

イチゴの茎頂切除が腋芽の発達に及ぼす影響

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Effect of Apical Pinching on the Development of Axillary Buds in Strawberry Plants

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Summary

Shoot apices in young, facultative, short-day strawberry plants (*Fragaria* × *ananassa* Duch. cv. Tochtotome) were removed to examine the role of apical dominance in the development of axillary buds into branch crowns and stolons. At planting, plants had 3 fully-expanded leaves associated with visible axillary buds and 2 expanding leaves. Young, expanding leaves were removed along with shoot apices one day after planting. Plants were grown in a glasshouse maintained at 25 °C from 6:00 to 18:00 and 19 °C from 19:00 to 5:00; day length was extended to 15 hr. Within a few days, new stolons were formed on the primary crowns in the intact control plants, whereas new stolons on treated plants formed on developing branch crowns 3 weeks after removal of their apices. Treated plants formed 3 branch crowns, while control plants formed single branch crowns just below the primary inflorescences. The results indicate that the lower axillary buds can develop into branch crowns even under long days and warm temperatures if the buds are released from apical dominance.

Key Words: apex excision, apical dominance, branch crown, *Fragaria* × *ananassa* Duch., stolon.

Introduction

Strawberry plants have compressed stems with short internodes that are called crowns. Axillary buds on the primary crowns become dormant or develop into either branch crowns or stolons, which are prostrate long, modified shoots with 2 nodes. At the bud stage, the first internode of a stolon bud is longer than that of a branch crown bud (Guttridge, 1955).

Stolons are usually formed under long day (Darrow, 1936; Piiriringer and Scott, 1964), warm temperature conditions (Darrow, 1936; Smeets, 1956), or after long periods of chilling (Guttridge, 1958; Kahangi et al., 1992; Piringer and Scott, 1964). Stolons form runners (daughter plants) which are used for vegetative propagation of strawberry plants. Branch crown buds, however, usually differentiate under conditions in which plants produce few stolons, i.e., under short photoperiods (Guttridge, 1985).

In Tochigi prefecture, Japan, strawberry plants derived from runners of a short-day cultivar are grown under a short photoperiod and cool night temperature for more than 3 weeks in summer. These flower-induced plants with 3 to 4 fully-expanded leaves are transplanted in beds in September, and forced into fruiting in December. At planting time in September, small dor-

mant buds differentiate in axils of the fully-expanded leaves. In the middle of the growing period, these dormant buds develop into branch crowns, and not into stolons. Possibly, the release of apical dominance is correlated with the development of the dormant buds into branch crowns. Lateral branch crowns at lower positions on the primary crowns are usually removed because fruit growth is inhibited if many branch crowns are allowed to grow. Removing branch crowns requires more labor than removing stolons. Therefore, it is desirable to make lower axillary buds develop into stolons by controlling environmental conditions, such as day length and temperature. However, it is not clear whether or not the dormant buds have already been destined to develop into branch crowns. The dormant buds at the lower position on the primary crown usually grow out in the middle of growing period, but they can be forced to grow if the apex is decapitated. Therefore, crown apices were removed in this study to test whether or not the lower axillary buds released from apical dominance will differentiate into branch crowns or stolons under long day condition.

Materials and Methods

Runners of strawberry plants 'Tochtotome', a facultative, short-day cultivar, were induced to flower under an 8-hr photoperiod and 13 °C at night from August 17 to September 7, 1999, in the Tochigi Branch Station, Tochigi Agricultural Experimental Station. On Septem-

ber 8, the plants were transplanted to pots (15 cm diam.) containing 1.5 liter of the plant growth medium (Soil Mix, Sakata Seed Co., Yokohama), and transferred to a temperature-controlled glasshouse. The pH of the medium was 5 to 6, and the N, P_2O_5 and K_2O contents were 180, 120 and 220 mg · liter⁻¹, respectively.

The glasshouse was kept at 25/19 °C (day/night). The day temperature was maintained from 6:00 to 18:00; the night temperature was kept from 19:00 to 5:00. Temperatures were shifted between 5:00 and 6:00 and between 18:00 and 19:00. Natural day length was extended to 15 hr by supplemental incandescent lamps (approximately 10 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ at the pot surface) from 4:00 to 6:00, and from 17:00 to 19:00.

At planting, each plant had a primary crown with 3 fully-expanded leaves and 2 expanding leaves. The apex flattened and enlarged into a dome, the first sign that flower induction had occurred (Jahn and Dana, 1970). Plants have 2 types of axillary buds, dormant and

stolon. External bracts completely cover dormant buds, but only the apical portion of stolon buds. As Guttridge (1955) stated, stolon buds are discernible because their first internodes are longer than those of dormant ones. In this study, dormant and stolon buds whose lengths become longer than 1 cm are called branch crowns and stolons, respectively. Bud length is measured from the top to the base of the axis, including immature leaves. At the axil of the fully-expanded leaves, there are 2 or 3 dormant buds or 1 or no stolon bud. The nodes were numbered acropetally; the node at which the oldest leaf is borne at planting is designated as node 1.

Apices were excised just above node 3 using a scalpel from 40 plants one day after planting (pinching treatment); an equal number of plants were left intact (control). Excising apices damages young leaves, and so the remaining 3 leaves were bound with plastic tape to reduce water loss from the wounds. Eight plants were sampled and dissected every 5 to 13 days for a total of 5 times up to 48 days after planting (DAP). On each sampling date, the number of branch crowns, stolons and buds of 8 plants in each treatment group were counted by the naked eye or by using a stereoscopic microscope. For scanning electron microscopic observation, samples were fixed in FAA and dehydrated in a graded ethanol series. Ethanol was replaced with 3-methylbutyl acetate. Samples were dried to a critical point, coated with platinum, and observed with a scanning electron microscope (Model S-4000, Hitachi, Tokyo) at an accelerating voltage of 10 kV.

Results

The scanning electron photomicrograph shows that the primary crown has one leaf primordium with 3 leaflets differentiating in dormant buds at nodes 1 to 3 at planting time (Fig. 1A). The image reveals stolon buds developing on the primary crowns that are surrounded with bracts and leaf primordium of the first runner (Fig.

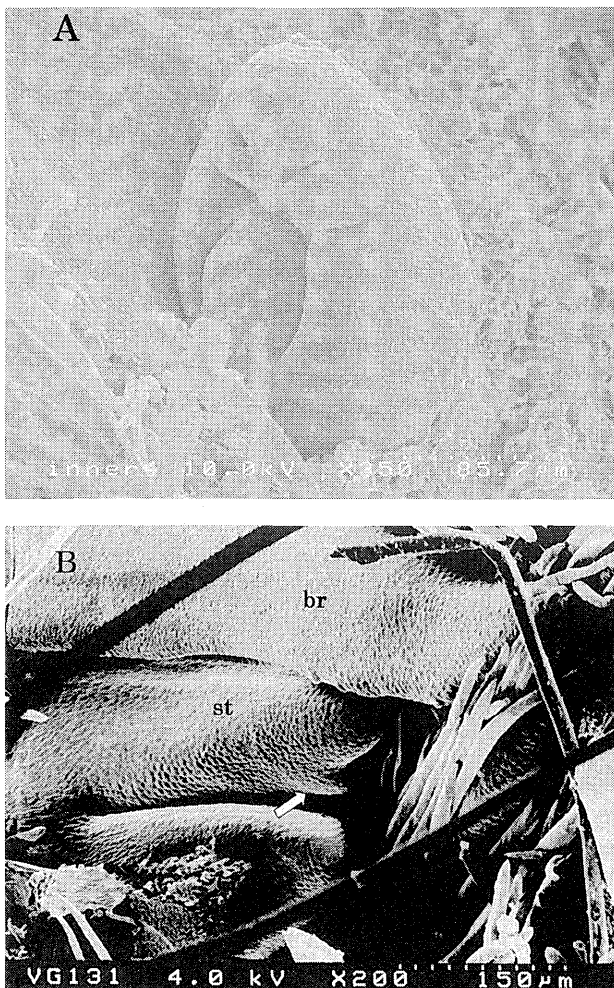


Fig. 1. Scanning electron photomicrograph of apex of an axillary dormant bud at planting (A) and stolon bud developing on the primary crown of control plants (B). The growing point of young stolon (st) is surrounded by bract (br) and the leaf primordium of the first runner (arrow).

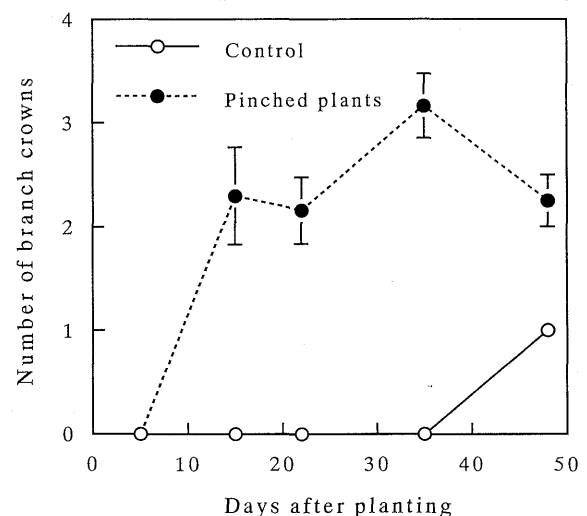


Fig. 2. Effects of excising apices on the number of branch crowns in 'Tochiotome' strawberry plants. Data are means $\pm$ SE (n=8).

Table 1. Effect of removing apices on the length and diameter of stolons on primary crowns four weeks after planting.

Treatment	Stolon length (cm)	Stolon diameter (mm)
Control	31.2 ± 2.2	2.1 ± 0.2
Pinching	9.6 ± 2.4	2.8 ± 0.2

Values are expressed as mean ± SE.

1B). Excising apices affected the growth of axillary buds as more than 2 dormant buds developed into branch crowns by 15 DAP (Fig. 2). On the contrary, each control plant produced a single branch crown just below the primary inflorescence by 48 DAP (Fig. 2). Axillary buds below node 1 did not develop into either branch crowns or stolons by 48 DAP in either control or pinched plants. Apices on newly-developed branch crowns on pinched plants started to flatten into a dome at 35 DAP, a sign that flower initiation had occurred, whereas flower buds were already visible in control plants.

Stolon buds on the primary crowns have elongated internodes so that they were discernible from the dormant buds. These stolon buds in the axils of the fully-expanded leaves at planting developed into stolons 5 days later in control plants, but 15 DAP in pinched plants (Fig. 3A). The stolons on the primary crowns on treated plants were shorter and thicker than those on control plants (Table 1). These stolons sometimes appeared as branch crowns because they expanded only 3 to 5 cm and did not produced any new stolons in the axil of the bract of the second node. On 22 DAP, new stolons grew out from the primary crowns in control plants and from newly-developed branch crowns in pinched plants (Fig. 3A); in the latter less than 0.5 new stolons per plant developed on the primary crowns. Stolon buds that had just started to elongate or ceased to elongate were present in the axil of expanding leaves on primary crowns of control plants. All four stolon buds developed into stolons so that none existed in the control plants at 48 DAP (Fig. 3B). On the contrary, 2 stolon buds on branch crowns developed into stolons in the pinched plants; the other 2 remaining dormant at the end of the experiment. Hence, the numbers of stolons at 35 DAP were 2 in pinched plants and 4 in control plants (Fig. 3A).

Discussion

Apical dominance has been defined as the control exerted by vegetative apical buds primarily over the breaking or sprouting of axillary buds, although floral buds exhibit weak apical dominance (Cline, 1997). Our results reveal that dormant axillary buds can be induced to grow immediately if the flower-induced, terminal apex is removed. Therefore, it appears that flower buds also dominate axillary buds in strawberry plants, at least immediately after flower induction.

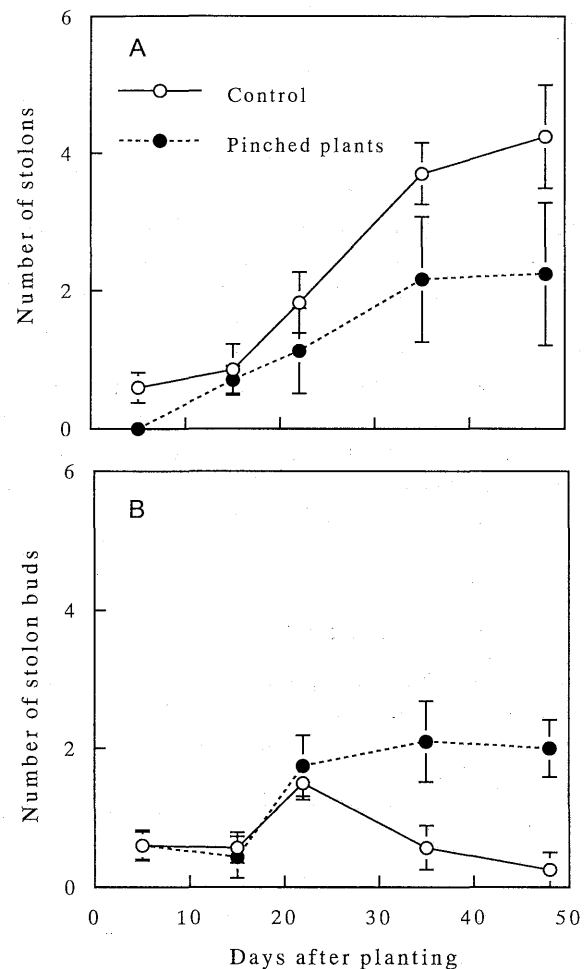


Fig. 3. Effects of excising apices on the number of stolons (A) and stolon buds (B) in 'Tochiotome' strawberry plants. Data are means ± SE (n=8).

Axillary buds become dormant, or develop into either stolons or branch crowns. Guttridge (1955) stated that differentiation probably occurs during the formation of the first 2 nodes. Stolons are usually formed under long day (Piringer and Scott, 1964), warm temperature conditions (Smeets, 1956) and after long periods of chilling (Guttridge, 1958; Kahangi et al., 1992; Piringer and Scott, 1964). This experiment was carried out under long photoperiod and warm temperature, conditions favorable for stolon development, and axillary buds were released from apical dominance by excision of the apices rapidly. These buds developed into branch crowns, supporting the view of Kumar and Wareing (1972) that axillary buds are capable of developing into stolons only when axillary buds are subject to apical dominance in potato plants. This may be the reason why the dormant buds at the lower position of primary crowns develop into branch crowns, and not into stolon, during the middle of a growing period. Furthermore, our findings suggest that it is difficult to regulate the fate of the lower axillary buds by controlling photoperiods and temperatures during their development. Buds are consid-

ered undifferentiated at the 1-leaf primordium stage (Guttridge, 1955), but this assumption has not been tested. Therefore, the possibility exists that the lower axillary buds at the 1-leaf primordium stage have already been predetermined to develop into either branch crowns or stolons, contrary to Guttridge's hypothesis. It is likely that the axillary buds at the lower position were programmed to develop into branch crowns at planting time in this experiment because plants were exposed to an 8-hr photoperiod and 13 °C for 3 weeks.

Furthermore, stolon buds on the primary crowns of pinched plants developed into stolons with thick and short internodes; no new stolons were formed in the axil of the bract of the second node. As a result, these stolons exhibited upright growth, with the appearance of branch crowns, indicating that apical buds play a role in the determination of whether or not axillary buds develop into normal stolons.

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摘 要

腋芽の2次クラウン、ストロンへの発達に対する頂芽優勢の役割を調べるため、一季成り性イチゴ‘とちおとめ’の茎頂を切除した。葉腋に腋芽が見られる完全展開葉3枚、展開中の葉2枚を持つ苗を定植した。定植1日後に茎頂部を展開中の葉とともに除去した。植物体は6時から18時まで25 °C、19時から5時までを19 °C、15時間日長に制御した温室で栽培した。対照の植物体では、定植後数日のうちにクラウンか

ら新しいストロンが発生した。茎頂部を切除した植物体では、切除後3週間目に2次クラウンから新しいストロンが発生した。茎頂部を切除した個体では2次クラウンが3つ形成されたが、対照の個体では第1花房の直下に1つしか形成されなかった。これらの結果は、1次クラウン下部の腋芽は頂芽優勢が破れると、長日、温暖な条件でも2次クラウンに発達することを示唆している。