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GROWTH, DEATH AND SIZE DISTRIBUTION CHANGE IN AN *IMPATIENS PALLIDA* POPULATION

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SUMMARY

(1) The growth and fate of individual plants in a natural self-thinning stand of *Impatiens pallida* located along a disturbed forest edge in southeastern Pennsylvania were followed from canopy closure to the onset of flowering (eight weeks). The primary study population consisted of 161 plants measured at the beginning and end of this period. Survivorship, lodging and herbivory of these individuals were monitored weekly, and flowering status was recorded at the end of the study. A second set of twenty representative but easily accessible plants at the same location were measured repeatedly the following year to determine the shape of the growth curve of individual plants during this same time interval.

(2) Mortality in the primary population was 25%. Lodging was an important cause of death. Smaller plants were more likely to lodge and to suffer herbivore damage than were larger plants. Lodging, independent of plant size, accounted for 16% of mortality explained by a path analysis model; the effects of herbivory on mortality (independent of plant size) were not significant, however. Death caused by lodging in a natural self-thinning population supports the hypothesis that biomechanical constraints may have substantial effects on self-thinning relationships and patterns of size structure change in herbaceous plant populations.

(3) A decrease in above-ground biomass (negative growth) was found to occur in 21% of the surviving plants in the main study population. Although models of plant competition usually assume that plants with zero or negative growth die, 88% of the surviving plants displaying negative growth flowered by the end of the study. Growth curves for the twenty repeatedly measured plants were approximately linear over the course of the study period.

(4) The survival of plants with negative growth affects the function relating biomass (B) to density (D) and the function relating size inequality (G) to mean plant mass (m) over the course of self-thinning. Had these plants died during the study period, the observed log B–log D slope ($-1{\cdot}73$) would have been very close to the mean thinning slope observed across many species ($-0{\cdot}85$). Because many non-growing and shrinking plants survived, size inequality did not decrease during self-thinning. We suggest that the ability of plants to survive sustained suppression may have a major and predictable effect on both the self-thinning trajectory and on changes in size variability over the course of stand development. Our results emphasize the importance of field studies aimed at understanding the behaviour of suppressed plants.

INTRODUCTION

The genesis of size distributions in monospecific plant populations has been investigated extensively in greenhouse experiments and in studies of agricultural and forest crops (Benjamin & Hardwick 1986 and Weiner & Thomas 1986 provide recent reviews). Much less research has been conducted on changes in size structure of natural monospecific populations. Natural stands differ greatly from greenhouse and crop populations in their

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exposure to herbivores, pathogens and 'random' sources of mortality, and in increased heterogeneity in soil quality and incident light levels. A major goal of ecology is to relate results from experiments performed under controlled conditions to the behaviour of natural populations. It is, therefore, imperative to quantify patterns of growth and mortality in (generally less tractable) natural systems in order to understand how such processes as size-distribution change and self-thinning occur in nature.

In general, changes in size distributions of a population are the product of four interacting processes: (i) the initial size distribution; (ii) the distribution of growth rates among individuals; (iii) changes in this distribution over time as plants grow, i.e. the growth curves of individuals; and (iv) the distribution of mortality among individuals. Here we describe the action of all of these processes over time in a natural, self-thinning stand of *Impatiens pallida* Nutt.

Previous studies on size-distribution change have generally relied on comparisons between stands of different 'developmental stages' measured at the same point in time or sequentially harvested, to reveal size distribution trends (e.g. Mohler, Marks & Sprugel 1978; Kohyama & Fujita 1981; Weiner & Whigham 1988). However, to construct a model that relates the growth and survival of individuals to changes in size distributions, it is necessary to follow the fate of individual plants within a population over time. A recent paper that does include information on individual growth and death is the study by Schmitt, Eccleston & Ehrhardt (1987) on size-dependent growth and self-thinning in a natural *Impatiens capensis* population. They have shown that density-dependent growth and mortality occur in natural *Impatiens* stands, and that there is higher inequality in biomass distribution in dense stands than in experimentally thinned stands. Their results agree with the general trend of higher inequality at higher densities recorded for a wide range of studied plants, a result which suggests that plant competition is generally 'one-sided' (Weiner & Thomas 1986). This study documents proximal causes of mortality and describes the growth of individual plants in a natural self-thinning population: the emphasis is thus on the relationship of growth and mortality at the individual-plant level to the population-level phenomena of self-thinning and size–distribution change.

Although describing individual fate and growth of plants over time is a conceptually simple task, it is difficult in practice. The most accurate measures of plant size are destructive. Researchers have generally either used sequential harvests, in which size is accurately measured but individuals cannot be followed (e.g. Koyama & Kira 1956; Obeid, Machin & Harper 1967; Naylor 1976) or, in demographically oriented studies, individual survivorship has been monitored with no or only very crude measurements of size or growth (e.g. Watkinson & Harper 1978; Leverich & Levin 1979; Watkinson, Lonsdale & Firbank 1983). *Impatiens pallida* possesses a number of characteristics which facilitate the direct observation of size distribution change as it occurs through the growth and death of individuals. This species is a common woodland annual with synchronous germination and characteristically forms monospecific stands. It is large and fast-growing, and possesses a highly reduced root system; total biomass is thus closely related to above-ground biomass, which may be accurately predicted using non-destructive measurements. In southeastern Pennsylvania *I. pallida* occurs at population densities up to 250 plants m^{-2} at which competition is important but not so high as to preclude measurement of plants without damaging individuals in the stand. While self-thinning and size structure changes may be easily followed over time in erect herbaceous annuals such as *Impatiens*, these plants still present a methodological dilemma in terms of size measurement: repeatedly disturbing plants in a dense stand is likely to have some effect on growth and mortality, especially of smaller individuals. From preliminary work it was concluded that this 'observer effect' had the potential to invalidate specific results. This study chooses to address the problem of damage during measurement by monitoring individual fate over time in a long, narrow plot in which plants were measured only once, soon after canopy closure, prior to the final destructive harvest at the onset of flowering. The next year, a smaller sample of easily accessible plants at this same location and at a similar density were repeatedly measured to determine the form of the growth curve of individual plants over this same time interval.

METHODS

Study area

All field work was conducted in the Crum woods of Swarthmore College (75°21′W, 39°54′N) in Delaware County, Pennsylvania, at a disturbed forest edge site on alluvial soils of the fifty-year floodplain of Crum Creek. *I. pallida* has formed dense stands in this same location for the last six years, covering 100–200 m^2. The study population was located beneath the crown of a *Prunus avium* L. tree, and was exposed to full sunlight only during a brief period in the mid-morning; such partial shading is typical of *I. pallida* populations in the area and other species of *Impatiens* that have been studied (Eliás 1987).

Initial measurements

One-hundred and sixty-one plants were measured and tagged on 7–23 July 1984 and harvested on 11 September. These individuals occurred within a strip measuring 5·8 m × 0·7 m running parallel to a path along the stand, bordered by a boundary zone approximately 0·7 m wide in which plants were disturbed as little as possible. For each tagged plant the following information was recorded initially: (i) height, measured to the nearest cm from the base to the terminal apical meristem; (ii) stem diameter, measured with callipers at the midpoint of the first internode to the nearest 0·1 mm; and (iii) leaf area, measured by visually estimating the length of all leaves on a given plant to the nearest cm and predicting surface area with an allometric function fit for this purpose. Leaf shape is relatively constant between individuals: in harvested plots these estimates predicted 93·9% of the variation in measurements made with an electronic leaf area meter. The initial plant biomass was estimated using a function that predicts above-ground dry mass (w) as a function of height (h), diameter (d) and leaf area (l): $w = \mathrm{a}h^{\mathrm{b}}d^{\mathrm{c}}l^{\mathrm{d}}$, where a,b,c and d are constants, fitted using multiple linear regression of a log–log transformed variables. This function accounted for 97·9% of the variance in log dry mass of individual plants in these stands. Because the parameters of such power functions may vary with density and over the course of stand development (J. Weiner and S. C. Thomas, manuscript in preparation), some bias in the estimates is inevitable. Potential errors were minimized by using a function which was based on harvested stands of similar density and canopy height. Bias-corrected regressions were not used (Baskerville 1972; Sprugel 1983) to estimate these functions because many of the analyses used log biomass, which is better estimated by uncorrected regressions, as a variable, and measures of inequality such as the Gini coefficient are insensitive to multiplicative transformations.

These initial measurements were made following canopy closure (leaf area index = 1·90), but before the onset of self-thinning. Observations of this and other stands of similar density, as well as the results presented below, indicate little or no density-dependent mortality before this point. Ideally, all plants would have been measured simultaneously, yielding an initial distribution at a single point in time. As extreme care had to be taken not to damage plants with metre sticks and callipers, the 'initial' measurement required more than a week to complete. The mean dry mass estimated for the last eighty-one plants measured was 0·345 g greater than that for the first eighty-one plants, but this difference was not statistically significant and thus unlikely to affect the general results of the eight-week study.

Monitoring individual fate

Following the initial measurements, the plot was inspected weekly and the following information recorded for each individual: (i) mortality—plants standing with no leaves or which were completely withered were considered 'dead'; (ii) lodging—plants which were leaning at an angle of greater than 30° from vertical were scored as 'lodged'; (iii) herbivory—plants were scored for herbivore damage if they had lost more than half of their leaf area to leaf-eating insects (a variety of lepidopteran larvae and adult coleoptera were seen) or had been chewed through at the base or, in some cases, pulled over by slugs. Many additional plants received more minor leaf or slug damage. To avoid problems of weight loss and mortality due to senescence, plants were harvested soon after the onset of flowering. At the final harvest, plants were also scored for presence of cleistogamous and chasmogamous flowers. Although diseased plants were observed frequently in nearby stands of *I. pallida*, very few plants in this stand showed any signs of disease, and so this factor is not included in the analysis.

Non-destructive measurements of plant growth

While it was possible to census plants repeatedly in the main study population for survivorship, lodging and herbivore damage, repeated size measurements were deemed likely to damage plants and invalidate census results: therefore, the main study population was only measured at the beginning and end of the study. To interpolate the growth curves of individuals between these initial and final states, height and diameter were remeasured over time for twenty plants, of varying size at the same location, over the same nine weeks during the subsequent year (1985). As hoped, the population at the same location during the following year was similar to the main study population with respect to density, canopy height and light conditions. From this population, plants were arbitrarily chosen as 'representative' individuals found in locations within the population which were accessible for repeated measurement with minimum damage to the plants and their neighbours. w was estimated at each point in time as a function of h and d, using a prediction equation based on the final harvest of the fifteen surviving plants. In this case the prediction function explained 97·7% of the variance in log dry mass. The use of a single allometric equation to estimate weights over the study period will introduce a small bias into the estimates of the weights for the earlier measurements. Such a bias is unavoidable in obtaining reasonable non-destructive measurements for a natural population. To study estimated plant growth curves, the twenty repeatedly measured plants were divided into four groups of five individuals, based upon initial size.

Statistical methods

To interpret the causes of death in the study population, path analysis was utilized (Sokal & Rohlf 1981); this has been advocated recently as a method for quantifying the effects and interactions of various sources of variability in plant performance (Waller 1985; Mitchell-Olds 1987). In employing this technique, one must make assumptions regarding the direction of causality of some set of correlated variables. It was assumed that initial size of individuals (*w*) potentially has some causal effect on lodging and herbivory in the population, as well as a direct effect on mortality; it was assumed that lodging and herbivory are potentially correlated, but that one does not necessarily cause the other; and, finally, it was assumed that lodging and herbivory potentially have independent causal effects on mortality. Thus one continuous variable was related to three categorical variables. Although standard linear regression was used to calculate path coefficients in this case, tests of significance based on linear regression of categorical variables are invalid because the standard assumptions of normality and homoscedasticity are not met. Therefore, logistic regression (Fienberg 1980) was used to provide tests of significance for the path coefficients: logistic regression may be used to test relationships between any combination of continuous and categorical variables, but does not itself yield partial regression coefficients (T. Mitchell-Olds, personal communication).

Distribution modifying functions (DMFs; Westoby 1982) were employed to provide a summary description of the effects of growth on size-distribution change. A DMF models the change in size of individual plants over a time interval as a function of their size at the beginning of the interval. Inequality of size distributions was measured using the Gini coefficient (Weiner & Solbrig 1984). The self-thinning trajectory was estimated using principle component analysis (Weller 1987a).

RESULTS

Mortality

Twenty-five percent of the main study population died during the study period. The path analysis model accounted for 34% of the total variance in mortality. There was a significant relationship between initial size (predicted above-ground dry mass at the first measurement) and all three categorical variables in the path analysis model: smaller plants were more prone to extensive damage by herbivores, were more likely to lodge, and more likely to die, regardless of the intervening effects of herbivory and lodging (Fig. 1). While lodging did contribute to mortality independently of size, accounting for 16% of the total explained variation, herbivory did not appear to have any direct effect on mortality in the population. Herbivory may, however, have contributed indirectly to mortality, because herbivore-damaged plants also tended to be those which lodged.

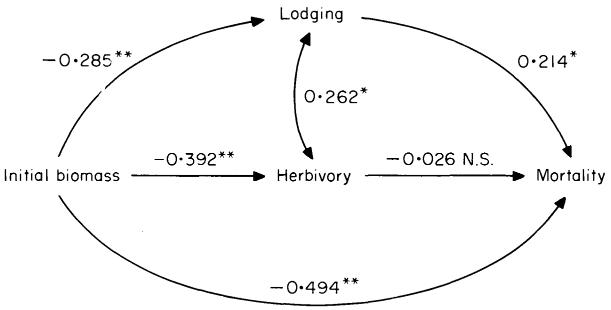

FIG. 1. Path diagram for factors influencing mortality in a natural population of *Impatiens pallida* in southeastern Pennsylvania. Paths for residual variance in lodging, herbivory and mortality are not shown; residual path coefficients (square root of the coefficient of nondetermination) are, respectively, 0·645, 0·628 and 0·636. $^{*}P<0{\cdot}01$; $^{**}P<0{\cdot}001$; N.S. not significant.

Growth

Growth curves for each size class in the repeatedly measured *I. pallida* stand (1985 data) were approximately linear (Fig. 2). Linear regression accounted for 92·3%, 83·8% and 77·8% of the variance in w over time for the three size classes with appreciable growth (slope >0 at $P<0{\cdot}01$ for all three). In no case did a second degree polynomial yield a significantly better fit to these growth curves in a step-wise regression procedure. More complex estimates of growth in which size is estimated using sigmoidal growth functions and allometric size estimates did not have a major effect on the estimated size distributions. Therefore linear growth of individuals in the main study population was assumed to interpolate sizes of individuals between the initial and final measurements. The DMF for this stand over the monitored growth period appeared to have a monotonically increasing slope (DMF3: Westoby 1984): small plants displayed a zero (or negative) growth rate, while many large plants increased in size three–five-fold during this period; among large plants growth rate ($\mathrm{d}w/\mathrm{d}t$) is significantly correlated with initial size ($r=0{\cdot}680$; $P<0{\cdot}01$) (Fig. 3). This pattern is represented as a discontinuous function comprised of two linear segments (West & Borough 1983).

The initial sizes of individuals that died during the course of the experiment were, as expected, at the low end of the initial distribution of predicted dry mass (Fig. 3). Forty-three percent of the surviving population had an initial w less than the largest individual which died; this group included all plants with negative growth rates. The average growth rate of these initially small survivors was 0·064 g week^{-1}, compared with 0·680 g week^{-1} for all other parts. Half of these smaller plants (21% of the surviving population) were found to have negative growth rates: the average for this group was $-0{\cdot}0274$ g week^{-1}. The growth rate for the smallest 43% of the population is not significantly different from

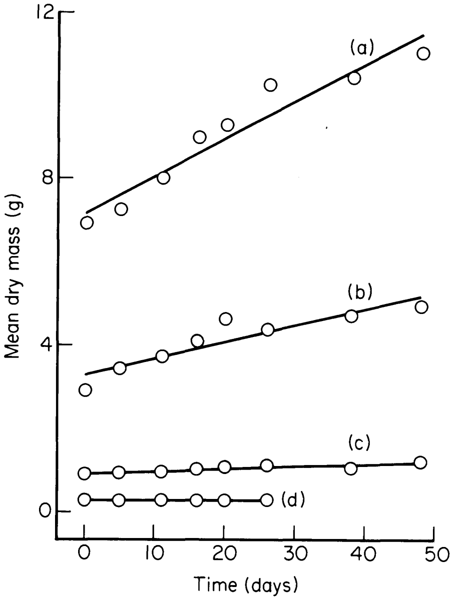

FIG. 2. Growth curves for groups of five out of twenty *Impatiens pallida* individuals repeatedly measured in 1985. (a) Mean for five largest individuals; (b) next five largest; (c) next five largest; (d) five smallest.

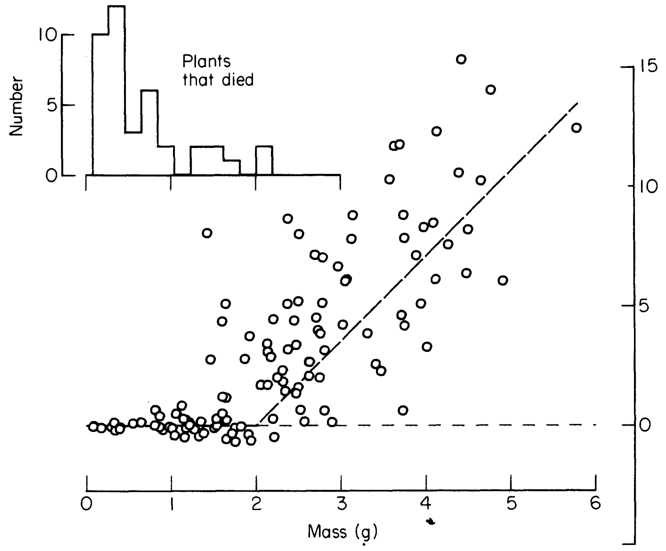

FIG. 3. Distribution modifying function (mass increment vs. mass) for survivors after eight weeks of growth in an *Impatiens pallida* population, and the distribution of initial sizes for those individuals that died. Data are from the main study population measured in 1984. The x-axis is the same for both graphs.

zero, and therefore a zero growth rate until death was assumed for all 'self-thinned' individuals in subsequent calculations.

Reproduction

By the time of the final harvest 94% of the main study population had produced floral structures, including twenty-three of twenty-six plants (88%) for which negative growth rates had been measured. Reproduction in the population was size-dependent: mean mass of plants which produced no flowers (2·36 g) and those which produced only cleistogamous flowers (0·75 g) were significantly smaller than the mean mass of plants which produced both cleistogamous and chasmogamous flowers (6·30 g) ($P < 0{\cdot}01$).

Combined effects of growth and motality on the size distribution

The effects of growth and death over time on the distribution of size (w) in the population are shown in Fig. 4. Extensive mortality of small individuals did not commence until approximately three weeks after the initial measurement period, suggesting that measurement and handling of plants was not an important contributing cause of mortality. The log biomass–log density trajectory for the stand displays an abrupt increase in mortality rate at this time (Fig. 5). The principle component analysis estimate of the thinning relationship is $\log B = -1{\cdot}73 \log D + 4{\cdot}79$ ($r^2 = 95{\cdot}9\%$; slope < 0 at $P < 0{\cdot}05$).

Inequality of the size distribution, as measured by the Gini coefficient, increases with increasing mean plant mass up to the start of self-thinning, and then levels off (Fig. 6). The coefficient of variation and skewness statistics (not shown) follow similar trajectories to the Gini coefficient.

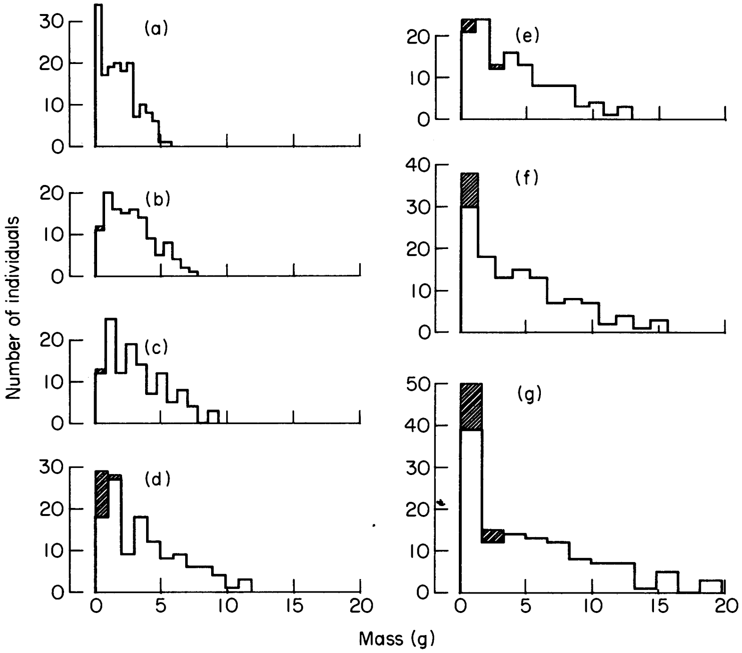

FIG. 4. Changing size distributions for an *Impatiens pallida* population in which individual fate was monitored weekly from (a) 23 July to (g) 11 September 1984. Initial and final distributions are based on direct size measurements. The intervening histograms are based on the assumption that individuals have linear growth (Fig. 2), and that individuals that subsequently died did not change in size (see text). Shaded columns represents individuals that died during a given time interval.

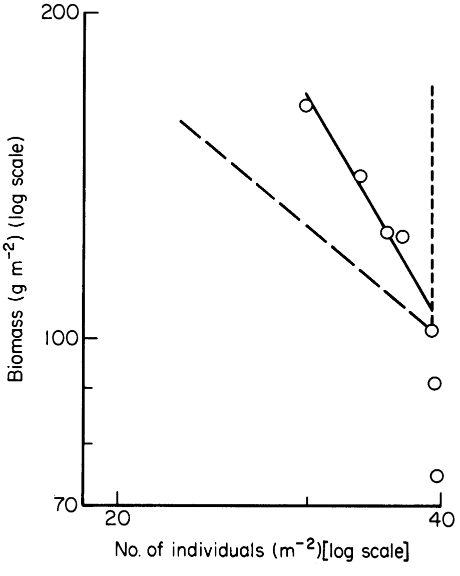

FIG. 5. Self-thinning trajectory (solid line) for *Impatiens pallida* population monitored weekly from 23 July to 11 September 1984. Mortality began on the third week, so the thinning line is based on the third to seventh weeks (inclusive). Dotted line represents a hypothetical thinning curve if no plants had died. Dashed line represents a hypothetical thinning curve if all plants with negative growth rates had died.

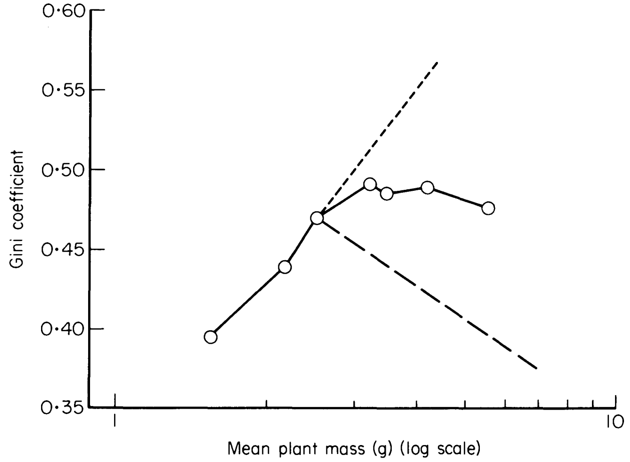

FIG. 6. Changes in size inequality (Gini coefficient) with increasing mean plant weight during growth and self-thinning in an *Impatiens pallida* population. Dotted line represents a hypothetical relationship if no plants had died. Dashed line represents a hypothetical relationship if all plants with negative growth rates had died.

DISCUSSION

While there is a very large literature on the form and nature of self-thinning relationships (Westoby 1984; Weller 1987a), little attention has been paid to the natural history of this process: i.e. what causes mortality in self-thinning stands? Ultimately this question should be answered in terms of physiological mechanisms. The implicit (and occasionally explicit) assumption of many models in the literature is that the smallest, suppressed plants simply fall below the compensation point and die (e.g. Perry 1984; Givnish 1986). The results (Fig. 1) here indicate that this is not the only way in which death may occur. Lodging was a major cause of death in this population, independent of size, implying that numerous fairly large individuals that would have survived had they remained upright died after falling over. The physiological mechanism behind this sort of mortality is almost certainly related to light-dependent growth patterns of individuals plants. Plants of intermediate size in *Impatiens* stands have higher height : diameter ratios than either very small or very large plants (J. Weiner and S. C. Thomas, manuscript in preparation), presumably due to extension growth at the expense of girth increases associated with the accumulation of woody tissue. Although these plants are reasonably large, they are susceptible to mortality through lodging. While lodging does not usually result in severe damage to plant tissues, it transports the individual's leaves into the low-light environment at the bottom of the stand, drastically reducing their capacity for carbon-gain. The observation that lodging (biomechanical failure) is a significant source of mortality supports the hypothesis (Givnish 1986) that biomechanical constraints are an important determinant of self-thinning trajectories. The data suggest that many of the plants which lodged would have otherwise survived. Only such observations of death due to biomechanical failure can provide strong evidence in support of the biomechanical constraint hypothesis.

Many theoretical discussions of plant growth and its effects on size distributions assume exponential growth (i.e. a constant RGR) over the course of stand development

(Benjamin & Hardwick 1986; Huston & DeAngelis 1987). The result here, that growth curves of individual plants in a competing *Impatiens* stand before and during self-thinning are approximately linear (Fig. 2), argues against an approach to stand development which assumes constant RGRs. Empirical evidence shows that the growth of plants is sigmoid with a nearly exponential phase, an approximately linear phase, and a levelling-off phase (Hunt 1982). While plant growth in general is best modelled using a sigmoid function such as the Richards equation (Causton & Venus 1981), *I. pallida* individuals during the period studied are in the central, approximately linear portion of the curve (although the data do suggest that growth is starting to level off as flowering begins).

There are also theoretical reasons to expect linear growth over much of the life-span of plants competing for light resources. As a non-competing plant grows, increases in size result in increased interception of resources. A non-competing plant, like an unrestrained population, could theoretically grow exponentially without limit. (In fact, allocation of resources to reproduction and support, and the process of senescence prevent this, and growth in non-competing plants is sigmoidal.) Competing plants, on the other hand, may also grow exponentially for a short period, but after most of the available light flux is being absorbed by the population, the population as a whole cannot continue to increase its resource base. Carbon fixation of the population (and therefore mean growth of individuals) will be limited by the total available light resource flux. As long as structural costs of maintenance or reproductive allocation do not greatly increase, individual growth in competing stands will be approximately linear after light interception by the population is close to the maximum.

Linear growth in competing stands is a fundamental assumption of empirical models which predict size distribution change using a constant function of change in size with respect to initial size (DMFs: Westoby 1982; $G(t,x)$ functions: Hara 1984a,b). If dw/dt changes over time, these models have relatively little predictive power because they are able to translate an initial distribution to a subsequent distribution for only one specific interval in time. If dw/dt is constant for a prolonged period (linear growth), such models will be able to predict stand structure over a much larger portion of stand development. Our results suggest that linear growth in competing stands may be a reasonable assumption for at least some plant populations.

The distribution of growth rates with respect to initial size (Fig. 3) reveals that many suppressed plants survive in spite of zero (or negative) growth rates in above-ground dry mass for much of their lives. Negative growth in this population was partially due to loss of leaves, though respiration of stored resources is also possible. Negative growth has also been reported in competing. *Impatiens capensis* populations (Schmitt, Eccleston & Ehrhardt 1987). Published models of plant competition usually assume that plants with zero or negative growth rates always die (e.g. Aikman & Watkinson 1980; Ford & Diggle 1981). This is clearly not the case for this population; most of the surviving plants with zero or negative growth rates had even produced flowers by the final harvest.

The survival of plants with negative growth rates also has major effects both on the self-thinning trajectory and on trends in inequality and distribution shape. The log biomass–log density thinning slope for this stand ($-1{\cdot}73$: Fig. 6) lies in the lower tail of the distribution of log B–log D slopes for the seventy-five field and experimental data sets analysed by Weller (1987a). What slope would have resulted if all plants with growth rates less than zero had died during the study period? The value in this case ($-0{\cdot}82$: Fig. 5) would be very close to Weller's mean of $-0{\cdot}847$. Variability in thinning slope has previously been attributed to differences in growth form or allometry (Miyanishi, Hoy &

Cavers 1979; Weller 1987b) and incident light levels (Lonsdale & Watkinson 1982; Westoby & Howell 1982). Weller (1987a) presents data indicating significant inter-specific differences in thinning slope related to shade tolerance, though the trend is in opposite directions for gymnosperms and angiosperms. The observation that the survival of plants with negative growth rates in the *I. pallida* stand greatly alters the slope of the thinning relationships from what would have resulted if all these plants had died, suggests that differences in the ability of suppressed plants to survive under adverse circumstances may account for some of the inter-specific variability documented by Weller.

The ability of many suppressed plants to survive is also a critical factor determining the relationship between mean plant weight and size inequality over the course of self-thinning. In this population, a slope of near zero for the curve describing changes in the Gini coefficient (G) with respect to log mean mass (m) during self-thinning was found (Fig. 5). If no plants had died, G would have continued to increase over the course of stand development following a linear trajectory of slope 0·406 as large plants continue to grow and small plants do not. If all plants displaying negative growth rates had died during the course of the observations, the slope of the relationship would have been $-0{\cdot}21$ as small plants were removed from the population. Weiner & Thomas (1986) found a slope of $-0{\cdot}2$ for the G–log m relationship for two conifer species, and Weiner & Whigham (1988) report a G–log m slope of $-0{\cdot}1$ for the annual grass *Zizania aquatica*. The results here indicate that the survival of small plants has a major effect on changes in size inequality during density-dependent mortality.

It is clear that *I. pallida* possesses a high degree of phenotypic plasticity which makes possible the survival (and reproduction) of highly suppressed individuals in competing stands. This survivability greatly affects self-thinning and size distribution change over the course of stand development. While research on size distribution change in plant populations has focussed on proximal causes, the potentially large influence of suppressed plant behaviour on this population-level phenomenon suggests some important questions which must be answered in evolutionary terms. One such question is 'why are suppressed plants able to survive sustained low-resource conditions?' We advance two alternative evolutionary hypotheses to explain this ability.

(1) Suppressed plants are following an alternative developmental pattern which is the product of natural selection. The environment of suppressed individuals differs greatly from that of dominant individuals; patterns of growth and reproduction which occur under high- and low-light conditions also differ markedly. This suggests that physiological responses which allow relatively high survivorship and reproduction in suppressed versus dominant environments are different, and that the ability to adapt physiologically to these conditions may have been selected for over evolutionary time. In essence, selection pressures have favoured phenotypic plasticity which makes possible tolerance of low resource levels among suppressed plants, though at the expense of high potential rates of growth and reproduction. Similarly, Waller (1980) has argued that selection pressures on small plants may favour the production of cleistogamous flowers as an evolutionary response to competition. Because many unpredictable variables strongly affect plant performance early in ontogeny (e.g. emergence site conditions, emergence time, neighbour relations), the future environment of a given plant is not predictable at the seed stage. Therefore, this alternative strategy is likely to be regulated by some sort of developmental switch which operates after germination.

(2) Dominant plants in competing stands give rise to the vast majority of offspring in the population; therefore, selection pressures will operate principally to increase the

likelihood of individual plants being dominant. Because there is probably a cost associated with maintaining an alternative developmental pathway for survival and reproduction under suppressed conditions, no such alternative pattern will evolve (Weiner 1988) even if the genetic basis for it exists in the population. According to this hypothesis, patterns of growth and reproduction under suppressed conditions are simply the result of patterns of growth and reproduction appropriate to dominant individuals: the behaviour of suppressed plants is an epiphenomenon, not a 'suppressed-plant strategy' which is the result of natural selection.

To distinguish between these two alternatives, future studies should look at differences in dominant versus suppressed plant behaviour under experimentally manipulated conditions.

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