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ROOT INFLUENCE ON SHOOT DEVELOPMENT IN TEA (*Camellia sinensis* (L.) O. KUNTZE) FOLLOWING SHOOT PRUNING†

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SUMMARY

The physiological interaction between the factors controlling the development of new shoots in pruned tea plants was investigated in an experiment using a widely cultivated TRI clone growing at low elevation in Sri Lanka. The functional importance during new shoot growth of root reserves, feeder roots and leaves and buds on unpruned branches (lung-shoots) is critically evaluated. A scheme for their interaction is presented, which highlights the need to maintain feeder roots alive during new shoot development, for which a large proportion of both reserve and current assimilates seem to be utilized. Mature leaves on lung-shoots, supplementing carbohydrate supply by current photosynthesis, may also serve to maintain the flow of metabolites from feeder roots to developing shoots and also function as ' sinks ' for excess, toxic levels of root metabolites. Removing all mature leaves, as is done during ' clean pruning ', leads to the depletion of reserves below the critical level for feeder root survival, resulting in death of feeder roots and failure of new buds to form shoots.

PERIODICAL shoot pruning is a critical cultural operation in tea plantations. Standard pruning necessitates that the bush is sustained from reserves until new shoots develop. In view of this, the turnover of carbohydrate reserves in tea has been investigated more intensively than in any other tropical evergreen perennial. However, it has not been possible to associate reserves with any particular aspect of recovery, and conflicting concepts of the turnover of carbohydrates during recovery from shoot pruning are found in the literature.

Tubbs (1937) advocated ' rim-lung ' pruning where one to three peripheral branches carrying *c.* 200 mature leaves, called ' lung-shoots ', are left unpruned on a pruned tea bush (Figure 1). Rim-lung pruning is known significantly to reduce the death of pruned bushes, especially in tea growing at low elevations in the tropics, where air temperatures are higher than at greater elevations. The lungs were assumed to supply photosynthates to developing new shoots.

Pethiyagoda (1964) and Nagarajah and Pethiyagoda (1965) noticed the absence of a direct correlation between root reserves and new shoot growth after pruning and inferred an indirect role for root reserves during recovery from pruning. They suggested that lung-shoots on pruned plants promote the mobilization of root metabolites to shoots as well as supplying photosynthates. Subsequently Roberts

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et al. (1976) provided evidence indicating that the lung-shoots could also serve as sinks for root metabolites that were injurious to shoots causing rim blight on new leaves.

Kandiah (1971) showed that the feeder roots formed a significant centre for the mobilization of root reserves during recovery from pruning. Further studies on feeder root growth indicated that a substantial amount of leaf assimilates are utilized by feeder roots during their growth and maintenance respiration (Kandiah, 1975; Kandiah and Wimaladharma, 1978). Kandiah (1971) indicated that bud break on pruned tea shoots *per se* may not directly consume large root reserves, as the pattern of leaf formation from shoot buds make them photosynthetically self-sufficient very early. Furthermore, Selvendran and Selvendran (1972) and Sivapalan (1975) found that stem bark reserves were potentially sufficient to meet the needs of buds developing on them.

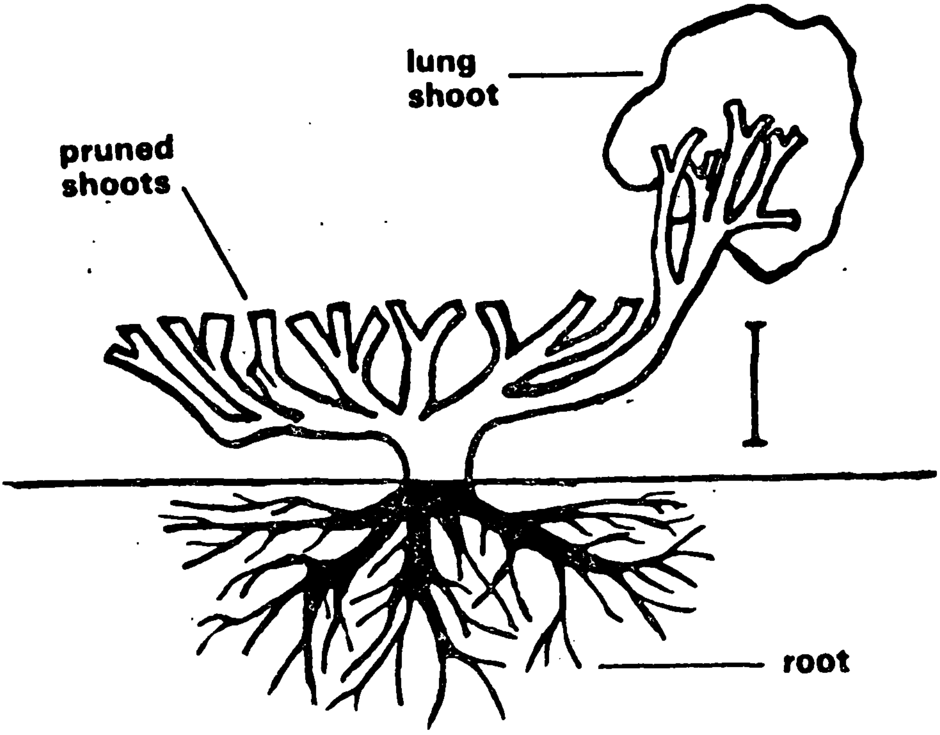

Fig. 1.—Diagrammatic sketch of a tea plant after shoot pruning with one lung shoot. Bar = 30 cm.

It appears necessary to examine critically the physiological significance of lung-shoots, root reserves and feeder root metabolism, all of which seem to be important in recovery from pruning and appear to interact functionally during the development of new shoots after pruning, and to elucidate such interactions.

MATERIALS AND METHODS

Eight-year-old tea plants of clone TRI-2025 growing at the low country station (30 m.a.s.l.) of the Tea Research Institute of Sri Lanka were used. Four pruning treatments were assigned to plots, each of 12 plants, in randomized blocks with six replications. The pruning treatments were :

1. RL — Rim-lung prune, where all shoots except the lung shoot were cut to a height of 30-45 cm above ground (Figure 1).
2. RL—R — As in 1, but with lung branches ring-barked at the base.
3. RL—D — As in 1, but the lung branches had all mature leaves removed.
4. CP — Clean prune, where all shoots were cut to a height of 30-45 cm above ground.

Recovery from pruning was assessed under the following criteria :

Shoot development

Four bushes per treatment and plot were selected at random and the following observations made at intervals :

(*a*) Bud break, estimated by counting the number of new bud sprouts on pruned shoots 3, 4, 5 and 8 weeks after pruning.

(*b*) Death of new buds : all buds did not develop into shoots, some aborted and this was estimated eight weeks after pruning by counting the dead buds.

(*c*) Shoot growth was estimated by counting the new shoots with more than two foliage leaves 14 weeks after pruning.

An overall estimate of ' rim blight ' and plant death was made. ' Rim blight ', characterized by marginal scorching of young leaves of growing shoots, which may retard growth or cause the death of new shoots, was assessed by visual scoring eight weeks after pruning. The percentage of plants that failed to re-establish new shoots, and hence died, after the pruning treatment was estimated 8, 12 and 16 weeks after pruning.

Bud, shoot, and plant counts (n) were transformed to $\sqrt{(n+1)}$ before analysis.

Feeder root activity

Feeder root activity was assessed by collecting all unsuberized feeder roots in 15 cm^3 soil samples. These were taken from below further random selections of one tree per treatment and plot, 4 and 8 weeks after pruning. Roots died to different extents after pruning, and activity was assessed as a score based on visual separation of : active ; white and inactive ; and brown roots.

Root reserves

Previous studies of feeder roots in tea showed that their reserves, consisting mostly of sugars and very little polysaccharide, underwent little change. Treatment effects on reserve levels in tea were reflected best by the wood of 1-1.5-cm-thick roots, so randomly selected bushes from each treatment and plot were sampled by excavating such roots for analysis. Normal growth was allowed to continue. The reserves were estimated by the routine methods used at the Tea Research Institute of Sri Lanka (Kandiah, 1971, 1975), that is, as two fractions corresponding to sugars (MeOH fraction) and starch + hemicelluloses (H_2SO_4 fraction). The values are expressed as percentages of dry residual matter after extraction (Priestley, 1962). Estimates were made 0, 3, 8, 11 and 13 weeks after pruning.

RESULTS

Shoot development

Bud break started two weeks after pruning and, by the end of the third week, bud break was evident in all plants irrespective of treatments; and differences in bud break between treatments were not significant up to four weeks. From the fifth week, bud break on lung-pruned plants (RL) was significantly best. Ring barking (RL—R) and defoliation (RL—D) of the lung shoot had adverse effects, RL—R or RL—D plants showing less bud break than even the clean pruned plants (CP) (Table I—NB).

The least death of new buds was in RL. Ring barking or defoliation of lung shoots (RL—R, RL—D) increased bud deaths compared to CP. Rim blight symptoms on new leaves were also least in RL, moderate in RL—R, but severe in RL—D and CP (Table 1—DB).

The cumulative effect on bud behaviour is reflected in the mean number of shoots with two or more foliage leaves per plant. Plants of RL were markedly better than those of other treatments, and RL—D plants carried the fewest shoots (Table I—NS).

The percentage of plants that died increased with time from pruning and deaths were significantly less in RL than in all other treatments. However, recovery from pruning in RL—R was better than in CP, whereas deaths in RL—D were more than even in CP (Table II—DP).

Feeder root activity

All pruning treatments reduced feeder root activity. This inactivation increased with time. However, in RL, in the sample studied eight weeks after pruning when bud break was almost complete in the pruned shoot, feeder root activity was markedly greater than in all other treatments which were characterized by very low activity (Table II—FR).

TABLE I

New buds—NB, dead buds — DB, new shoots—NS per plant, and rim blight assessment — RB, on new shoots. Analysis of NB, DB and NS made on $\sqrt{(n+1)}$ - transformed data. Figures in parentheses indicate back-transformed numbers.

	Weeks after pruning						
Pruning treatment	3	4	5	8	8	8	14
	NB	*NB*	*NB*	*NB*	*DB*	*RB*	*NS*
RL ..	3·23 (9·40)	3·66 (12·42)	4·31 (17·6)	4·99 (23·88)	1·05 (0·1)	Nil	4·80 (22·0)
RL—R ..	2·64 (5·98)	3·03 (8·18)	3·30 (10·01)	3·75 (13·03)	2·12 (3·51)	Moderate	2·34 (4·46)
RL—D ..	2·42 (4·83)	2·65 (6·00)	2·87 (7·3)	3·42 (10·66)	2·10 (3·43)	Severe	1·35 (0·83)
CP ..	2·97 (7·81)	3·26 (9·61)	3·57 (11·73)	4·11 (15·86)	1·91 (2·63)	Severe	2·27 (4·13)
LSD P=0.05 ..	NS	NS	0·9	0·51	0·28	—	0·38

TABLE II

Scores for feeder root activity —FR. and percentage of plants that died following shoot pruning—DP. Analysis of DP made on $\sqrt{(n+1)}$ - transformed data. Figures in parentheses indicate back transformed numbers.

	Weeks after shoot pruning				
Pruning treatment	4	8	8	12	16
	FR	*FR*	*DP*	*DP*	*DP*
RL ..	58	33	1·00 (0)	1·92 (2·68)	2·14 (3·58)
RL—R ..	56	7	3·00 (7·98)	7·14 (49·92)	7·44 (54·30)
RL—D ..	41	0	4·53 (19·52)	9·17 (83·07)	9·49 (89·05)
CP ..	51	3	4·35 (17·92)	7·89 (61·29)	8·64 (73·63)
LSD P=0.05 ..	—	—	0·91	0·96	0·92

Root reserves

The variation of root wood reserves is shown in Figure 2. Even though depletion of root wood reserves was evident three weeks after pruning there was no significant difference between treatments. In the sample taken after eight weeks the H_2SO_4 fraction (starch+hemicelluloses) was markedly less than the level at pruning. The 11th-week sample indicated a beginning of replenishment of reserves in RL. Replenishment of reserves in other treatments was not evident even in the sample taken at the 13th week from pruning and, in RL—D and CP, a large percentage of plants died and so were unavailable for sampling.

Reserve fluctuation was mostly associated with the H_2SO_4 fraction and the MeOH fraction was found less affected by the treatments.

DISCUSSION

The object of this study was to assess critically aspects of root-shoot interaction, especially in relation to the functional importance of lung shoots, in tea recovering from shoot pruning. The treatments were expected to modify the lung shoots so that their functions became restricted. The effect of such functional restriction was compared with treatments having unrestricted lungs or no lungs.

Plants of CP had no lungs and RL had unrestricted lungs. RL—R differed from RL in that the lung shoots had no bark connection to the pruned shoots or the root system, thereby restricting the supply of photosynthates, but transpiration could be maintained, and so xylem sap metabolites could be drawn from the root. In RL—D the lungs mainly carried only young leaves and buds, and so provided a stimulus free of both active transpiration and the supply of photosynthates.

Plants of RL recovered best from shoot pruning. Even though recovery in RL—R was poorer than in RL, it as better than in RL—D or CP (Tables I, II). Thus, the lungs have had some benefits in RL—R, even though a supply of carbohydrates from them was prevented from reaching the new buds or shoots. The benefits of lungs in RL—R is probably attributable to maintenance, by transpiration, of a stream of xylem sap from root to shoot.

In RL—D the lung shoots afforded active centres of auxin synthesis in the young buds they carried, which was initially absent in CP. Nevertheless, the poor recovery of plants in RL—D indicated that auxin supply from lungs is not an important factor contributing to recovery after shoot pruning. On the other hand , it seemed that such centres of auxin synthesis on unpruned shoots may be detrimental to bud development on pruned shoots since shoot growth was poorer in RL—D than CP (compare RL—D and CP, Tables, I, II). Possibly the extra buds on the lungs of RL—D plants increased interbud competition for restricted nutrients.

RL also proved to be distinctively better in restoring higher levels of root reserves (Figure 2), reducing rim blight symptoms, and maintaining feeder root activity (Tables, I, II). Even here RL—R was found less harmful than RL—D or CP. Priestley (1976) had observed a comparable effect of shoot ringbarking on root reserves in apple.

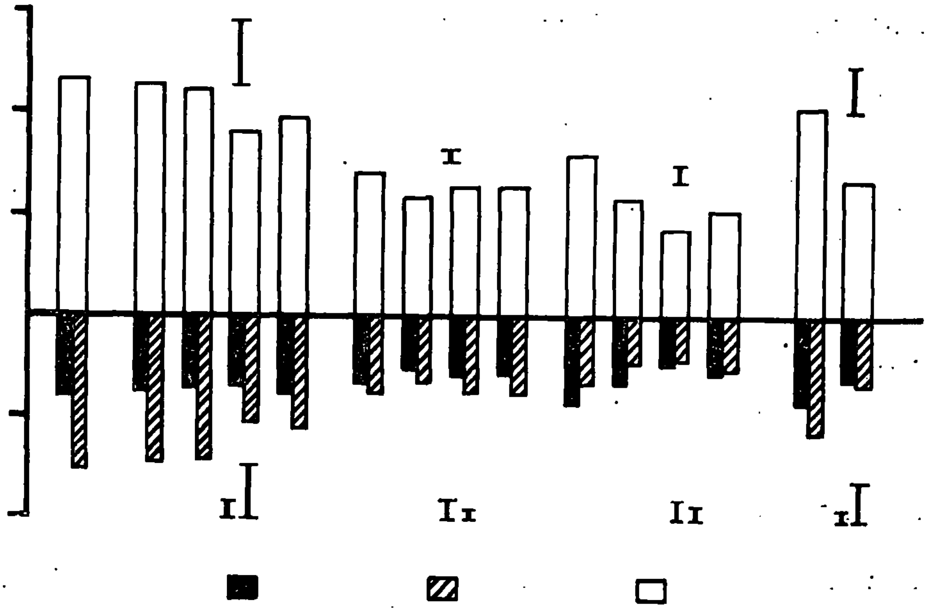

Fig. 2.—Variation in root wood reserves estimated in two fractions corresponding to sugars (MeOH fraction) and starch + hemicelluloses (H_2SO_4 fraction) at 0, 3, 8, 11 and 13 weeks after shoot pruning. Bushes of treatments RL - D and CP were dead at 13 weeks. Bars = LSD (0.05).

The net result was evident in the percentage of plants that failed to recover from pruning and died (Table II—DP). RL—D had most deaths, followed by CP and RL—R. Recovery was most successful in RL.

These results imply two major functions of lung shoots : supplying carbohydrates to the roots and maintaining the flow of metabolites from roots to shoots. It seems that the feeder roots form the primary sites of utilization of lung carbohydrates rather than the shoot buds as was originally proposed (Tubbs, 1937). Feeder roots, promoted by the retention of lung branches, use appreciable quantities of carbohydrate but assist the development of new shoots in supplying them with xylem-and phloem-translocated metabolites. Previous studies also support this view of shoot-root interaction (Kulasegaram, 1969 ; Kulasegeram and Kathiravetpillai, 1972 ; Selvandran, 1970 ; Kandiah and Wimaladharma, 1978). In temperate deciduous trees, also, the root system has been shown to be a strong sink for carbohydrates during shoot bud development in spring (Kandiah, 1979a; 1979b). Metabolites leaving the roots probably include sugars, amino acids and amides, and phytohormones such as cytokinins or gibberellins.

Furthermore, lung shoots in tea seem to dilute any harmful root metabolites which arise from dead feeder roots and may cause rim blight symptoms on new leaves (Roberts *et al.*, 1976).

By incorporating the findings of this experiment with the results of previous studies it is possible to compile a scheme indicating the flow of metabolites following pruning of a tea plant (Figure 3).

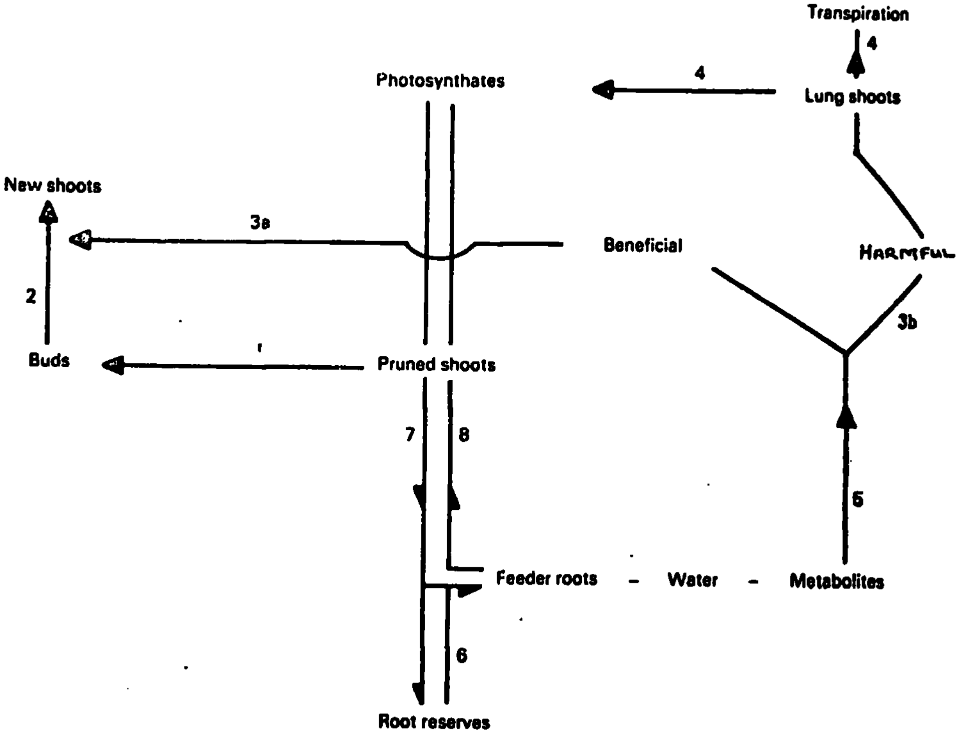

Fig. 3.—*Scheme indicating the flow of metabolites during the development of new shoots following shoot pruning of tea plants. The flow directions of metabolites from source to sink are indicated by arrows. Paths* 1 *to* 8 *are described in the text.*

Buds develop on pruned shoots independently of the presence of lung shoots (1). Further development of bud sprouts into new shoots (2) depends on the flow of root metabolites to them (3a) which is assisted by the transpiration pull and by photosynthates originating from the leaves of the lungs (4). Shoot growth results shown in Table I support this deduction. The root metabolites are provided by the feeder roots (5) which are kept active by carbohydrates supplied from root reserves (6) and by photosynthates from the leaves of lung shoots (7) (Table II—FR), the latter in response to a phloem-translocated feeder root stimulus (8) (Kandiah and Wimaladharma, 1978). Death of bud sprouts results from interbud competition for limited root metabolites ; the poor shoot growth in RL—D supports this (Table I). Some of the root metabolites may be harmful to developing shoots (3b) and the mature leaves on lungs may act as sinks and dilute this effect (Roberts *et al.*, 1976). Photosynthates translocated from the lungs (7) also help maintain root reserves above a critical level for the survival of the plant (Figure 2). At low elevations in the tropics with high ambient temperatures, root reserves in the absence of lungs are often depleted below the critical level needed for recovery, followed by death of feeder roots and bud sprouts.

In lung-pruned plants the functions of the lungs are taken over by the new shoots when they have formed four or five mature leaves. Retention of lung shoots thereafter is of no benefit to the plant.

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