

COMPETITION AND GROWTH FORM IN A WOODLAND ANNUAL

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SUMMARY

(1) Distributions of several variables of above-ground growth form, including plant height, vertical distribution of leaf area and vertical distribution of primary and secondary branch length, were compared for crowded (naturally occurring) and uncrowded (naturally occurring and experimentally thinned) populations of *Impatiens pallida* in south-eastern Pennsylvania. Growth form was examined at the population, individual plant and sub-individual levels.

(2) There were major differences in the growth form of crowded and uncrowded plants. Although they were smaller in stem diameter and had less total leaf area and branch length, crowded plants were taller than uncrowded plants.

(3) Uncrowded plants had significantly more leaf area, and this leaf area was located lower along the main axis of the plant than in crowded plants. Similarly, uncrowded plants had more, longer and lower branches than crowded plants. Uncrowded plants had more second-order than first-order branches, and the vertical distributions of both first and second-order branches were similar. Crowded plants had very few second-order branches, and the secondary branches were located higher on the plants than the more numerous and longer first-order branches.

(4) In uncrowded populations there was a linear relationship between the height of an individual and its total leaf area or branch length, but these relationships were curvilinear or discontinuous for crowded populations. This suggests different patterns of growth for canopy and sub-canopy individuals within crowded stands.

INTRODUCTION

Neighbours can affect the form as well as the size, survival and reproductive output of plants (Harper 1977). The influence of competition on plant form, however, has been less studied than its other effects. While there has been much interest in the evolution of plant form in response to different regimes of competition (e.g. Abrahamson 1979; Givnish 1982), studies addressing the evolution of plant form usually assume that the growth form of a given species is the result of natural selection and is genetically fixed. Plants show great plasticity in form as well as size, but little is known about how competition changes a plant's growth form (Franco 1986; Jones & Harper 1987).

Competitive interactions between plants are mediated by their growth forms. For example, plant allometry has been seen as a primary determinant of self-thinning (density-dependent mortality) trajectories (Miyanishi, Hoy & Cavers 1979; White 1981; Weller 1987). Species with different growth forms show different degrees of 'one-sided' competition in monoculture (Ellison & Rabinowitz 1989; Geber 1989; Thomas & Weiner 1989b). Similarly, differences in growth forms determined by allocation patterns can determine their competitive relationships between species in different environments (Tilman 1988). However, the relationship between plant form and competition is interactive: plant growth form is, in part, the product of competition between plants. Because of changes in plant growth form induced by competition, *Salicornia europaea*

does not show 'one-sided' competition or self-thinning (Ellison 1987). Competition changes the allometric relationships between plant height, stem diameter and plant weight in *Polygonum pennsylvanicum*, *Tagetes patula* and *Impatiens pallida* (J. Weiner and S. C. Thomas, in preparation). Thus, differences in growth form within a population play a critical role in stand structure.

Competition between plants can be studied at several levels of analysis (Allen & Starr 1982). The construction of reductionist theory of competition between plants begins with density dependence: the relationship between mean size and density (e.g. Watkinson 1980; Vandermeer 1984). The next level looks at different individuals within the population, the interaction of density, mean size and the distribution of sizes within the population (Weiner & Thomas 1986; Benjamin 1988). However, interference also generates systematic, predictable (and therefore quantifiable) variation in the form as well as the size of crowded individuals and this variation is fundamental to the dynamics of stand structure and development.

Plants vary greatly in their degree of modular integration (Watson & Casper 1984), but a wide variety of plant growth forms can be explained in terms of modular birth and death (Harper, Rosen & White 1986). For example, Franco (1986) has interpreted differences in the radial growth form of *Kochia scoparia* individuals in terms of the responses of modules to local resources levels as determined by neighbours. Uncrowded plants had no net horizontal vectoral component to their branch growth, whereas horizontal branching of competing pairs of *Kochia* plants tended to be in the directions away from each other. Franco reasoned that the competing individuals altered their growth form in response to competition through the reduced growth and/or increased death of modules experiencing interference from neighbouring plants relative to those modules that did not. Franco's approach can be applied to the vertical, as well as the radial-horizontal dimension of plant growth. In the present study, the changes that competition induces in the vertical dimension of above-ground plant form of *Impatiens pallida* were investigated.

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 often forms dense monospecific stands (Thomas & Weiner 1989a). *I. pallida* has a reduced root system, is restricted to moist, shaded habitats and shows early canopy closure, suggesting that competition for light is an important source of interference.

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 the fifty-year flood plain of the Crum Creek. A more complete description of the study area is given in Thomas & Weiner (1989a). Plots of *I. pallida* were established in 1984 and 1988. Leaf-area measurements were made on the 1984 experimental plot, which had a density of 39.66 individuals m⁻² ($n = 103$). Branch-length measurements were made on the 1988 plot, which had a density of 31.20 individuals m⁻² ($n = 30$). The 1984 experimental plot was located in the inner portion of an undisturbed, dense stand of *I. pallida*. The 1988 experimental plot was an inner region of an undisturbed, dense stand in the same location as the 1984 experimental plot. This site contained *I. pallida* populations of similar stature and density during the period 1983–88 (Thomas & Weiner 1989a). Because spatial

variation between stands can be as great as or greater than variation between years at the same site, the same site was used in a subsequent year for a control population in one of the studies, and a contemporaneous nearby site for a control population in the other study. Thus, a control population for the 1984 population was established in the same location in 1985. This population consisted of seventeen plants that were found near the 1984 plot and were growing a distance of at least 1.5 m to the nearest erect plant. All of these plants were surrounded by a mat of *Microstegium vimineum* and other low-lying herbs that rose approximately 20 cm up the main stem. A contemporaneous control population was established near the 1988 plot. This population consisted of thirty plants that were experimentally thinned soon after germination in early May. Plants in this control plot were separated from their nearest neighbour by 1–2 m. All low-lying herbs were removed biweekly. All measurements were taken during the second week in July, when the canopy had closed ($LAI > 1$), but extensive self-thinning had not begun. To avoid edge effects in the crowded populations, no plants near the periphery of these stands were measured.

For each plant, height was measured to the nearest cm, from the base to the terminal apical meristem, and stem diameter was measured to the nearest 0.1 mm with digital calipers at the midpoint of the first internode. For the 1984 and 1985 populations, the size and vertical location of all leaves were also recorded. The length, to the nearest cm, of each leaf was measured, and its vertical position was recorded as the height, to the nearest cm, of the point of attachment of the leaf petiole or primary branch to which the leaf was attached. The area for each leaf was estimated from leaf length with an allometric function relating leaf length to leaf area. The allometric function was fitted to the leaf areas, measured with an area meter (LI-COR, Lincoln, Nebraska, U.S.A.), and lengths of seventy-six leaves, and accounted for 95.3% of the variation in log leaf area.

For the 1988 plots, the vertical location and size of all the primary (attached to the main stem) and secondary (attached to primary) branches were recorded. The vertical position of each primary branch was recorded as its point of attachment to the main stem, to the nearest cm, and its angle off the main stem. The vertical position of each secondary branch was recorded as the height of the primary branch to which it was attached. All branch lengths were recorded to the nearest cm. To make comparisons between the vertical distribution of leaf area and branch length within individuals and populations, vertical frequency distributions of leaf area and branch length for individuals and populations were constructed, and weighted mean height measurements for leaf area and branch length were calculated. Procedures for calculating weighted means and corresponding standard deviations were taken from Sokal & Rohlf (1981).

Second-order polynomial regression was used to test for curvilinearity in the relationships between different measures of plant size and growth form. A significant second-order polynomial term was considered evidence that a relationship was curvilinear or discontinuous.

RESULTS

Whole-plant comparisons

Measures of main stem height and diameter were similar for both sets of crowded plants and for both sets of uncrowded plants. Mean main stem height and height:diameter ratios were significantly greater in crowded plants than in uncrowded plants (Table 1). Mean stem diameter was greater in the uncrowded plants, but this difference

TABLE 1. Comparison between means per plant (± 1 S.D.) of several measures of main stem size and leaf area for crowded and uncrowded populations of *Impatiens pallida*.

Variable	Crowded 1984		Uncrowded 1985
Height (cm)	93.1 \pm 27.3	**	69.4 \pm 20.6
Diameter (cm)	0.70 \pm 0.23	N.S.	0.71 \pm 0.25
Height/diameter	137.9 \pm 27.8	**	100.6 \pm 16.8
Leaf area (cm ²)	463.2 \pm 294.7	*	667.6 \pm 510.3
			1988
Height (cm)	76.3 \pm 13.3	***	56.7 \pm 11.8
Diameter (cm)	0.72 \pm 0.14	**	1.06 \pm 0.19
Height/diameter	107.6 \pm 10.6	***	54.1 \pm 11.0
Total primary branch length (cm)	27.6 \pm 25.7	***	173.7 \pm 73.9
Total secondary branch length (cm)	1.1 \pm 5.1	***	143.6 \pm 88.8

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

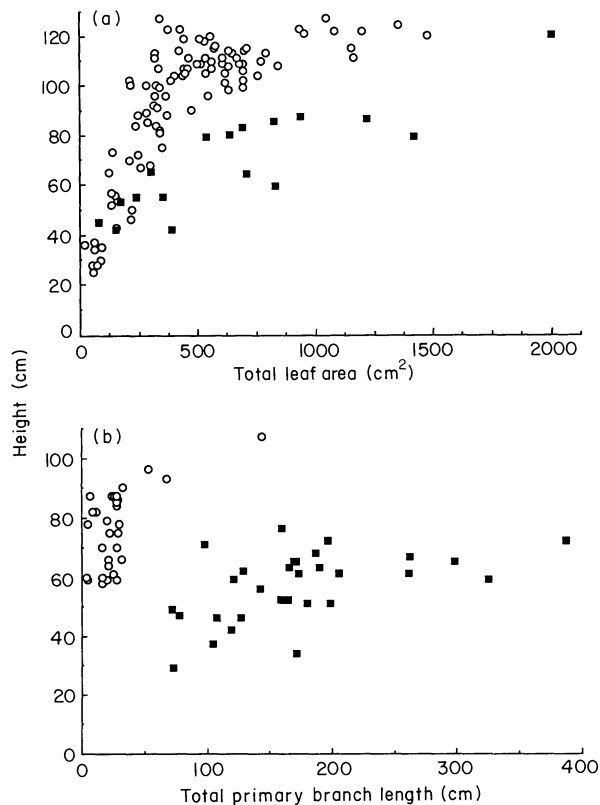


FIG. 1. The relationship between plant height and (a) total plant leaf area, and (b) plant height and total length of primary branches, for crowded (O) and uncrowded (■) populations of *Impatiens pallida*.

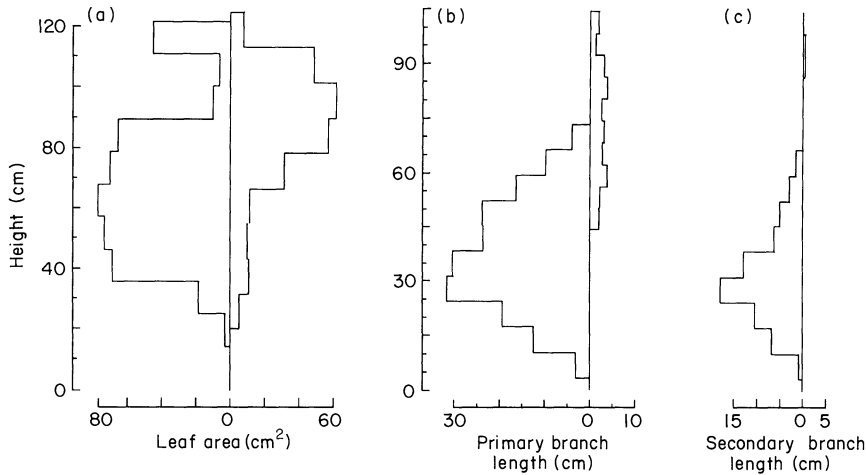


FIG. 2. Stand-level (mean plant) vertical distributions of (a) leaf area (cm^2) (1984, 1985), (b) primary and (c) secondary branch length (cm) (1988) for crowded (right side of axis) and uncrowded (left side of axis) populations of *Impatiens pallida*.

was significant only for the 1988 data. Mean leaf area per plant and total branch length per plant were significantly greater in the uncrowded plants (Table 1). Uncrowded plants had more and longer branches than crowded plants. Except for the smallest plants, crowded plants were taller than uncrowded plants of the same leaf area (Fig. 1a). The relationship between the height of a plant and its total leaf area was significantly curvilinear in the crowded population ($P < 0.01$) but not in the uncrowded population ($P > 0.8$; Fig. 1a). Similarly, the relationship between the height of a plant and total primary branch length was also significantly curvilinear in the crowded population ($P < 0.01$) but not within the uncrowded population ($P > 0.9$; Fig. 1b).

The thirty uncrowded plants in 1988 had a total of 357 primary branches and 566 secondary branches, whereas the thirty crowded plants had 211 primary branches and only eight secondary branches: a 1.69-fold difference in primary branch number and a seventy-fold difference in secondary branch number.

Individual growth forms and population structure

There were major differences for crowded and uncrowded populations in the vertical distribution of leaf area and branch length. The vertical distributions of leaf area and branch length were higher for the crowded than the uncrowded populations (Fig. 2). In crowded populations most of the leaf area was located in a canopy near the top of the stand, and there was a tail of leaf area towards the ground (Fig. 2a). Competition reduced branch lengths and increased branch height (1988, Fig. 2b, c).

The crowded plants had all their primary branches in the top-most 60% of the plant; secondary branches were restricted to the top-most 17%. For uncrowded plants, primary and secondary branches were found along the entire height of the plants. The mean elevation of branch length for uncrowded plants was close to half of their height.

The mean elevation of secondary branches was slightly lower than that of primary branches in the uncrowded population ($P < 0.001$; Fig. 2b, c). The crowded population had very few secondary branches. These branches were restricted to a very narrow vertical

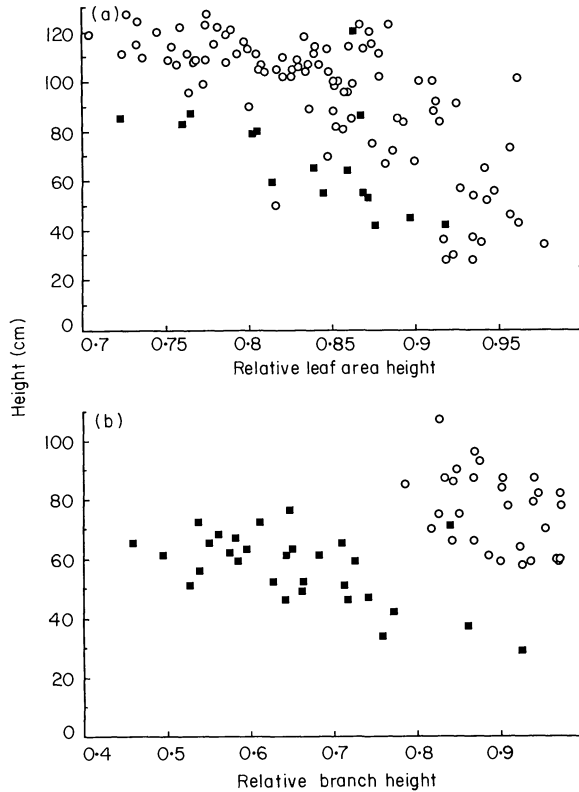


FIG. 3. The relationship between plant height and (a) relative height on plant of a unit of leaf area (mean height of a unit of leaf area/plant height), and (b) relative height on plant of a unit of branch length (mean height of a unit of branch length/plant height) for crowded (○) and uncrowded (■) populations of *Impatiens pallida*.

range near the top of the stand and had a mean elevation higher than that of the primary branches.

The relationship between the height of a plant and the relative height of its leaves and branches was different for crowded and uncrowded populations (Fig. 3). Crowded plants had the mean elevation of leaf area and branch length higher on the plant than did uncrowded plants of the same height.

The vertical distributions of leaf area and primary branch length for individual crowded and uncrowded plants were very different (Figs 4 and 5). Within crowded populations, the smaller plants have their leaves and branches restricted to the top of the plant, while the larger plants have a larger vertical spread of leaves and branches. Uncrowded plants generally have leaves and branches spread out over more of the height of the plant. The modal height of a unit of branch length is almost always close to the top of a crowded plant, but is usually much lower on uncrowded plants. The mean horizontal angle of primary branches was 17° for both crowded and uncrowded populations.

DISCUSSION

Crowded and uncrowded individuals show pronounced differences in growth form. Despite the presence of many small plants in the crowded populations, mean height of

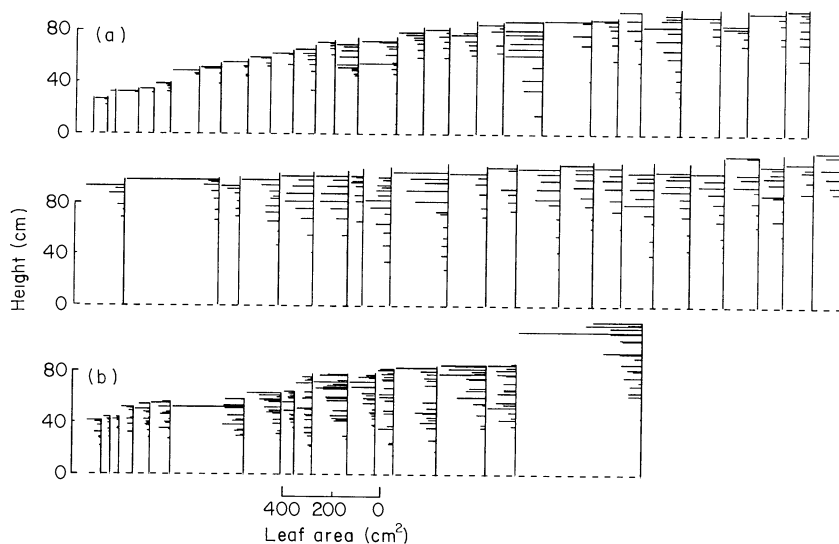


FIG. 4. Schematic representation of the vertical distribution of leaf area for (a) a random subset of the crowded (1984) and (b) the uncrowded (1985) populations of *Impatiens pallida*. Vertical lines represent main stems, and horizontal lines represent leaf area.

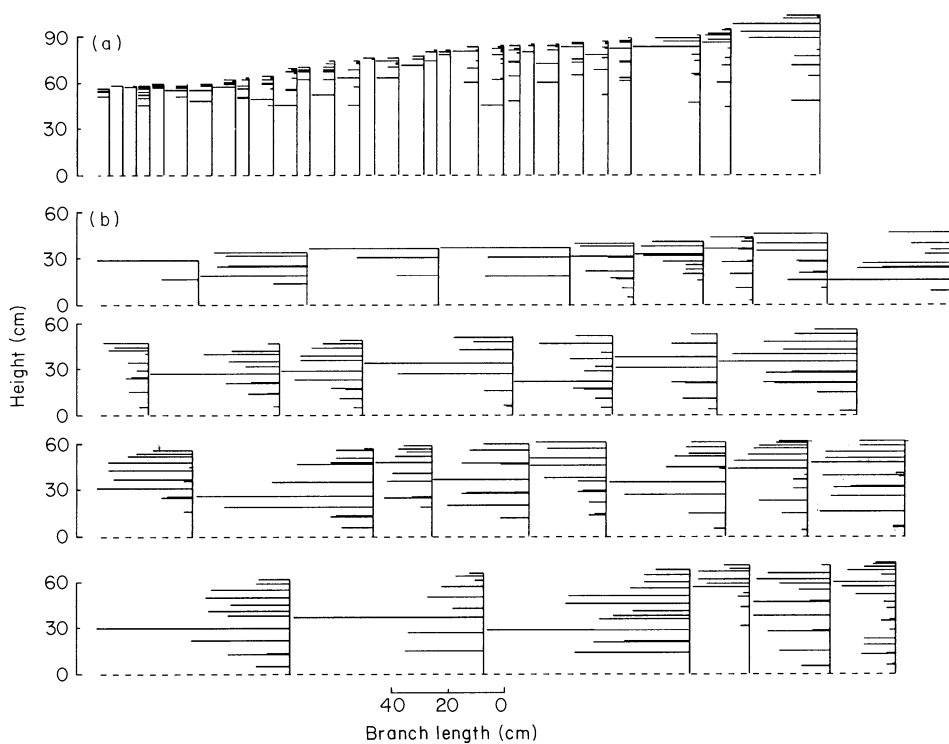


FIG. 5. Schematic representation of the vertical distribution of primary branch length for (a) crowded and (b) uncrowded (both 1988) populations of *Impatiens pallida*. Vertical lines are main stems, and horizontal lines represent primary branch length.

TABLE 2. Summary of observed differences in above-ground growth form of crowded and uncrowded populations of *Impatiens pallida*.

Measure	Uncrowded	Crowded
Population level		
Height-leaf-area relationship	linear	non-linear
Height-branch-length relationship	linear	non-linear
Vertical distribution of leaf area and branch length	lower and more spread	higher and more concentrated
Individual level		
Height/stem diameter	low	high
Height/leaf area	low	high
Leaf area/plant weight (leaf 'allocation')	high	low
Height/total branch length	low	high
Primary branch length/secondary branch length	low	high
Vertical position of leaf area and branch length	low	high
Relative height of primary and secondary branches	similar	primary lower than secondary
Mean height of leaf area/plant height	low	high

crowded plants was greater than that of uncrowded plants (Table 1). Crowded plants are thinner (higher height:diameter ratio) and have less leaf area and branch length. Uncrowded plants have extensive leaf and branch development along the entire length of the main stem (Figs 4 and 5). Secondary branches of uncrowded plants have a vertical distribution similar to that of primary branches. Crowded plants, on the other hand, have very few secondary branches, and the vertical distribution of secondary branches is restricted to the top of the distribution of primary branches from which they originated. Observed differences in growth form of crowded and uncrowded plants are summarized in Table 2.

Some of the differences in growth forms between crowded and uncrowded *I. pallida* populations in this study have been observed in other populations. Plants in high-density populations are taller and thinner in *Laportea canadensis* (Menges 1987) and *Populus tremuloides* (King 1981). Foliage development was restricted to the top portion of individuals grown in dense populations of *P. tremuloides* (King 1981), *I. capensis* (Schmitt, Eccleston & Ehrhardt 1987), *Glycine max* (Monsi, Uchijima & Oikawa 1973) and *Ambrosia artemisiifolia* (Al-Fatih & Bazzaz 1979). Open-grown saplings of *Abies mariesii* have branches along the entire length of the main stem, whereas branches of suppressed saplings are restricted to the very top of the plant (Kohyama 1980). At the population level, interspecific competition changes the vertical distribution of leaf numbers in wheat and several weeds (Maillette 1986).

The changes in above-ground plant form in response to neighbours are probably caused by changes in quantity and spectral composition of light as plants shade one another. Beneath a photosynthetically active canopy, the quality (red:far-red ratio) as well as the quantity of light is decreased (Smith & Morgan 1983). Several studies have demonstrated that decreases in the red:far-red ratio and quantity of light have a profound effect on the amount of branching, internode lengths, total leaf area (Morgan & Smith

1979; Solangaarachchi & Harper 1987; Mitchell & Woodward 1988) and the internode length of clonal plants (Slade & Hutchings 1987).

Natural populations of *I. pallida* form a dense canopy that acts as a boundary layer between the relatively high-quantity, high-quality (i.e. high red:far-red ratio) light environment at the top of the canopy and the poor light environment below the canopy. In crowded populations of *I. pallida*, those individuals that were initially large enough to be within the canopy when it formed tend to be those which remain relatively large throughout the growing season (Thomas & Weiner 1989a). The discontinuous or curvilinear relationship between height and leaf area and height and branch length (Fig. 1) supports the idea that there are distinct dominant and suppressed growth forms in crowded *I. pallida* populations. The taller individuals within the canopy have a high degree of leaf area and branch development, resulting in an umbrella shape, whereas the smaller subcanopy individuals more closely resemble a lollipop shape (Figs 4 and 5), perhaps because taller individuals are partially within a light-rich environment. Lower internodes were relatively barren due to the abscission of leaves and branches. This probably occurs because local interference causes a significant increase in leaf and bud mortality rates, as shown in *Floerkea proserpinacoides* (Smith 1983) and *Betula pendula* (Jones & Harper 1987). It is the larger individuals whose leaves and branches comprise the canopy, whereas smaller individuals live below the canopy. Dominant individuals grow with their tops in a high-quality light regime, while their smaller suppressed neighbours grow completely below the canopy in a poor light environment. These differences in the light environment generate differences in growth form. The leaf area towards the bottom of a crowded *I. pallida* stand is primarily composed of leaves at the top of smaller individuals, not leaves towards the bottom of larger individuals.

The differences in growth form between crowded and uncrowded, and between dominant and suppressed individuals within the crowded populations may be due, to a large extent, to differential proliferation of modules in areas of high and low resource availability. Uncrowded plants proliferate leaf and branch modules all along their vertical dimension. Larger crowded plants have extensive modular proliferation only towards the top of the plant, and suppressed crowded plants have very few modules, which are located only at the very top of the plant. The lack of evidence for any effect of competition on the angles of primary branches supports the simple modular interpretation of the observed differences in growth form, i.e. modules proliferate differentially, but their organization does not change. The plants may be understood in terms of '... relatively simple rules of growth, rather than complex [growth] strategies' (Weiner 1988a).

While there are similarities between the effects of competition on growth form described here and the well-documented phenomenon of etiolation in shade-grown seedlings (Smith & Morgan 1983), there are also important differences. The subcanopy plants described in this study are adults, and many of them flowered later in the summer (Thomas & Weiner 1989a). There was no evidence of abnormal development in the smaller individuals. The lack of foliage towards the bottom of crowded plants was due to leaf abscission; leaf development was reduced but not absent (G. M. Berntson and J. Weiner, in preparation).

It has been argued that the increase in the size variability of a population of plants which is caused by competition is the result of asymmetric competition for light (Weiner & Thomas 1986). Light is intercepted by a two-dimensional surface while plants grow in three dimensions. Thus, even if plants are modelled as organisms whose shape is constant in space and time, slightly larger (taller) individuals are able to intercept a

disproportionately large amount of the available light (Ford & Diggle 1981; Weiner 1988b). However, plants do not maintain their shape in the presence of competition. The forms, as well as the sizes, of individuals within the population are a product of their competitive interactions.

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