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Effects of the spatial arrangement of aerial stems and current-year shoots on the demography and growth of *Hydrangea hirta* in a light-limited environment

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SUMMARY

This study investigates the effects of the spatial arrangement of aerial stems and current-year shoots on patterns of herbivory, competition and on the requirements for mechanical support in *Hydrangea hirta* Sieb. et Zucc. growing in a light-limited environment. Stem demography was followed for three consecutive growing seasons. Stem mortality rates decreased with increasing stem age. Age-specific mortality rate was highest for new stems owing to the high incidence of herbivory. Mortality due to herbivory was low in older stems and was attributed to the dispersion of the risk of herbivore attack as a result of the increase in number of current-year shoots per stem. Clumping of stems led to intense intra-clonal competition as inferred from size-dependent mortality and density-dependent turnover of stems, and higher maximum stem length in clumps with higher stem density. Analysis of the spatial distribution of current-year shoots within the stem crown revealed a uniform, mono-layered crown architecture. The horizontal distribution of buds within the mono-layer was aggregated as a result of their opposite position, but as current-year shoots grew, their apices became uniformly distributed, resulting in efficient leaf display for light capture and shading out competing stems. However, limits on stem growth were observed in crown expansion, shoot production rate and current-year shoot size. Crown width increased with increasing basal diameter to reach a maximum. Both shoot production rate and current-year shoot size decreased with stem growth and a minimum current-year shoot size was defined. These limits on stem growth were attributed to suppression from intra-clonal competition and to the requirements for mechanical support of the mono-layered crown.

Key words: Herbivory, *Hydrangea hirta*, intra-clonal competition, growth, demography.

INTRODUCTION

It has been suggested that plant growth pattern is largely a consequence of foraging by the plant for resources such as light, water and nutrients (Hutchings & de Kroon, 1994), and many studies have interpreted the spatial arrangement of modular units in plants (plant architecture), such as clonal perennial herbs, as patterns of resource acquisition by the plant (Hutchings & Barkham, 1976; Lovett Doust, 1981; Bell, 1984; Evans & Cain, 1995). Plant growth pattern is also the result of the interaction between plant growth and the factors which influence it, such as herbivory (Mopper *et al.*, 1991; Tolvanen *et al.*, 1992), competition (Turkington & Harper, 1979*a*; *b*), and environmental factors such as stress (Salzman, 1985; Salzman & Parker, 1985). In shrubs and trees, growth occurs in three dimensions and introduces another influencing factor: the requirements for mechanical support (MacMahon, 1975; Niklas & O'Rourke, 1982; Gartner, 1991; Mattheck, 1995). This study investigates the effects of the spatial arrangement of aerial stems and current-year shoots on the interaction between plant growth and three factors which may influence it; herbivory, competition and the requirements for mechanical support, in the shrub *Hydrangea hirta*. Demographic study of the aerial stem population and morphological analysis of aerial stem growth were used to infer these effects.

H. hirta is a clonal shrub, often found in the shrub layer of mesic forests in temperate Japan. A single shrub consists of numbers of aerial stems of various ages and sizes growing in tight clumps from a single

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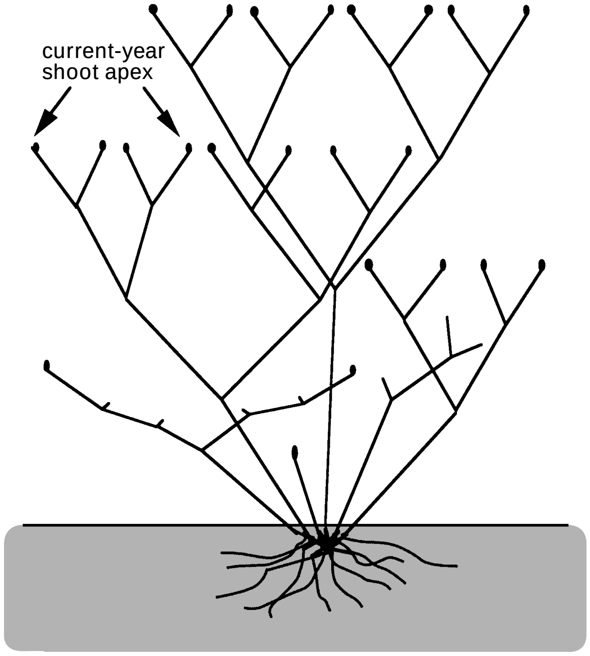

Figure 1. A schematic diagram of a clump of aerial stems of *Hydrangea hirta* consisting of five live and one dead stem. Aerial stems have characteristic mono-layered crown architecture. The clumps are made up of aerial stems of various age and size, including dead stems and new stems, suggesting stem turnover.

underground root mass (Fig. 1). The crown of each stem consists of current-year shoots arranged in a horizontal mono-layer. The clumps include both many dead stems and numbers of new stems suggesting stem turnover within the clump. Demographic studies of clonal plants have revealed continuous turnover of ramets in clonal perennial herbs (Sarukhan & Harper, 1973; Hutchings & Barkham, 1976; Noble, Bell & Harper, 1979; Lovett Doust, 1981; Nault & Gagnon, 1993) and stems in woody species (Ford & Newbould, 1970; Kurmis & Sucoff, 1989; Tappeiner *et al.*, 1991). Various causes for turnover have been discussed. Sarukhan & Harper (1973) found that ramet mortality in three species of *Ranunculus* depended upon ramet age and density. Hutchings & Barkham (1976) found that ramets of *Mercurialis perennis* conformed to the competition–density equation, and ramet mortality was caused by environmental factors such as light and nutrients. Ford & Newbould (1970) found size-dependent mortality in coppices of *Castanea sativa*.

In the case of *H. hirta*, the effects of herbivory might play an important role in causing stem turnover. Newly emerged stems of *H. hirta* are often attacked by Hymenopteran and Lepidopteran larvae (H. Ishii, unpublished). Although the larvae are not confined to *H. hirta*, they can completely defoliate new stems, causing them to die. We hypothesized that new stems may have high mortality due to herbivory because they consist of a single current-year shoot and apical meristem and its loss would result in death of the stem. Cook (1985) raises 'risk-spreading' as one of the benefits of clonality that leads to higher rates of plant survival. Older stems consisting of larger numbers of current-year shoots and meristems may be able to spread the risk of herbivore attack and decrease the chance of stem mortality due to herbivory.

Secondly, we hypothesized that clumping of aerial stems of *H. hirta* would result in intense *intra-clonal competition* among neighbouring stems for space in the light-limited shrub layer and lead to stem mortality and turnover. Harper (1985) defined competition among modules of the same plant in terms of 'resource depletion zone(s)'. Wilson (1995) also refers to 'competition for stored materials between stems of the same clone' in shrubs. Givnish (1982) showed that, where plant density is high, vertical growth is important in displaying foliage above those of competitors. The mono-layered crown architecture of stems would shade out other stems, creating a resource depletion zone, once a stem has emerged above other stems in the clump. The capture and allocation of resources among stems may be considered as competition in a broader sense (intra-clonal competition) albeit different from competition among individual plants.

Thirdly, we hypothesized that the growth of those stems which survive herbivory and intra-clonal competition may still be constrained by the requirements for mechanical support of the mono-layered crown. In light-limited environments, such as the shrub layer, leaves of many woody species are arranged in a mono-layer so as to capture light efficiently (Nicola & Pickett, 1983; Ardhana *et al.*, 1988; Givnish, 1988). The mono-layered crown architecture of the stem results from repeated sympodial branching: terminating the apical bud each year and then branching from one or both of the opposite lateral buds in the following year. A similar branching pattern has been modelled in *Tabebuia rosea* by Borchert & Tomlinson (1984) who predicted that the cost of mechanical support for such crown geometry would eventually limit its growth. Niklas (1994) found an allometric relationship which constrains the lateral spread of crowns relative to trunk diameter in trees. The growth of *H. hirta* stems may be limited by similar requirements for mechanical support.

MATERIALS AND METHODS

A population of *H. hirta* was sampled at Mt Hiei, Ohtsu City, Shiga Prefecture, Japan, before and after three consecutive growing seasons from 1993 to 1995. A 10 m × 40 m study site was set up under the canopy of a 40-yr-old *Chamaecyparis obtusa* Endl. plantation forest (mean dbh: 21·33 cm, mean tree height: 16·54 m, density: 1000 trees ha^{-1}, closed canopy).

The 115 clumps in the study area were numbered and their positions mapped. Crown height of clumps (from ground to top of foliage) and crown width (at widest part of crown) were measured to the nearest 5 cm. Relative light intensity (RLI: percent light relative to open sky) above each clump was measured using the Minolta T-1H illuminance meter. The mean ratio of three consecutive simultaneous measurements on an overcast day above each clump and in a nearby open area was used.

All aerial stems were marked, and stem length (distance from emergence at ground level to centre of the crown) and crown width (at widest part of the crown) were measured to the nearest 5 cm. Diameter at the base of the stem was measured with calipers to the nearest mm and number of current-year shoots per stem counted. Stem age was determined by counting the number of times the stem had branched from its base (the year of stem emergence being year zero). All measurements were taken toward the end of each growing season in late August when all growth had ceased for that year.

Stem demography and intra-clonal competition

Recruitment, survival and mortality of stems were followed for three growing seasons from 1993 to 1995. Stem mortality for a given year was determined by non-production of foliage in the following year. Causes of mortality were classified as either herbivory or non-herbivory. Mortality due to herbivory was defined as complete defoliation during the growing season due to herbivore attack resulting in stem mortality.

Based on the stem age counts, the age structure of the aerial stem population was determined for each year of observation. Age-specific mortality rates were calculated to investigate patterns of stem mortality in relation to stem age.

The relationship between stem mortality and stem morphology was investigated for size-dependent mortality. Stems were divided into size classes based on length, crown width and number of current-year shoots per stem, and mortality rates were calculated for each size class. Stems which died of herbivory were excluded from this analysis.

The relationship between stem turnover (recruitment and mortality) in each clump and the number of stems in the clump was investigated for density-dependent turnover of stems. Stem recruitment was examined relative to the number of stems in the clump at the *beginning* of the growing season, and mortality relative to the number of stems *during* the growing season. Because stem recruitment occurs at the beginning of the growing season, it is likely to be influenced by the number of stems before the emergence of new stems. On the other hand, stem mortality occurs during and after the growing season, and mortality is likely to be influenced by the number of stems during the growing season, i.e. number of stems at the beginning of the growing season plus recruitment. Spearman's rank correlation was used for this analysis because the frequency distributions of stem recruitment and mortality in the clumps and number of stems per clump were not normal.

Based on the theory by Givnish (1982), the relationship between number of stems per clump and the length of the longest stem in the clump was investigated to infer the intensity of intra-clonal competition in the clumps. If our second hypothesis holds true, maximum stem length should be higher for clumps with higher stem density as a result of more intense intra-clonal competition. The number of stems in the clump during the growing season was used for this analysis.

Stem morphology and growth

Thirteen aerial stems of various age and size were chosen for morphological analysis in the field to characterize the mono-layered crown architecture of stems and the spatial distribution of current-year shoots within the crown. A 1 m × 1 m grid with 5-cm lattices was set up above the crown of each stem to map positions of current-year buds in spring. Bud positions were mapped by dropping a rod vertically from the grid to the bud to record the three-dimensional position of each bud. The grid was set up in the same position above the crown at the end of the growing season to map the position of current-year shoot apices. The vertical distributions of buds and shoot apices were analysed by calculating the coefficient of variance of bud and shoot apex heights for each stem. The horizontal distributions were analysed using the Clark & Evans statistic, R (Clark & Evans, 1954):

$$R = r_A \,/\, r_E,$$

where r_A is the mean distance to nearest neighbour of the sample distribution, and

$$r_E = \frac{1}{2\sqrt{p}}$$

the mean distance to nearest neighbour in a spatially random distribution with density ρ. The Clark & Evans statistic was chosen for its ease of application in that it uses mean distance to nearest neighbour and avoids analyses using Monte Carlo simulations (Diggle, 1983). Although, corrections to the Clark & Evans statistic have been suggested (Donnelly, 1978), the uncorrected statistic was chosen for two reasons. First, the stem crown was irregular in shape and could not be defined as a 'reasonably smooth boundary' (Donnelly, 1978) for calculation of edge effects. Second, corrections for edge effects assume that an arbitrary boundary has been drawn in a continuous distribution and that neighbours outside the boundary equally influence the distribution of points within the boundary. This assumption does not hold in this case because the boundary is the circumference of the stem crown (i.e. not arbitrary), and neighbours outside the boundary belong to other stems and do not have equal influence on the distribution within the boundary. The uncorrected Clark & Evans statistic is biased towards a uniform distribution (Sinclair, 1985). However, the patterns of aggregation observed in this study were strong enough to be detected using the uncorrected Clark & Evans statistic.

Stem growth was analysed by investigating the changes in crown width, shoot production and current-year shoot size with stem age and size. The relationship between crown width and basal diameter of stems was investigated for evidence of limits on the horizontal expansion of the mono-layered crown.

The year to year growth or decline of stems can be expressed by calculating the *shoot production rate*, analogous to 'bud production rate' (Maillette, 1982):

$$\text{shoot production rate in year } (t) = \frac{\text{number of current-year shoots in year } (t+1)}{\text{number of current-year shoots in year } (t)}.$$

Shoot production rates of all stems in the field were calculated as the ratio of the number of current-year shoots per stem in consecutive years. In addition, 28 stems of various age and size (hereafter: harvested stems) were taken for morphological analyses in the laboratory. For the harvested stems, shoot production rates for past years of stem growth were estimated as ratios of the number of branches of age $x+1$ to number of branches of age x. Shoot production rates of stems of various age and size in the field can be considered a chronosequence, whereas shoot production rate of harvested stems is an estimate of the past changes in shoot production rate during the growth of a single stem.

Harvested stems were also used to investigate changes in current-year shoot morphology in relation to stem age and size. Current-year shoot sizes (shoot length, total leaf area, and number of leaves per current-year shoot) of harvested stems were measured, and mean current-year shoot size was calculated for each stem. In addition, the lengths of all branches in each harvested stem were measured, and mean length for branches of the same age (mean branch length) calculated to give estimates of the mean current-year shoot length from past years of stem growth. Current-year shoot sizes from harvested stems of various age and size can be considered a chronosequence, whereas mean branch length is an estimate of the past changes in current-year shoot length during the growth of a single stem.

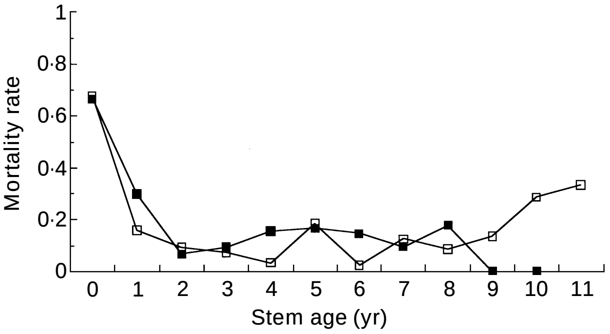

Figure 2. Age-specific mortality rate of stems. ■, 1993; □, 1994. Age-specific mortality rate was calculated based on the age structure of the stem population in each year of observation.

RESULTS

Mean height and crown width of clumps in 1993 were 99·5 cm and 99·8 cm, respectively, and the clumps consisted of an average of four to five live stems. Clump sizes were normally distributed and mean clump size was relatively constant among years. RLI above each clump ranged from 4 to 11 % and was normally distributed. There was a positive correlation between clump size and RLI above the clump ($r = 0{\cdot}460$, $P < 0{\cdot}01$ for crown height, $r = 0{\cdot}348$, $P < 0{\cdot}01$ for crown width; $n = 115$). However, the narrow range of RLI values and the low correlation coefficient despite the large sample size suggests that variation in light environment does not sufficiently explain the variation in clump size. Clump size might depend more on other factors such as time, since clump initiation or local soil conditions. The clumps were concentrated in a small depression (*c.* 1 m deep and 3 m wide) which cut diagonally across the study area. However, there was sufficient spacing between clumps to disregard interaction among clumps.

Stem demography and intra-clonal competition

Age-specific mortality rate was highest for new stems (0-yr-old) with values of 0·67 in 1993 and 0·68 in 1994 (Fig. 2). Mortality rate declined sharply from new stems to 1-yr-old and 2-yr-old stems, and remained relatively low thereafter, except for a slight increase from 7-yr-old to 11-yr-old stems in 1994. Mortality in new stems was mainly due to herbivory as assessed by complete defoliation. Herbivory accounted for 58·0 % of mortality in new stems in 1993 and 55·6 % in 1994. However, herbivory accounted for only 6·1 % (1993) and 12·8 % (1994) of mortality in all older stems (1-yr-old and older) combined.

Stem mortality rate decreased with increasing stem size, indicating size-dependent mortality of stems (Fig. 3). The sharpest decline was observed in the size classes based on the number of current-year

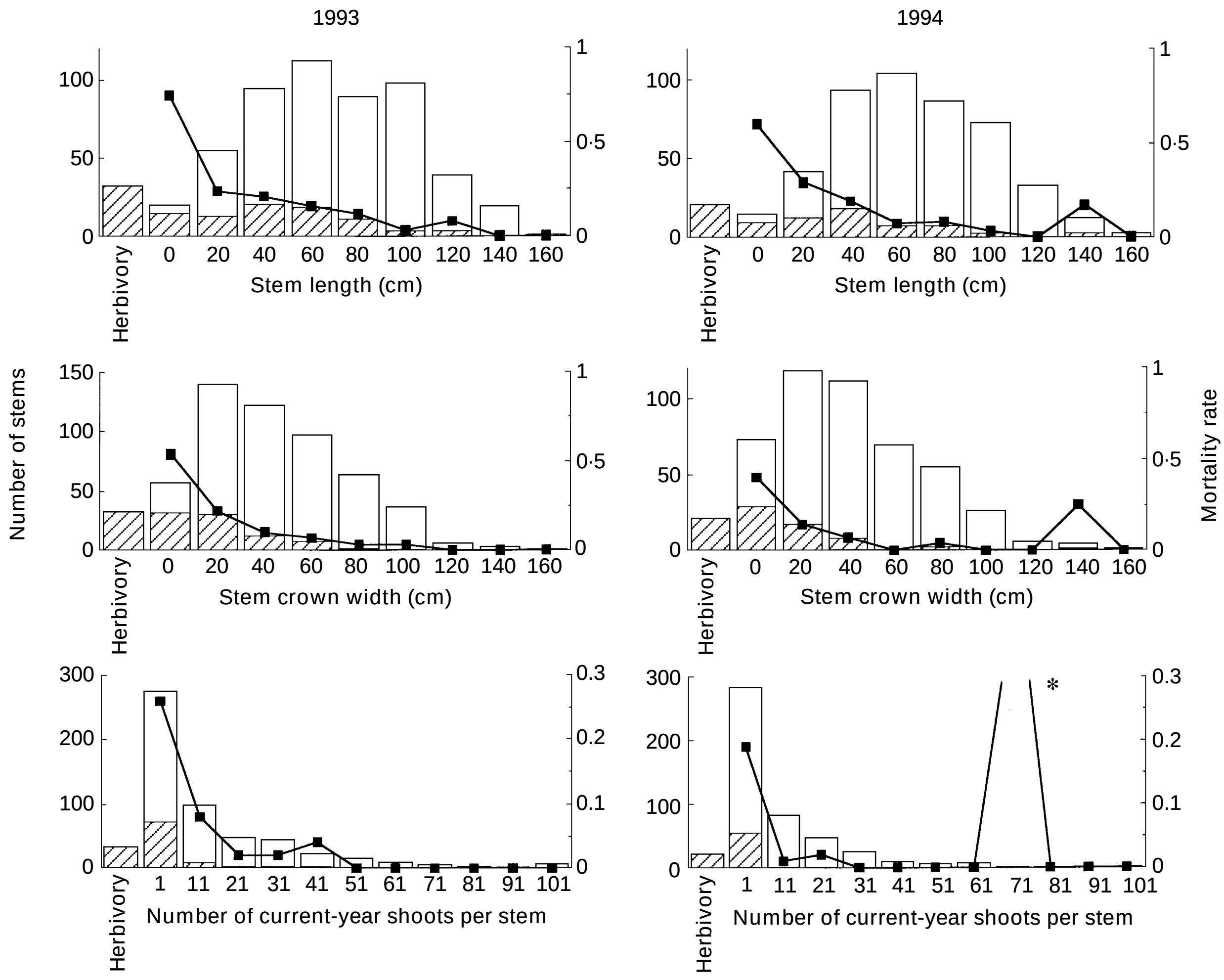

Figure 3. Survival (□), mortality (▨) and mortality rate (■-■) of stems in relation to stem size (length, crown width, and number of current-year shoots per stem) showing size-dependent mortality of stems (note varied y-axis range). Size classes are labeled with the minimum values in each class. The mortality rate in * equals 1 owing to the death of the only stem in the size class.

shoots per stem, and this was used as a measure of stem size in later analyses.

The overall relationships between stem mortality, stem age and stem size were summarized by dividing stems into four size classes based on the number of current-year shoots per stem and calculating the age-specific mortality rates in each size class (Fig. 4). The trend in stem mortality with stem age, observed above, was reflected in the two smaller size classes (1–10 and 11–20 current-year shoots per stem). However, in the two larger size classes (21–30 and > 31 current-year shoots per stem) mortality seldom occurred. The highest mortality rate was observed in new stems (which are all in the smallest size class because they consist of one current-year shoot), mainly owing to high incidence of herbivory. Mortality in older stems was mostly in the two smaller size classes, reflecting size-dependent mortality.

Stem recruitment in each clump was positively correlated with the number of stems at the beginning of the growing season (Spearman's rank correlation coefficient: $r_s = 0{\cdot}546$, $P < 0{\cdot}01$ in 1993, $r_s = 0{\cdot}400$, $P < 0{\cdot}01$ in 1994; $n = 115$) indicating density-dependent recruitment of stems. Stem mortality was positively correlated with the number of stems during the growing season ($r_s = 0{\cdot}205$, $P < 0{\cdot}05$ in 1993, $r_s = 0{\cdot}321$, $P < 0{\cdot}01$ in 1994; $n = 115$) indicating density-dependent mortality. The combined effect was higher stem turnover in clumps with higher stem density.

Maximum stem length showed a wide range of values for clumps with fewer stems, but became restricted to higher values in clumps with larger numbers of stems (Fig. 5), resulting in a positive overall correlation between maximum stem length and number of stems in the clump ($r_s = 0{\cdot}305$, $P <$ 0·01 in 1993, $r_s = 0{\cdot}324$, $P < 0{\cdot}01$ in 1994, $n = 115$). This suggested that intra-clonal competition becomes more intense with increasing stem density, resulting in higher maximum stem length.

Stem morphology and growth

Spatial analyses of stem crowns confirmed observations of the mono-layered vertical distribution of

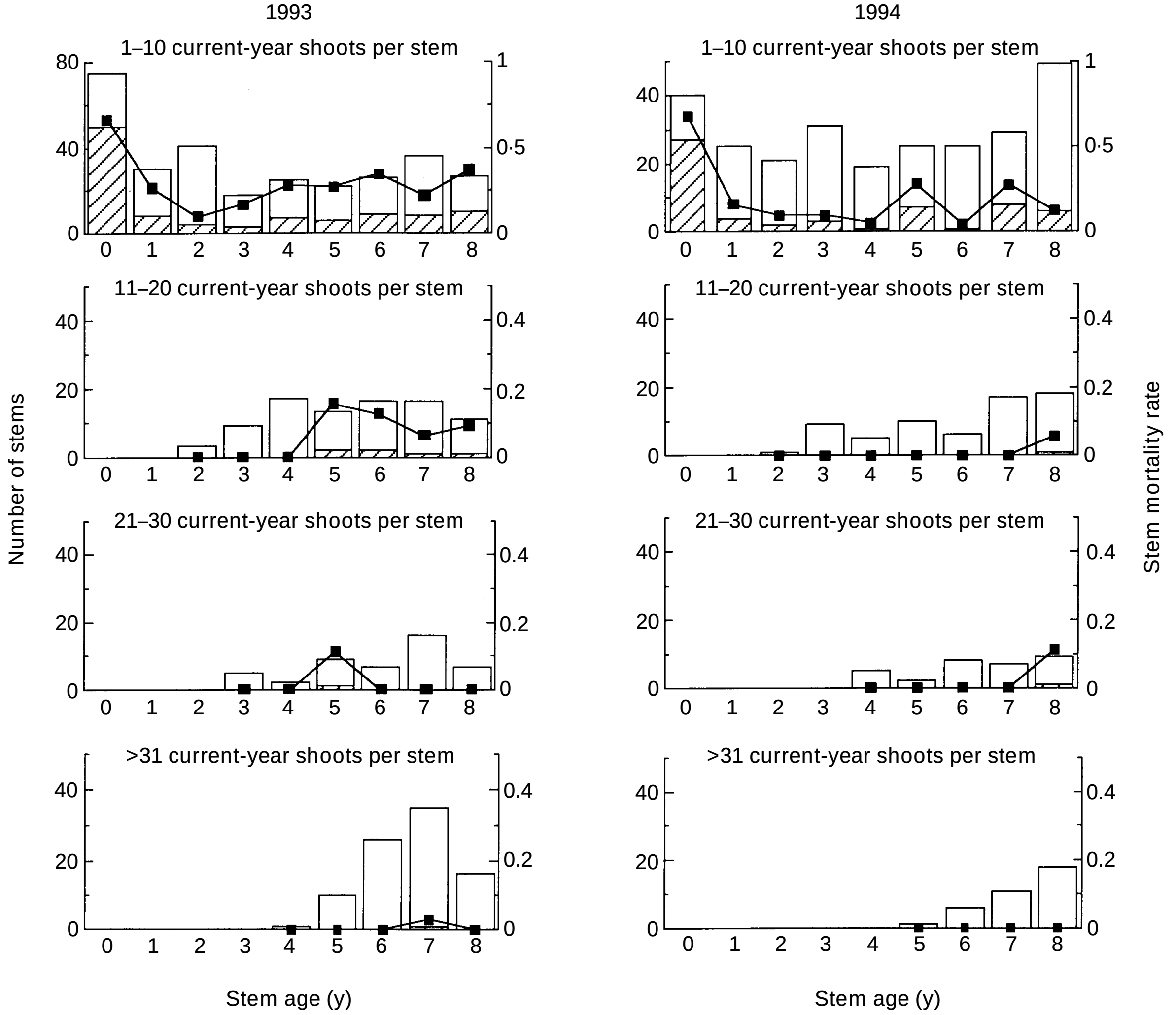

Figure 4. Survival (□), mortality (▨), and mortality rate (■-■) of stems in relation to stem age and size in each year of observation. Stems were divided into four size classes based on the number of current-year shoots per stem and age-specific mortality rate was calculated in each size class (note varied *y*-axis range). Stems older than 8 yr were excluded due to small sample size.

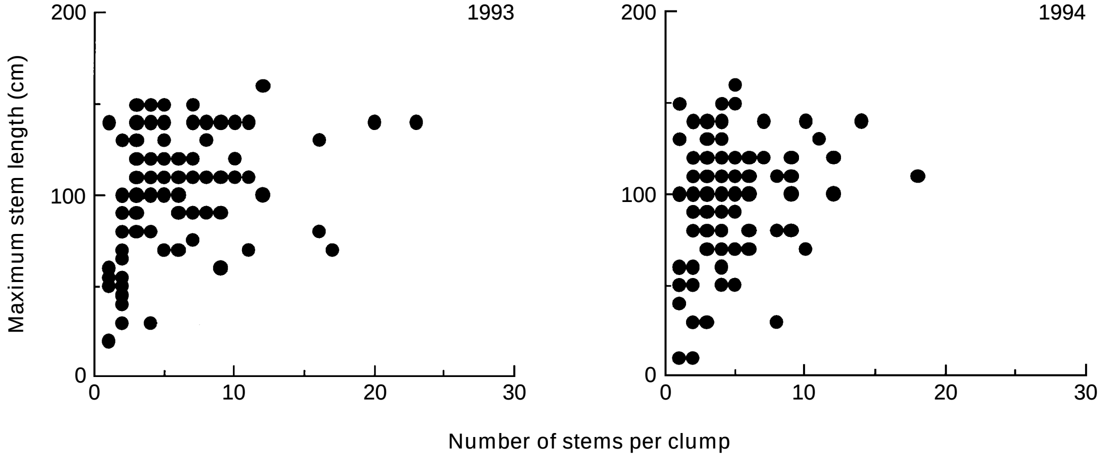

Figure 5. The relationship between maximum stem length and number of stems during the growing season in each clump.

current-year buds and shoot apices. Coefficients of variation in bud and shoot apex heights within stems ranged from as low as 1·53 % to 28·38 % (Table 1).

As a result of their opposite position, the horizontal distribution of buds showed deviation from random towards an aggregated distribution ($R < 1$) in 12 of

Table 1. *Spatial distribution of current-year buds and shoot apices in the crown of stems*

Buds

Stem	No. of buds	Height CV (%)	*R*
1	4	13·99	0·913
2	4	1·53	0·106**
3	10	7·30	0·528**
4	10	5·39	1·020
5	12	3·23	0·369**
6	13	10·01	0·892
7	24	19·09	0·559**
8	26	5·31	0·235**
9	28	2·85	0·241**
10	35	5·46	0·214**
11	76	6·75	0·319**
12	77	12·16	0·589**
13	73	13·93	0·564**

Shoot apices

Stem	No. of shoots	Height CV (%)	*R*
1	3	13·01	1·793**
2	4	1·71	1·244
3	8	4·63	0·982
4	10	9·52	1·273**
5	11	6·64	1·254
6	12	10·23	1·188
7	19	28·38	1·082
8	20	7·38	1·230*
9	24	3·12	1·264*
10	28	6·40	1·551**
11	42	8·15	1·035
12	42	16·15	1·221**
13	64	12·46	1·125

The Clark & Evans statistic: $R = r_A/r_E$, *where* r_A = mean distance to nearest neighbour, $r_E = 1 \;/\; 2\sqrt{\rho}$, ρ = density. $0 < R < 2·1491$ ($R < 1$: aggregated, $R = 1$: random, $R > 1$: uniform distribution)

Significance of deviation from randomness: $*P < 0·05$, $**P < 0·01$.

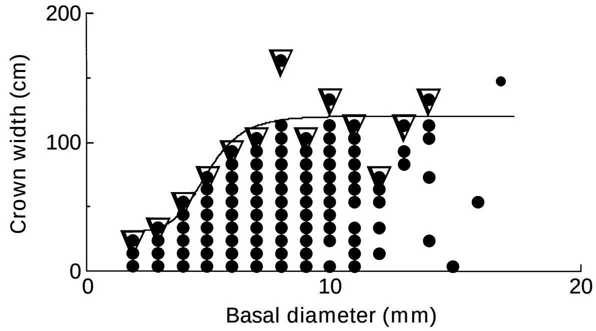

Figure 6. Crown width of stems in relation to basal diameter for all stems in the field with a logistic curve drawn through the maximum observed crown width for each basal diameter (▽), excluding values with single observations for a given basal diameter. Maximum crown width is estimated to asymptote around 125 cm.

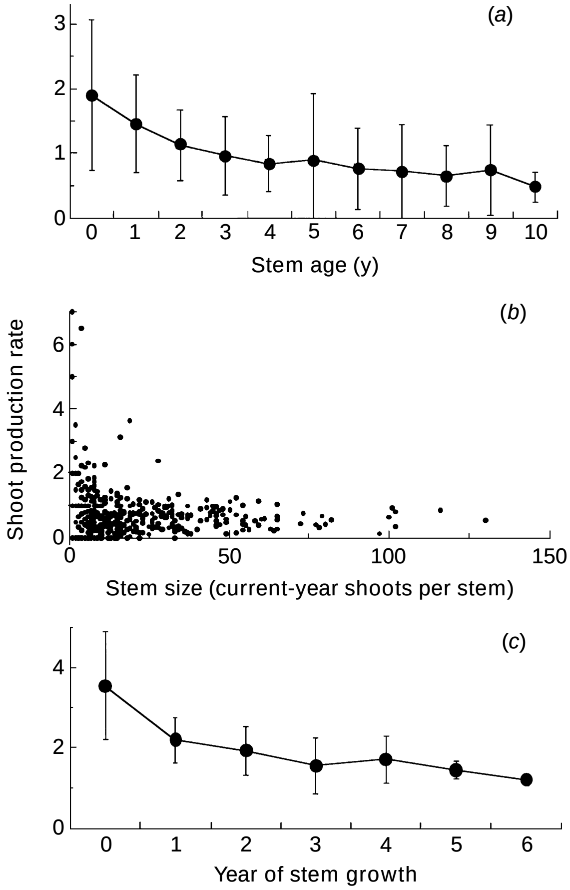

Figure 7. Shoot production rate (1993) of stems in relation to (*a*) stem age and (*b*) stem size (number of current-year shoots per stem) observed in the field (±1 SD). Shoot production rates of stems in the field were calculated as the ratio of the number of current-year shoots per stem in consecutive years. (*c*) Shoot production rates for past years of stem growth estimated from the 28 harvested stems (±1 SE). Shoot production rates for past years of stem growth were estimated as the ratio of the number of branches of age $x+1$ to number of branches of age x. SD is used for the mean of all stems in the field as opposed to SE for the mean of harvested stems which are a sub-sample of the stem population.

13 stems sampled. However, as current-year shoots grew, their apices became uniformly distributed within the mono-layered crown. The horizontal distribution of shoot apices showed deviation from random toward uniform distribution ($R > 1$) in 12 of 13 stems sampled. The Clark & Evans statistic for uniform distribution of shoot apices must be interpreted with caution. However, the increase in the statistic in all stems indicates that the distribution is tending from aggregated toward uniform distribution with current-year shoot growth.

Limits on stem growth were observed in crown expansion, shoot production rate and current-year shoot size. Maximum observed crown width increased with increasing basal diameter to asymptote around 125 cm (Fig. 6). Shoot production rates of stems in the field showed a decreasing trend with stem age (Fig. 7*a*). The range of values was quite wide for all age classes, indicating that stems of the

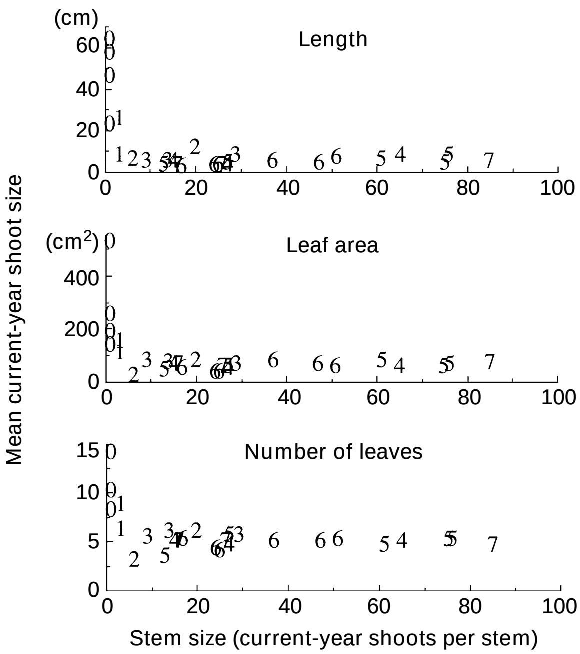

Figure 8. Mean current-year shoot sizes of the harvested stems in relation to stem age and size (number of current-year shoots per stem). Current-year shoot sizes (shoot length, total leaf area, and number of leaves per current-year shoot) were measured, and mean current-year shoot size was calculated for each stem. Numbered symbols denote stem age.

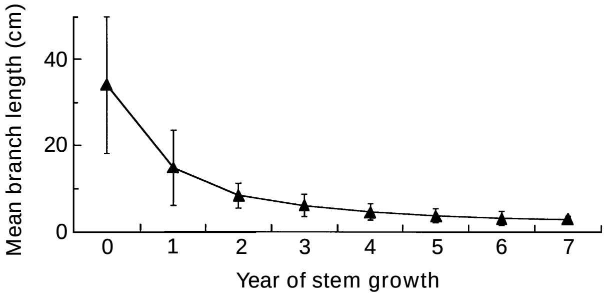

Figure 9. Mean branch length of the harvested stems (± 1 SE), used to estimate mean current-year shoot length for past years of stem growth. Mean branch length for branches of the same age was calculated for each stem and averaged across all stems for each year of stem growth.

same age can have widely different rates of growth. Shoot production rates showed a wide range of values for smaller stems (Fig. 7*b*), ranging from a shoot production rate of zero for stems which died to shoot production rates > 4 for vigorously growing new and 1-yr-old stems. However, shoot production rates became restricted to smaller values with increasing stem size. The estimated shoot production rate of harvested stems showed a wide range of values for the early years of stem growth, decreasing toward shoot production rates near-unity in later years (Fig. 7*c*), indicating that during the growth of a single stem, shoot production rate decreases with each year of stem growth. Mean current-year shoot size showed a decreasing trend with wider ranges of values in the younger stems, becoming restricted to smaller values with increasing stem age and size (Fig. 8). Stems with large current-year shoot sizes were vigorously growing new and 1-yr-old stems. Older stems had consistently small mean current-year shoot size independent of stem size, defining a minimum current-year shoot size: 2–4 cm in length, 20–50 cm^2 total leaf area, and four to six leaves per current-year shoot. Mean branch length of harvested stems showed a similar decreasing trend with each year of stem growth to approach the minimum mean current-year shoot length (Fig. 9), indicating that during the growth of a single stem, current-year shoot size decreases with each year of stem growth.

DISCUSSION

The trends in mortality rates with plant age and size observed in this study are well established for other subcanopy species. Researchers have found declining mortality with increasing age and size in various plants with the steepest declines in saplings (Harcomb, 1987; Silvertown, 1987). In clonal plants the probability of initial survival of vegetatively produced offspring is higher than that of seedlings because of the physiological connectivity with the parent plant (Cook, 1985). Mortality rates have been found to be relatively constant for ramets of clonal perennial herbs (Sarukhan & Harper, 1973; Hutchings, 1983; Cook, 1986) and stems of clonal shrubs (Balogh & Grigal, 1987). However, Hutchings (1983) notes that initial mortality rates can be higher if the number of ramets which fail to develop ('shoot initials') were taken into account. In the case of the aerial stems of *H. hirta*, the trends in mortality rates can be explained by the effects of herbivory and intra-clonal competition.

The effects of herbivory led to the high mortality rate in new stems of *H. hirta*. Evidence of herbivory was also observed in older stems, but was dispersed among the larger number of current-year shoots, and stem mortality due to herbivory was considerably lower. As our first hypothesis suggested, mortality due to herbivory might have been higher for new stems because they only consist of a single current-year shoot and apical meristem, and its loss would result in death of the stem. However, other hypotheses cannot be excluded. The susceptibility of new stems to herbivory might be due to their palatability; high nutrient content, or lack of deterrent chemicals (Bernays & Chapman 1994). The process of host–plant selection for the herbivores of *H. hirta* needs further investigation to answer this question.

Evidence of size-dependent mortality and density-dependent turnover of stems supports our second hypothesis of intra-clonal competition among stems. Clumping led to intense intra-clonal competition among stems and higher stem turnover in clumps

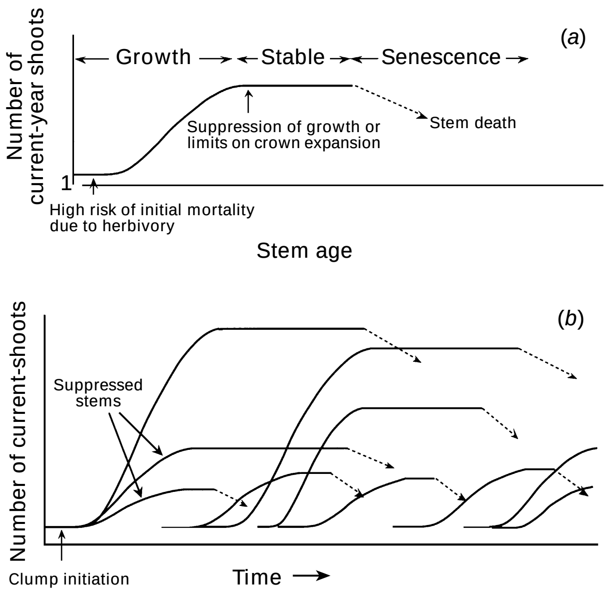

Figure 10. (*a*) Schematic diagram of the changes in the number of current-year shoots with stem age showing the three stages of stem growth. (*b*) Schematic diagram of the growth and dynamics of stems within the clump showing continuous turnover of stems with different growth rate, maximum size and longevity resulting in a clump composed of stems of various age and size.

with higher stem density. Higher maximum stem length suggested more intense intra-clonal competition in clumps where stem densities were higher. However, the latter relationship was not that of simple density-dependence as suggested by Givnish (1982). Although Cook (1985) points out that evidence for intra-clonal competition has seldom been found in clonal herbs, clumping of stems and vertical competition for light may enhance intra-clonal competition among aerial stems in *H. Hirta*.

The uniform, mono-layered distribution of current-year shoots in the crown of *H. hirta* stems would result in less mutual shading among leaves and a more efficient leaf display for light capture in the light-limited shrub layer (Nicola & Pickett, 1983). The mono-layered crown architecture would also effectively shade out other stems once a stem has out-grown competing stems in the clump as a result of the vertical competition for light. However, we found limits on stem growth in crown expansion, shoot production rate and current-year shoot size. The growth of smaller stems may become limited by suppression from larger stems as a result of intra-clonal competition. The growth of those stems which survive intra-clonal competition by out-growing competing stems may still be limited by the requirements for mechanical support of the mono-layered crown, as predicted by Borchert & Tomlinson (1984). The limits we found on crown expansion support our third hypothesis of limits on stem growth due to the requirements for mechanical support. Holbrook & Putz (1989) showed that intense competition and lateral shading resulted in thin, elongated stems with less mechanical stability in *Liquidambar styraciflua*. Stems that were able to survive intra-clonal competition are likely to have out-grown competing stems by allocating to elongation growth, and might lack mechanical stability. In such stems, shoot production rate and current-year shoot size might decline to avoid further crown expansion to where it could not be supported mechanically. However, limits on the minimum current-year shoot size suggest that there is a minimum amount that a stem must grow each year in order to produce new foliage. Stems might die when they are suppressed or have expanded their crown to the point where they are no longer able to produce the minimum-sized current-year shoot.

In summary, the growth pattern of the *H. hirta* stem can be divided into three phases (Fig. 10*a*). The initial 'growth phase' is characterized by a steady increase in the number of current-year shoots as a result of sympodial branching. In this stage, shoot production rate is high and stem mortality decreases abruptly once the stem has escaped the high risk of mortality due to herbivory in the initial year, and has accumulated an abundance of current-year shoots. Elongation growth during this stage is important in order to survive intra-clonal competition by out-growing competing stems in the clump, especially in clumps where stem density is high.

The 'stable phase' of stem growth is reached when the stem ceases to increase in the number of current-year shoots (shoot production rate $= 1$). In the 'stable phase' the *H. hirta* stem was observed to abort one of the pair of opposite buds and cease to branch, maintaining a constant number of current-year shoots. The age and size at which a stem reaches this phase would depend on the spatial relationship with other stems in the clump, i.e. stem density in the clump and the amount of space available for growth of the stem. The wide range of shoot production rates and current-year shoot sizes in the younger stems suggests that suppression due to intra-clonal competition can have profound effects on the earlier stages of stem growth: smaller, suppressed stems experience reduced growth, whereas larger stems which survive intra-clonal competition can expand until their growth is constrained by the requirements for mechanical support.

The 'senescence phase' is characterized by a decline in the number of current-year shoots. Stems are presumed to die when they are no longer able to produce the minimum-sized current-year shoot. Smaller, suppressed stems might die after being shaded out by larger stems. Larger stems which survive intra-clonal competition might senesce as a result of intrinsic factors such as mechanical instability. Stems with shoot production rates < 1, consisting of very few current-year shoots and many dead branches are presumed to be at this stage.

As stems of *H. hirta* go through the three phases of growth, they experience three types of mortality and different mortality rates: initial high mortality rate due to herbivory, followed by size- and density-dependent mortality due to intra-clonal competition, and mortality due to senescence. The rate of growth in the 'growth phase,' maximum size, and longevity might differ between stems depending on the spatial relationship with neighbouring stems in the clump. As a result, individual stems go through the three phases of growth at different rates. The continuous turnover of stems of different growth rate, maximum size and longevity would result in clumps consisting of stems of various ages and sizes (Fig. 10*b*).

Hutchings & de Kroon (1994) postulated a cost–benefit analysis of foraging in plants and re-evaluated plant growth pattern in terms of the economics of resource acquisition. Foraging and resource acquisition are important factors determining plant growth pattern and the spatial arrangement of modular units within the plant (plant architecture). We found that the spatial arrangement of stems and current-year shoots influenced patterns of herbivory and intra-clonal competition in *H. hirta* which in turn influenced stem demography and growth. This feedback between plant growth and factors such as dispersion of mortality risks and competition needs to be considered when evaluating plant growth pattern. In woody plants, where growth occurs in three-dimensions, the requirements for mechanical support might also play an important role in determining plant growth pattern.

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