STUDIES ON THE DORMANCY OF TEA SHOOTS
1—HORMONAL STIMULATION OF THE GROWTH OF DORMANT BUDS

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Observations made on free-growing tea plants indicated that the formation of dormant buds and the resumption of growth of these buds follow a definite pattern suggesting that the change in the condition of the buds is under the control of endogenous growth regulators. This view was supported by the results of experiments in which growth regulators were applied exogenously to dormant buds. It was shown that the gibberellins (gibberellic acid) and kinins (kinetin and adenine) promoted the growth of dormant buds while the auxins (indolyl-3-acetic acid and naphthalene acetic acid) had no effect in stimulating the growth of such buds.

Analysis of gibberellins made in dormant buds, in buds resuming growth from dormancy and in active buds did not show any deficiency of native gibberellins in the dormant buds compared with the levels in the other two types of buds to account for their apparent inactivity. The acidic fraction of the extracts of dormant buds showed greater inhibition than that found in the same fraction of buds resuming growth while the acidic extract of active buds showed no inhibition. The possible significance of this in relation to dormancy has been pointed out and discussed in the light of other studies in the hormonal regulation of morphogenesis.

Dormancy may be defined as a temporary suspension of visible growth. It is convenient here to distinguish between *'physiological dormancy' and 'imposed dormancy'. In the absence of any external factors restricting growth (like low temperature or rainfall), the dormant state of buds may be assumed to be 'physiological'.

Relatively little attention has been devoted to the study of dormancy in the tea plant. Bond (1942) reported in some detail on the anatomy and periodic growth of the young unplucked shoots of the tea bush and in a later paper, Bond (1945) analysed the flushing behaviour in terms of apical activity and primordial growth rate. Wight & Barua (1955) studied the nature of dormancy in the tea bush and introduced the concept of 'dormancy index'—the ratio of the length of the terminal bud to that of the topmost leaf—as a measure upon which the morphological expression of dormancy is dependent. They also showed a high correlation between the dormancy indices of unplucked and plucked bushes suggesting that the changes in the morphological condition of buds in the two sets of bushes proceeded simultaneously in the same direction although the magnitude of the index was reduced as a result of plucking. They concluded that the condition of the buds was presumably caused by factors inherent in the proximal parts of the plant which are plucked. Pethiyagoda (1964) reported some observations in the study of dormancy and suggested that growth regulators and/or inhibitors may be involved. The growth-promoting effect of gibberellin on the growth of tea shoots was reported by Torii & Nakagawa (1960), and Ahmed, Chakraborty & Hasan (1965) showed that low concentrations of gibberellic acid were effective in increasing the height of six-month-old tea seedlings and indicated that gibberellic acid may break dormancy in mature tea bushes and enhance quick flushing of the young shoots.

*Physiological dormancy is used to describe a suspension of visible growth which continues even under a favourable external environment. It is synonymous with the term rest. Imposed dormancy will be used to refer to a cessation of growth caused by unfavourable external conditions. It is used in the same sense as quiescence.

The extent to which dormancy (frequency of occurrence and duration of each dormant phase) affects yield by restricting growth is generally not realized as it is not confined to any particular age of the plant and also the fact that a plant in plucking has several shoots all of which do not generally become dormant (banji) at the same time.

Dormancy can be observed at frequent intervals during the growth and development of the plant and differs only in degree. At the nursery stage, a seven-to eight-months-old nursery plant may generally have gone through about three periods of dormancy producing only about three to four leaves during each of the active growth periods. Nevertheless, this will vary from clone to clone. Aperiodic shoots that are produced following pruning will often produce about 20 to 25 leaves before entering the dormant phase, the duration of which is also much shorter. Plants in plucking will be observed to have a greater proportion of shoots becoming dormant towards the latter stages of the plucking cycle; and even plucking which results in the removal of leaves and buds, including the dormant buds, at this stage does not appear to be effective in inducing the dormant buds to grow out. This is reflected in yields.

The duration of the dormant phase and the frequency of its occurrence are influenced by several factors. Generally, conditions resulting in restricted growth of the plant like the inadequacy of water and of nutrients (Bond 1945) especially nitrogen (de Haan 1941), very low light intensity (dense shade), pest and disease attacks *etc* lead to early dormancy which may persist for prolonged periods, *ie* imposed dormancy. In the absence of severe restricting factors referred to above—physiological dormancy—the dormant phase lasts for about four to six weeks on the average and not infrequently for a longer period. The incidence of dormancy does not, therefore, permit the full growth and cropping potential of the plant to be realised; the limitations set by dormancy to tea yields are not readily apparent except in cases of prolonged periods of dormancy.

Any treatment or cultural operation which can minimize, if not altogether eliminate, the occurrence of dormancy and/or shorten the duration of the dormant phase would, therefore, appear to result in increased growth and probably increased crop. In order to achieve this, it was thought that an understanding of the natural pattern of growth and dormancy in a free-growing plant, which is free from the imposition of complicating factors, may be helpful in formulating a working hypothesis on which subsequent work on physiological dormancy may be developed.

GROWTH PATTERN IN FREE-GROWING PLANTS

Observations made on free-growing tea plants indicate that tea exhibits two unusual growth characteristics:

1 — There is a cyclical growth pattern of individual free-growing (unpicked) shoots consisting of phases of the production of actively-growing buds (flush) alternating with phases of production of dormant buds (Bond 1942).

2 — The dormant phase may occur in all shoots of the plant at the same time or only in some shoots depending on whether the main shoot in a free-growing plant is producing active or dormant buds.

The latter growth characteristic in tea is peculiar in that when a terminal dormant bud becomes an active one, the axillary buds immediately below it, which have remained dormant, also tend to grow out to form axillary shoots. As growth proceeds, the main and lateral shoots grow at different rates, the former dominating the latter.

FIGURE 1—*Eighteen-months-old free-growing clonal plants in polythene bags showing the condition of the terminal buds on the different shoots—Left : generalized dormancy—Right : localized dormancy*

FIGURE 2—*Sequence of bud-break in an eighteen-months-old, free-growing clonal plant following generalized state of dormancy*

FIGURE 3—*Induction of bud-break in clone TRI 2026 by 200 ppm solution of gibberellic acid (GA_3), applied daily for 6 days commencing on 8th January, 1967—Left : Control—dormant shoot—Right : Dormant shoot treated with GA_3—Shoots photographed on 29th January 1967*

After a period of time, when the main shoot is growing vigorously, the terminal buds of the lateral shoots tend to become dormant. Dormancy sets in first in the lowest lateral shoots and progressively affects the upper lateral shoots. Eventually, the growth of the main shoot is also arrested and when it enters the dormant phase, all the terminal buds of the lateral shoots have generally become dormant, so that, when the main shoot has a dormant terminal bud, all the terminal buds of the lateral shoots are also dormant whereas when the main shoot has an active terminal bud, all the buds in the lateral shoots are not necessarily active. This pattern of growth suggests that the factor governing dormancy may sometimes be 'generalized' affecting all the buds in the plant or at other times be 'localized' affecting only some of the buds (Fig. 1). Tea plants in plucking exhibit the latter type of dormancy and rarely, if ever, exhibit the generalized state of dormancy, as operations like bending and the removal of parts of the plant at harvesting or pruning tend to prevent the occurrence of the 'generalized' state of dormancy. Following generalized state of dormancy when growth commences again, the terminal buds of the uppermost shoots first become active, followed progressively downwards by the terminal buds of the lower lateral branches. The activity may or may not extend to the buds of the lowest branch depending on the strength of the stimulus (Fig. 2).

Concurrently, the axillary buds immediately below the terminal buds also begin to grow out. The growth of the buds following generalized dormancy takes place from the top downwards, whereas when dormancy becomes 'generalized' after a period of active growth, the sequence of the shoots becoming dormant (banji) is from the lowest shoot upwards. This observation has not been reported previously. The different tree forms of free-growing tea plants (*eg* seed bearers) is largely attributable to differences in the number of alternating phases of active and dormant periods and the relative rates of growth of the main and lateral shoots.

It appeared from the peculiar nature of growth and the formation of the dormant buds that this phenomenon may be mediated through the action of endogenous growth regulators. A preliminary study was, therefore, made of the effects of exogenous application of selected growth regulators in breaking dormancy.

EFFECT OF EXOGENOUS APPLICATION OF GROWTH REGULATORS

Experiments were carried out using the following growth regulators : gibberellic acid (GA_3), indolyl-3-acetic acid (IAA), both at concentrations ranging from 200 to 800 ppm; naphthalene acetic acid (NAA) as Phyomone at 500 ppm, adenine (AD) at 100 ppm and kinetin (K) at concentrations of 20 to 80 ppm, on different tea clones.

Shoots with dormant terminal buds were selected in bushes which had been previously pruned or in young free-growing plants. Only main shoots arising from the pruned frames were selected and for quantitative studies ten such shoots were assigned to a treatment. The isolated shoots were treated daily for six to eight days with the respective solutions, all of which had a wetting agent (Teepol at 0.05%) incorporated. The solutions were applied to the terminal bud and the two adjoining leaves with a soft brush. When the treatment neccessitated the use of two or more different solutions, they were applied separately at different times in the day.

It was found that GA_3 and combinations of GA_3 and IAA, but not IAA alone, each when used at a concentration of 200 ppm, on clone TRI 2026 caused 100% of the dormant buds to grow in two weeks while the untreated buds showed no evidence of a break in dormancy at that time. Fig. 3 shows the effect of GA_3 in breaking dormancy three weeks from the date of first application. The mean lengths of the terminal bud from the scale-leaf node to the tip of the shoot with the significant difference between treatments (at $P = 0.05$) are given in Fig. 4, for the same clone which

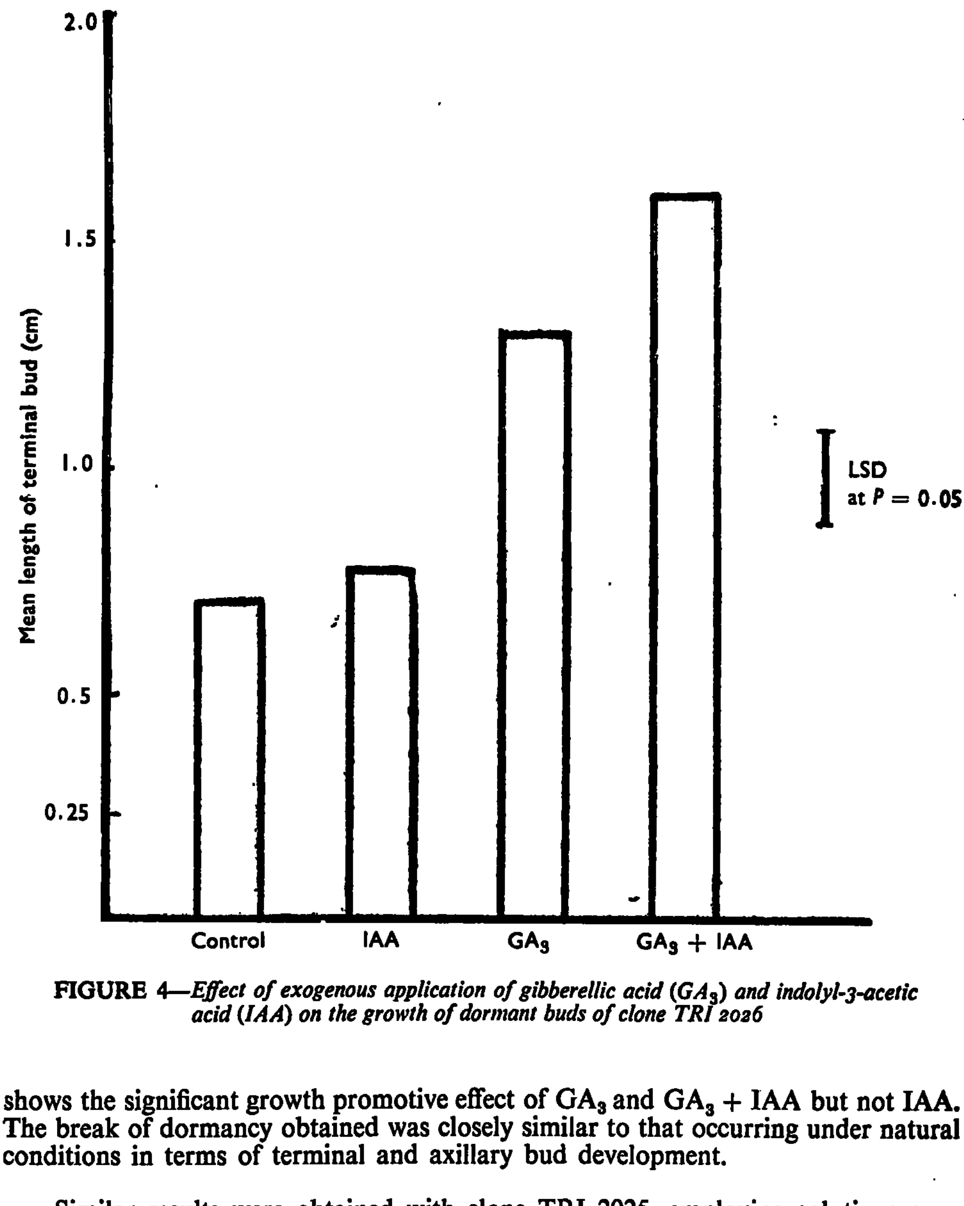

FIGURE 4—*Effect of exogenous application of gibberellic acid (GA_3) and indolyl-3-acetic acid (IAA) on the growth of dormant buds of clone TRI 2026*

shows the significant growth promotive effect of GA_3 and GA_3 + IAA but not IAA. The break of dormancy obtained was closely similar to that occurring under natural conditions in terms of terminal and axillary bud development.

Similar results were obtained with clone TRI 2025, employing solutions containing 800 ppm but the higher concentrations tended to promote greater terminal extension growth at the expense of axillary bud development. Kinetin (80 ppm) applied alone and in combination with GA_3, but not combination with IAA, was also effective in breaking dormancy. The action of IAA was antagonistic to that of kinetin. Comparative effects of these growth regulators on breaking dormancy in clone TRI 2025 are shown in Fig. 5. Adenine was as effective as kinetin but NAA like IAA had no effect on bud-break. Shoots induced to grow actively from the dormant state produced more active buds and the duration of the active phase was generally longer than that of the corresponding control shoots.

Active shoots treated with GA_3 differed from the corresponding control shoots in that they showed greater extension growth with pale green leaves. GA_3 did not promote axillary bud development in active shoots (Fig. 6). GA_3 applications also

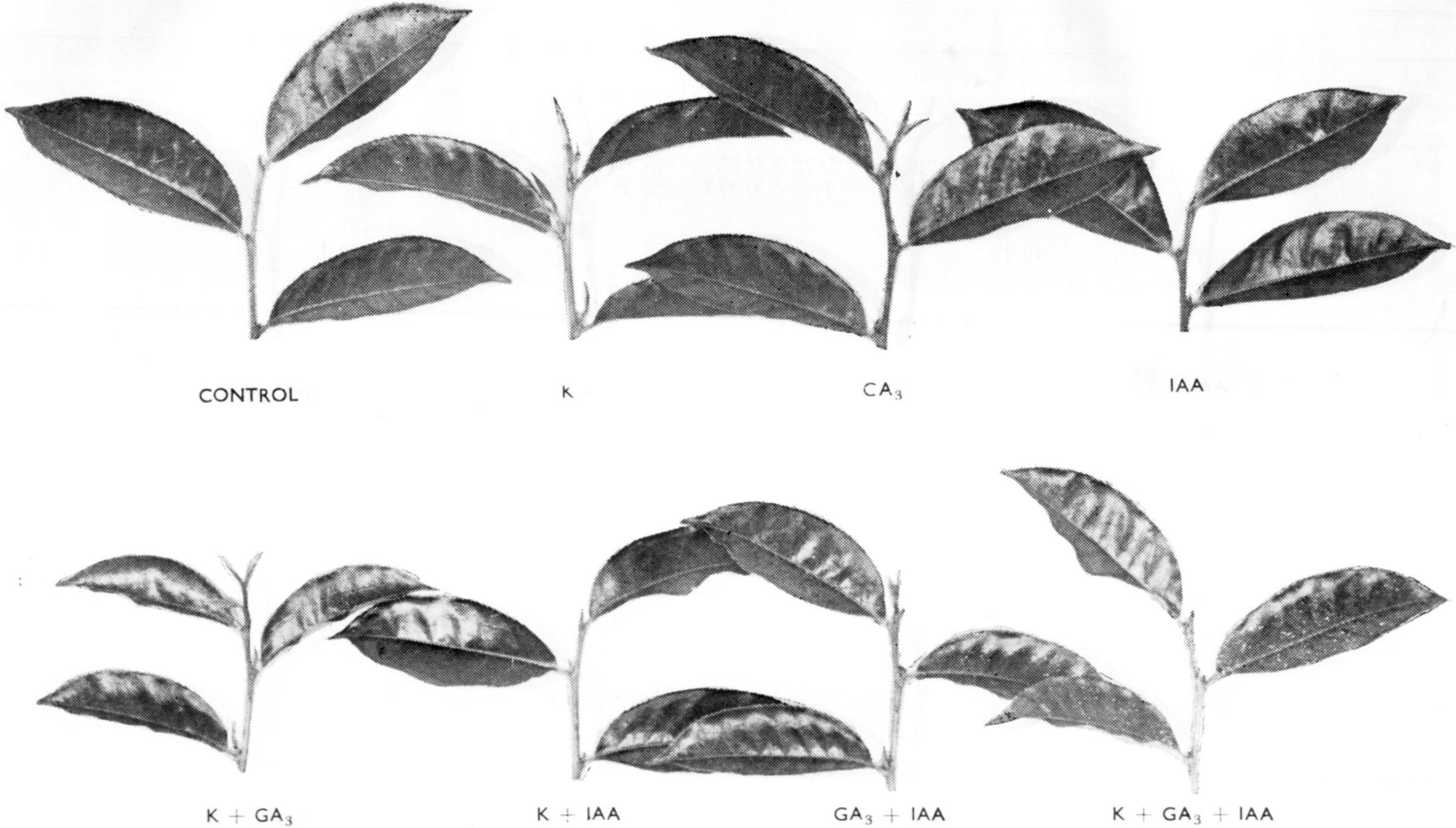

FIGURE 5—*Comparative effects of 80 ppm solution of kinetin (K) and 800 ppm solutions of gibberellic acid (GA_3) and indolyl-3-acetic acid (IAA) applied daily for 8 days commencing on 18th June 1967, on bud-break in clone TRI 2025—Shoots photographed on 15th July 1967*

Initially active shoot

Initially dormant shoot

FIGURE 6—*Active and dormant buds treated with GA_3 (200 ppm)*
Note : *No stimulation of axillary bud growth in active shoot by GA_3*

resulted in increased total fresh and dry weights of actively-growing shoots but these had a lower percentage dry weight *ie* GA_3 increased the moisture content of the tissues. Treated shoots tended to wilt on dry days more readily than the untreated shoots. The moisture content of actively-growing shoots is normally greater than that of dormant shoots.

Following the observations made on the sequence of bud-break from a generalized state of dormancy in a free-growing plant, it was of interest to see if localized applications of growth regulators to the terminal buds of the main or lateral shoots at various positions on the main axis will be able to reverse the natural sequence of budbreak.

Eighteen-to 24-months-old clonal plants which had all the buds dormant were selected and terminal buds at various positions were treated. It was found that when GA_3 or AD solutions were applied, the treated buds resumed growth earlier than the terminal bud in the main axis irrespective of its position. Application of GA_3 to any terminal dormant bud in the plant was effective in breaking all the dormant buds indicating its ease of mobility in the plant but as referred to earlier, application of higher concentrations of GA_3 (500 to 800 ppm) to a dormant terminal bud in a lateral shoot while breaking dormancy and forcing terminal growth generally tended to inhibit the development of the axillary buds immediately below in that shoot, but stimulated growth of dormant buds in shoots above and below the treated shoot. Lower concentrations of GA_3 (100 to 200 ppm) did not have the inhibiting influence on axillary bud growth and permitted their growth.

Adenine (100 ppm) appeared to be as effective as GA_3 but showed limited mobility in the plant. The vigour on axillary bud growth was greater when a kinin (AD or K) was used, than when GA_3 was used and more closely resembled that occurring under natural conditions.

ANALYSIS OF GIBBERELLINS IN SHOOTS

No information is available on the concentrations of native hormones in tea shoots. In view of the efficacy of exogenously applied GA_3 in breaking dormancy, it was thought that an analysis of the levels of endogenous gibberellins in dormant buds, in buds growing out of dormancy and in actively growing buds, may help resolve the question of the mechanism of dormancy. Analysis was, therefore, done for gibberellins in clone S 106 for the three types of buds. Samples of buds for analysis (50 g) were taken with the two adjoining leaves. The extracts from each of the three samples were partitioned into the acidic, neutral and basic fractions (Pegg 1966), chromatographed in iso-propanol: ammonia: water (10:1:1) and assayed for activity using the lettuce hypocotyl assay technique (Frankland & Wareing 1960). There did not appear to be any marked difference in the overall levels of endogenous gibberellins in the three samples of buds analysed. The acidic fractions of all three samples showed acitvity over a range of *Rf* 0.2 to 0.6 equivalent to about 0.1 ppm of authentic GA_3. There was a greater amount of inhibition in the dormant buds than in the buds resuming growth while the active buds showed no inhibition at all. The inhibition was observed at *Rf* 0.1. Further work is necessary to discriminate between its toxic effects and any possible regulatory function. An analysis of auxins and inhibitors may shed light on this aspect of work.

The neutral fractions showed lesser overall gibberellin activity over a similar range of *Rf* as in the acidic fractions but again no differences could be observed between samples. There was relatively little promotive activity in the basic fraction which showed marked inhibition in all three samples to the same extent at *Rf* 0.6 to 0.8. Whether the inhibition observed is physiologically significant is doubtful because of the toxic symptoms observed in the lettuce plants. This was presumably because of the basic polyphenols which are present in high concentrations in tea shoots. As all the samples showed inhibition to similar extents, it may not have much significance. Gibberellin analysis, therefore, did not show any marked difference between the samples that could account fully for the differences in activity of the three samples of buds. Nevertheless, the inhibitory effects are interesting; and may be worth following. They may possibly explain the setting of dormancy. A search will have to be made for the other classes of important growth regulators, the *kinins, which are known to stimulate bud initiation and growth amongst other things. This view is supported by the fact that kinins (kinetin and adenine) are both effective in breaking dormancy. Although these synthetic kinins are less mobile in the plant it is probable that native kinins will have greater mobility and, therefore, a wider range of efficacy. There is evidence to show that native inhibitors (*eg* dormin) an be antagnoised by kinins and gibberellins.

DISCUSSION

The observations made on the natural sequence of growth and dormancy in free-growing tea plants indicate that there is a regulatory mechanism which appears to be hormonal in nature. Bond (1945) observed that there was a reduction in the vascular tissue below the growing point of rapidly-elongating periodic tea shoots and concluded that restricton of the supply of nutrients to the apex interrupts the sequence of the production of leaf initials which results in dormancy. Wight & Barua (1955) point out that whilst this may be the immediate cause their results suggest that a more remote cause has to be considered. It is generally agreed that there is a close interdependence between the shoot system and the root system and any prolonged restriction imposed on one can affect the efficient functioning of the other. The buds and young leaves are the sources for the production of auxins which in conjunction with inhibitors are known to be involved in the correlative inhibition of lateral buds (Snow 1937; Libbert 1954; 1955; see Wareing 1966).

Libbert (see Wareing 1966) showed that auxin-induced bud inhibition is greater in the presence of roots and green leaves than in stem segments lacking these. He also showed that the level of inhibitor in the stems is reduced in the absence of leaves and roots, in which a precursor of the inhibitor is presumably formed. The shoot system supplies the roots with substances like sugars, Vitamin B *etc,* which are essential for root growth. The root system in turn supplies the shoot with considerable quantities of inorganic as well as organic nutrients such as a wide variety of nitrogenous compounds, organic acids, alkaloids, phosphorus-containing compounds and sulphur containing organic compounds (Carr 1966). In addition, it has been shown that the root system exports to the shoot growth regulators such as the gibberellins, kinins and specific and unspecific growth inhibitors (Loeffler & van Overbeek 1964; Carr, Reid & Skene 1964; Carr 1966) and that these are transported in the xylem in the transpiration stream. It has also been shown that the root system can regulate metabolic activities in the shoot and exerts a profound effect on the rate of assimilation in the leaves, by acting as a sink and that a reduction of the size of the root system reduces the rate of photosynthesis (Humphries 1963; Humphries & Thorne 1964). White & Barua (1955) reported that the longitudinal growth of the feeder-root system in tea exhibits periodic fluctuations similar to that of the shoot system. This may be reflected in a periodic fluctuation in the uptake of nutrients and may present a nutritional basis of dormancy.

It is also possible that the supply of native growth regulators will follow the pattern of root activity. Many woody plants have vascular systems which show reasonable separation into distinct channels of transport and this is presumed to be

*The term kinin is used as a synonym for cytokinin or phytokinin to describe the group of substituted purine derivatives promoting kinetin-like responses in plant tissues.

so in tea. If root growth shows periodicity, then it is conceivable that those shoots which are in direct vascular contact with particular roots will also show periodicity of growth similar to roots. It is known that growth regulators can promote the transport of substances to the point of application (Mothes 1964) and auxins promote transport of these to sites of production (Carr 1966). Dormancy would appear to be due to lack of the essential growth promoters and/or the build-up of some endogenous inhibitor like dormin (Abscisin II now called abscisic acid). There is sufficient evidence to suggest that growth promoters play a prominent role in morphogenesis and changes in the levels of these have been shown during resumption of growth following dormancy and other morphogenetic phenomena (Nitch 1957; 1963; Frankland & Wareing 1966; Pegg 1966 *etc*). There is also some evidence which seems to suggest that native inhibitors regulate bud dormancy and this view is gaining considerable support (Wareing 1966; Phillips & Wareing 1958; 1959; Nitsch 1957; Eagles & Wareing 1963; 1964; Robinson & Wareing 1964.)

It was shown in this paper that GA_3, K and AD, representing the gibberellins and the kinins were effective but that the auxins (IAA and NAA) had no effect on budbreak. It was also shown that the auxins (IAA and NAA) were antagonistic to the action of kinins (K, AD). Analysis of native gibberellins did not show any acute deficiency of natural gibberellins in the dormant buds and this cannot, therefore, account for the setting of dormancy. It was pointed out that the natural sequence of budbreak in a free-growing plant could be partly reversed by the application of a kinin (or a gibberellin) to the terminal bud of a lateral shoot. As no difference between the levels of gibberellins in the different bud samples of shoots was detected it may be assumed that kinins rather than gibberellins are of greater relevance. Kinins are also known to be effective in overcoming the action of inhibitors. It has been reported (Skoog & Miller 1957; Selman & Kulasegaram 1967) that the ratio of auxin to kinin plays a dominant role in morphogenesis and that a low ratio is favourable to bud initiation and growth. That this is applicable in breaking dormancy was shown by the application of a kinin to dormant buds. This would also explain the vigorous growth obtained following decapitation and defoliation (pruning, plucking and even bending the shoots and branches) which reduces the supply of auxins and inhibitors, and permits the kinin to have its full effect.

The lack of sufficient information on the hormone status of the tea plant is quite apparent and until more information on the levels of auxins, inhibitors and kinins becomes available, attempts to explain dormancy and the resumption of growth on the basis of the action of growth regulators would be largely speculative. Nevertheless the observations made and results obtained indicate the direction along which future work could be pursued.

CONCLUSIONS

1 — Observations made on free-growing tea plants indicate that the factor governing dormancy may be generalized affecting all the buds in the plant or be localized affecting only some of the buds, depending on the condition of growth of the terminal bud of the main shoot.

2 — The factor governing dormancy of buds in bushes in plucking appeared to be localized. This is presumably because of decapitation and defoliation which prevented the occurrence of the generalized state of dormancy.

3 — It was shown that gibberellins (GA_3) and kinins (K and AD) were effective in causing the dormant buds to grow earlier than the untreated dormant buds. The auxins (IAA and NAA) had no effect in promoting the growth of dormant buds.

4 — It was pointed out that the natural sequence of bud break in free-growing plants can be altered by localized application of the effective hormones to terminal buds of lateral shoots.

5 — The results of gibberellin analysis showed that dormancy of the buds could not be attributed to a deficiency of endogenous gibberellins nor the activity of buds to a higher level of endegenous gibberellins.

6 — It was pointed out that while the inhibition observed in the basic fraction of the extracts was of little physiological significance, the inhibition observed in the acidic fraction in the dormant buds and to a lesser extent in the buds resuming growth may have some significance in relation to dormancy. The acidic extract of active buds showed no inhibition.

7 — The bearing of these results on the possible mechanisms that may be involved are discussed in relation to earlier work on other plants.

ACKNOWLEDGEMENT

The gift of samples of gibberellic acid and Phyomone by Chemical Industries (Colombo) Ltd., is gratefully acknowledged.

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(*Accepted for publication — 20th February 1969*)