

Size structure of populations within populations: leaf number and size in crowded and uncrowded *Impatiens pallida* individuals

Glenn M. Berntson* and Jacob Weiner**

Department of Biology, Swarthmore College, Swarthmore, PA 19081, USA

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Summary. We compared the size distributions of leaves on naturally-occurring crowded and experimentally thinned “uncrowded” individuals of *Impatiens pallida* in southeastern Pennsylvania. Crowding decreased the number of leaves on individual plants and altered the distribution of leaf size. Crowded individuals had smaller leaves, but the size (length) inequality of the leaf population did not change. The relationships between the height of a plant and the mean and maximum length of its leaves were significantly different for crowded and uncrowded plants. There were weak positive relationships between height and total leaf area, and height and total number of leaves for uncrowded plants, whereas crowded plants showed tighter but curvilinear relationships between these variables. Our results point out the strengths and the limitations of viewing canopies as populations of modules.

Key words: Competition – Demography – Modules – *Impatiens pallida* – Size

The effects of competition between plants have usually been evaluated in terms of whole-plant parameters (biomass or relative growth rate). However, we can gain insights into the process of competition by looking at its effects on the modules that comprise an individual plant and, ultimately, a population of plants. Leaves can be viewed as modules (Harper 1988), and information on the population structure of leaves can be obtained by comparing the size distributions of leaves on plants in different environments. Modules on an individual plant are to some extent physiologically integrated, but the degree of integration varies greatly between species (Wat-

son and Casper 1984). To the degree that modules are physiologically independent, the size or age structure of a population of modules can be viewed as analogous to the size or age structure of a population of organisms (Bazzaz and Harper 1977; Harper and Bell 1979). The present study does this by investigating the effect of crowding on the leaf populations of individual plants. If a canopy of leaves is analogous to a population of individuals, then we would expect the response of individual leaves to crowding to be similar to the responses of individual plants to crowding. For example, we would expect crowding to result in a decrease in mean leaf size (Silvertown 1987), and an increase in the variation in leaf size (Weiner and Thomas 1986). If, on the other hand, leaf populations on individual plants do not behave as independent individuals, but are physiologically integrated, then the behavior of a population of leaves on a plant will not be similar to the behavior of a population of plants.

The leaf population of a plant at any point in time can be described in terms of the number and size of leaves on the plant. A complete demographic account of the population of modules (e.g. leaves or buds) on a plant would require information on the birth, growth and death rates of those modules (see Bazzaz and Harper 1977; Jones and Harper 1987; Maillette 1982, 1986; Smith 1983). Because this is extremely time-consuming, it can only be done on relatively few individuals. While information on the size distribution of leaves on a plant at one point in time does not yield a complete demographic description of a population of leaves, it allows the collection of comparative data on many individuals, and therefore the description of a whole stand, rather than just a few individuals.

The size distribution of leaves on a plant is the result of three processes: the birth, growth and death of leaves. The birth of leaves is influenced by the population which already exists on the individual (Harper 1989a, b). When a population of leaves receives sufficient light, water and nutrients, the birth rate of new modules within that population is high. Newly emerged leaves are small and

* *Current address:* Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA

** *Offprint requests to:* J. Weiner

leaf expansion follows a sigmoidal growth curve (Causon and Venus 1981). Thus, to some extent, size and age are correlated. However, if leaves vary greatly in their growth rates (e.g. because of variation in environmental factors such as the duration, intensity and spectral composition of light [Dale 1982]), this correlation will be weak: the only inevitable relationship between leaf size and age is that large leaves cannot be very young. Distributions of leaf size will also be strongly influenced by the impact of the local environments of the leaves on leaf birth and death rates. For example, Bazzaz and Harper (1977) found that at high plant densities the birth rates of leaves of *Linum usitatissimum* was decreased. Jones and Harper (1987) found significantly greater rates of mortality in buds of *Betula pendula* that were in close proximity to their neighbors. To some extent, leaves on a plant "compete" for resources (mineral nutrients and carbohydrates during leaf expansion), but leaves also produce photosynthate which is exported to other parts of the plant (Harper 1989b; Watson and Casper 1984).

Here, we report on a field experimental study on the effects of crowding on the size structure of leaf populations on *Impatiens pallida* individuals.

Materials and methods

Impatiens pallida Nutt. (Balsaminaceae) is a large, erect, summer annual of mesic woodlands of eastern North America. It is usually found in moist, partially shaded woodland areas and it often forms dense monospecific stands (Thomas and Weiner 1989) like other closely-related species (Winsor 1983). *I. pallida* has a reduced root system, is restricted to moist, shaded habitats, and shows early canopy closure, suggesting that competition for light is important (Weiner et al. 1990).

All field work was conducted in the Crum Woods of Swarthmore College (75° 21' W, 39° 54' N) in Delaware County, Pennsylvania, at the edge of a disturbed forest, on a flood plain of the Crum Creek. A more complete description of the study area is given in Thomas and Weiner (1989). In May of 1987, just after *I. pallida* populations had germinated, several plots were thinned, leaving at least 0.8 m between the remaining *I. pallida* seedlings (<0.5 individuals m⁻¹). All other vegetation was removed bi-weekly. Thus, these individuals experienced no competition during the course of the study. A rectangular plot within a dense undisturbed population nearby was used as the crowded population (40 individuals m⁻¹). To avoid edge effects, the sides of the plot were 0.25–0.5 m from the periphery of this population. Both populations were in locations which had been *I. pallida* monocultures for several years before this study (Thomas and Weiner 1989; Weiner et al. 1990). These naturally-occurring monocultures reach a height of 1.5 m by mid-July. All measurements were taken in the third to fourth weeks in July, when the canopy was completely closed and self-thinning was in progress. On each of the 125 plants, the length of every leaf and the height of the plant from the ground to the apex were measured to the nearest centimetre with a ruler. The area for each leaf was estimated from leaf length with an allometric function relating leaf length to leaf area. This allometric function was obtained by regressing log leaf area (measured with an area meter; LI-COR, Lincoln, Nebraska) on log leaf length for a sample of 76 leaves. This function accounted for 95.3% of the variation in log leaf area.

To test for deviations from linearity in the relationships between plant height and measures of leaf population size, we used second-order polynomial regression. A significant second-order term was considered evidence that a relationship was curvilinear or discontinuous (rejecting the null hypothesis of linearity).

Table 1. Mean values of whole-plant variables measured in crowded ($n=69$) and an uncrowded ($n=56$) *Impatiens pallida* plants

Parameter	Crowded		Uncrowded
Height (cm)	92.899	**	42.339
Leaf Area (cm ²) ^a	330.208	**	752.792
Number of Leaves ^a	34.464	*	54.804
Maximum Leaf Length (cm)	8.913	**	11.286
Mean Leaf Length (cm)	4.149	*	4.601

* $P < 0.01$, ** $P < 0.001$, t -test

^a t -test on log-transformed data

Results

Crowded plants had fewer leaves, less total leaf area, and smaller mean and maximum leaf lengths than uncrowded plants (see Table 1). As observed in a previous study (Weiner et al. 1990), crowded plants were, on average, taller than uncrowded plants. Crowded populations showed negatively skewed height distributions ($g_1 = -0.205$), whereas uncrowded populations showed positively skewed height distributions ($g_1 = 0.394$).

For both crowded and uncrowded plants there were positive relationships between the height of a plant and summary statistics of its leaf population. The slope of the relationship between a plant's height and its mean leaf length was substantially lower for crowded than for uncrowded plants (Table 2, Fig. 1). This pattern was even stronger if maximum leaf length was used instead of mean leaf length (Table 2, Fig. 2). Here the relationship was curvilinear in the uncrowded population (significant second-order term in polynomial regression). Crowded and uncrowded plants also showed different relationships between height and leaf population size. For uncrowded plants there was a weak positive correlation between the height of a plant and its total leaf area (Table 2, Fig. 3) and a somewhat stronger relationship between the height of a plant and its number of leaves (Table 2, Fig. 4). These relationships were not significantly curvilinear (Table 2). Crowded plants showed tighter and curvilinear or discontinuous relationships between height and total leaf area or number of leaves ($P < 0.001$ for second-order term), in which plants within a large range of total leaf area were near to an asymptotic height of approximately 140 cm.

Within the crowded population the distribution of leaf length in the few tallest individuals was noticeably different from that of the smaller plants (Fig. 5). Within the uncrowded population there was no apparent discontinuity in the distributions of leaf length ranked by height. The mean size inequality of leaf length on a plant was greater in the crowded than in the uncrowded population, but this difference was not significant ($CV = 0.623$ and 0.608 , respectively, $P > 0.05$, t -test). The population-wide distributions of leaf length for crowded and uncrowded plants were significantly different (Fig. 6; crowded $n = 2378$, uncrowded $n = 3069$, $P < 0.01$, Kolmogorov-Smirnov, two-tailed), but the inequality in leaf length for the crowded population was the same as that

Table 2. Summary statistics for linear and polynomial regressions of leaf population variables (dependent variables) versus individual plant height (independent variable) in crowded ($n=69$) and an uncrowded ($n=56$) *Impatiens pallida* plants. Linear regression: $y=b_0+b_1x$; polynomial regression: $y=b_0+b_1x+b_2x^2$. Significance of second-order term (b_2) is evidence for curvilinearity; nonsignificance is consistent with linear relationship

	Leaf Area (cm ²)	Number of Leaves	Maximum Leaf Length (cm)	Mean Leaf Length (cm)
<i>Crowded plants</i>				
Linear regression:				
Intercept	-360.9	-29.1	3.92	3.25
Slope	7.44	0.68	0.05	0.01
$P(H_0: b_1=0)$	0.0001	0.0001	0.0001	0.0015
r^2	0.447	0.42	0.617	0.141
Polynomial regression:				
$P(H_0: b_2=0)$	0.0003	0.0002	n.s.	n.s.
r^2	0.545	0.528	—	—
<i>Uncrowded plants</i>				
Linear regression:				
Intercept	97.4	-19.6	4.77	3.49
Slope	15.48	1.76	0.15	0.03
$P(H_0: b_1=0)$	0.0008	0.0001	0.0001	0.0001
r^2	0.19	0.579	0.584	0.380
Polynomial regression:				
$P(H_0: b_2=0)$	n.s.	n.s.	0.0022	n.s.
r^2	—	—	0.652	—

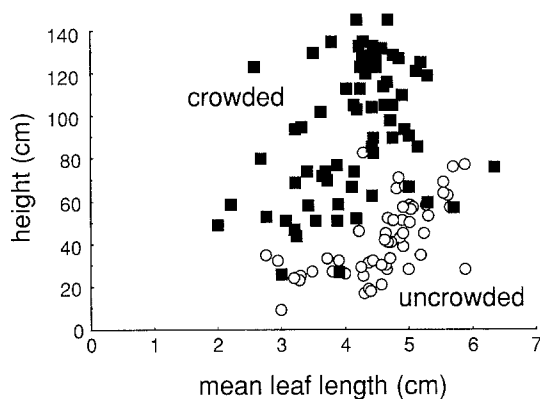


Fig. 1. The relationship between plant height and mean leaf length for crowded and uncrowded *Impatiens pallida* plants. The filled squares (■) indicate crowded plants; open circles (○) indicate uncrowded plants

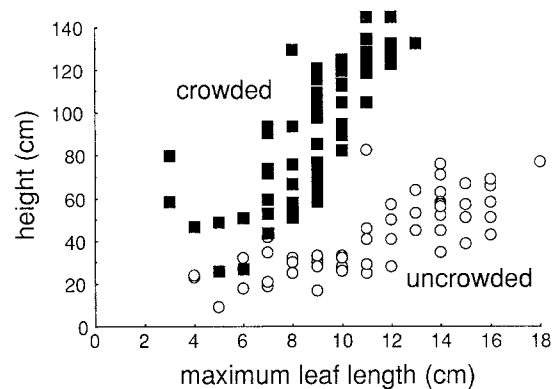


Fig. 2. The relationship between plant height and maximum leaf length for crowded and uncrowded *Impatiens pallida* plants. The filled squares (■) indicate crowded plants; open circles (○) indicate uncrowded plants

of the uncrowded population (CV = 66.08% and 66.10%, respectively).

Discussion

Crowding caused a reduction in mean and maximum leaf length, total leaf area, and the number of leaves on each plant, but had no effect on the variability (inequality) in leaf length within the population. Crowding also made the distribution of plant heights negatively skewed and the relationship between plant height and leaf number or

total leaf area non-linear. Those plants that were slightly taller than their neighbors had a disproportionately greater total leaf area (Fig. 3) and more leaves (Fig. 4).

Leaf populations respond to plant competition primarily through their number (37% reduction in mean leaf number) and secondarily through their size (9.8% reduction in mean leaf length). This is consistent with the idea that plants are modular in construction and that leaf modules may be considered as unitary organs, comparable to unitary individuals in a population of animals (Harper 1989a). However, the fact that modules on a plant are to some degree physiologically integrated (e.g.

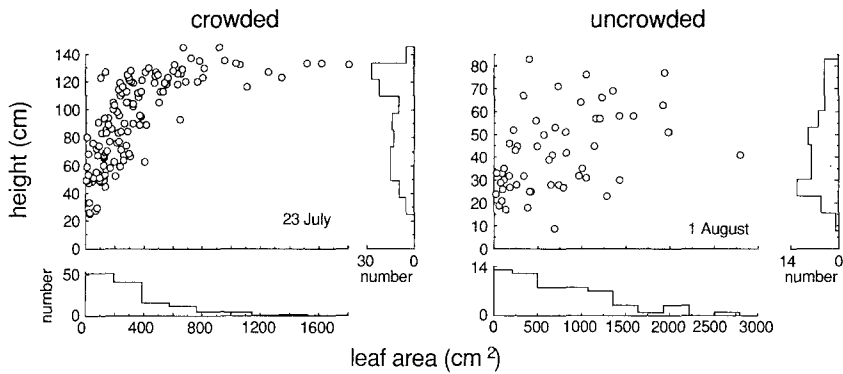


Fig. 3. The relationship between plant height and total plant leaf area for crowded and uncrowded *Impatiens pallida* plants. Frequency distributions of plant height are to the side of each scatter-plot. The axes are the same for the scatter-plot and its corresponding frequency distributions

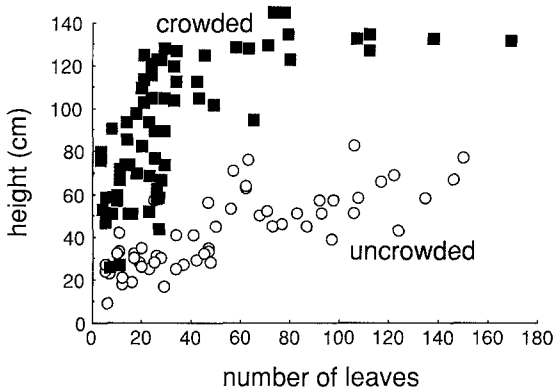


Fig. 4. The relationship between plant height and its number of leaves for crowded and uncrowded *Impatiens pallida* plants. The filled squares (■) indicate crowded plants; open circles (○) indicate uncrowded plants

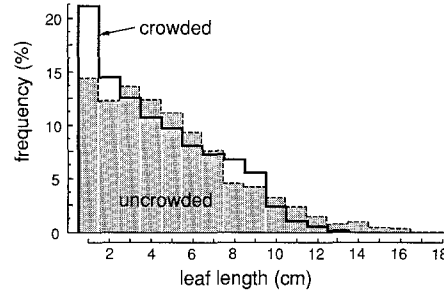


Fig. 6. Leaf length distributions for the entire crowded ($n=2378$) and uncrowded ($n=3069$) populations of *Impatiens pallida*. The thick line corresponds to the crowded population. The dashed line and shaded area correspond to the uncrowded population

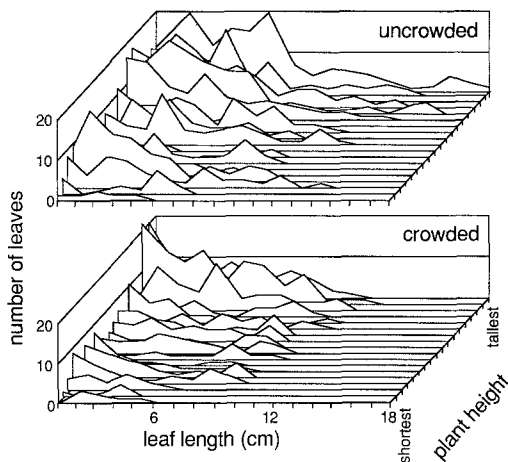


Fig. 5. Leaf length distributions for sub-samples of the crowded and uncrowded *Impatiens pallida* individuals. Each horizontal line in the figures corresponds to a single plant. Each population of plants was sorted by height and every fourth individual in the crowded population ($n=18$) and every third individual in the uncrowded population ($n=19$) are shown. The shortest plant in the sample is at the front of each figure, the tallest is in the back

Novoplansky et al. 1989) means that the analogy between modules on an individual plant and individuals within a population should not be taken too far. Leaves on a plant are not as independent as individuals in a population.

The differences in the size distributions of leaves on crowded and uncrowded plants must occur through the processes of leaf birth, growth and death. The crowded plants did not have very large (> 12 cm) leaves, but had more very small (1–2 cm) leaves than the uncrowded plants (see Fig. 6). The reduction in the number of large leaves and the absence of very large leaves on crowded plants could be due to the death of large leaves or to reduced leaf growth, such that no leaves achieved these sizes. The largest leaves on *I. pallida* individuals usually occur on the main stem and are among the oldest leaves on the plant. They develop relatively early in the season, before crowding is intense. Leaf scars are present on the crowded plants at the nodes where the largest leaves occur on the uncrowded plants. Therefore, it seems likely that crowding resulted in their loss.

Although there was a significant difference in the length distribution of leaves in the crowded and uncrowded population (Fig. 6), one aspect of these distributions, inequality, was almost identical in both. There are several possible non-exclusive explanations for this. (1) There may be as much local variation in the local environments (e.g. light levels) of leaves on crowded and uncrowded plants. For example, lower and inner leaves on an isolated plant are shaded by leaves on the same individual, and variation in local light levels may be as great as that occurring in a crowded stand. (2) Leaves on a plant “compete” for some resources, but to the degree that plants are physiologically integrated, the outcome of

competition between leaves is under the control of the plant. Therefore, we might expect competition among leaves on a plant for resources distributed internally to be "symmetric". According to current models, symmetric competition does not increase size variation (Weiner and Thomas 1986). (3) Inequality in leaf length may reflect a fundamental structural aspect of a leaf population which is maintained at (or constrained to) a relatively constant level regardless of plant density.

Our results point to the usefulness of applying population models to modules, and they also point to the limitations of this approach. The latter are probably a reflection of the differences in the degree of independence of an individual organism and a module on an organism.

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