *Am. Nat.* **129:** 876–896.

— & — (1987b): Reproductive effort in plants: 2. Does carbon reflect the allocation of other resources? *Am. Nat.* **129:** 897–906.

— & — (1987c): Reproductive effort in plants: 3. Effect of reproduction on vegetative activity. *Am. Nat.* **129:** 907–919.

Reinartz, J.A. (1984): Life history variation of common mullein (*Verbascum thapsus*). II. Plant size, biomass partitioning and morphology. *J. Ecol.* **72:** 913–925.

Schaffer, W.M. (1974): Selection for optimal life histories: the effects of age structure. *Ecology* **55:** 291–303.

— & Schaffer, M.V. (1977): The adaptive significance of variation in reproductive habit in *Agavaceae*. In: Stonehouse, B. & Perrins, C.M. (eds): *Evolutionary Ecology*. MacMillan, London.

— & — (1979): The adaptive significance of variation in reproductive habit in *Agavaceae* II: Pollinator foraging behaviour and selection for increased reproductive expenditure. *Ecology* **60:** 1051–1069.

Schat, H., Bos, A.H. & Scholten, M. (1984): The mineral nutrition of some therophytes from oligotrophic dune slack soils *Acta Oecol. Oecol. Plant.* **5:** 119–131.

Schweizer, C.J. & Ries, S.K. (1969): Protein content of seed: increase improves growth and yield. *Science* **165:** 73–75.

Silvertown, J.W. (1983): Why are biennials sometimes not so few? *Am. Nat.* **121:** 448–453.

Snell, T.W. & Burch, D.G. (1975): The effects of density on resource partitioning in *Chamaesyce hirta* (Euphorbiaceae). *Ecology* **56:** 742–746.

Thompson, K. & Stewart, A.J.A. (1981): The measurement and meaning of reproductive effort in plants. *Am. Nat.* **117:** 205–211.

Tutin, T.G., Heywood, N.A., Burgess, D.H., Walters, S.M. & Webb, D.A. (1964): *Flora Europaea.* Cambridge University Press, Cambridge.

Werner, P.A. (1975): Predictions of fate from rosette size in teasel (*Dipsacus fullonum* L.). *Oecologia (Berlin)* **20:** 197–201.

Williams, R.B. & Bell, K.L. (1981): Nitrogen allocation in Mojave Desert winter annuals. *Oecologia (Berlin)* **48:** 145–150.