Structural demography of *Oxalis corniculata* L. — The fate of buds
(Struktur demografi pokok *Oxalis corniculata* L. — Penentuan kudup)

B. Baki*, S. Kamarudin**, O. Ahmad Shokri***

Abstrak

Pembahagian kudup pokok *Oxalis corniculata* L. kepada tiga potfolio pelaburan iaitu kudup yang dorman (D) kudup yang membesar menjadi sejambak bunga (F) atau kudup yang membesar menjadi stolon (S) berbeza mengikut masa dan susunan-susunan hiraki (kelas-kelas stolon) yang ada pada pokok tersebut. Pelaburan potfolio yang berlainan ini tidak menampakkan perbezaan yang nyata bagi tempoh 10 minggu selepas percambahan biji. Pelaburan kudup pada minggu ke−11 dan minggu-minggu berikutnya adalah mengikut bentuk susunan D > F > S. Bagi stolon-stolon utama, bilangan kudup yang membesar menjadi ranting stolon melebihi kudup-kudup lain yang membesar menjadi sejambak bunga atau yang dorman, dengan bererti. Kudup-kudup yang ada pada stolon-stolon yang kelas pelaburannya tinggi pada amnya berbentuk mengikut susunan: D > F > S.

Keputusan ini telah dibincangkan mengikut hubungkait di antara strategi pertumbuhan pokok dengan penawanan sumber, perhubungan di antara modul-modul secara holistik.

Abstract

The allocation of buds in *Oxalis corniculata* L. into three 'investment portfolios' viz. remaining dormant (D), growing into inflorescences (F) or stolon branches (S) differed with time and hierarchical positions (stolon class) within the plant. No differences were registered among these investment portfolios for the first 10 weeks after seedling emergence. Investments of buds post from the 11th week onward were in the order of D > F > S. In primary stolons, buds growing into stolon branches significantly exceeded those remaining dormant or growing into inflorescences. In higher stolon class, the investments of buds, generally were in the following order: D > F > S.

The results are discussed in relation to the growth strategy of the plant *vis-a-vis* resource capture, and to the inter-relationship between modules and holistic approach.

---

*Central Research Laboratories Division, MARDI, P.O. Box 12301, 50774 Kuala Lumpur, Malaysia
**Computer Centre, MARDI, P.O. Box 12301, 50774 Kuala Lumpur, Malaysia
***Techno-Economy and Social Studies Division, MARDI, P.O. Box 12301, 50774 Kuala Lumpur, Malaysia
Authors' full names: Baki Bakar, Kamarudin Saadan and Ahmad Shokri Othman

Introduction

The architecture of a plant reflects 'successful' meristems, and both the static and dynamic structure of the plant thus depends on its meristem bank, meristem potential, position and fate (Harper and Bell 1979). In essence, the population of meristems on a plant is a reflection of the potential of that plant for further growth as well as reflecting the history of the plant. By considering meristem potential, position and fate, it becomes possible to combine an understanding of the organized structure of a plant with an appreciation of the demography of its parts.

The buds of a plant form a population in which births and deaths occur. A bud may die, remain dormant, develop into shoot or produce flowers. In essence, clonal branches are formed from the reiteration of the basic units, while flowers and inflorescences come from the reiteration of units bearing modified leaves. Flowering in particular may produce great changes in the morphology when meristems which have contributed to clonal growth are diverted to sexual reproduction. Halle et al. (1978) cited an extreme case, found in species such as Corypha elata (Palmae) where the stem is unbranched, the inflorescence is terminal and flowering ends the life of the tree.

Mailette (1982) likened the population of buds on a tree, as did Noble (1976) for a rhizomatous herb as analogous to a bank. The fates of various buds change with position on the plants and represent different 'investment portfolios' available for its buds viz. investments in highly profitable but expensive enterprises (long shoots) (*sensu* Mailette 1982) and low revenue ventures (short shoot) (*sensu* Mailette 1982); or in low cost, high risk speculation (flowering) (*sensu* Mailette 1982). Buds that remain dormant act as a guarantee, but can be mobilized as capital invested in an emergence, e.g. regeneration after damage. There are risks and running costs at all levels: predation and diseases (taxation), senescence (devaluation and depreciation). A flow of organic and inorganic resources (a currency) is both under internal control but tied to external physiological and biological constraints.

Oxalis corniculata L. spp. *corniculata* var. *atropurpurea* van Houtte ex Planchon is a cosmopolitan weed belonging to the family Oxalidaceae Sect. Corniculatae. The weed occurs from sea level to snow line (Eiten 1963; Holm et al. 1977; Lourteig 1979) infesting many horticultural and ornamental crops and pastures, in tropical and temperate zones. The species possesses some of the characteristics of an 'ideal weed' (cf. Baker 1965). Arguably, it is these characteristics (e.g. the ability to proliferate and produce ample numbers of colonal and sexual reproductive modules within a short period of 4−5 months) which made *O. corniculata* an appropriate candidate for ecological studies not least in the context of population biology.

The present work is an attempt to determine and describe the fates of buds on plants of *Oxalis corniculata* L. and the dynamics of the bank of buds on which the growth and architecture of the plant depend.

Materials and methods

Fresh seeds of *Oxalis corniculata* L. spp. *corniculata* var. atropurpurea van Houtte ex Planchon collected in October 1985 from horticultural greenhouses at Plas Newydd, Anglesey, U.K., were sown in plastic trays (21 cm x 15 cm x 5 cm) previously filled with John Innes No. 1 compost. Two weeks after emergence, six seedlings were selected for uniformity and transplanted individually into the centre of 1 m x 1 m x 8 cm wooden box and filled with John Innes No. 1 compost. The plants were grown under heated glasshouse conditions at Pen-y-Ffridd Research Station, UCNW, Bangor, U.K.
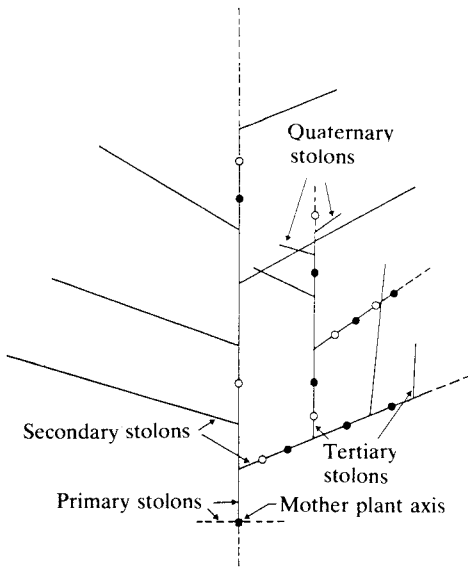
*Figure 1. Diagrammatic view of stolon production and growth of **Oxalis corniculata** showing various classes of stolons, dormant buds (○) of fruits/flowers (●) and their relative positions*

where the temperatures ranged from 15 °C to 27 °C (day) and 14 °C to 20 °C (night) with supplementary illumination from 400 watt high pressure lamps from the 16th day. The plants were watered from above when necessary using a fine spray. The boxes were arranged in a completely randomized manner.

At weekly intervals and for 22 weeks after emergence, the number of buds that were dormant (D), or grew into inflorescences (F) and those that grow into stolon branches (S) on the primary, secondary, tertiary and quaternary stolons were recorded. The number and fate of buds on the mother plant axis that were dormant or grew into inflorescences were not taken into account. The experiment commenced on 5 November 1985 and was terminated on 14 April 1986.

Figure 1 illustrates diagrammatically the orientation of growth of stolon of O. corniculata 22 weeks after emergence.

Generalised Linear Model (GLM) was used to assess the competition effect between dormant buds, inflorescences and stolons over time at four different orders of branching. Logarithmic transformation was thought to be the most appropriate since the effects were multiplicative and the data covered quite a wide range of values.

Results

The allocations of buds (or meristems) in *Oxalis corniculata* into stolon branches (S), inflorescences (F) or remaining dormant (D), differed considerably with time and stolon class *(Table 1* and *Figure 2)*. These differences were more pronounced and significant from week 11 onward in the following order: $D > F > S$. At the end of the experiment (i.e. 22 weeks after seedling emergence), the D fractions accounted for about 733 buds (or 49.4% of the total buds) borne on the plant while the remaining bud populations were shared among the F (590 or 39.8%) and the S (158 or 10.8%) fractions.

In primary stolons, the plant invested significantly more buds in stolon branches than either inflorescence or buds that remained dormant. The population of buds that grew into stolon branches was consistently higher than the D or F types at each time interval. The S fractions formed about 44.9% of total bud counts on primary stolons *[Figure 2(b)]*.

Buds borne on secondary stolons were mostly dormant forming about 43.4% of the total bud counts on such stolon class. No differences were registered up to week 13 between the number of buds destined to remain dormant and the number of buds to grow into inflorescences *[Figure 2(c)]*, while from week 9 onwards buds growing into stolon branches were consistently and significantly lower than the D and F fractions. In tertiary stolons, the D fraction from 9 weeks onward likewise outnumbered both the S and F

Table 1. Relationship between Log (n+1) mean total number of buds of *Oxalis corniculata* that grew into stolon branches (S), inflorescence (F) or remaining dormant (D) over time

Bud type		Weeks after emergence																
		6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Overall stolons	D	0.10b	0.34a	0.44a	0.61a	0.88a	1.07a	1.21a	1.32a	1.38a	1.68a	1.81a	1.89a	1.96a	2.03a	2.08a	2.10a	2.11a
	F	0.0 c	0.31a	0.46a	0.57a	0.89a	1.07a	1.23a	1.32a	1.40a	1.64a	1.78a	1.87a	1.94a	2.00a	2.06a	2.08a	2.09a
	S	0.20a	0.37a	0.46a	0.57a	0.77a	0.91b	1.02b	1.10b	1.16b	1.20b	1.23b	1.26b	1.27b	1.28b	1.28b	1.29b	1.29b
Primary stolons	D	0.38c	0.76b	0.84c	0.92c	1.02c	1.16c	1.22c	1.25c	1.25c	1.27c	1.30c	1.31c	1.33c	1.34c	1.35c	1.35c	1.37c
	F	0 b	0.73b	1.01b	1.15b	1.25b	1.36b	1.41b	1.44b	1.47b	1.50b	1.53b	1.55b	1.57b	1.58b	1.59b	1.60b	1.60b
	S	0.54a	1.06a	1.22a	1.33a	1.42a	1.55a	1.58a	1.59a	1.60a	1.63a	1.65a	1.66a	1.68a	1.69a	1.70a	1.71a	1.71a
Secondary stolons	D	0 b	0.58a	0.91a	1.18a	1.60a	1.83a	2.00a	2.07a	2.12a	2.16a	2.19a	2.20a	2.22a	2.23a	2.24a	2.24a	2.25a
	F	0 b	0.50a	0.82a	1.14a	1.54a	1.76a	1.94a	2.03a	2.09b	2.13b	2.15b	2.17b	2.19b	2.20b	2.20b	2.21b	2.21b
	S	0.28a	0.44a	0.62a	0.94b	1.30b	1.48b	1.61b	1.66b	1.72c	1.75c	1.77c	1.79c	1.80c	1.81c	1.82c	1.82c	1.83c
Tertiary stolons	D				0.34a	0.90a	1.29a	1.64a	1.95a	2.15a	2.30a	2.39a	2.44a	2.49a	2.51a	2.52a	2.53a	2.54a
	F				0 b	0.77a	1.16a	1.55a	1.82b	2.03b	2.18b	2.25b	2.31b	2.35b	2.37b	2.38b	2.39b	2.39b
	S				0 b	0.37b	0.60c	0.98c	1.13c	1.30c	1.43c	1.51c	1.57c	1.60c	1.61c	1.62c	1.63c	1.63c
Quaternary stolons	D										0.98a	1.37a	1.62a	1.81a	2.04a	2.21a	2.25a	2.28a
	F										0.74a	1.18b	1.44b	1.64b	1.84b	2.07b	2.12b	2.15b
	S										0.0 b	0.0 c	0 c	0 c	0 c	0 c	0 c	0 c

Values with similar letter in a column for each stolon class do not differ significantly at *p* >0.01 (Tukey's HSD Test)
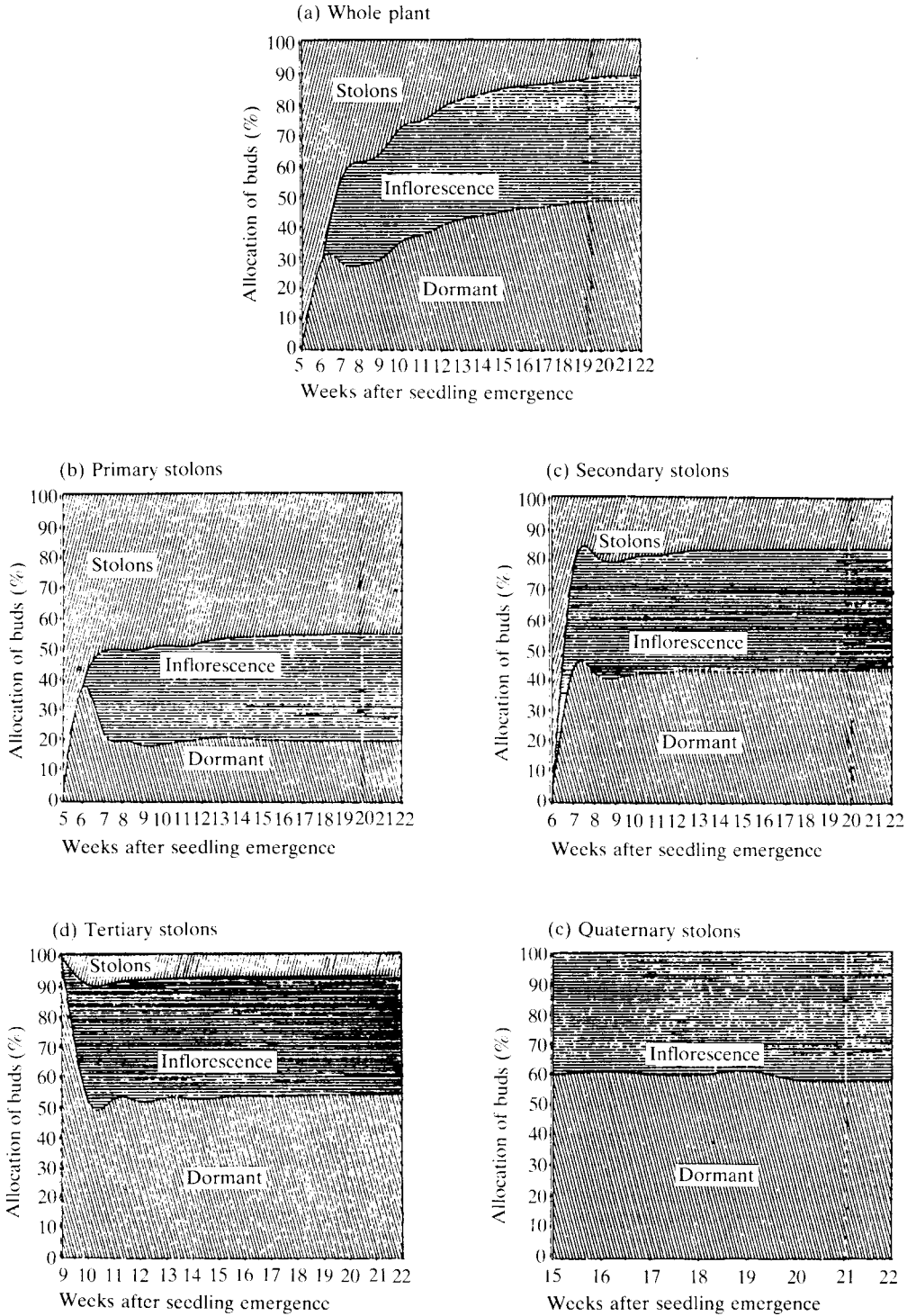
Figure 2. Proportional allocations (%) of bud numbers of different fates in **Oxalis corniculata** as a function of time

populations, although these differences may not always be significant at all time intervals *[Table 1* and *Figure 2(d)]*. In the quaternary stolons order, no buds grew to form stolon branches; buds were either dormant or grew into inflorescences. The hierarchial counts were consistently D > F at each time interval *(Table 1)*.

Discussion

Knowledge of the fate of axillary buds is an important prerequisite in any understanding of the dynamics of a plant species (Maillette 1982; Chapman 1983; Solangaarachchi 1985; Baki 1986). Bell (1979) argued that in rhizomatous plants, it is the number of developing buds or more precisely meristems that governs the potential of a clone i.e. its productivity. In this study on *O. corniculata*, a plant which proliferates by both clonal and sexual reproductive means, the central issue is the fate of axillary buds, which develop either into stolon branches, flowers and fruit, or remain dormant.

The distinct differences in the population of stolons of different orders or the production of buds growing into inflorescence on such stolons at each time interval *(Table 1* and *Figure 2)* may be interpreted as evidence that the law of allometric growth prevails within the whole plant of *O. corniculata*. This is in line with the view that the growth of modular plants is clearly programmed and that 'allometries must necessarily arise in modular organisms when the genet as a whole has indeterminate growth but the size of individual modules is essentially determinate' (Harper 1985). Further, it appears that some kind of regulatory mechanism was operating in *O. corniculata* which determined the number of axillary buds that developed into stolon branches and inflorescences or remained dormant in the phasic (*sensu* Watt 1947) development of the plant. Implicit to this was the greater tendency of buds on primary stolons to develop into

stolon branches − an evident of growth strategy which laid emphasis on clonal growth for greater exploration and exploitation of resources (space) *(Table 1* and *Figure 2)*. In higher order stolons, growth emphasis was mainly sexual reproductive − a modification of tactics (*sensu* Van Der Pijl 1972) to ensure dispersal colonization (through seed). It would be intriguing to ascertain that the mechanics of such regulations were through integrative hormonal control *per se* or as local adjustments and responses to the presence of neighbour modules or both.

Generally, there was an apparent display of asymptotic relationships between the number of buds that developed into the different fates (S, F or D) with time *(Table 1)* and these were similar to those observed for ramet production in *Eichornia crassipes* (Watson 1984). Such relationship may be reflections of one or more of the following possibilities: (i) the system is running out of finite resources and competition between stolons of different orders for such resources prevail and (ii) the onset of flowering from 7 weeks after seedling emergence onwards and the production of fruit and seed thereafter may mean that resources, that might otherwise have been allocated for further production of stolons and their growth, were diverted to fruit and seed production or were limitedly available. Further, asymptotic relationship between the rate of recruitment of S, D or F modules *(Table 1)* may be considered as manifestation of law of diminishing returns operating in larger plants whereby the accumulation of further numbers of such modules did not increase the birth rate. Similar arguments have been first forwarded by Clegg (1978) to explain the asymptotic relationships between leaf birth rate and time in *Ranunculus repens*.

Both hypotheses were based on the Harperian view of the Candollean

Doctrines (Cusset 1982) which laid emphasis on the individual plant as an organized whole, and as such emphasize holistic aspects of construction, modular interdependence and integration within clonal plants of which *O. corniculata* is one.

Baki (1986) reported an enhancement in the rate of primary stolons recruitment in *O. corniculata* following detachment of existing stolons from the mother plant axis; these observations may be construed as evidence that modular integration prevailed in the plant. Evidence for modular interdependence and integration with clonal plants have been reported elsewhere (Marshall and Sagar 1966; Noble 1976; Harnett and Bazzaz 1985).

The second hypothesis is based on traditional resource allocation model which proposes that sexual reproduction inhibits clonal growth by intra-plant competition (Cohen 1968, 1971; Harper and Ogden 1970; Abrahamson 1975; White 1979). Harper (1977) wrote 'perennial interoperous plants often show an inverse correlation between clonal growth and production of fruit and seed which suggests that fecundity and clonal activity are not wholly compatible'. Watson (1984) suggested that one appropriate explanation for the inverse correlation between production of inflorescence and ramet population growth rates observed in *Eichornia crassipes* was the outcome of competition among life history functions for a limited number of meristems available for differentiation, rather than competing for available assimilate. This argument is consistent with and complimentary to the evidence of carbon economy of various plant modules. It would be interesting to ascertain that the observed reduction in the production of stolons *vis-a-vis* inflorescence and dormant buds with time for higher order stolons *(Table 1)* was the consequence of competition with other life history functions (reproductive and other clonal modules) for the limited resources or competition for limited numbers of meristems available for differentiation or both; the subject remains for further research.

The sigmoid patterns of cumulation of the S, F and D modules with time in *O. corniculata (Table 1)*, besides being interpreted as a consequence of intra-plant competition among members of a metapopulation (White 1980), may be attributed to 'time-mediated resource depletion' within the environment that these plants were subjected to. The fact that stolons, inflorescences and dormant buds emerged at different times, their rates of population growth differed considerably (at leasts initially) and this may be explained by the initially high C.V. values *(Figure 3)*. The reduction and apparent stability of C.V. values with time help to explain that the rates of recruitment among these modules (of the same type) were getting similar. Solangaarachchi (1985) and Franco (1985) forwarded similar arguments to help explain the approaching similar growth rates of *Trifolium repens* L. and *Kochia scoparia* L. respectively with time.

The disparity in the proportion (%) of buds fated to become the S, F and D modules with time in *O. corniculata (Figure 2)* may also be related for the light environment within the canopy. Arguably, based on first principles, at the later stage (say from the 14th week onwards) there must have been a corresponding increase in shading, thereby reducing the photosynthetically active radiation (PAR) or PR/PF values in the canopy and at ground level. Such reductions in PAR or PR/PF may have led to failures of bud break of axillary buds or stolons *(Table 1* and *Figure 2)*. Similar arguments have been made by several workers e.g. Bogorad and McIlrath (1960) in *Xanthium* spp. and Kasperbauer (1971) in *Nicotiana tabacum* L. Solangaarachchi
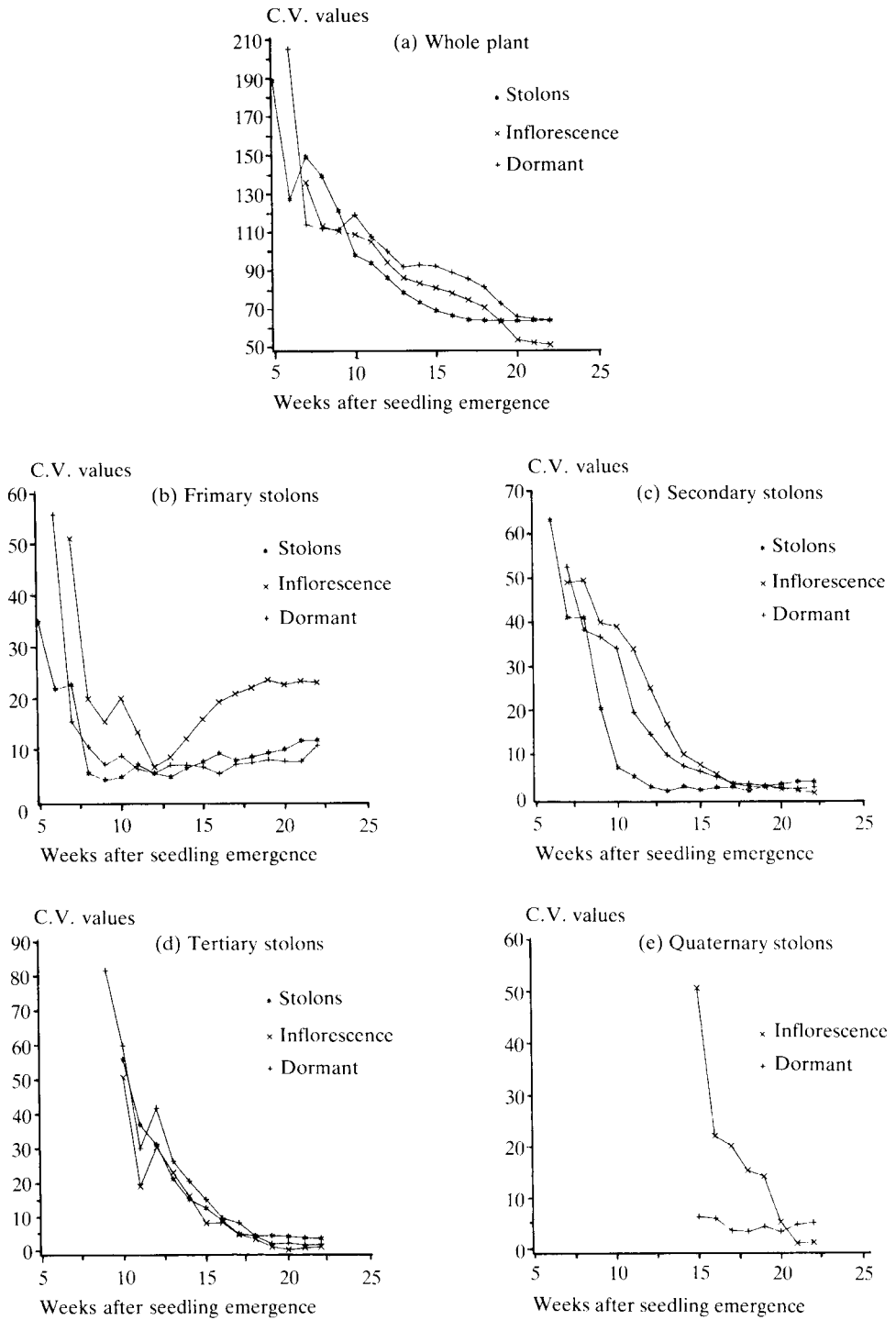
*Figure 3. C.V. values of bud numbers of different fates in **Oxalis corniculata** as a function of time*

(1985) observed that the number of stolons of *Trifolium* spp. decreased with reduced light intensity or PAR. Beinhart (1963), Harvey (1979) and Davies and Evans (1983) recorded the inhibition of the development of axillary buds in *Trifolium repens* with reduced PAR.

Acknowledgements

References

Abrahamson, W. G. (1975). Reproductive strategies in dewberries. *Ecology* **56:** 721–6

Baker, H. G. (1965). Characteristics and modes of origin of weeds. *Proc. of 1st. internl. union on biol. sci.* Asilomar, California (Theme: The Genetic of colonizing species)

Baki, B. B. (1986). The propulations biology of *Oxalis corniculata* L. Ph.D thesis, Univ. of Wales

Bell, A. D. (1979). The hexagonal branching pattern of *Alpinia speciosa* L. (Zingiberaceae). *Ann. of Botany* **43:** 209–23

Beinhart, G. (1963). Effects of environment of meristematic development, leaf area and growth of white clover. *Crop Sci.* 3: 209–13

Bogorad, L. and McIlrath, W. J. (1960). Effect of light quality in axillary bud development in *Xanthium*. *Pl. Physiol.* **35:** (suppl, 32)

Chapman, D. F. (1983). Growth and demography of *Trifolium repens* stolons in grazed pastures. *J. appl. Ecol.* **20:** 597–608

Clegg, L. M. (1978). The morphology of clonal growth and its relevance to the population dynamics of perennial plants. Ph.D thesis, Univ. of Wales

Cohen, D. (1968). A general model of optimal reproduction in a randomly varying environment. *J. Ecol.* **56:** 219–28

——— (1971). Maximizing final yield when growth is limited by time or limiting resources. *J. Theor. Biol.* **33:** 299–307

Cusset, G. (1982). The conceptual bases of plant morphology. In *Axioms and principles of plant construction.* Sattler R., ed.), p. 8–86. Martinus Nijhoff/Dr. W. Junk, The Hague

Davies, A. and Evans, M. E. (1983). Branching in white clover. *Working Group On Detailed Sward Measurement, Newsletter. Issue No. 12.* Aberystwyth: Welsh Plant Breeding Station

Eiten, G. (1963). Taxonomy and regional variation of *Oxalis* section Corniculate. I. Introduction, keys and synopsis of the species. *American Midl. Naturalist* **69:** 257–309

Franco, M. (1985). The architectural and dynamics of tree growth. Ph.D thesis, Univ. of Wales

Halle, F. Oldeman, R. A. A. and Tomlinson, P.B. (1978). *Tropical Trees and Forests: an architecture analysis* Springer Verlag, Berlin

Harnett, D. C. and Bazzaz, F. A. (1985). The integration of neighbourhood affected by clonal genets in *Solidago canadensis* L. *J. Ecol.* **73:** 416–29

Harper, J. L. (1977). *Population biology of plants.* London: Academic Press

——— (1985). Modules, branches and the capture of resources. In *Population biology of clonal organisms* (Jackson J. B. C., Buss, L. W. and Cook, R. E., ed.) p. 1–33. New Haven: Univ. Press

Harper, J. L. and Bell, A. D. (1979). The population dynamics of growth form in organisms with modular construction. *Population dynamics, Symp. of the British Ecol. Soc.,* **20:** 29–52

Harper, J. L. and Ogden, J. (1970). The reproductive strategy of higher plants. I. The concept of strategy with special reference to *Senecio vulgaris. J. Ecol.* **57:** 681–98

Harvey, H. J. (1979). The regulation of repetitive reproduction. Ph.D thesis, Univ. of Wales

Holm, L. G., Plucknett, D. L., Pancho, J. V. and Herberger, J. P. (1977). The world's worst weeds. Honolulu: Univ. Press of Hawaii

Kasperbauer, M. J. (1971). Special distribution of light in tobacco canopy and effects of end-of-day light quality of growth and a development. *Pl. Physiol.* **47:** 775–8

Lourteig, A. (1979). Oxalidaceae extra-Austroamericanae, 2. Oxalis L. sectio Corniculatae DC. A revision of *Oxalis* section Corniculatae. *Phytologia* **42:** 57–198

Maillette, L. (1982). Structural dynamic of silver birch 1) the fate of buds. *J. appl. Ecol.* **19:** 203–18

Marshall, C. and Sagar, G. R. (1968). The distribution of assimilates in *Lolium multiflorum* Lam. following differential defoliaton. *Ann. Bot.* **32:** 715–19

Noble, J. C. (1976). The population biology of rhizomatous plants. Ph. D thesis, Univ. of Wales

Ogden, J. (1974). The reproductive strategy of higher plants II. The reproduction strategy of *Tussilago farfara* L. *J. Ecol.* **62:** 291–324

Solangaarachchi, S. M. (1985). The nature and control of branching pattern in white clover. Ph.D thesis, Univ. of Wales

Van Der Pijl, L. (1972). *Principles of dispersal in higher plants*, 2nd ed. Springer, Berlin

Watson, M. A. (1984). Developmental constraints; Effect on population growth and patterns of resource allocation in a clonal plant. *The American Naturalist* **123:** 441–32

Watt, A. S. (1947). Pattern and process in the plant community. *J. Ecol.* **35:** 1–22

White, J. (1979). The plant as a metapopulation. *Annu. Rev. of Ecol. and Systematics* **10:** 109–45

—— (1980). Demographic factors in populations of plants. In *Demography and evolution in plant populations* (Solbrig, O. T., ed.) p. 21–8. London: Blackwell Scientific Publication