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Gravitropic Reaction in the Growth of Tea Roots

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Abstract : In Japan, tea (*Camellia sinensis* (L.) Kuntze) seedlings are propagated by cutting. A root system of clonal plants by cutting consists of adventitious roots and lateral roots. Most of the roots grow horizontally, which results in a shallow distribution of the root system. Such a shallow root system could be one of the factors contributing to the deterioration of nutrient uptake and resistance to water stress. Gravitropism of the roots is considered to be a decisive factor that controls the depth of a root system. The authors have investigated changes in the growth direction of roots to gravitative stimulus, using several kinds of roots (seminal roots, lateral roots and adventitious roots). Furthermore, amyloplasts in the root-cap cells, which are considered to be an equipment sensing gravistimulus, were observed. Seminal roots prominently showed orthogravitropism and contained many amyloplast particles in their root cap cells. Most lateral and adventitious roots showed plagiogravitropism, growing in an angle to gravistimulus, and lacked observable amyloplast particles in their root cap cells. The results suggest that the shallowing of root systems of clonal tea plants could be attributed to a gravitropic reaction of the adventitious and lateral roots composing the root system. There could also be a close relationship between the growth direction of roots and the presence of amyloplasts in root-cap cells.
Key words : Adventitious root, Amyloplast, *Camellia sinensis* L., Gravitropism, Lateral root, Plagiogravitropism, Seminal root, Tea plants.

チャの根の生長における重力屈性反応：山下正隆・武弓利雄・佐波哲次（野菜茶業試験場久留米支場）
要　旨：わが国におけるチャの育苗は挿し木による栄養繁殖がほとんどである．挿し木個体の根系は不定根と側根により構成されるが，これらの根のほとんどは水平方向に伸長し，根系の分布を浅くしている．このような挿し木によるチャの根系の浅根化は養分吸収効率，水ストレス抵抗性等を低下させる要因となっている．根系分布の深さを決定する基本的な要因の一つは根の重力屈性であると考えられることから，著者らは種子根，種子根から分枝した側根，褐色の太い木化根に形成された側根および挿し穂から発生した不定根を用いて重力刺激に対する生長反応を調査した．また，根における重力の感知装置とされている根冠細胞内のアミロプラスト粒子の観察を行った．その結果，種子根は明らかな正の重力屈性を示したが，側根，不定根の多くは鉛直方向には伸長せず，重力刺激に対してある角度を保って伸長するといわゆる傾斜重力屈性の現象を示した．さらに，正の重力屈性を示した種子根はその根冠細胞内に多量のアミロプラストを含有したが，傾斜重力屈性を示す側根，不定根の多くが，その根冠細胞内にアミロプラストを観察できなかった．これらのことから，栄養繁殖によるチャの根系の浅根化は根系を構成する不定根，側根の重力屈性反応に大きく依存すると考えられた．また，種子根と不定根，側根の伸長方向の違いには根冠細胞内のアミロプラストの有無との関係が示唆された．
キーワード：アミロプラスト，*Camellia sinensis* L.，傾斜重力屈性，重力屈性，種子根，側根，チャ，不定根．

Tea plants (*Camellia sinensis* (L). Kunze) in Japan are generally reproduced by cutting to keep genetic uniformity. The root system of clonal plants, however, shows significant differences from that of seedling plants. The most remarkable difference appears to be in distribution. Although seedling plants have a deep root system with thick seminal root growing downward no 1 m or greater depth[5], clonal plants have no seminal root but show seven to eight thick adventitious roots growing obliquely[10]. In clonal plants, the change in composition of roots leads to a shallow root system in which most of roots distribute within a range of 30～50 cm in depth[2] (Fig. 1). The change in the root system by clonal propagation could affect the efficiency of nutrient uptake and resistance to water stress. Heavy manuring culture in tea fields[6,7] and severe damage to

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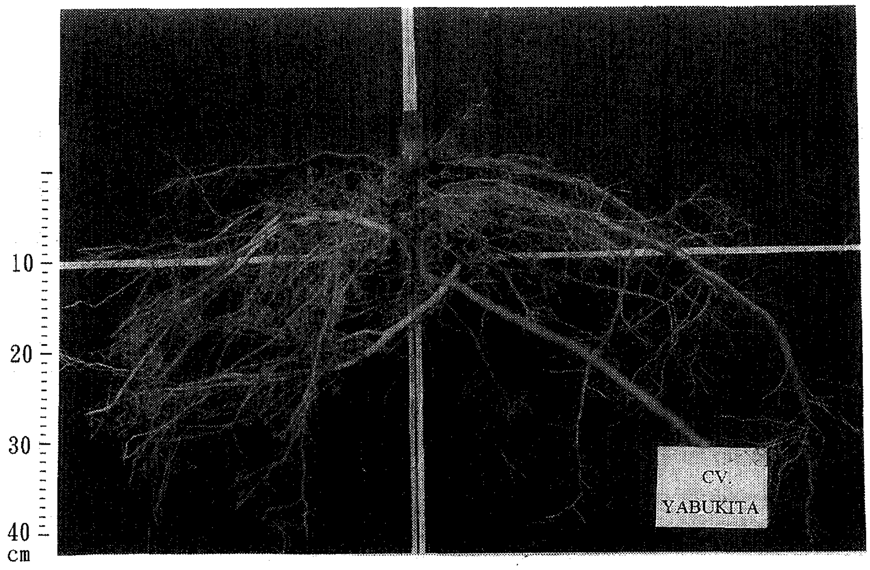

Fig. 1. Root system of a four-year-old clonal tea plant by cutting.
Five to six thick adventitious roots grew almost transversely and most of the roots distributed up to 40 cm in depth.

the root system by the drought in 1995 and 1996[11] are considered to be closely related to the distribution of roots in the clonal plants. Several techniques, such as cutting with nursery pots or vinyl chloride pipes and trenching in fields prior to transplantation, have been invented to promote a deeper root system[1]. Their effects, however, are limited to only young plants. To continuously control the formation of root systems, morphological and physiological approaches to root growth of tea plants are indispensable. The authors have studied the relationship between root variety and gravitropism and considered the relationship between the sensitivity to gravity and the amyloplasts in root-cap cells for several kinds of roots.

Materials and Methods

Experiment I : Growth direction of seminal roots

The seedlings of Chinese variety (cv. Yabukita) and Assam variety (Ai37) were used. Two seeds each were sown in 10 transparent acrylic root boxes (length : 200×width : 200× depth : 20 mm) filled with wet vermiculite in late May 1995. The plants were grown under room temperature. The angle to the gravitative direction and length of each seminal root were measured 2 weeks after rooting. Thereafter, the box was laterally turned by 90° and an angle of roots to the direction of gravity and length were measured 2 weeks later (Fig. 2). The root boxes were covered with aluminum foil during the experimental period to shade the roots.

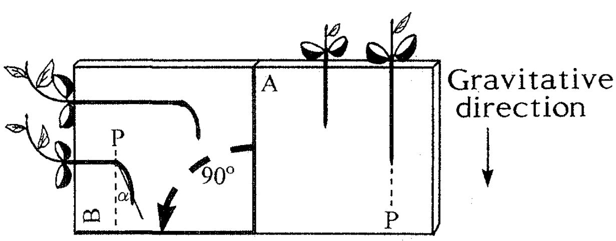

Fig. 2. Diagram showing root box turning and change in direction of gravistimulus affecting roots by turning.
A : Growth direction of roots before turning a root box by 90°. B : Growth direction of roots after turning a root box by 90°. α : Angle to the perpendicular line (P).

Experiment II : Growth direction of lateral roots on a seminal root

The seminal roots of Chinese and Assam varieties that were grown in L-shape in Experiment I, at which no lateral roots were initiated yet, were used for the experiment. Twenty seminal roots were replanted in transparent acrylic root boxes (length : 200×width : 200× depth : 20 mm) in late June 1995 after they were removed the tips by about 10 mm in length. The seedlings were grown under room temperature. Lateral roots formed on seminal roots were classified into 4 types (A-D) according to the site of their initiation (Fig. 3). The angle of lateral roots to the gravitative direction and length were measured 2∼3 weeks after rooting. Thereafter, the root boxes were laterally turned by 90° and the angle of roots to the gravitative direction and length were measured 2∼3 weeks later. The root boxes were covered with aluminum foil during this period.

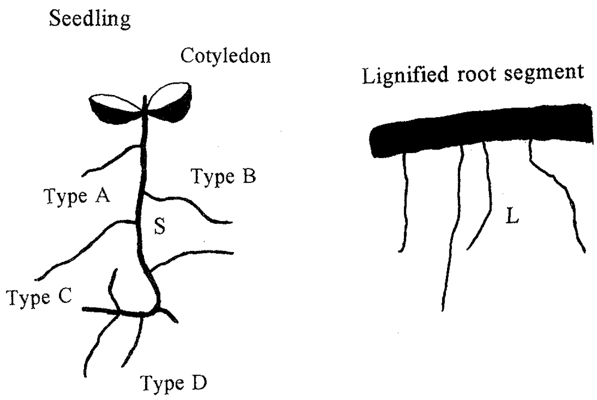

Fig. 3. Seminal and lateral roots exercised in the experiments.
S indicates a seminal root bending to L-shape through growth reaction in Experiment I. Type A-D roots show lateral roots newly initiated on seminal root removed about 10 mm of the tip just after Experiment I. L shows a lateral root initiated on a lignified root segment incubated with wet vermiculite.

Experiment III : Growth direction of lateral roots on lignified roots

Twenty segments of lignified roots (5～7 mm in diameter and 50 mm in length) were sampled from 3-year-old plants of Chinese variety (cv. Yabukita) in August 1995. Each segment was horizontally placed in a transparent acrylic root box (length : 200×width : 200×depth : 20 mm) filled with wet vermiculite and kept at room temperature. The angle of the lateral roots on the segments to the direction of gravity and the length were measured 3 weeks after rooting. Thereafter, the boxes were laterally turned by 90° and the angle of the lateral roots to the direction of gravity and the length were measured 3 weeks later. The root boxes were covered with aluminum foil during this period.

Experiment IV : Morphology of root-cap cells

The seedlings, cuttings and 3-year-old clonal plants of Chinese variety (cv. Yabukita) were used. About 40 seeds and 15 segments of lignified roots of 5 cm in length obtained from the root systems of clonal plants were incubated using wet vermiculite under room temperature from July to August, 1995. Cuttings were rooted in a nursery bed during the same season. When each young root grew sufficiently, about 3 mm of root tips were cut from seminal roots, lateral roots and adventitious roots of cuttings. They were sliced longi tudinally to a thickness of 30 μm with a microtome without being fixed and immediately stained by an iodine potassium iodide solution. The sections showed amyloplast particles in the cells with an optical microscope (×40 -1000).

Results and Discussion

Experiment I : Growth direction of seminal roots

Seminal roots of Chinese and Assam varieties grew almost vertically not only in the early stage of growth but also in the latter stage after turning a box by 90° during growth. When the direction of gravistimulus affecting the roots changed, they immediately reacted toward the gravistimulus and tilted toward the gravistimulus in 12 hours (Table 1). This growth reaction, showing the strong orthogravitropism, indicated that the seminal roots of tea seedlings have a high sensitivity to gravistimulus. The marked orthogravitropism of the seminal roots was considered to be an essential factor to also determine direction of root growth in tea plants. The deep root system of the seedling plants could be attributed to the orthogravitropic property of the seminal root.

Experiment II : Growth angle of lateral roots on a seminal root

The lateral roots were initiated on various

Table 1. The length and growth angle to the gravitative direction of seminal roots.

Variety	Length 1	Angle 1	Length 2	Angle 2
Assam	47.2±15.1	11.0±8.9°	27.2± 9.5	11.2±7.1°
Chinese	41.4±14.9	12.1±8.8°	37.6±12.7	10.1±8.6°

Values are means of 20 roots±S.D.
Length 1 : Length of roots before turning (mm).
Length 2 : Length of roots after turning (mm).
Angle 1 : Growth angle before turning.
Angle 2 : Growth angle after turning.

parts of a seminal root. They were grouped into 4 types (A–D) according to parts initiated on an L-shaped seminal root. The type A roots were initiated on the lateral face of a vertical axis and grew toward gravistimulus after reorientation. The type B roots were initiated on a lateral face of the vertical axis and grew against gravistimulus after reorientation. The type C roots were initiated on the upper side of transversal axis and grew horizontally after reorientation. The type D roots were initiated on the lower side of the transversal axis and grew horizontally after reorientation. Each type of lateral root elongated by 10～30 mm in the early stage, and by 5～20 mm in the latter stage of the experiment (Table 2). Among all root-types, type D roots were most numerous (Table 2). The phenomenon was more definite in the Chinese than the Assam variety and suggested that the lower side of the horizontally growing roots was the most active part of the lateral-root formation. The lower side facing the gravistimulus might be favorable in the distribution of hormones relative to initiation of the lateral roots.

The Lateral roots on the seminal roots demonstrated a different reaction to gravistimulus according to their types (Table 3). Type A and B of the lateral roots grew at a 50～60° angle in the gravitative direction for the first 2 weeks. Type C roots grew at an angle of 100～110° for the first 2 weeks. Meanwhile, type D roots grew at an angle of about 16° near the gravitative direction for the first 2 weeks. When they were reoriented after 2 weeks, the type A roots grew at an angle of about 20° to the gravitative direction with regard to the Chinese variety, but at about 80° for the Assam variety as if the roots were against the gravistimulus. The type B roots grew at about 60° for the Assam variety, and at about 130° for the Chinese variety as if the roots of both varieties did not sense the change in the gravitative direction. Type C and type D roots grew at about 100° and 70° in both varieties, respectively.

The results suggest that gravitropism of lateral roots was different from that of the seminal roots. The phenomenon of roots growing at a certain angle to the gravitative direc-

Table 2. The number and length of lateral roots on seminal roots.

Type of lateral roots	Assam variety			Chinese variety		
	Number	Length 1	Length 2	Number	Length 1	Length 2
A	34	11.9±5.1	4.8± 4.2	31	26.8±14.4	14.3±14.3
B	38	13.7±7.5	6.0± 5.8	20	26.7±14.1	10.8±11.2
C	32	9.9±4.7	7.4±10.0	21	24.8±12.7	13.0± 6.0
D	50	11.1±5.6	8.1±10.0	73	34.8±17.7	23.6±20.8

Values are means±S.D.
Length 1 : Length of roots before turning (mm).
Length 2 : Length of roots after turning (mm).

Table 3. Growth angle to the gravitative direction of lateral roots on seminal roots.

Type of lateral roots	Assam variety		Chinese variety	
	Angle 1	Angle 2	Angle 1	Angle 2
A	50.8±23.9°	80.4±35.4°	66.9±17.7°	22.9±14.7°
B	53.4±15.7°	62.5±21.6°	59.3±14.9°	126.6±31.2°
C	114.2±27.3°	98.6±32.2°	108.6±25.3°	105.7±33.5°
D	15.3±11.3°	65.9±24.7°	17.4±12.2°	70.2±21.3°

Values are means±S.D.
Angle 1 : Growth angle before turning.
Angle 2 : Growth angle after turning.

tion is known as plagiogravitropism[4]. Growth reaction of lateral roots that seemed less sensitive to gravistimulus was considered to be an example of plagiogravitropic phenomena. Furthermore, the formation and gravitative reaction of lateral roots seemed to differ genetically between the Chinese and Assam varieties.

Experiment III : Growth direction of lateral roots on segments of lignified roots

Lateral roots produced on the lower side of the lignified roots which grew downward at 20° for the first 3 weeks and grew at an angle of about 80° after they were oriented horizontally (Table 4). Although the lateral roots grew toward gravistimulus in the early stage, they did not react sensitively to a change in the gravitational direction inducing by root-box turning as well as the lateral roots on the seminal roots. This growth reaction also seemed to show plagiogravitropism of the lateral roots.

Experiment IV : Morphology of the root-cap cells

Amyloplasts in the root-cap cells of the seminal roots, lateral roots on the seminal roots, lateral roots on thick lignified roots and adventitious roots of cutting could be observed with a optical microscope (Table 5). Root-cap cells of the seminal roots contained a large number of amyloplast particles. The particles were relatively large and distributed in the colmela cells and neighoboring cells (Fig. 4). Lateral and adventitious roots were 1 mm or less in diameter. Many of the lateral roots and adventitious roots lacked amyloplast particles in their root-cap cells. Furthermore, the particles were much smaller than those in the root-cap cells of seminal roots (Fig. 5). Amyloplast particles in root-cap cells are considered to be an equipment sensing gravistimulus in the roots of many higher plants[3,8,9]. Therefore, the strong orthogravitropism that was observed in the seminal roots was considered to be caused by a large number of amyloplast particles in their root-cap cells. While many lateral roots showing plagiogravitropism contained no observable amyloplast particles in their root cap cells. These results implied

Table 4. The length and growth angle to the gravitative direction of lateral roots on lignified root segments.

Number	Length 1	Angle 1	Length 2	Angle 2
26	24.8±12.3	17.3±12.4°	6.8±7.8	77.0±16.6°

Values are means±S.D.
Length 1 : Length of roots before turning (mm).
Length 2 : Length of roots after turning (mm).
Angle 1 : Growth angle before turning.
Angle 2 : Growth angle after turning.

Table 5. Relationship between variety of roots and amyloplasts in root cap cells.

Variety of roots	Diameter (mm) Base	Diameter (mm) Apex	The rate of roots without amyloplasts
Seminal root	—	1.26±0.18	0 % (n=43)
Root 1	0.48±0.11	0.38±0.03	92 (n=81)
Root 2	1.06±0.14	0.68±0.15	82 (n=20)
Root 3	—	—	72 (n=25)
Root 4	0.88±0.02	0.56±0.12	37 (n=70)

Values of diameter are means±S.D. (n=15).
Root 1 : Thin adventitious roots on cuttings.
Root 2 : Thicker adventitious roots on cuttings.
Root 3 : Lateral roots on seminal roots.
Root 4 : Lateral roots on lignified roots.
Number in parenthesis shows the total number of roots observed.

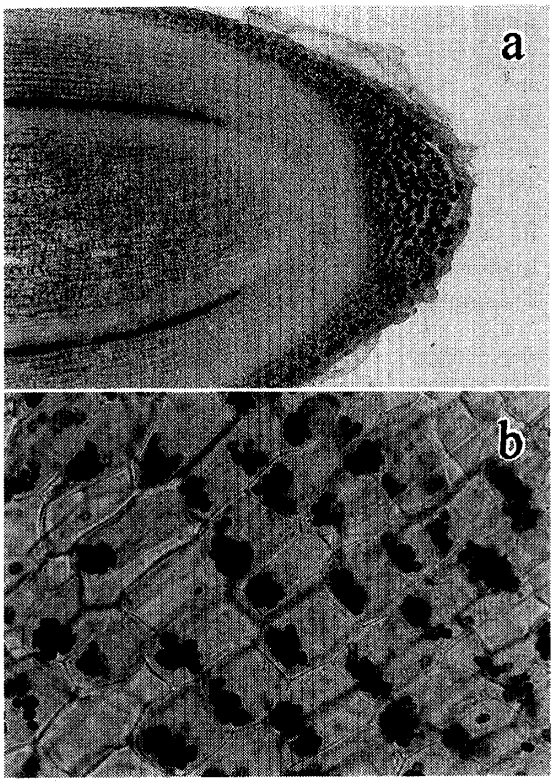

Fig. 4. Root cap cells of a seminal root.
Black particles in cells are amyloplasts.
a : Top (×25), b : Bottom (×250).

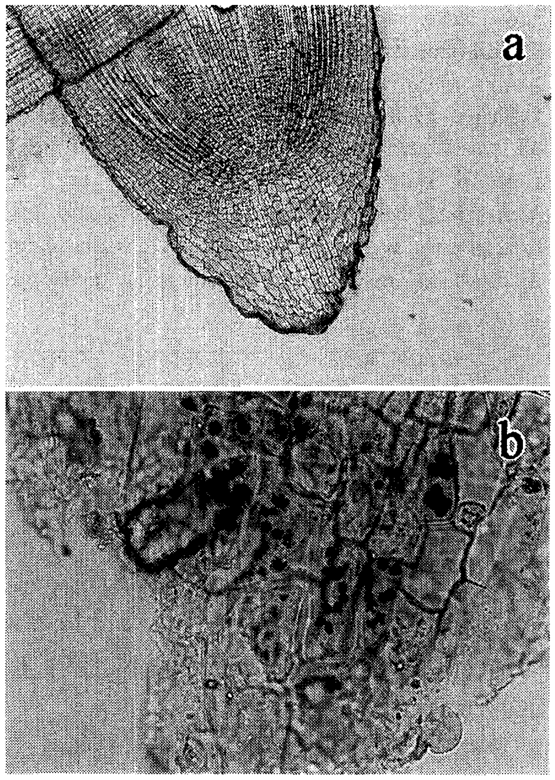

Fig. 5. Root cap cells of a lateral root produced on a seminal root.
Black particles in cells are amyloplasts. A lateral root (a) contains no amyloplasts particles in the cells and other lateral root (b) contains amyloplasts.
a : Top (×50), b : Bottom (×250).

that there was a close relationship between plagiogravitropism and the presence of amyloplast in the root-cap cells. Moreover, the results that many adventitious roots did not contain observable amyloplast particles in their root cap cells suggested that they could also show plagiogravitropic growth as well as the lateral roots.

Seedling plants having a seminal root with strong orthogravitropism construct a deep root system. On the contrary, clonal plants with plagiogravitropic lateral and adventitious roots construct a shallow root system. However, the manifestation of plagiogravitropism in lateral and adventitious roots seemed to be changeable depending on various growth conditions of the roots. It might be indispensable for controlling the formation of the root system of clonal tea plants to clarify the mechanism of plagiogravitropism in roots.

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* In Japanese with English abstract.
** In Japanese with English summary.
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