THE INFLUENCE OF 'LUNGS' ON CARBOHYDRATE RESERVES AND GROWTH OF SHOOTS

S. Nagarajah & U. Pethiyagoda

Studies are in progress to evaluate the importance of various factors regulating recovery from pruning. The retention of 'lungs' has been shown by previous workers to minimize the risks of die-back and death from pruning. This benefit is presumed to result from the lungs synthesizing carbohydrates to supplement root stores as they are used up in recovery. This paper presents the results of a scrutiny of the physiological activities of lungs. Lungs affect the carbohydrate balance of the pruned bush. In addition to contributing to the supplies in the roots, they also perhaps promote the utilization of such reserves in the earlier stages of recovery. Lungs exert a depressing effect on the buds developing on the frames. They reduce the numbers of such buds and also retard their subsequent growth. The balance between the beneficial and harmful effects of lungs is determined by the duration of their retention on the recovering tea bush. When kept for a long period, their harmful effects are likely to be dominant. In practical terms, this underlines the need to determine under any given set of conditions, the minimum period after which lungs may be safely removed.

Introduction

Since the investigations of Tubbs (1937) on the causes leading to heavy die-back in tea bushes pruned in the low-country, it has been an accepted view that adequate levels of carbohydrate reserves in the roots are important to enable satisfactory recovery from pruning. Following from his observations there developed the practice of 'lung pruning', the function of the 'lungs' being to supplement the root reserves as they are used up in recovery. Recently, Priestley (1962) suggested the possibility that lungs are required to enable the recovering bushes to utilize such reserves as are stored in the roots. They could for instance, be important in the 'mobilization' of reserves and not solely in their production. The latter function has been considered hitherto, perhaps to the exclusion of other possible influences on recovery. The aim of the present paper is to consider rather more broadly the effect of lungs on carbohydrate reserves and on recovery, in the light of the results of certain experiments conducted recently.

Changes in carbohydrate reserves following pruning

Details on the methods of sampling and of estimating carbohydrate reserves in tea roots have been presented elsewhere (Pethiyagoda 1964 ; 1965). It would suffice to mention here that the method used was one which estimated jointly, the quantity of starch and sugars present in samples prepared from root segments of standard size. The term 'total available carbohydrates' (TAC) is used to define these two classes of compounds which represent the principal form of carbohydrates utilized for growth. All figures are expressed as percentage dextrose equivalent based on the initial dry weight of the sample.

It has been consistently found that depletion of reserves follows pruning. Figure 1 represents graphically the results obtained from a typical experiment. In this study 400 bushes of clone TRI 2024 were pruned leaving one generous lung per bush. Another comparable group was clean pruned at the same time. Weekly samples were taken from groups of five randomly selected bushes. A single root sample was taken from each bush and the five samples bulked to yield a single composite sample. Observations continued for six months from pruning.

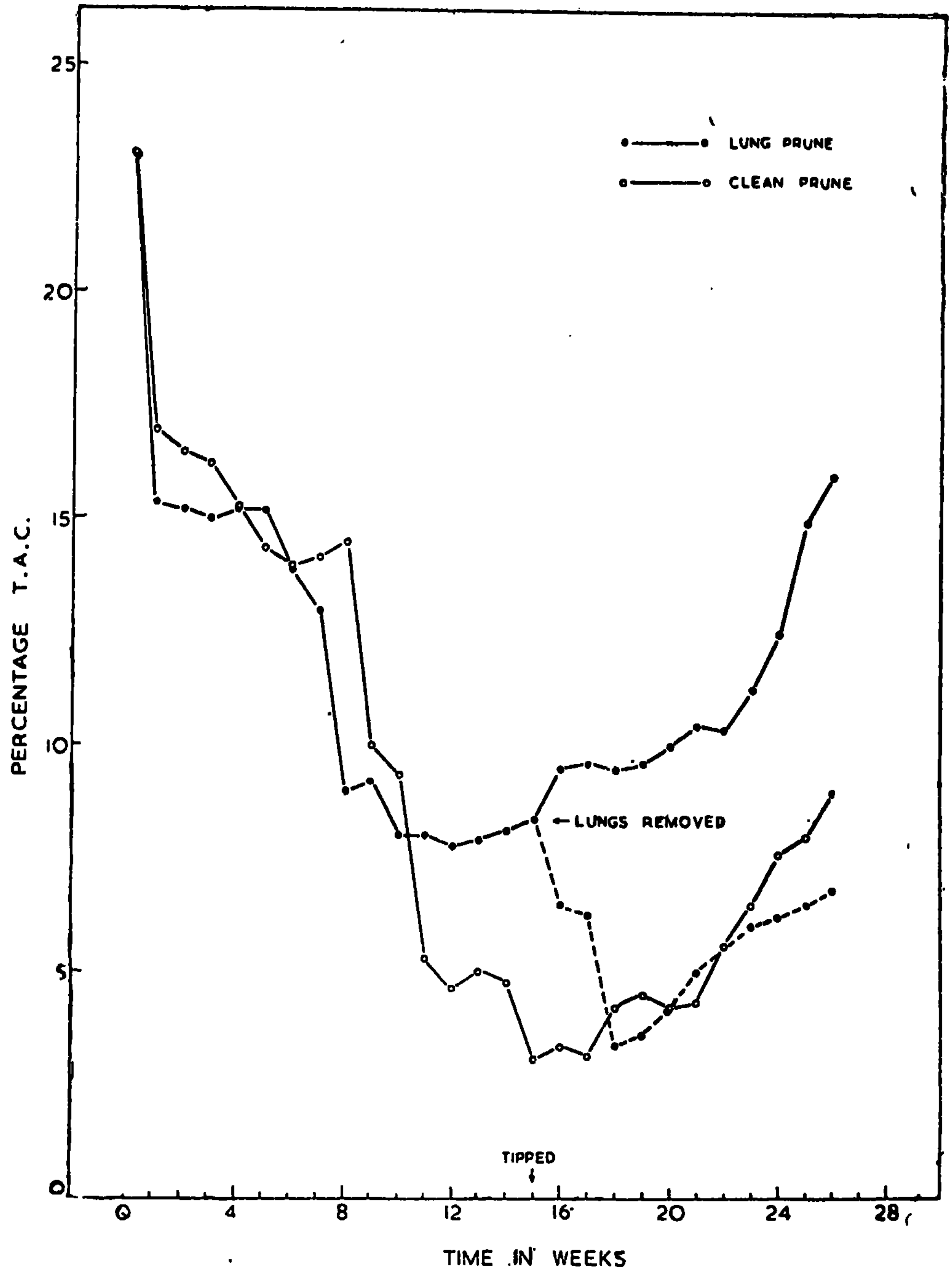

FIGURE 1 — *Changes in 'total available carbohydrates' (TAC) in tea roots following pruning. All results are expressed as percentage 'dextrose equivalent' based on the initial dry weight of the sample*

The following main features were noted:

1 At the time of pruning, root reserves (TAC) were about 23%. There is then evidence of an immediate decline of reserves which continues steadily in both clean and lung pruned bushes. This decline commenced before any signs of bud break became evident.

2 During the first 10 weeks, this decline appears to be somewhat more rapid in lung pruned than in clean pruned bushes. During this initial phase it was also noticed that there was an earlier initiation and faster growth, of buds commencing growth on the lung pruned bushes. These observations are in agreement with the earlier quoted suggestion (Priestley 1962) that lungs aid recovery by enabling faster mobilization of root reserves by the new growth.

3 The decline of reserves in lung pruned bushes ceased after about 10 weeks and they thereafter remained fairly constant at about 8% until tipping. In contrast, reserves in clean pruned bushes continued to decline until they reached a level of about 3% at tipping.

4 The removal of lungs at tipping (in half the number of lung pruned bushes) simulated the effect of clean pruning, reserves immediately declining sharply to a level equivalent to that of clean pruned bushes.

The results show that the presence of lungs while initially increasing the rate of decline of reserves, also enables them to be stabilized at a higher level relative to clean pruned bushes. They presumably do so by themselves synthesizing carbohydrates partially to meet the needs of the growing buds, or alternatively, by latterly inhibiting the utilization of root reserves. Confirmation for the synthetic activities of lungs was obtained from another similar experiment but including a third treatment where a half an inch wide band of bark near the bases of all lung branches was removed in the form of a complete ring ('bark-ringing' or 'ring-barking'). This treatment prevents the transport of materials synthesized by the lungs into the roots. From the point of view of root reserves this treatment thus amounts to clean pruning. Results of root analysis are summarized in Table 1.

TABLE 1— *'Total available carbohydrates' in roots of pruned bushes at the time of tipping— Clone TRI 2025 which had an initial level of TAC of 18.23% at time of pruning*

	Lung pruned	Clean pruned	Lung pruned but lungs bark-ringed
Mean TAC	11.66%	6.64%	6.70%

The results show that the higher level of reserves at tipping time in lung pruned bushes is due to the contribution of the lungs.

Lungs and the growth of shoots

While the foregoing section has presented evidence for the beneficial effect that lungs have on maintaining root reserve levels, it is a matter of common observation that lungs reduce the numbers of buds developing on pruned frames.

In Plate 1 are photographs of bushes of TRI 2024 taken about three months after tipping. On comparing 1*a* and 1*b*, the marked difference in growth and spread of the new shoots is clearly evident. In 1*c* the lungs have been retained for long after tipping. The lungs show marked growth while the shoots on the pruned frame are considerably retarded in their growth.

PLATE 1 — *Photographs of bushes of TRI 2024 taken about three months after tipping*

a — *A clean pruned bush showing dense growth on the pruned frame*

PLATE 1 b — *A lung pruned bush – note poor recovery relative to* 1*a* (*Lungs were removed before photographing*)

PLATE 1 c — *Another lung pruned bush showing good growth of lungs but reduced growth of pruned frame*

In Figure 2 are plotted the mean numbers of buds counted on the frames of bushes pruned with and without lungs. These particular counts were made on bushes of TRI 2025 that had been rested for three months, but the pattern is similar for all cases investigated.

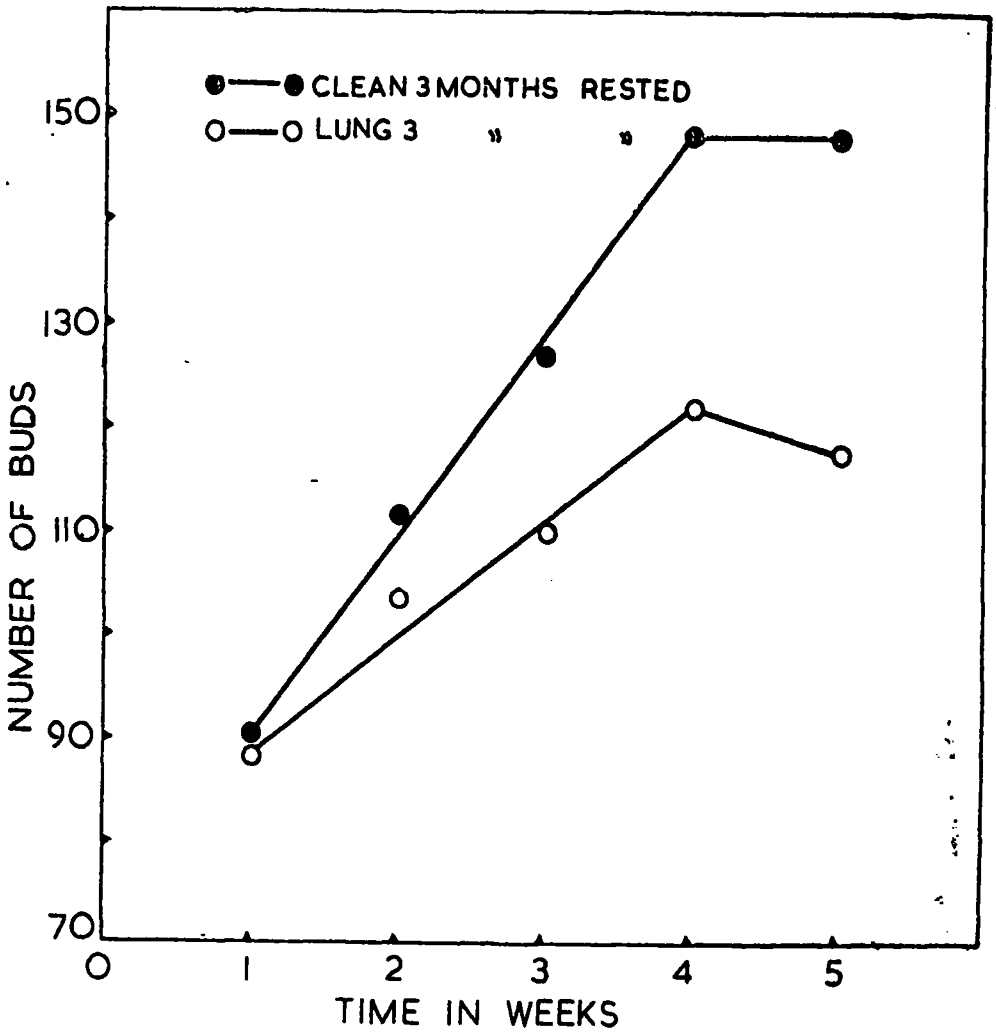

FIGURE 2 — *Frequency of buds following two types of pruning*

Despite this marked depressing effect of lungs on the growth of shoots, records of tipping weights, however, suggest an opposite effect. In Table 2 are the mean weights of tippings obtained in the above trial.

TABLE 2—*Tipping weights from clean and lung pruned bushes of TRI 2024—Each figure represents the mean tipping weight in pounds per bush*

	Clean pruned	Lung pruned
1st tipping	3.42	4.64
2nd tipping	0.17	0.06
Total	3.59	4.70

This apparent contradiction is easily explained on examining the nature of the tippings removed in each case. Five pound samples were randomly drawn from the bulked tippings from each of the treatments, and were separated into shoots carrying differing numbers (1-8) of fully expanded leaves. The numbers of each category are presented in Table 3.

TABLE 3—*Types of tipping shoot occurring in representative five pound samples from plots of clean and lung pruned bushes—Shoots are classed according to the number of fully expanded leaves present*

Number of leaves	Number of shoots	
	Clean pruned	Lung pruned
1	52	26
2	174	86
3	146	116
4	137	114
5	37	65
6	10	23
7	—	4
8	—	2
Total	556	436

The samples drawn from the clean pruned bushes have more shoots of the smaller categories (1-4 leaves) and less of the larger (5-8 leaves). Thus the explanation for the greater tipping weights recorded from lung pruned bushes is that although smaller numbers of shoots develop, they grow to a larger size than shoots of clean pruned bushes. This perhaps underlines the need for caution in using 'tipping weights' as a criterion of recovery from pruning—for the visibly better recovering bushes have yielded lower tipping weights. The bias is in favour of the greater frequency of larger shoots in lung pruned bushes.

The inhibitory influence of lungs

Further evidence of the inhibition of the growth ot buds was obtained from a series of bark-ringing experiments on lung-pruned bushes. It is a common observation that new buds do not sprout along the frame of lung branches, although the lungs themselves grow freely on top (Plate 2*a*).

This downwardly operating inhibitory influence appears to be exerted through the bark, for the removal of a complete ring of bark along the lung at a point below the lowest leafy branch, permits the growth of buds below the ring (2*b*). This operation has the further influence of checking top growth of the lung. It appears that the inhibitory influence is now confined within the lung and reaches a level when the growth of the lung itself is prevented. Since buds can grow in the region between two rings (Plate 2*c*), it cannot be concluded that the cessation of growth of ringed lungs is due to their isolation from materials necessary for growth and passing upwards in the bark from the roots. Further, it is evident from Table 1 that there is a net production of carbohydrates by the foliage carried by lungs. It was also noted that bark-ringed lungs soon acquire a prominent pink coloration (due presumably to accumulation of anthocyanin pigments) and also flower profusely—circumstantial evidence that they accumulate soluble carbohydrates.

PLATE 2 — *Photographs showing the inhibitory influence of lungs on new growth —*

a — *A normal lung showing good top growth – note the absence of buds along the main stem*

PLATE 2. b — *A ring-barked lung showing the lack of new top growth but with the development of new shoots below the ring*

PLATE 2 c — *A double ring-barked lung showing the lack of new top growth but with shoot development between the rings*

The following tentative hypothesis is proposed for the inhibition by lungs of the development and growth of buds. The (mature) foliage carried by lungs is a source of a certain inhibitory substance (or substances). These move downwards within the bark. Where a lung branch carries a pruned, upwardly directed spur, buds grow only on the latter. This is suggestive of a direct downward passage of the inhibitors into the roots, which possibly act as a 'sink'. Certain amounts also perhaps find their way into the pruned frame where they reduce the numbers of buds sprouting. Where a girdle of removed bark interrupts the pathway to the roots, the substances remain within the lung to retard its own growth at the top. The part of frame below the ring is then freed from the influence and buds are able to grow out.

Instances of similar synthesis of growth inhibiting substances have been reported for other plants (*eg* Eagle & Wareing 1963). The production of such substances by the mature foliage of tea might lead to a gradual accumulation as the pruning cycle advances and would explain the diminished vigour of growth of bushes towards the end of the cycle and why partial defoliation at this stage does not result in proportionate losses of crop (see also Pethiyagoda 1965a).

Discussion

The benefits to be derived from the retention of lungs when pruning at lower elevations have been exhaustively dealt with by Tubbs (1937). Even at higher elevations, there is fair opinion that lung pruning is advantageous in special circumstances; *eg* at the first pruning of young tea and in dealing with debilitated or poor fields. It is not the intention of this paper to suggest abandoning such practices. In an operation like pruning, sound individual judgement on all points is critically important. Practices which experience have shown to be useful, should continue unless concrete evidence to the contrary is forthcoming.

In regard to the role of lungs at pruning, we have been able to show certain salient features. It is clear that lungs provide carbohydrates to supplement the losses of root reserves (Table 1). It is also suggested that lungs may help in the more rapid mobilization of reserves in the early stages of recovery (Figure 1). The stabilization of reserves at a higher level in lung pruned bushes than in clean pruned ones reflects the photosynthetic role of foliage on the lungs. It was noted that bud-break occurs somewhat earlier on the frames of lung pruned bushes. However, actual numbers of buds showing growth is smaller on such bushes in comparison with clean pruning (Figure 2). Consequently, the spread and density of the new shoots is also more limited (Plate 1 *a* & *b*). However, tipping weights appear greater in lung pruned bushes (Table 2). It is suggested that this can be accounted for by the faster growth of the more limited number of shoots with the result that a smaller number of tipped shoots could furnish a greater weight of tippings (Table 3). Thus it would appear that despite the enhancement of carbohydrate resources by lungs, this is not reflected in appreciable improvements in recovery—there actually being evidence that except for hastening the start of recovery, they actually hold back the growth of the new shoots. This lack of a direct relationship between the concentration of carbohydrate reserves and the amount of new bud growth at recovery has become evident in certain other studies too. This aspect will, however, be discussed in another paper which will be published shortly.

There is evidence that lungs restrict the growth of newly formed shoots on the pruned frames. Thus, if they are retained for long (*eg* after tipping), they themselves grow but check the new shoots (Plate 1*c*). It is possible that this dominating influence resides in their ability to channel nutrients or other factors necessary for growth, to themselves at the expense of the younger shoots. It is, however, also evident that lungs (probably the more mature leaves) produce substances inhibiting the growth of buds (Plate 2). This aspect is dealt with in detail in the relevant section above.

It seems, therefore, that retained lungs speed up the commencement of recovery while they depress subsequent growth. This earlier recovery may well be the basis of the reduction of die back with lung pruning (Tubbs 1937). The most rational approach would, therefore, be to remove them as early as practicable when their provision at pruning is dictated by particular situations. It is not possible to formulate a general rule for timing the removal of lungs. The evidence indicates that the present general practice of delaying this operation until tipping is not advisable. The sooner they could be removed after they have performed the function of hastening recovery, the greater will be the advantage in terms of new growth. Experimental removal of lungs at varying times between bud-break and tipping would most satisfactorily resolve the question for individual cases. In addition to the factors indicated, inordinate delays in the removal of lungs often results in heavy die-back of the pruned lung branches themselves.

Summary

The effects of lungs on carbohydrate reserves and shoot growth have been investigated. Lungs supplement root reserves as they are used up in recovery. They may also help in mobilizing reserves. Lungs further exert a depressing effect on the numbers of buds beginning growth and also their subsequent rate of growth. The commencement of recovery, however, seems advanced.

In order to utilize the benefits and minimize the disadvantages of lungs, it is suggested that the earliest time at which they could be safely removed be sought.

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