STUDIES ON THE DORMANCY OF TEA SHOOTS.
2—ROOTS AS THE SOURCE OF A STIMULUS ASSOCIATED WITH THE GROWTH OF DORMANT BUDS

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Six-month-old plants of clone TRI 2023 having either active or dormant terminal buds were used in intra-clonal reciprocal top-grafts in an attempt to study shoot growth and dormancy in tea. It was shown that plants having actively growing terminal buds supplied a stimulus from the roots, which caused early growth of dormant buds, increased the number and size of leaves and produced longer internodes in grafted scion shoots. This response was observed eight weeks after grafting.

The results also suggested that roots may differ in their activity like shoots and this may have a controlling influence on shoot growth. Discussed in the light of other work, the results suggested that a component of the root-stimulus may be hormonal in nature.

In a previous paper Kulasegaram (1969) reported some observations on the sequence of growth and dormancy in free-growing tea plants. He showed that certain classes of growth regulators such as the kinins (kinetin and adenine) and gibberellins (gibberellic acid) when applied to dormant terminal buds of free-growing shoots caused earlier growth compared with untreated dormant buds.

It has been reported by Bond (1943 ; 1945) that restriction of the supply of nutrients to the growing apex interrupted the sequence of the production of leaf initials resulting in dormancy. Bond arrived at this conclusion from anatomical studies where he observed poor vascular connections to the growing apex in rapidly elongating shoots. Wight and Barua (1955) reported that the growth in length of the feeder root system in tea exhibits periodicity of growth similar to the top parts of the tea bush and have taken this as indicative of a periodic rise and fall in the uptake of nutrients. Thus, the poor vascular connections below the growing terminal bud and the periodicity of growth of the feeder root system might be controlling factors in shoot growth and dormancy, by way of nutrition. Further, De Haan (1941) has shown that a deficiency of nitrogen prolonged dormancy.

It is now known that the root system in addition to supplying the shoot with nutrients also synthesizes and supplies the shoot with gibberellins, kinins and specific and unspecific growth inhibitors (Carr, Reid & Skene 1964 ; Kende 1964 ; Loeffler & van Overbeek 1964 ; Carr 1966 ; Letham 1967 ; Sitton, Richmond & Vaadia 1967). These substances are known to be transported in the xylem, along with the transpiration stream, and have been detected in the root exudate and bleeding sap of plants. They have also been shown to exert profound morphogenetic effects. Kulasegaram (1969) suggested that in addition to nutrition, hormones may also play an important role in shoot growth and dormancy. If the root system in tea shows periodicity of growth, it is conceivable that the supply of growth hormones, in as much as the supply of nutrients, will also be subject to periodicity.

Morphogenetic changes in plants are generally associated with changes in the type and levels of plant hormones. Various methods have been used to estimate the levels of endogenous hormones in attempts to interpret morphogenetic changes. Grafting is one of the methods employed by plant physiologists as a biological means of demonstrating various hormonal stimuli associated with morphogenetic development (Howard 1949 ; Gregory 1956 ; Okazawa & Chapman 1962 ; Kulasegaram 1966 ; Selman & Kulasegaram 1967).

In the present study an attempt was made using intra-clonal reciprocal top-grafts to see if there was a stimulus associated with shoot growth in tea and if there was one, the source of this stimulus.

Preliminary grafting experiments using plants of clone TRI 2025 with terminal buds in the active or dormant condition indicated that the root system of plants with active terminal buds supplied a growth stimulus that was greater than that supplied by the roots of plants with dormant terminal buds. An indication of the strength of this stimulus was obtained from the growth of the scion in the different graft combinations. The results obtained from further work are presented in this paper.

Materials and methods

Six-month-old plants of the vigorously growing clone TRI 2023 were used in the present study. The plants were raised under standard nursery conditions. The majority of plants had gone dormant at least twice and carried 7-8 leaves at the time of grafting. The plants were selected according to the condition of the terminal bud as either distinctly active or dormant. Top-grafting was carried out at a level on the stem between the second node and the base of the plant, with only the mother leaf being retained on the stock. The scion shoot was taken with three mature leaves below the terminal bud which was either active or dormant depending on the graft combination. The following four combinations of grafts were made :

1 — active scion shoot on a stock which carried an active terminal bud (A/A)

2 — active scion shoot on a stock which carried a dormant (banji) terminal bud (A/B)

3 — dormant (banji) scion shoot on a stock which carried an active terminal bud (B/A), and

4 — dormant (banji) scion shoot on a stock which carried a dormant (banji) terminal bud (B/B).

The plants were grafted on 27th March 1969 and kept in a mist chamber until 13th May, and then transferred to an outdoor nursery. The polythene tapes used to secure the grafts were removed a month following grafting. The grafts were carefully examined and only those that had shown good union were selected for further observation. Growth measurements were periodically recorded.

Perenox was sprayed every fortnight following grafting at the rate of 1 oz per 2 gallons of water to control Blister Blight and Kelthane was sprayed once on 15th April at the rate of 15 fl. oz. per 50 gallons of water to control mites. Fertilizer (T65) was applied on 25th May at the rate of 2 g per plant.

Results

Of a total of 69 grafts made in this instance, only 27 good grafts were obtained. One of the main reasons for the low success was lack of adequate control of watering, which resulted in several shoots dying due to excess moisture. Final records were maintained for the following number of plants :

5 (A/A) ; 10 (A/B) ; 7 (B/A) and 5 (B/B).

In just over 8 weeks from grafting, differences between the four graft combinations were clearly observable. Figure 1 shows the type of differences observed which

FIGURE 1—*Reciprocal top-grafts of plants of clone TRI* 2023. *Left to right: active on active* (A/A); *active on banji* (*A/B*); *banji on active* (*B/A*) *and banji on banji* (*B/B*). *Grafted on* 27th *March* 1969. *Photographed on* 1*st June* 1969.

Note :—The tapes in the figure represent positions of the scion terminal buds immediately following grafting.

confirmed the findings of preliminary grafting experiments mentioned earlier. The black tapes in the figure represent the original positions of the terminal buds immediately following grafting. The lengths above the tapes, therefore, indicate new growth.

Comparing the growth in grafts A/A and A/B it will be seen that the former combination produced shoots with more and bigger leaves and longer internodes compared with the latter graft combination. Furthermore, the terminal bud remained active in graft A/A, while in graft A/B, it had become dormant after producing only three leaves. In the grafts B/A and B/B, it was noted that the dormant terminal bud of B/A resumed growth earlier than that of B/B. The length of the internodes and number of leaves produced were greater in B/A than in B/B. Moreover, the terminal bud remained active in B/A while in B/B, it had already become dormant.

In the graft combinations A/A and B/A, the former produced more growth presumably because of the initial advantage of the terminal bud of the scion being active, while in the latter graft B/A, the scion had to grow out of the dormant condition which probably used up some of the stock stimulus. In grafts A/B and B/B, both scion terminal buds had become dormant and no clear differences could be

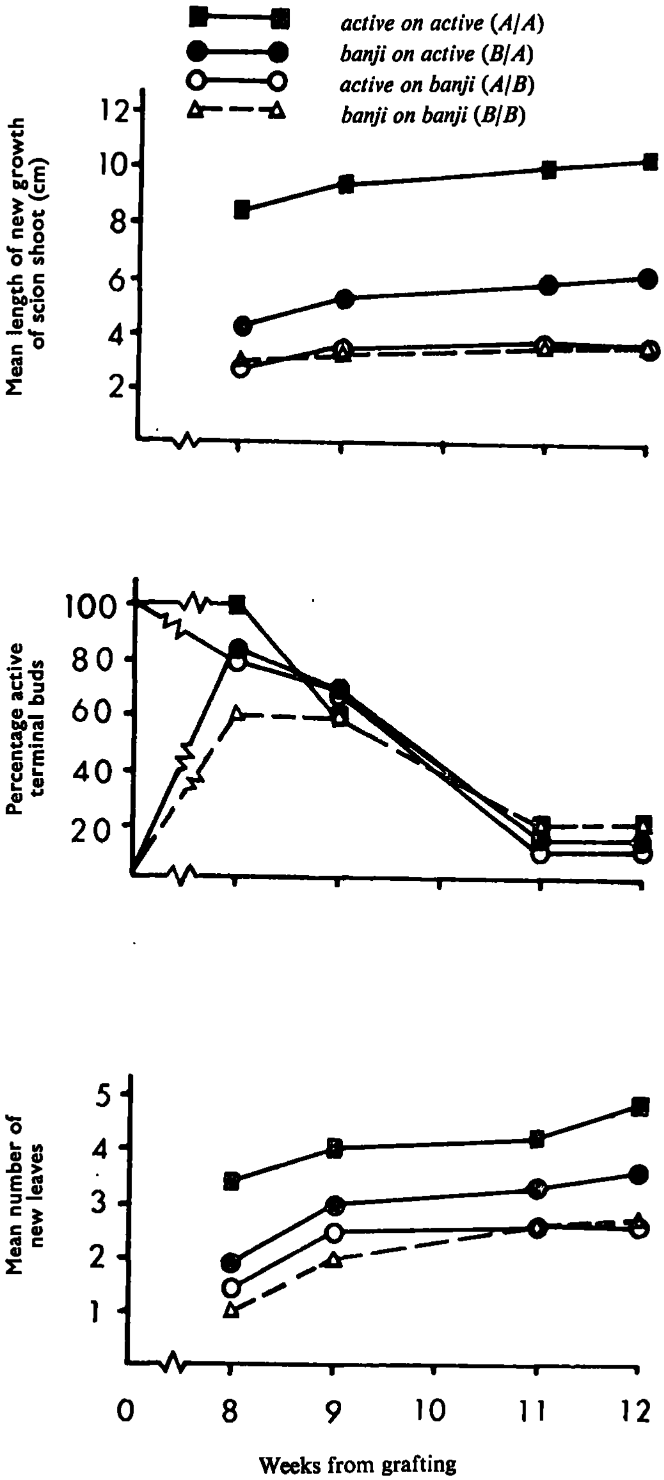

FIGURE 2—*Effect of stock condition on the growth of the scion*

observed although one might have expected growth to be better in A/B than in B/B. Nevertheless, the four graft combinations indicate that the stock which originally carried an active terminal bud produced a stimulus that was greater compared with the stimulus produced by the stock which carried a dormant terminal bud.

An attempt was made to quantify the above effects by observations and measurements of growth periodically. Figure 2 shows the effects produced by the stock on the growth of the scion in respect of mean length of new growth (Fig. 2A), percentage active scion terminal buds (Fig. 2B) and mean number of new leaves produced on the scion shoot (Fig. 2C) over a period of 12 weeks from grafting.

It will be evident from Fig. 2A that by 8 weeks following grafting, when the first measurements were made, the scion shoots in the different treatments had already produced sufficient growth to show the differences due to the stocks. From 8 to 12 weeks following grafting, the growth rates appeared to be maintained at more or less similar rates for the different combinations. It appeared from the above that whatever stimulus that was transmitted from the stock via the grafts to the scion, was supplied within 8 weeks from grafting.

The effects on the percentage of active terminal buds of scion shoots were also evident 8 weeks after grafting, and a week later all combinations showed that the terminal buds were becoming dormant (Fig. 2B). Twelve weeks after grafting, the treatments did not differ appreciably in respect of the condition of the terminal bud.

Fig. 2C again shows a similar trend for the rate of leaf production. By eight weeks following grafting the effects of the grafts were already evident showing that the condition of the stock influenced the growth of the scion.

In Fig. 3, the effects of the graft combinations on length of internodes have been presented in a histogram. Old growth in the scion shoot is represented by internode 1 and 2 and internode 3 and those following represent new growth in the scion shoot. It will be seen that the mean length of the internodes from position 3 to 7 shows a similar trend as seen in the earlier figures.

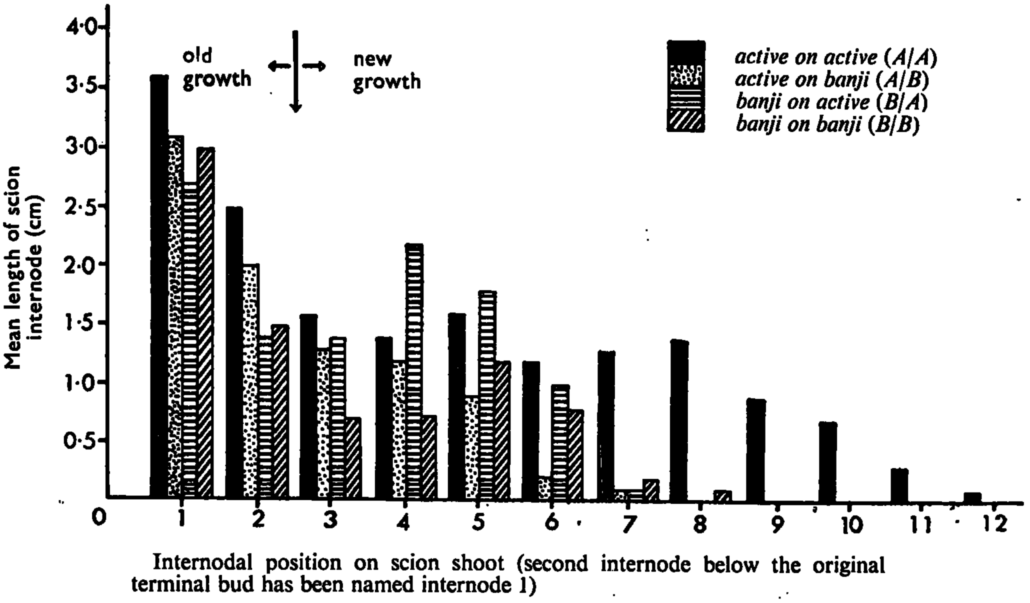

FIGURE 3—*Effects of different graft combinations on the growth of scion internodes. Grafted on 27th March 1969. Growth measurements taken on 25th June 1969.*

Discussion

The results reported in an earlier paper (Kulasegaram 1969) showed that kinins and gibberellins were effective in causing early growth of dormant buds. In addition, it was reported that in free-growing plants there was a definite sequence in the occurrence of 'generalized' dormancy and in the resumption of growth from such dormancy. This indicated that hormones may be involved in shoot growth and dormancy. The pattern of growth showed that apical dominance was least intense when plants commenced growth following 'generalized' dormancy and most intense when the terminal bud of the main axis was growing vigorously. This is reflected in the release and control respectively of terminal and axillary bud growth of the lateral branches.

Current theories on the mechanism of apical dominance in the control of form in plants take into account hormonal as well as nutritional aspects as these appear to be closely linked (Gregory & Veale 1957, McIntyre 1964, Phillips 1968). It is known that growth regulators (*eg* auxins and kinins) can promote the transport of organic and inorganic nutrients towards the site of application and there is evidence for the auxin-directed transport of these towards the main apex (Booth, Moorby, Davies, Jones & Wareing 1962 ; Mothes 1964 ; Davies & Wareing 1965). Cytokinins and gibberellins may also interact with auxins in bud inhibition, growth and other morphogenetic effects (Skoog & Miller 1957 ; Wickson & Thimann 1958 ; Sacks & Thimann 1964 ; Kulasegaram 1966 ; Selman & Kulasegaram 1967 ; Catalano and Hill 1969). These hormones can also influence the accumulation of nutrients (Seth & Wareing 1964).

Auxins are known to be produced in high concentrations in meristematic apices and young leaves, while gibberellins and kinins have been shown to be synthesized in the roots and transported via the xylem to the shoots where they regulate shoot growth. Since resumption of growth from 'generalized dormancy' commences first in the terminal bud of the main axis, it is possible that any root stimulus associated with shoot growth reaches the terminal bud first and only thereafter the buds of the lower lateral shoots. As growth proceeds, greater control is exercised by the terminal bud probably by drawing a greater portion of any root-stimulus and depriving the lateral shoots of same.

Root growth in tea has been shown to be subject to periodicity (Wight & Barua 1955). If this was so, then any stimulus from the roots will also be subject to periodicity. It is conceivable then that there may be times when the roots do not supply this stimulus or supplies limited amounts only, resulting in 'generalized' dormancy. The results of the grafting experiment clearly showed that a stimulus was necessary for the growth of dormant buds and that this stimulus came from the roots of actively growing plants. The roots of plants with dormant terminal buds did not appear to produce such a stimulus. This suggested that the root-stimulus may be subject to periodicity similar to root growth and this may regulate shoot growth.

It must be pointed out that internodal cuttings normally take 4 to 6 weeks in most clones to initiate roots. In preliminary grafting experiments with 18-month-old plants of clone TRI 2025, it was observed that it took about 8 weeks for the grafts to become effective. In this study 6-month-old plants of clone TRI 2023 were used and the grafts became effective in just over 4 weeks. Mention was made earlier of the graft transmission of various stimuli. Withrow & Withrow (1943) reported that the flowering stimulus in Xanthium and soya bean is able to pass a graft union only when phloem connections have been established, while Hamner & Bonner (1938) reported that the stimulus can pass across a barrier of lens paper without actual fusion of tissues. In this study it was shown that at 8 weeks following grafting the effects of the root-stimulus were clearly observable for growth measurements to be made. If the root stimulus is able to pass across a graft only after fusion of the tissues, it will be able to do so in this instance only after four weeks, as this is the minimum period taken for the grafts to become effectively united. If the transfer of the stimulus took place after 4 weeks from grafting, it took only about 3 to 4 weeks then for the stimulus to express its effect on the growth of the scion. It is interesting to note that exogenous application of hormones to dormant buds also takes about 2 to 4 weeks to induce growth.

Previous workers have suggested restricted supply of nutrients as the cause of dormancy (Bond 1942 ; 1945 ; Wight & Barua 1955). De Haan (1941) showed that a deficiency of nitrogen prolonged dormancy. The plants used in the above experiment were regularly manured with T 65 which is considered quite adequate in respect of N, P, K and Mg and it appears unlikely that lack of the above nutrients resulted in dormancy. Nutrient supply to the buds can still be restricted if absorption by roots is affected by periodicity of growth of the feeder roots. While the root-stimulus may have a nutritional component, the results reported indicate that the stimulus may have a hormonal component as well. Since roots are known to synthesize gibberellins and kinins, and in view of the efficacy of these in causing early growth of dormant buds, it appears very tempting to suggest that the hormonal component of the root-stimulus may be the gibberellins and kinins. But since gibberellin analyses did not show marked differences between active buds, buds resuming growth and dormant buds, it appears that kinins rather than gibberellins are more relevant (Kulasegaram 1969).

In this study no attempt was made to examine root-growth or to analyse the root stimulus. No information is available on the endogenous levels of auxins, kinins and inhibitors in the tea plant. These indicate lines along which future investigations may be usefully directed.

Conclusions

1 — A root-stimulus was associated with plants having actively growing terminal buds but not with those having dormant terminal buds.

2 — The root-stimulus caused early growth of dormant buds, produced more and bigger leaves and increased the length of internodes in grafted scion shoots.

3 — The response of this stimulus was observed eight weeks after grafting.

4 — The root-stimulus may have a hormonal component.

5 — The root systems of plants with active terminal buds and those with dormant terminal buds probably differ in activity.

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References

Bond, T. E. T. (1942). Studies in the vegetative growth and anatomy of the tea plant (*Camellia theae* Link) with special reference to the phloem. I. The flush shoot. *Ann. Bot. N.S.* **6**, 607–630.

Bond, T. E. T. (1945). Studies in the vegetative growth and anatomy of the tea plant (*Camellia theae* Link) with special reference to the phloem. II. Further analysis of flushing behaviour. *Ann. Bot. N.S.* **9**, 183–216.

Booth, A., Moorby, J., Davies, C. R., Jones, H. & Wareing, P. F. (1962). Effects of indolyl—3—acetic acid on the movement of nutrients within plants. *Nature, Lond.* **194**, 204-205.

Carr, D. J. (1946). Metabolic and hormonal regulation of growth and development. pp. 253-283. In "Trends in Plant Morphogenesis". Ed. E. G. Cutter. Longmans, Green & Co. Ltd., London. 2nd imp. (1967) 329 pp.

Carr, D. J., Reid, D. M. & Skene, K. G. M. (1964). The supply of gibberellins from the root to the shoot. *Planta* **63**, 382-392.

Catalano, M. & Hill, T. A. (1969). Interaction between gibberellic acid and kinetin in overcoming apical dominance, natural and induced by IAA, in tomato (*Lycopersicum esculentum* Mill. Cultivar Potentate) *Nature, Lond.* **222**, (5197), 985-986.

Davies, C. R. & Wareing, P. F. (1965). Auxin-directed transport of radiophosphorus in stems. *Planta* **65**, 139-156.

De Haan, I. (1941). Deficiency symptoms on tea, caused by an insufficient supply with the most important nutrient elements except potassium. *Arch. Theecult. Ned. Ind.* **15**, 1-32 (Dutch with English summary).

Gregory, L. E. (1956). Some factors for tuberization in the potato plant. *Am. J. Bot.* **43**, 281-288.

Gregory, F. G. & Veale, J. A. (1957). A reassessment of the problem of apical dominance. *Symp. Soc. exp. Biol.* **11**, 1-20.

Hamner, K. C. & Bonner, J. (1938). Photoperiodism in relation to hormones as factors in floral initiation and development. *Bot. Gaz.* **100**, 388-431.

Howard, H. W. (1949). Potato grafting experiments. 1. The effect of grafting scions of Epicure on the short-day species, *Solanum demissum*. *J. Genet.* **49**, 235-241.

Kende, H. (1964). Preservation of chlorophyll in leaf sections by substances obtained from root exudate. *Science* **145**, 1066-1067.

Kulasegaram, S. (1966). Studies in the morphogenesis and developmental physiology of kohl rabi (*Brassica oleracea* cultivar Caulo-rapa). *PhD Thesis*, University of London.

Kulasegaram, S. (1969). Studies on the dormancy of tea shoots. 1. Hormonal stimulation of the growth of dormant buds. *Tea Q.* **40**, (1), 31-46.

Letham, D. S. (1967). Chemistry and physiology of kinetin-like compounds. *A. Rev. Pl. Physiol.* **18**, 349-364.

Loeffler, J. E. & Van Overbeek, J. (1964). Kinin activity in coconut milk. pp. 77-82. In "Regulateurs Naturels de la Croissance Vegetale". Centre National de la Recherche Scientifique, Paris.

McIntyre, G. E. (1963). Mechanism of apical dominance in plants. *Nature, Lond.* **203**, 1190-1191.

MOTHES, K. (1964). The role of kinetin in plant regulation. pp. 131-140. In "Regulateurs Naturels de la Croissance Vegetale". Centre National de la Recherche Scientifique, Paris.

OKAZAWA, Y. & CHAPMAN, H. W. (1962). Regulation of tuber formation in the potato plant. *Physiologia Pl.* **15**, 413-419.

PHILLIPS, I. D. J. (1968). Nitrogen, phosphorus and potassium distribution in relation to apical dominance of dwarf bean (*Phaseolus vulgaris* c. v. Canadian Wonder) *J. exp. Bot.* **19**, (60), 617-627.

SACHS, T. & THIMANN, K. V. (1964). Release of latent buds from apical dominance. *Nature, Lond.* **201**, 939-940.

SELMAN, I. W. & KULASEGARAM, S. (1967). Development of the stem tuber in kohl rabi. *J. exp. Bot.* **18** (56), 471-490.

SETH, A. & WAREING, P. F. (1964). Interaction between auxins, gibberellins and kinins in hormone-directed transport. *Life Sci.* **3**, 1483-1488.

SITTON, D., RICHMOND, A. & VAADIA, Y. (1967). On the synthesis of gibberellins in roots. *Phytochem.* **6**, (8), 1101-1105.

SKOOG, F. & MILLER, C. O. (1957). Chemical regulation of growth and organ formation in plant tissues cultured in vitro. pp. 118-131. In "Symposia for the Society of Experimental Biology XI. The biological action of growth substances". University Press, Cambridge, 344 pp.

WICKSON, M. & THIMANN, K. V. (1958). The antagonism of auxin and kinetin in apical dominance. *Physiologia Pl.* **11**, 62-74.

WIGHT, W. & BARUA, D. N. (1955). The nature of dormancy in the tea plant. *J. exp. Bot.* **6**, 1-5.

WITHROW, A. P. & WITHROW, R. B. (1943). Translocation of the floral stimulus in Xanthium. *Bot. Gaz.* **104**, 409-416.