Flowering in Bougainvillea

A FUNCTION OF ASSIMILATE SUPPLY AND NUTRIENT DIVERSION

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ABSTRACT

Reproductive development, whether expressed as first node to flower or numbers of inflorescences developing, is promoted in direct relationship to leaf area and in inverse relationship to the numbers of axillary branches developing. Per cent soluble solids in the reproductive shoots vary with reproductive development. Cytokinin treatments promote inflorescence development and per cent soluble solids, further supporting a nutritional hypothesis in the control of flowering in Bougainvillea “San Diego Red.” Gibberellin treatments inhibit reproductive development completely without significant lowering of per cent soluble solids, which is counter to expectations for a nutritional hypothesis. A closer examination of the reproductive axes, the tissues in which morphogenetic change occurs, must be made for the gibberellin-treated tissues.

Early concepts of the control of reproductive development emphasized the importance of nutritional parameters (7, 8, 11, 14), particularly C/N ratios in the entire plant (12). Many of these ideas were not sustained in subsequent studies (13), and, hence, nutritional hypotheses were assigned a supportive rather than regulatory role in reproductive development. Numerous studies with monocarpic and polycarpic species showed that flower initiation and development have apparently higher light flux requirements than continued leaf initiation (18). There is also considerable evidence, for many photoeriotic species, that high photon flux may replace all or part of the day length requirements for the transition from vegetative to reproductive development (2, 3, 9, 15, 18). Since the high light flux is generally in the photosynthetically active range, it seemed as if changed levels of photosynthesis, or assimilates derived therefrom, played an important role in inductive processes in the leaves and/or as a morphogenetic signal in the shoot apical meristem (5, 10). Bodson (2) obtained evidence for an early increase, before cytological evidence for evocation, in carbohydrate levels in apical buds of Sinapis following induction by LD³ or disordered SD.

In a comprehensive review of the effects of nutritional factors, acting as substrates or osmotica, on tissue differentiation and organogenesis, Allsopp (1) assigned a determining, not merely supporting, role to sugars and other metabolites. Generally the same views were expressed in a recent symposium concerned with flowering (18) with additional emphases given to the role of nutrients in regulating energy transduction in leaf and apical meristematic tissues and the potential significance of energy supply in regulating morphogenesis.

In Bougainvillea “San Diego Red” clear evidence was obtained that day length, cytokinin, and selective defoliation treatments increased assimilate supply to the inflorescence axis before morphological change was observed (19, 20). We proposed, therefore, that assimilate supply limited reproductive development and that environmental and chemical parameters regulated primordial initiation and development through their influence on assimilate supply to the responsible meristematic tissues (16, 17). Specifically, promotion of development should result from treatments that increase assimilate supply to the inflorescence axes and from treatments that decrease assimilate supply to competing meristems. This is the essence of nutritional (nutrient diversion, resource allocation) hypotheses proposed to account for apical dominance (14), fruit set, abscission and growth (4), and partitioning of assimilates to establish root to shoot ratios. In the context of such hypotheses the terms “source” (photosynthetic assimilate-producing) and “sink” (assimilate-consuming), are useful, as is “hormone-directed transport,” which suggests a relatively nonspecific role for hormones, namely that of diverting assimilates to hormone-activated growth centers (sinks).

In these studies we have attempted to test the nutritional hypothesis as it applies to the control of flowering in Bougainvillea by studying inflorescence development as a function of leaf area (source activity), number of developing shoots (competing sink activity), and GA and cytokinin treatments that may alter sink activity close to or at the inflorescence axes.

MATERIALS AND METHODS

Rooted cuttings of Bougainvillea “San Diego Red” were grown routinely in a 26 C/21 C (approximate day and night temperatures) greenhouse under LD conditions which were 8 h daylight, approximately 675 µE m⁻² s⁻¹, summed for the 400 to 700 nm interval, and 16 h under black cloth with supplemental incandescent light, 9 µE m⁻² s⁻¹; from 4:30 pm to midnight. SD conditions were on adjacent greenhouse benches with 8 h daylight and 16 h under black cloth. Plants of 35 nodes and with at least 10 fully exposed leaves were used for experiments.

Different photosynthetic assimilation was obtained by varying the leaf area. Six expanded leaves were cut to conform to rectangular templates of known area; four different leaf areas were used: 10, 20, 30, and 40 cm². Final leaf area was also determined at the end of each experiment, since many of the leaves continued growing during treatments. All of the leaves above those selected for photosynthesis were removed; young leaves unfolding from terminal buds were also removed as described previously (20).

To study inflorescence development as a function of branch
number, decapitated plants were permitted to develop (one, two, three, four, or five) axillary branches above the uppermost leaf. Six leaves were maintained on each plant and leaf areas were approximately the same, 40 cm², for all decapitated plants. Young leaves unfolding from the terminal bud of branches were removed as described previously.

In both experiments treatments were with PBA (500 mg/l) and GA (100 mg/l). The chemicals were applied every 4 days in 10-μl droplets to the terminal buds. After all of the manipulations were done, plants were moved to SD conditions (black cloth 4:30 PM to 8:30 AM).

Fresh weight, dry weight, and soluble solids of the plants and component parts were determined at the end of the treatment. Dry weight per cent was computed from the ratio of dry weight (70 C oven, 24 h) and fresh weight. Dried tissue was extracted three times with 80% methanol, dried in a 70 C forced air oven for 24 h and then reweighed. The difference between the initial and final dry weights divided by the fresh weight and expressed as per cent, is the per cent soluble solids. Inflorescence development was evaluated by counting the number and node position of inflorescences greater than 2-mm diameter. Earlier studies have shown that these inflorescences will proceed to anthesis. Linear regression analysis was performed for that data.

RESULTS

Inflorescence development as a function of leaf area is shown in Figure 1, A and B, with the computed first order linear regression line; the data provide convincing evidence of correlation between earliness to flower or number of inflorescences developing and leaf area. As expected per cent dry weight during the experimental period, 21 days, was a function of leaf area (Fig. 1C). Results showed also a direct correlation between leaf and soluble solids in the shoot apical region (Fig. 1D). The correlation coefficients and the statistical analyses of intercepts and slopes of the regression lines shown in Figure 1 are presented in Table I. Cytokinin treatments of the shoot apex: (a) increased per cent dry weight and soluble solids as much as 30 to 40%; (b) reduced the first node to flower; and (c) increased the number of infloresccences. The difference between initial and final dry weights divided by the fresh weight and expressed as per cent, is the per cent soluble solids. Inflorescence development was evaluated by counting the number and node position of inflorescences greater than 2-mm diameter. Earlier studies have shown that these inflorescences will proceed to anthesis. Linear regression analysis was performed for that data.

![Fig. 1](https://academic.oup.com/plphys/article-lookup/doi/64/5/810/6077666)

**Fig. 1.** Regression lines for relationships between leaf area and inflorescence development expressed as first node to flower (A) or number of inflorescences developing (B), dry weight gain (C), and soluble solids (D) in shoots.

![Fig. 2](https://academic.oup.com/plphys/article-lookup/doi/64/5/810/6077666)

**Fig. 2.** Regression lines for relationships between number of axillary branches and inflorescence development expressed as first node to flower (A) or number of inflorescence developing (B), dry weight gain (C), and soluble solids (D) in shoots.
cences developing. Plants with the smallest leaf area developed inflorescences when treated with PBA, but the control plants did not. GA treatments completely inhibited inflorescence development, regardless of leaf area, but did not reduce per cent dry weight and soluble solids. In fact, there was a small, but not statistically significant, increase of both per cent dry weight and soluble solids.

Experiments studying inflorescence development, per cent dry weight gain, and soluble solids as a function of the number of axillary branches also revealed strong correlations (Table II). Again, the number of axillary branches was closely related to inflorescence development, whether expressed as first node to flower or number of inflorescences, per cent dry weight, or soluble solids (Fig. 2). Cytokinin treatments enhanced first node to flower, number of inflorescences developing, per cent dry weight, and soluble solids, whereas GA treatment completely inhibited inflorescence development, regardless of axillary bud number, without reducing per cent dry weight and soluble solids.

Plotting number of inflorescences as a function of per cent dry weight or soluble solids (grouped data obtained from the leaf area, branch number, and PBA experiments) reveals highly significant correlations as indicated in the linear regression analyses (Fig. 3).

**DISCUSSION**

If per cent soluble solids is an acceptable indicator of the nutritional status of a developing shoot (and the inflorescence axes), then the results for leaf area, axillary branch number, and PBA treatment support the hypothesis that reproductive development in *Bougainvillea* is a function of nutrient supply to the inflorescence axis. However, the dramatic inhibition of primordial initiation in the GA-treated shoots without a concomitant decrease in soluble solids indicates that the nutritional hypothesis, as formulated, is in error, or that soluble solids, when derived grossly for the entire shoot, are an inadequate measure of nutrient supply to the inflorescence axis.

Micromeasurements sensitive to the initial changes that determine morphogenetic events in apical meristematic tissues are required. Such determinations are possible but technically very difficult. For example, Sachs, in collaboration with Drs. G. Berrier, M. Bodson, and A. Jacqmaud of the University of Liège, attempted soluble solid determinations for apical buds of *Sinapis alba*. Employing freeze substitution, then dissection of the dried buds into meristems, leaves, and stem, followed by 80% methanol extraction of the tissues, relatively accurate gravimetric determinations were obtained of soluble solids for tissues weighing in excess of 50 µg, i.e. of the order of the third or fourth leaf primordia below the meristem. Apical meristems weighed (dry) less than 3 µg each; both dissections and weighing were highly variable for these tissues. Apical meristems of *Bougainvillea* reproductive axes appeared to be of similar dimensions. Preliminary results for glucose, fructose, and sucrose determinations in *Bougainvillea* inflorescence tissues have been highly variable; thus, it is not yet possible to evaluate treatment effects on sugar or soluble solid concentration. Recent experiments on BA metabolism in GA-treated *Bougainvillea* revealed that GA inhibits formation of BA riboside and other polar derivatives (6) which may be important for primordial initiation. If this effect of GA on BA metabolism reflects similar changes in metabolism of the naturally occurring cytokinins, it is possible that the primary reason for GA-induced inhibition of flowering in *Bougainvillea* is due to altered cytokinin metabolism and only indirectly to nutrient displacement in meristems.

Control of flowering in *Bougainvillea* would appear to involve both nutritional and hormonal parameters which may ultimately depend upon strategies of resource allocation and energy transduction and the effects of the latter on morphogenetic events (18).

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