

## Density and the commitment of apical meristems to clonal growth and reproduction in *Hieracium pilosella*

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**Summary.** We examined responses to population density in the commitment of apical meristems to reproduction and clonal growth in a rosette-forming, stoloniferous herb (*Hieracium pilosella*). Despite close physiological coupling between the evocation of the terminal inflorescence bud and the development of one or more axillary buds into stolons, the allocation of meristems was extremely plastic.

Genets at the higher sowing densities showed density-dependent mortality consistent with self-thinning along a  $-3/2$  trajectory. The probability of inflorescence evocation and associated stolon development was negatively dependent on surviving density. The proportional distribution of primary stolons amongst genets became strikingly more unequal (expressed as the Gini coefficient) with increasing density. Clonal growth was resolved into the number of primary stolons per stoloniferous genet and the extent of stolon branching (i.e. number of apices per primary stolon); both showed strongly negative density-dependence. Reproduction, expressed as the mean number of flowering capitula per stoloniferous genet, declined 15-fold with increasing density; although theoretically expected to be unity, greater values resulted from capitulum production by attached secondary rosettes and lower values reflected the increasing abortion rate of inflorescence buds with increasing density.

Both the total number of apices produced per unit area and the corresponding number of reproductive apices were maximal at intermediate surviving densities ( $700\text{--}1,000\text{ m}^{-2}$ ). The balance between reproductive and clonal growth may be expressed as the probability of an apical meristem producing a capitulum, that also peaked sharply at intermediate density. This finding does not conform with linear models that predict a shift from vegetative growth to sexual reproduction with increasing population density.

have proved a singularly rewarding series of subjects, especially in relation to the idea of reproductive strategy (Harper and Ogden 1970; Abrahamson and Gadgil 1973; Ogden 1974; Gaines et al. 1974; Solbrig and Simpson 1974; Bostock and Benton 1979). Less often, limiting inorganic nutrient resources such as nitrogen and phosphorus have served as the currency (Lovett Doust 1980 a, b) in allocation studies. A third alternative is to consider the disposition of the fundamental units of dividing cells, the shoot meristems or apices (Tripathi and Harper 1973; Watson 1984; Eriksson 1985). This has the merit of, on the one hand, integrating various individual resources irrespective of which of them is actually constraining growth at any instant, whilst on the other hand recognising that the total number of meristems is itself a resource limited by morphology.

*Hieracium pilosella* is a composite with modular growth. Each rosette is a distinct ramet that comprises a single terminal shoot apex and 3–9 leaves, each with a dormant axillary bud. The shoot apex may remain vegetative for four years or longer in the field; sooner or later it may undergo floral evocation and in due course produce a terminal capitulum of about 50–100 florets, each of which potentially can produce a wind-dispersed achene, with its embryonic shoot apex. British races of the species generally produce seed by the sexual process (Sell and West 1975) and therefore are reproductive; elsewhere, many races are substantially or obligately apomictic (Turesson and Turesson 1960; Delcourt 1972; Gadella 1972; Makepeace 1981), their achenes merely contributing to clonal growth. The inevitable consequence of floral evocation is the development of one or more of the axillary buds into stolons that bear further apical meristems at their tips and further dormant buds in the axils of their scale-leaves; under certain conditions stolon axillary buds may break dormancy and produce branching stolons. Each branch potentially is capable of developing into a new rosette; these daughter rosettes root adventitiously and their stolon connections atrophy. Daughter rosettes may also develop in situ from the axillary buds of the parent rosette, without a stolon. As rosettes are monocarpic (semelparous), the parent then senesces and dies. The capitulum may abort at an early stage of development or be grazed off, but in either case stolon development continues normally. Consequently, despite the close physiological coupling of flower and stolon production, there is considerable scope for shifts in the balance between the contributions of apices to reproduction and clonal growth.

Variations in the partitioning of resources between reproduction and vegetative growth are important determinants of evolutionary fitness in plants. Despite wide recognition of this idea, the interpretation of particular plant responses is complicated by the need to express reproduction and clonal growth in a common currency appropriate to the questions asked. Most commonly energy (carbon) has been the preferred currency and members of the Compositae

Populations of *H. pilosella* in the East Anglian Breckland of Britain are regulated within a moderate range of density by the annual commitment of a proportion of apices to the initiation of capitula (Bishop and Davy 1984; Davy and Bishop 1984). This proportion is negatively density-dependent, a phenomenon also observed in spreading patches of *H. floribundum* in Canada (Thomas and Dale 1974). The 'strawberry-coral' model of Williams (1975), perhaps appropriate to other, stoloniferous, rosette-forming herbs, predicts that in stable environments there should be a shift from clonal growth to reproduction with increasing population density; Abrahamson (1980) has reviewed evidence for such a relationship in a number of species. Models developed by Armstrong (1982, 1983, 1984) for rhizomatous perennials suggest more complex relationships, however, that depend upon growth form.

Unfortunately the precise relationships between density and apex allocation in *H. pilosella* are obscured in the field by many factors: the inability reliably to identify genets, the presence of competitor species and grazers, and the nutrient- or drought-limited stolon growth on the impoverished Breckland soils. The purpose of the experiment described in this paper was to examine the density response of *H. pilosella* under conditions where its potential was more fully and unequivocally expressed, and using a seed population of genetic individuals, sown in monoculture at a much wider range of density than has been found in the field.

## Materials and methods

### Experimental material

Mature capitula of *Hieracium pilosella* were collected in late July 1978 from plants growing at a density of about  $880 \text{ m}^{-2}$  in Breckland grass-heath at Deadmans Grave, Icklingham, Suffolk, U.K. This is a species-rich sward with *Festuca ovina* as the most abundant constituent and a long history of rabbit grazing. The site is an extensive plateau of sandy calcareous loam overlying chalk to a depth of about 0.5 m. Details of the site and behaviour of *H. pilosella* populations there have been given previously (Bishop et al. 1978; Bishop and Davy 1984; Davy and Bishop 1984).

### Experimental procedure

Capitula were hand-rubbed to separate the achenes and to remove the pappus from each achene. Mature well-filled achenes were sown on the surface of John Innes No 2 potting compost in 216 mm ( $366 \text{ cm}^2$ ) plastic pots on 19 February 1979. Then they were covered with a thin (1 mm) layer of sharp sand. Six densities were sown in the range  $10^1$  to  $10^{4.5} \text{ m}^{-2}$  (i.e. 1, 4, 37, 115, 366 and 1,157 achenes per pot respectively). The three lower densities were adjusted accurately after germination by pricking out seedlings of the same age to make good any losses; the three higher densities were made with weighed quantities of rubbed achenes, after suitable calibration by mass. There were five replicate pots of each density.

The pots were arranged in randomized blocks in a heated glasshouse with supplementary lighting from high pressure sodium lamps for 14 h per day. The small seedlings were watered with a mist spray to prevent disturbance.

Flowering was recorded as the total number of elon-

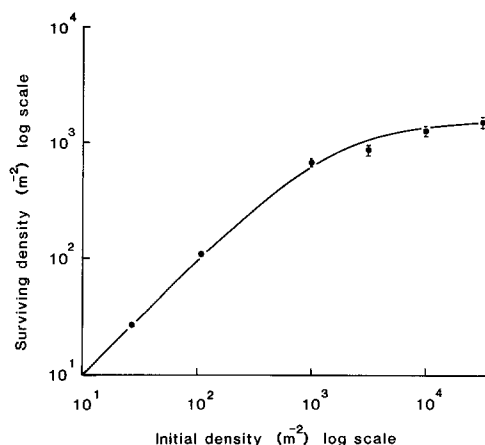


Fig. 1. Relationship between surviving genet density of *Hieracium pilosella* at harvest and the initial density of achenes sown. Vertical bars represent  $\pm 1$  standard error ( $n=5$ )

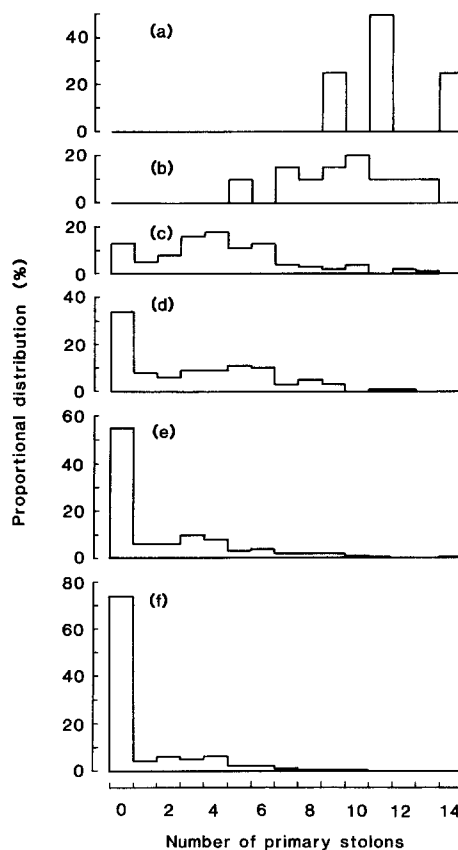


Fig. 2a-f. Proportional distribution of genets of *Hieracium pilosella* according to the number of primary stolons produced, at six genet densities: a  $27 \text{ m}^{-2}$ ; b  $109 \text{ m}^{-2}$ ; c  $683 \text{ m}^{-2}$ ; d  $874 \text{ m}^{-2}$ ; e  $1,280 \text{ m}^{-2}$ ; f  $1,530 \text{ m}^{-2}$

gated peduncles observed on eight occasions between 27 April and 24 June 1979. The plants were finally harvested 150 days after sowing. The surviving genets were carefully separated and counted. The number of primary stolons and stolon apices on each were recorded; primary stolons were defined as those directly attached to the primary (parent) rosette, although frequently they were highly branched with numerous apices. Dormant buds in the axils of rosette

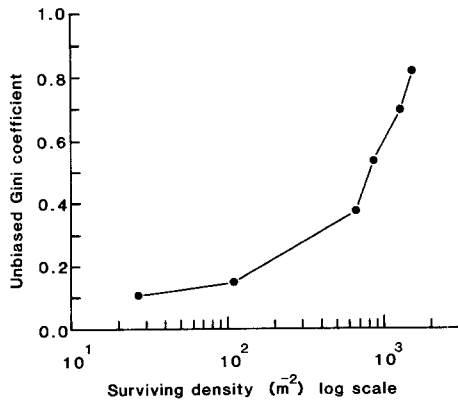


Fig. 3. Relationship between the inequality of primary stolon production amongst genets of *Hieracium pilosella*, expressed as the unbiased Gini coefficient, and surviving genet density

leaves or stolon scale-leaves were not considered. In the case of large luxuriant genets, the leaves of the primary rosette were often absent by the time of harvest. The root system associated with the parent rosette, however, was readily located and all stolons emanating from this point were defined as primary. The total dry mass per pot was determined after oven drying at 80° C for 48 h.

## Results

### Mortality and dry mass in relation to density

Mortality was density-dependent. There were no losses in the lower two densities and progressively higher mortality with increasing density in the higher four densities. Comparison of the surviving (harvest) genet density ( $N_s$ ) with the initial (sowing) genet density ( $N_i$ ) reveals an asymptotic relationship (Fig. 1). A model of the form employed by Watkinson (1980):

$$N_s = N_i(1 + aN_i)^{-1}$$

with  $a=0.0062$  fits the data extremely closely (Fig. 1). This implies an asymptote ( $a^{-1}$ ) of about 1,600 m<sup>-2</sup> for surviving density under these experimental conditions.

Both this relationship and a consideration of the mass-density relationships at sowing and harvest indicate that the mortality observed was entirely consistent with self-thinning along a  $-3/2$  gradient. The mean achene dry mass was 0.101 mg and the mean harvest dry mass per genet ranged from 7.9 g at the lowest density to 0.31 g at the highest density. A line of slope  $-3/2$  fitted to the highest surviving density has an intercept of 4.29, which is within the usual range (3.5–4.5) for herbaceous plants (White 1980). Hence, although the trajectory of thinning with time was not followed, *H. pilosella* grown under these conditions conformed with theoretical expectation.

### Stolon apex production

The proportional distribution of primary stolons produced per genet (Fig. 2) became strikingly more unequal with increasing density; the mode at 27 m<sup>-2</sup> was 11 primary stolons per genet whereas at the highest three densities the mode was 0 stolons per genet. The largest number of prima-

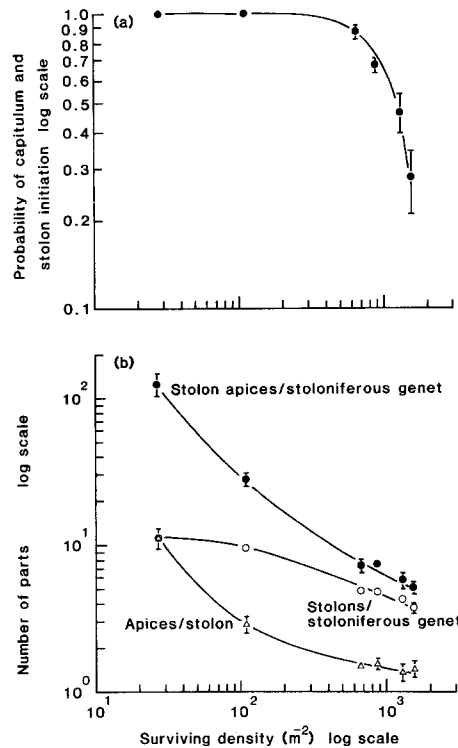


Fig. 4. a Probability of a genet of *Hieracium pilosella* initiating a capitulum and stolons in relation to surviving genet density. b The mean number of apices per stolon, the mean number of stolons per stoloniferous genet and the mean number of stolon apices per stoloniferous genet in relation to surviving genet density. Vertical bars represent  $\pm 1$  standard error ( $n=5$ )

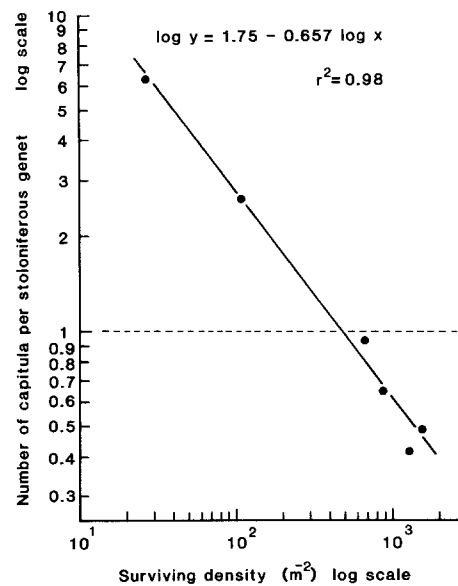


Fig. 5. The mean number of capitula produced per stoloniferous genet in relation to surviving genet density in *Hieracium pilosella*

ry stolons per genet recorded (14) however, was observed in plants at densities as different as 27 and 1,280 m<sup>-2</sup>. Even at 1,530 m<sup>-2</sup> a single genet produced as many as 10 primary stolons. The inequality of distribution of primary stolons between genets probably can best be examined in the same way as for dry mass using the Gini coefficient (Weiner and

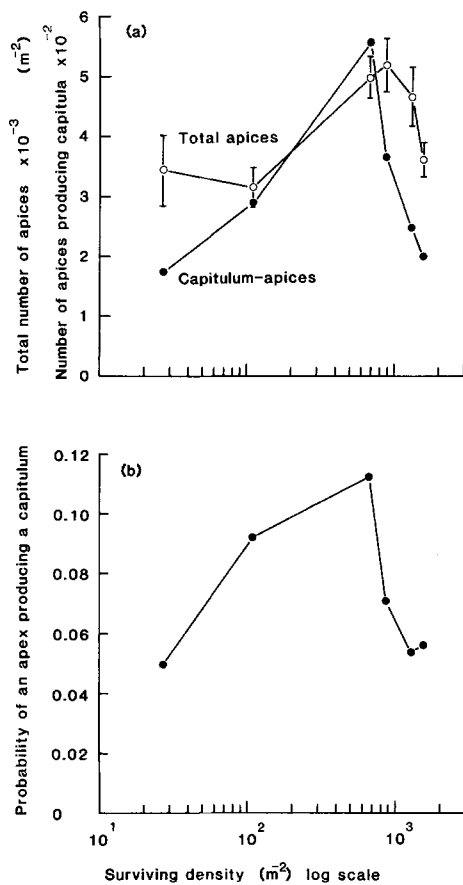


Fig. 6. **a** The total apex density ( $m^{-2}$ ) and the density of apices producing capitula ( $m^{-2}$ ) of *Hieracium pilosella* in relation to surviving genet density. Vertical bars represent  $\pm 1$  standard error ( $n=5$ ). **b** Probability of an apex producing a capitulum in relation to surviving genet density

Solbrig 1984) that ranges from 0 for equality to a theoretical maximum of 1. Values of the unbiased Gini coefficient, i.e. corrected for sample size, increase progressively from 0.11 at the density of  $27 m^{-2}$  to 0.82 at a density of  $1,530 m^{-2}$  (Fig. 3). Variability has perhaps been exacerbated by the absence of 'guard rows' at the edges of the pots, but for the range of density investigated this precaution would have enormously increased the scale of the experiment and the quantity of achenes required.

The average probability of a genet producing at least one stolon (and therefore also of its terminal apex having undergone floral evocation) showed strong negative density-dependence (Fig. 4a). Furthermore, both the mean number of stolons per stoloniferous genet and the extent of their branching – i.e. the mean number of apical meristems per stolon – declined with increasing density (Fig. 4b); hence their product, the total number of stolon apices per stoloniferous genet declined dramatically with increasing density (Fig. 4b).

#### Reproductive apex production

Capitula collected in the field yielded a mean of  $70 \pm 7$  achenes (S.E.,  $n=20$ ). In the absence of direct counts for this experiment the number of capitula is used therefore as an indication of the number of embryonic shoot apices

produced. The mean number of capitula per stoloniferous genet was negatively density-dependent (Fig. 5), ranging from about 0.4 at high density to 6.25 at the lowest density ( $27 m^{-2}$ ). A mean value of greater than one indicates that certain stolon apices or axillary daughter apices had undergone floral evocation even though their rosettes had not yet rooted and assumed a separate existence. Because of the close coupling between stolon production and flowering, and the absence of flower bud predation in the glasshouse, a mean value of less than one implies that a proportion of evoked apices aborted before peduncle elongation and flowering. The notional value of 1 capitulum per stoloniferous genet in the first growing season would be predicted only at a density of  $460 m^{-2}$  from this relationship, and for the conditions of this experiment.

#### The balance between vegetative and reproductive apices

The total number of apical meristems produced and the number culminating successfully in a capitulum in response to variations in density may be examined on an area basis (Fig. 6a). Both increase with density to a pronounced peak and decline sharply at the higher surviving densities. The maximal production of apices lies at a density of about  $900 m^{-2}$ , but the maximal production of capitula was at a distinctly lower density. It would not be possible to define this density precisely without further treatments in the density range of  $200\text{--}500 m^{-2}$ , but from the shape of the curve (Fig. 6a) it ought to be  $500 m^{-2}$  or lower.

The relative commitment of apical meristems to reproduction and clonal growth is expressed as the mean probability of an apex producing a capitulum that reached the stage of peduncle elongation by the end of the experiment (Fig. 6b). The greatest probability (0.11) was achieved at neither the lowest or highest surviving densities, but near the middle of the range ( $683 m^{-2}$ ); mean probability fell strikingly to about 0.05 either side of this density. Again, the actual peak probably would have been between the 109 and  $683 m^{-2}$  treatments.

#### Discussion

The responses of *Hieracium pilosella* under the artificial conditions of this experiment were consistent with the behaviour of populations in the field and serve to illuminate some of the mechanisms underlying such behaviour. In grass-heath, the probability of a rosette initiating an inflorescence, and therefore of producing at least one stolon, declined markedly with increasing population density; this was the more striking because the *H. pilosella* was embedded in a matrix of other species, mainly *Festuca ovina* and *Koeleria macrantha* (Bishop and Davy 1984). The present experiment confirms this relationship in monoculture and reveals certain of its potentially important features. The linear model used previously to test field data is clearly not applicable to the much wider range of density of the glasshouse experiment, where densities fall low enough to permit all plants to flower. The use of more appropriate types of model has been discussed by Watkinson and Davy (1985).

The increasing inequality of stolon production amongst the individuals of populations with increasing density parallels the findings for the negatively skewed dry mass distributions of numerous species (e.g. Turner and Rabinowitz

1983), especially other dicotyledons. It seems likely that the number of stolons produced is largely a function of rosette dry mass, with the first stolon determined by the minimum threshold size for floral initiation. The pattern of density-dependent mortality suggests that this inequality of stolon production reflects increasing hierarchical structure, with dominant and suppressed individuals, rather than just the skewness associated with a shift to a log-normal distribution because of variance in exponential growth rate (Turner and Rabinowitz 1983). At comparable density, the inequality shown in the relatively nutrient-rich, monocultural conditions of the experiment was substantially greater than in the nutrient-limited grass-heath, where very few plants indeed produce more than two stolons; even at the highest density used, where 74% of genets produced no stolons, three genets produced 8, 9 and 10 respectively. This is further indirect evidence for the importance of plant mass for stolon-production.

If we consider further just the stoloniferous genets, there are some remarkable plastic refinements to the density response. The number of stolon apices per stoloniferous genet varied nearly 25-fold with whole population density. This effect could be resolved into two components with contrasting response curves but similar overall contributions: the number of apices per primary stolon, which is a measure of stolon branching, was the greater determinant at low density, whereas the number of primary stolons per stoloniferous genet was the more significant influence at high density (Fig. 4b). Similar patterns of plasticity for numbers of plant parts in response to density have been recorded for annuals such as *Agrostemma githago* (Watkinson 1981) and *Salicornia europaea* (Jefferies et al. 1981). This potential is rarely realized in the field by *Hieracium pilosella*. The local population that was the seed source for this experiment averages 1.79 stolons per stoloniferous genet and the stolons are typically unbranched. Another, nearby population, however, with a lower density and subject to more intensive rabbit activity on a chalky soil, averages 2.73 stolons per stoloniferous genet and these stolons are often branched. The capacity to produce numerous heavily branched stolons is likely to be of advantage in exploiting small patches of bare ground (such as rabbit scratchings) or nutrient enrichment (such as rabbit latrines).

The number of flowering capitula per stoloniferous genet was similarly density-dependent (16-fold variation over the range of surviving population density). The mature capitula were not collected in this experiment but as material from the field yielded an average of 70 achenes per capitulum, it is likely that conservative estimates of mean seed production per stoloniferous genet range from about 440 at the lowest density to about 30 at the highest density. Mean numbers of capitula per stoloniferous genet of less than one are of particular interest because they imply the abortion of a proportion of reproductive apices. At high (self thinning) densities the probability of abortion was high (0.51–0.58). At an intermediate density (874 m<sup>-2</sup>) the probability of abortion (0.36) was strikingly similar to the average probability observed over four summers in the field (0.35 for grazed and 0.30 for ungrazed populations). Abortion was decreasingly significant at lower densities such that at the lowest density all of the primary rosette apices produced a capitulum. It must be recognized however that the linear relationship shown in Fig. 5 is actually the product of two opposed processes: the propensity of the second-

ary rosette apices (both at the ends of stolons and in the axils of the primary rosette) to produce capitula at low density *versus* abortion of reproductive apices that increases with density. Abortion is clearly an important component of the response of *H. pilosella* to density and the mechanism deserves further study.

The maximal commitment of apices to both vegetative and reproductive growth was at intermediate surviving density rather than either extreme; in both cases it occurred at densities within the characteristic range of the parent population in the field. Maximal inflorescence production occurred at rather lower density than maximal stolon apex production with the result that there was a striking pattern in the probability of any apex successfully producing an inflorescence (Fig. 6b). The probability was also greatest (0.11) at intermediate density and had declined by more than half at both extremes of density. It is probable that the peak would have been considerably greater had there been treatments with a surviving density in the range 200–600 m<sup>-2</sup>. The response to density of this measure of the balance between reproductive and clonal growth contrasts strongly with the linear predictions of the “strawberry-coral” model (Williams 1975) and responses of several species on the basis of dry mass distribution reported by Abrahamson (1980). The data conform with neither the predictions for ‘stable’ nor ‘unstable’ habitats. The predictability of the environment for *H. pilosella* is itself a moot point. Its growth form allows the exploitation of the spatial and temporal patchiness associated with grazing herbivores, particularly rabbits. Yet Breckland grasslands and heaths remain classical examples of plant communities with cyclical processes that are largely predictable and therefore arguably stable (Watt 1947, 1962). A more appropriate analysis of the underlying principles might be akin to models that take account of the geometry of growth form in energy partitioning in rhizomatous plants (Armstrong 1982, 1983, 1984).

The approach of assessing the allocation of resources to clonal growth and reproduction in terms of the commitment of apices has been used previously by Tripathi and Harper (1973) in a comparison of a rhizomatous species (*Elymus repens*) with a closely similar non-rhizomatous one (*Elymus caninus*). The allocative strategies of the two species could be regarded as different partitioning of a limited number of meristems, as axillary buds directed to become rhizomes reduce the number available to become flowering tillers. Watson (1984) has demonstrated a similar effect in *Eichhornia crassipes*, a stoloniferous plant whose development has certain important parallels with that of *H. pilosella*; inflorescence production was inversely correlated with the growth rate of the ramet population because the overall meristem population was limited by developmental anatomy. Eriksson (1985) reports recent findings that take account of density for *Potentilla anserina*, a stoloniferous herb with axillary flowers. Plants at the upper end of a five-fold range of density committed a greater proportion of meristems exclusively to clonal growth and a lower proportion to flowering plus clonal growth; there was no trend in the proportion committed exclusively to flowering. The intriguing corollary of this pattern was an invariant allocation to reproduction and clonal growth in carbon terms. It is not clear whether flower bud abortion plays a role in shaping this response of *P. anserina*, as it appears to in the comparable responses of *H. pilosella*.

Examination of meristem partitioning in *Hieracium pilosella* indicates that the responses of stoloniferous plants to density may be complex. Both *Hieracium floribundum* (Thomas and Dale 1974) and *H. pilosella* show a decline in flowering with increasing density in the field and over restricted ranges of density the relationships are approximately linear as predicted by Abrahamson (1980). Nevertheless it seems that a diminished relative allocation to reproduction, and hence dispersal by the wind-borne achenes, may be a response common to both of two opposite circumstances; colonizing populations with low density behave similarly to self-thinning populations with high density and severe competition for resources, in this respect. The former is a plastic response that would be expected to confer fitness in a patchy environment. Investigation of the physiology of the way in which reproductive and vegetative sinks compete for nutrient within a genet may be necessary to interpret the latter response.

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