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Growth and Development of a Carnation Shoot

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This investigation was primarily to study the growth and development of the meristem region of carnation shoots and to describe and photograph differences in anatomical and staining characteristics that may be associated with vegetative and reproductive shoot tips. This paper is limited primarily to gross characteristics of the developing shoots that are detectable by the observing grower. Microscopic changes and changes in reaction of the regions of the meristem to biological stains will be published elsewhere.

Methods

On October 27, 1966, 600 carnation cuttings (cv. White Pikes Peak) were taken from a commercial propagation greenhouse. The clones used were special stock selected to be of uniform high quality. The stock plants at this time were unpinched, and the main stem terminated in an unopened floral bud. Cuttings were obtained from axillary shoots found on the lower 8 inches of the main stem. Two nodes from each cutting were left on the stock plants. Three hundred cuttings weighing from 5-10 grams were selected. These cuttings averaged 9 nodes in length and observations disclosed that the fourth node from the base of the cutting contained a bud averaging 1.2 mm and varying little from cutting to cutting.

The cuttings were rooted in a mist propagation bed under normal greenhouse conditions and transplanted to a bench containing soil in one of the carnation greenhouses at Colorado State University. The experiment began on December 27, 1966, when axillary bud growth at the fourth node was apparent; the terminal bud was removed leaving the lower 5 nodes.

December 30, 1966, (4 days after the beginning of the experiment) 40 shoots were taken from the node fourth from the base of the plant. Thereafter, similar samples were taken on 19, 36, 52, 70, 90, and 117 days after the date the terminal bud was removed. Samples were processed between 8:00 and 10:00 A.M. on the sample dates. To process the sample, the 40 shoots were divided into four subgroups. Three of the subgroups were used for microscopic examination of staining characteristics.

Ten shoots of each sample were examined for gross characteristics of the shoot and included measurements of length of each node, leaf, axillary bud, and total stem length, obtained by measuring the most distal portion of the shoot to its insertion on the main stem. The data from these measurements were averaged to form an estimate of a shoot representing the sample group. Figure 1 contains drawings of representative shoots in the first five samples.

The greenhouse growing conditions during the period of the experiment, Dec. 28, 1966 to April 19, 1967, were determined with a recording thermometer, a max-min thermometer, and a hygrometer. A daily greenhouse record of the temperature and relative humidity at 9 A.M. was kept. Table 1 summarizes these data. No pathogen or insect infestation was found on the experimental plants. Water containing a complete nutrient solution was applied to the soil at

This a condensed section of the author's thesis in partial fulfillment of the requirement for the Ph.D. degree at Colorado State University.

Fig. 1. A drawing showing the development of the carnation shoot. The groups were considered to represent the transition from the vegetative state in the seedling to the floral initiation in the 70 day old sample. The meristems of these shoots were studied cytologically.

intervals from 4 to 14 days depending on plant demand. General growth and vigor of the plants was considered excellent.

Table 1. Monthly averages of the daily greenhouse temperatures and relative humidities during the experimental period

	Temperatures °F			Relative humidity
	High	Low	9:00 AM	9:00 AM
Jan.	69	51	60	82
Feb.	74	52	64	79
Mar.	75	51	66	78
Apr.	7 6	52	70	7 6

Results

Axillary bud growth was first evident in the 10 node sample (19 days). The buds born at the basal nodes showed slow and sporadic growth, while the mid-stem and distal buds grew in a consistent pattern. The axillary bud length appeared greatest at

mid-stem of all shoots, with development of the distal 3 or 4 buds occurring only after node formation had ceased. Individual axillary shoots grew rapidly, but there was a tendency for growth rates of buds produced on nodes after the 10th to decrease. The buds produced after 10 nodes may be considered as part of the inflorescence, since after 90 days these axillary shoots terminated in a flower. The inhibition of axillary bud growth until 10 nodes have formed and the slower rate of axillary bud development found on nodes formed after this stage suggest the flowering process may be correlated with these developments.

The length of the internode varied between the samples with respect to time and stem position. In the 4, 7, and 10 node samples a rapid increase in length of all the internodes showed a similar relationship between internode length. The length intrastem relationships changed in the 14 node sample. Here a low ratio between the length of the distal 5 or 6 nodes and a nearly constant ratio between the basal 4 nodes existed. Finally this pattern was augmented in the 17 and 18 node samples when these apparently slowly elongating internodes began to expand rapidly, as was indicated by the plots of the growth of the internodes versus time (Fig. 2). The internode elonga-

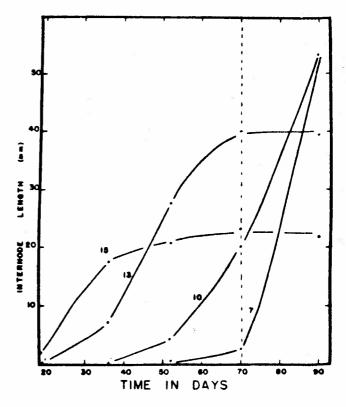


Fig. 2. A graph of the length of the internodes of a carnation stem with time measured in days. Each point represents the average of 10 measurements. The numbers on the lines (7, 10, 13, 15) indicate the position of the internode on a stem of 18 nodes. The most distal node on the stem is number 1. The dotted line indicates the time of flower formation.

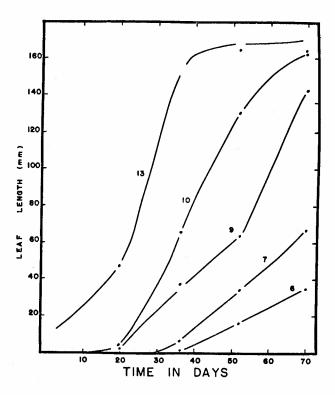


Fig. 3. A graph of the length of the leaves of a carnation stem with time measured in days. Each point represents the average of 10 measurements. The numbers on the lines (6, 7, 9, 10, 13) indicate the position of the leaf on a stem of 18 nodes. The most distal node on the stem is number 1.

tion may be divided into three phases: (1) vegetative, where the elongation of all internodes is rapid; (2) an intermediate stage, where the youngest internodes expand slowly, mid-stem internodes elongate rapidly, and the basal internodes are nearly equal in length and elongate slowly; (3) a floral stage, where elongation of the youngest distal internodes is rapid and progresses acropetally with respect to stem position, and the mid-stem and basal internode elongation is slow.

The development of leaves on the sample stem indicated some variation of leaf expansion. The rate of leaf development early in the growth of the shoot differed from the rate of development for leaves formed later. This was expressed by graphing the average leaf length for a given stem position versus time in days (Fig. 3). There appeared to be a slowing in the leaf expansion after 10 nodes had developed on the shoot. It was at this time (the 10 and 14 node samples) that a mature or fully-expanded leaf was first encountered near the base of the shoot. Thus leaves found near the middle of the shoot on the 18 node sample shoot were largest at maturity and developed most quickly.

Discussion

The process of flowering is the product of numer-

ous interrelated changes. These changes are especially tied to the photoperiod, but are clearly affected by other environmental factors (Holley and Baker, 1963). This experiment was conducted under daylength conditions (about a 12-hour day) unfavorable to flowering. However, it was consistent with the view of Nougarede (1967) because the changes leading to flowering were slow. It is also consistent with his point of view that the intermediate stage starts when the plant is sensitive to photoperiod. This appears true for the carnation, and changes from the vegetative to the prefloral stages may be more discrete under long days. If the number of nodes involved in the inflorescence is variable, the day-length influence could extend the intermediate stage, resulting in a greater number of nodes on the stem grown under short days. The numerous factors which introduce variability in the timing and development of flowering and shoot development (Blake, 1956, 1962; Hanzel, 1955; Harris and Harris, 1962; Holley and Baker, 1963) must be considered before the proposed phases are accepted and a general theory of flowering can be developed for the carnation. Careful investigation of the number of axillary buds in the inflorescence as a function of day-length and stem position would probably add additional information and understanding in regards this problem. The attempt at classification of the growth stages of carnation as outlined in this paper may allow for a more critical analysis of the underlying causes of environmental effects. The use of in vitro shoot tip culture (Phillips and Mathews, 1964) appears to be an excellent way of exploring the reality of these stages. Thus future avenues for research are found in the defining of floral induction and the exploration of the effects of exogenous hormone levels on floral induction.

Summary

Analysis of growth of the carnation shoot indicated various changes associated with flower development occurred. Changes occurred in: (1) staining reaction of the meristem; (2) mitotic index and nucleolar volume of cells in the flanking and axial zones; (3) size and shape of the meristem; and (4) the elongation of leaves, axillary buds, and internodes. Based on these criteria three phases of growth are proposed: vegetative; intermediate; and prefloral. Shoot elongation is rapid and cytohistological zonation clear in the vegetative stage. The intermediate phase may be most sensitive to the influence of photoperiod. In the intermediate phase, node formation continues but a preparation for reproductive growth is suggested. Determinant growth and a preparation for flower development marks the prefloral phase.

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