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Effects of Defoliation and Root Heating during Rest on Leaf Growth in Strawberry Plants

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Summary

'Premier' strawberry plants were defoliated and chilled at 5°C in the dark for 35 days (chilling), and then forced at day/night temperatures of 22°/20°C under a 12-hr photoperiod. The petioles of the 2nd and 3rd leaves which emerged during forcing conditions became longer than those of the plants defoliated but not chilled on account of the increase in the petiolar cell length. The area of the first 5 leaves which emerged during forcing were also greater for the chilled plants. This increase, however, was attributed mainly to the increase in the number of laminar cells. Thus, it appeared that strawberry plants without mature leaves might respond to chilling, although it is unknown whether or not the effect obtained was comparable to that expected for the plants with mature leaves.

In the undefoliated plants of which the roots were kept at 26°C during chilling, both the petiole length and lamina area of the leaves which emerged during forcing were greatly inhibited on account of the decrease in the petiolar cell length and laminar cell area, respectively, suggesting that root temperature was an important factor participating in breaking the rest in strawberry plants.

Strawberry plants require a certain amount of low temperatures near the freezing level (chilling) to break the rest (4, 6). In most deciduous trees, the chilling requirement is localized in the bud (7, 9). Differing from deciduous trees, strawberry plants enter the rest without losing their leaves. Thus, there arises a question whether or not the existence of mature leaves might be necessary to break the rest of strawberry plants by chilling. Young and Werner (9) indicated that the exposure of roots to low temperatures was requisite to maximize the budbreak of dormant apple trees. Concerning the importance of root temperatures during chilling, however, there is no information in strawberry plants.

The objectives of this study were to elucidate the chilling effects on breaking rest affected by defoliation before chilling and root temperatures during chilling. The chilling effect is usually evaluated by the petiole elongation and laminar expansion of newly developed leaves under the subsequent forcing conditions. The growth of strawberry leaves is regarded as a function mainly of cell division and cell enlargement (4, 5, 6). Therefore, it was also investigated how the increase in petiole length and laminar area was related to the number of cells and cell size in the petioles and laminae.

Materials and Methods

On September 10, 1991, 'Premier' strawberry plants were planted one per 1 l plastic pot with 5 soil : 3 vermiculite : 2 peat (v/v/v) medium amended with 1.5 g of a controlled release fertilizer (10N-10P_2O_5-10K_2O), and grown in an unheated plastic film greenhouse until the beginning of the experiments. Before experiments, axially buds were removed leaving one just below the primary cluster. Flowers and runners were removed as soon as they emerged.

Experiment 1. Chilling Effect on Breaking Rest in Defoliated Plants.

On November 15, all the leaves were removed in 14 plants, of which the 7 plants were chilled in a growth chamber kept at 5°C in the dark for 35 days and then forced in a growth chamber kept at day/night temperatures of 22°/20°C under a 12-hr photoperiod. The remaining plants were forced immediately from November 15 without chilling. Light in the growth chambers used for chilling and forcing was provided from 6 : 00 to 18 : 00 by 40W fluorescent lamps and 20W incandescent lamps at photosynthetic photon flux of 270 and 10 μmol m^{-2} s^{-1}, respectively, at the leaf surface.

The first leaf which emerged during forcing was designated as L-l, and successively developed leaves were numbered as L-2, L-3, L-4 etc. Five leaves from L-1 to L-5 were harvested when L-5 ceased to expand. The petioles were cut into 3 sections with equal length, and fixed in a FAA solution (5 formaldehyde : 5 acetic acid : 90 50% ethanol by volume). The lengths of 15 epidermal cells on the abaxial side of each section were measured as reported previously (4, 6) and designated as petiolar cell length. The number of epidermal cells along the petiole length (abbreviated as the number of petiolar cells) was calculated by dividing the petiole length by the mean petiolar length. The mean epidermal cell area on the adaxial side of laminae (abbreviated as the laminar cell area) was measured by means of Ishihara *et al.* (3) using the terminal leaflet. The number of epidermal cells of a lamina (abbreviated as the number of laminar cells) was calculated by dividing the lamina area by the mean laminar cell area.

Experiment 2. Chilling Effect on Breaking Rest as Affected by Root Temperature.

On November 20, plants with a single bud were transferred into a growth chamber and chilled at day/night temperatures of 6°/5°C under a 12-hr photoper-

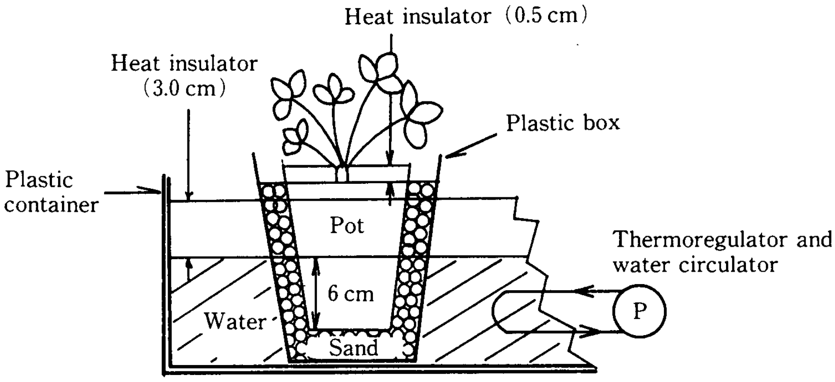

FIG. 1. Schematic diagram of water-bath to control root temperature.

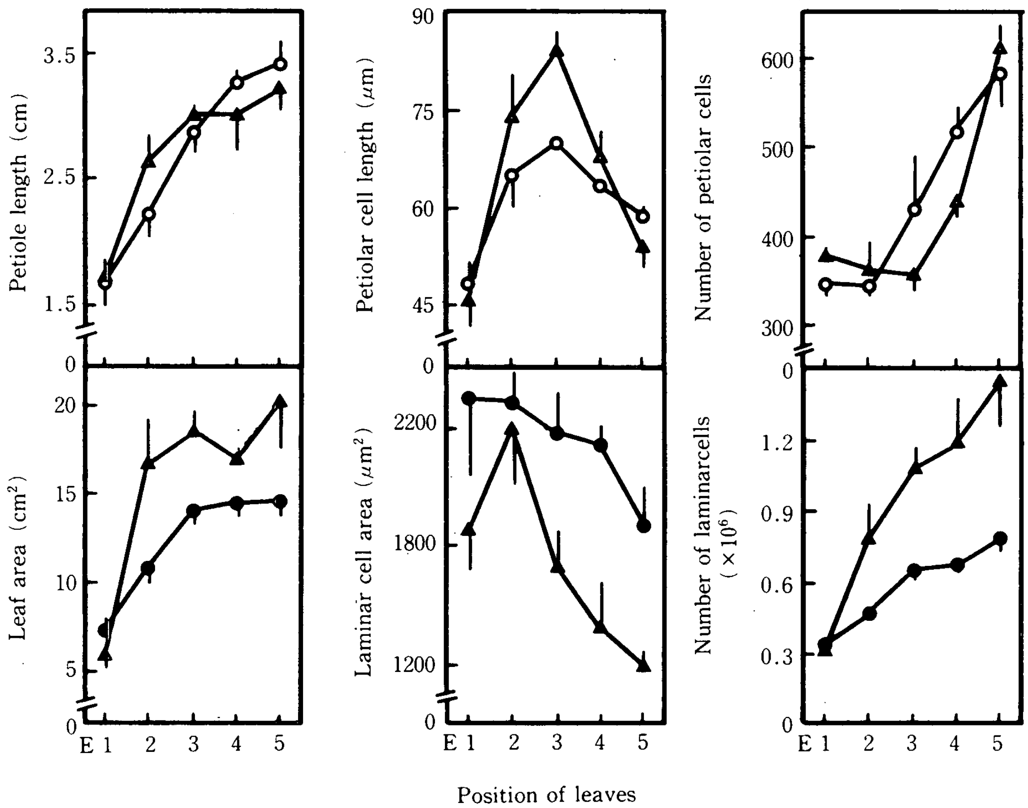

FIG. 2. Growth of petioles, laminae and their epidermal cells of the defoliated plants. Defoliated plants were chilled at 5°C for 35 days and then forced at day/night temperatures of 22°/20°C under a 12-hr photoperiod (△, ▲). Control plants (○, ●) were forced without chilling. The newly-developed leaves during forcing were designated as L-1, L-2, L-3, etc. from the basal one. L-1 to L-5 were harvested when L-5 ceased to expand and their growth was measured. Cell number and cell size were of epidermal cells of petioles and laminae, and values represent means of 7 plants ± SE.

iod for 35 days. They were divided at random into 3 groups of 7 plants. The roots of the 1st and 2nd groups were subjected to 5°C (abbreviated as root-chilled plants) and 26°C (abbreviated as root-heated plants), respectively, during chilling using water baths shown in Fig. 1. Then the plants were forced under the same conditions as in Experiment 1. The 3rd group was forced immediately from November 21 without chilling (abbreviated as unchilled plants). Sampling and measurements were carried out as in Experiment 1.

Results and Discussion

Experiment 1. Chilling Effect on Breaking Rest in Defoliated Plants.

Petioles of L-2 and L-3 of the chilled plants were longer than those of the unchilled plants on account of the increase in the petiolar cell length. The lamina areas of L-2 to L-5 were also greater in the chilled plants. This increase, however, was attributed to the increase in the number of laminar cells instead of in the laminar cell area (Fig. 2 and Fig. 3). Thus, it seems that the presence of mature leaves during chilling is not necessarily required for breaking rest, although strawberry plants during rest usually have several mature leaves. However, it is unknown whether or not the chilling effect obtained in the defoliated plants is comparable to that in the plants with mature leaves, because of the lack of treatment where the intact plants were chilled and then defoliated just before forcing.

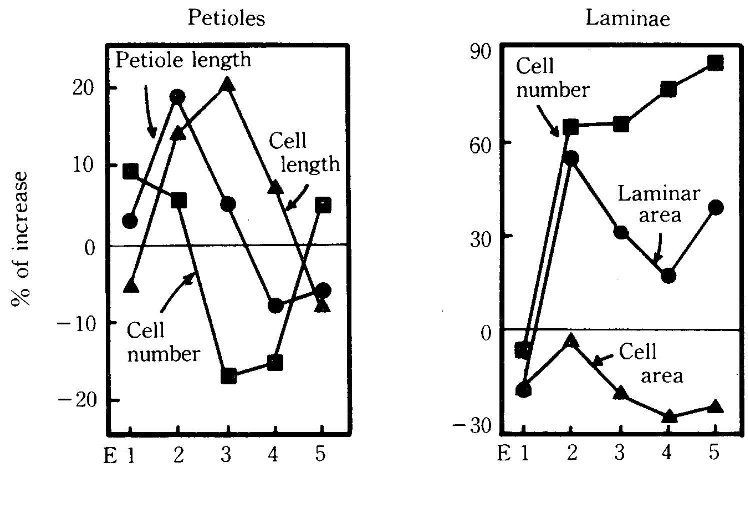

FIG. 3. Percent of increase in the leaf growth of chilled plants over that of unchilled control plants. Calculated from Fig. 2. Cell number and cell length/area are of epidermal cells.

Experiment 2. Chilling Effect on Breaking Rest as Affected by Root Temperature.

In the root-heated plants, a leaf per plant emerged during chilling but did not unfold, hence they were sampled as L-1.

In the root-chilled plants, the petioles of L-1 to L-3 were longer than those of the unchilled plants on account of the increase in the petiolar cell length. The lamina areas of L-2 and L-3 were also greater in the root-chilled plants. This increase, however, was attributed mainly to the increase in the number of laminar cells (Fig. 4 and Fig. 5).

In the root-heated plants as compared with the root-chilled plants and the unchilled plants, the growth of new leaves was inhibited during the subsequent forcing period. The petiole lengths and lamina areas of L-1 to L-5 were often inferior even to those of unchilled plants on account of the decrease in the petiolar

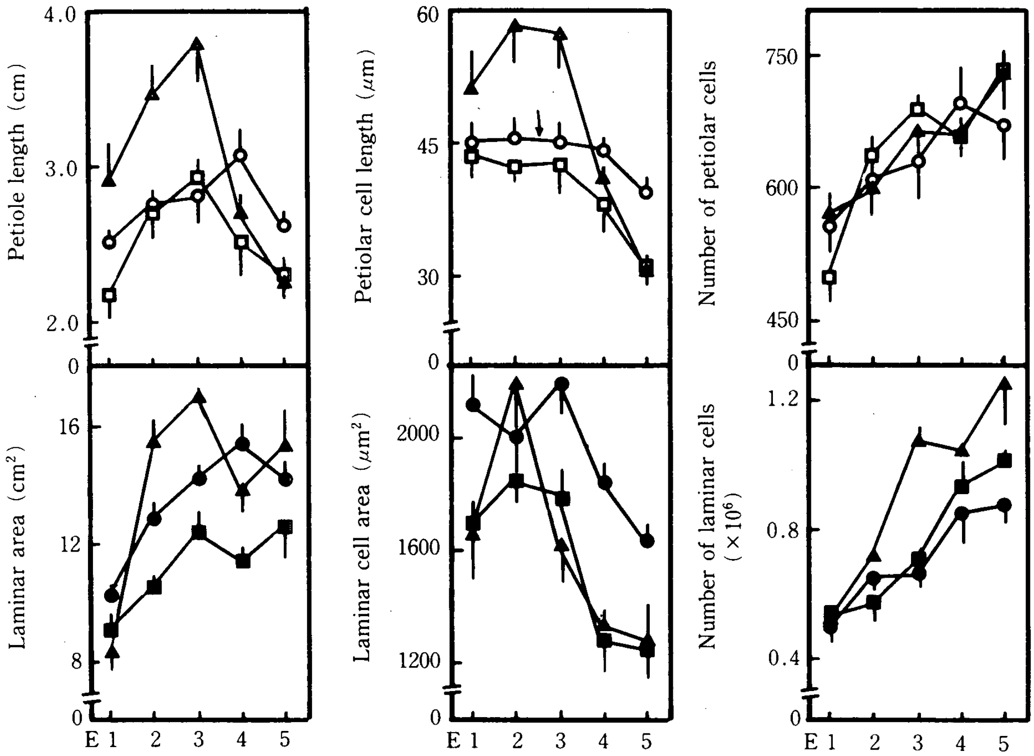

FIG. 4. Growth of petioles, laminae and their epidermal cells of chilled plants as affected by root temperature during chilliing. Plants were chilled at day/night temperatures of 6°/5° under a 12-hr photoperiod for 35 days. During chilling, their roots were kept at 5°C (root-chilled plants, △, ▲) or 26°C (root-heated plants, □, ■) and the plants were forced at day/night temperatures of 22°/20°C under a 12-hr photoperiod. Control plants (○, ●) were forced without chilling. Sampling and mearurement were carried out as in Fig. 2. Values represent means of 7 plants ± SE.

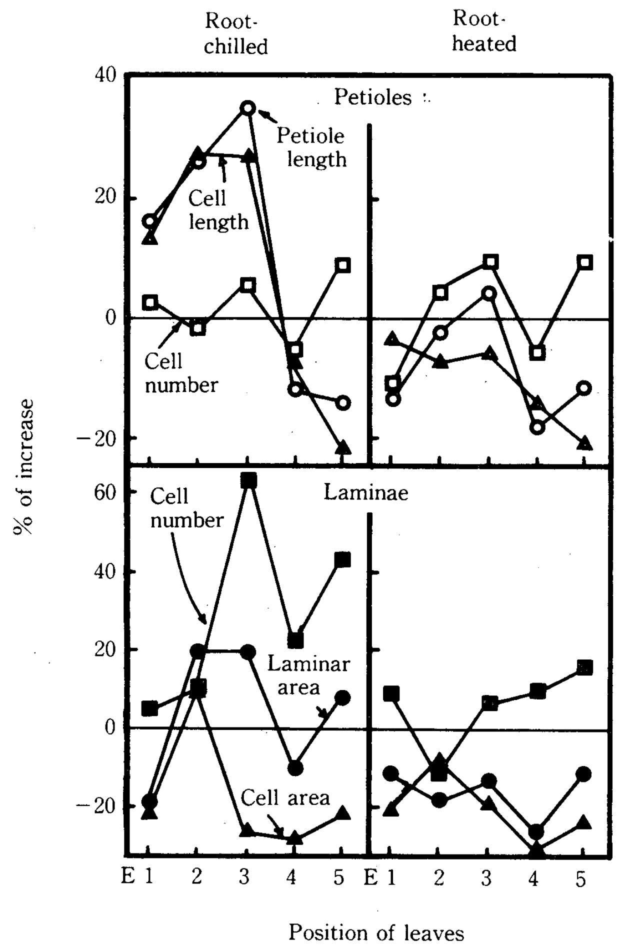

FIG. 5. Percent of increase in the leaf growth of root-chilled and root-heated plants over that of unchilled control plants. Calculated from Fig. 4. Cell number and cell length/area are of epidermal cells.

cell length and laminar cell area, respectively (Fig. 4 and Fig. 5). Thus, the vigorous growth of the root-chilled plants was nullified by the exposure of roots to high temperature during chilling. Consequently, root temperature during chilling seems to be an important factor for the chilling effect to emerge. Similar results have been shown in apple trees, where exposure of roots to low temperature was necessary to maximize the budbreak in next spring. Further, the leaf growth of root-heated plants was inferior even to the unchilled plants. Thus, it appears that the low root temperature is requisite for breaking rest itself or the high root temperature inhibited the subsequent growth by depletion or immobilization of carbohydrates and some endogenous growth regulators involved in rest (7, 8, 9, 10).

The increase in the petiole length of chilled (except root-heated) plants compared to unchilled plants was attributed to the increase in the petiolar cell length, while the increase in the lamina area was attributed mainly to the increase in the number of laminar cells. In strawberry plants, cell division ceases earlier in petioles than in laminae (1, 2). Consequently, it is probable that at the time of chilling, the petiolar cells are about the end of cell division and preconditioned to increase their size (length), while the laminar cells are yet in active division and preconditioned to increase their number by chilling.

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