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COPPER: ITS EFFECTS ON THE GROWTH AND COMPOSITION OF THE RUBBER PLANT (*HEVEA BRASILIENSIS*)

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Copper was long recognised (Sommer [15]) as one of the essential nutrient elements required by higher plants. Investigations showed that copper was a constituent of at least three important plant enzymes and that it played a vital function in the process of respiration (Arnon [1]). But published information did not exist on the effect of a restricted copper supply on the growth and composition of the rubber plant; neither was a description of the symptoms of copper deficiency available. There was a lack of information on the effect of copper status on the concentration of rubber in the tissues. However, Beaufils and Compagnon [2 3 4 9] claimed that copper played an important role in the rubber tree's absorption of potassium from the soil and that the concentrations of copper and potassium, in the latex, were correlated.

Copper deficiency frequently occurs in plants grown on soils rich in organic matter (Gilbert [11]), particularly peat soils, such as may be found in some Malayan coastal areas. Bearing this in mind, the present studies were initiated with the following objectives; to produce and record symptoms of copper deficiency in the rubber plant; confirm some of the claims made by Beaufils (*loc. cit.*) regarding a copper-potassium interrelationship, and to determine the direct effect, if any, of copper supply on the concentration and distribution of other mineral elements and of rubber within the plant.

Rubber seedlings were grown in purified sand at varying levels of copper supply. Severe symptoms of copper deficiency were produced and the importance of the element in the nutrition of the rubber plant was established beyond doubt.

EXPERIMENTAL METHODS

Four treatments, or levels, of copper supply were applied to the plants grown in sand:—

Cu_1 .... 0.001 ppm of Cu: this very low level of copper was not deliberately supplied and mainly arose from casual contamination of the nutrients.

Cu_2 .... 0.008 ppm of Cu: a subnormal or low level of copper.

Cu_3 .... 0.064 ppm of Cu (or 0.002 milligram equivalent per litre of copper): a level usually sufficient to permit healthy growth.

Cu_4 .... 0.512 ppm of Cu: a level anticipated to be greater than the plant's requirement but not, so it finally ensued, sufficient to induce marked toxicity effects.

Each treatment was applied in duplicate and each replicate contained five vessels (described below) in which the plants were grown.

Sifted river sand, particle size 0.5–1.5 mm, was purified by three successive seven-hour washings with a boiling mixture of (by weight) 14% hydrochloric acid and 1% oxalic acid. The purified sand was placed in 4-gallon capacity pyrex glass, freely drained vessels and subsequently well leached with water and copper-free nutrients to restore it to neutrality. The basal nutrient solution, supplied to all plants during the course of the experiment, contained the following concentrations of nutrient ions (in milligram equivalents per litre): NH_4^+ 3.0, NO_3^- 5.0, SO_4^{--} 7.5, PO_4^{---} 3.0, Mg^{++} 2.5, K^+ 3.0, Ca^{++} 4.0, Na^+ 1.0, Fe^{+++} 1.0, Mn^{++} 0.02, Zn^{++} 0.002, BO_3^{---} 0.033, Mo^{VI} 0.001, Al^{+++} 0.001, Ga^{+++} 0.0002, Co^{++} 0.0002, Ni^{++} 0.0002.

Stock solutions containing the macronutrient elements were purified by the phosphate-adsorption autoclaving process followed by subsequent dithizone extraction. Copper-free ferric citrate was prepared by combining ether-extracted ferric chloride with dithizone-extracted, copper-free, ammonium citrate. The purification procedures used were essentially those developed and used by Hewitt and Bolle-Jones [13] and which have been more fully described elsewhere (Hewitt [12]). The purified nutrients, diluted ready for application, possessed a pH of approximately 5.0.

Demineralised water, resulting from the passage of rain water through "Zeokarb", "Deacidite" and "Deminrolit" ion-exchange resins, was used for the preparation of nutrients; this water was contaminated to the extent of 0.001 ppm with copper.

Eighteen, "selfed" clone Tjirandji-1 seeds, each weighing more than four grams, were sown in each vessel in December 1954. The seedlings, after emergence were thinned out to nine plants per vessel and subsequently progressively removed at each sampling date so that by the end of the experiment, February 1956, one seedling, only remained. At each sampling (March '55, May, July, September '55, February '56) complete plants were removed and the nutrient element concentrations within roots, stems, and leaves were determined. All tap and fibrous roots of plants removed from each replicate were bulked, dried and ground before analysis. The stems were treated similarly. Leaves were usually bulked according to storey position; some of the results are expressed as the concentration of nutrients in the dry matter of the laminae, which excluded midribs and petioles, while for the computation of the total nutrient per plant, account of the midrib and petiole composition was taken. The methods of analyses employed have been given (Bolle-Jones [5]), except for the procedure used for the determination of rubber in tissues, which was based on the method described by Meeks *et al* [14].

VISUAL OBSERVATIONS

The first definite signs of copper deficiency appeared in the Cu_1 plants in April 1955; the plants were noticeably shorter than those of other treatments and showed a paling and marginal cupping of the uppermost leaves.

The symptoms first appeared near the shoot tips. Leaflets were produced which tended to remain pendulous, for longer than usual, and which developed a lime or olive-green appearance. The laminae cupped inwardly near the tip; this cupped margin turned to a grey wilted appearance (Plate I). Occasionally the cupping occurred towards the ventral surface of the lamina. The wilted margin changed to a straw-coloured or brown scorch which spread down the lamina away from the tip (Plate I). During these changes the lamina hardened but the scorch grew progressively worse. Finally the leaf would be shed; frequently a large number of leaves were shed at about the same time leaving behind a bare stem (see Plate IV). The stem growing point usually died after such a defoliation and necrosis or rotting of the stem tip was often extensive. New shoots were then put out lower down the main stem, away from the original growing point (Plate III), and the sequence of leaf expansion, cupping, scorching and abcission was repeated. In severe instances many of the lower laminae of these new side shoots did not expand at all and they become withered or atrophied prematurely so that finally a new side shoot might have several stems clothed with numerous dead and shrunken petioles, which appeared much like hairs (Plate III).

The older leaves of the Cu_1 plants developed a pale-green or even bright-yellow mottling which was at first marginal but then spread inwardly between the veins; this was followed by a brown tip and marginal scorch of the lamina (Plate III). Although these symptoms

PLATE I. View of topmost olive-green leaflets showing inrolled margins and tip and marginal scorch, prior to abcission.

PLATE II. Roots of fourteen-month old Cu_1, Cu_2 and Cu_3 plants. Note weak appearance of Cu_1 roots and abundance of Cu_3 roots.

PLATE III. Shoot of Cu_1 plant, about 14 months old. Note numerous sideshoots, arisen as a result of terminal dieback, and scorched older leaves.

PLATE IV. Cu_3 plant (left), Cu_1 plant (right). Plants 13 months old; each scale division represents 3 inches. Note healthy growth of Cu_3 plant and dieback of stunted Cu_1 plant.

of the older leaves were relatively much more severe in their extent and occurrence in the Cu_1 plants they were not thought to be directly due to a deficiency of copper as similar, but milder, symptoms were seen in the older leaves of the Cu_3 and Cu_4 plants.

The symptoms in the upper region of the shoots of the Cu_1 plants which were most characteristic of copper deficiency, became so severe that it was necessary to supply the plants with Cu_2 nutrient for the period July 19–August 29, to prevent death and to resuscitate growth.

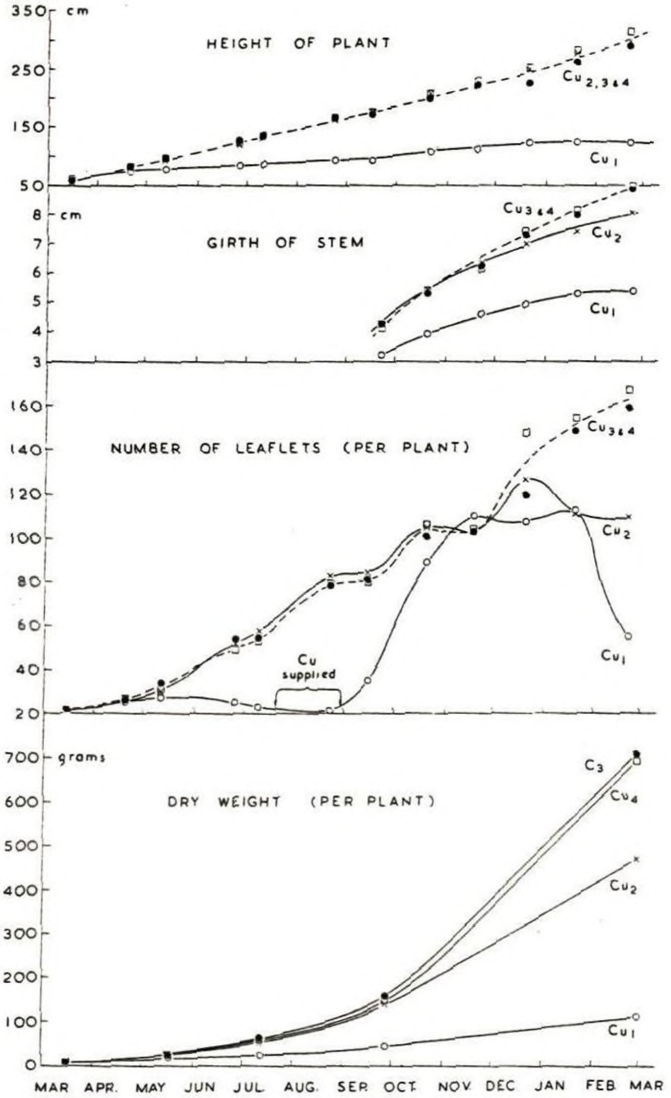
The Cu_2 plants suffered from a very mild deficiency of copper and olive-green young laminae with scorched edges were seen from July onwards. Severe dieback was not recorded. The Cu_3 plants presented a thriving appearance and appeared slightly more vigorous than the Cu_4 plants. Visually, the impression was gained that the tolerance of the rubber plant to a high copper level increased as the plant grew older so that any mild toxicity effects which may have been exerted on the Cu_4 plants in the earlier part of the experiment became less marked and the plants improved in vigour, in relation to the Cu_3 plants, towards the end of the experiment.

Figure 1 summarizes the effect of copper level on height, girth and number of leaflets per plant. The leaflet count values do not include the leaflets of the top storey or uppermost leaves; this method was adopted to avoid difficulties which would be encountered in deciding at which stage of development should the youngest leaves be included in the count. The girth of stems was measured 7 centimetres above sand level.

For each of these growth measurements it was obvious that the Cu_1 plants showed a marked inferiority to those of other copper treatments. But it was also quite clear that girth measurement and leaflet count gave a much more sensitive index to copper status than did height. Thus, towards the end of the experiment, it was possible to make a clear distinction between the Cu_2 and the Cu_3/Cu_4 values for girth and leaflet count, but not for height. The leaflet count records also showed (Fig. 1) the marked response by the Cu_1 plants to copper addition in July–August 1955; a smaller and relatively less marked response was also obtained in terms of height.

The total dry weight per plant (shoot plus root) varied according to copper level (Fig. 1). The Cu_1 plants produced the least weight and the Cu_3 the greatest. The Cu_4 plants were heavier than the Cu_2 plants but lighter than those of the Cu_3 treatment. The vast dis-

FIG. I



parity between the weights of the Cu_1 and Cu_3 plants at the end of the experiment indicated the decisive importance of copper to the health and wellbeing of the rubber plant which were well reflected in terms of root growth and general vigour (Plates II and IV).

CHEMICAL DATA

The concentration of rubber and nutrients in the tissues

It is not feasible to present all the chemical data here. The variation in chemical composition of roots and stems at different copper levels is summarized in graphical form and the concentration values are expressed in terms of oven-dried material. The effect of copper level on laminar composition is given for the expanded laminae of the top storey only: similar effects for the laminae of other storeys are not presented as, generally, they do not add any extra information. The effect of copper level on composition of laminae might vary, as measured arithmetically, according to storey position of leaves but this usually did not alter the nature of the effect. An examination of the data, for the top storey laminae, showed that there was no obvious indication of a change in treatment effect according to data for the samplings carried out in July, September and February. The data from these samplings were therefore combined for the purposes of the statistical analyses reported here.

The concentration of copper within the roots reflected the copper status of the plant with greater amplitude than did the stems and laminae (Fig. 2). At the end of the experiment the Cu_4 and Cu_1 roots contained 246 ppm and 6 ppm of copper, respectively, as compared with values of 11 ppm and 2 ppm obtained for the corresponding stems. In general, for any one copper level at any one sampling date the roots contained a higher concentration of copper than did the laminae, which, in turn, was higher than that of the stems. The difference between the copper concentrations of Cu_1 and Cu_2 laminae was always discernible (Table I), but this was not always so for the stems (Fig. 2). As the copper-deficiency symptoms were mainly localised towards the top of the plant, it was expected that analysis would show that the younger laminae possessed a smaller concentration of copper than the older laminae. However, the analytical results did not show any well-marked trend; they indicated, for the Cu_2 plants, that the younger or top storey laminae possessed about the same or a slightly smaller concentration of copper than those of the older second and third

TABLE I

Rubber, chlorophyll and mineral nutrient concentrations in laminae and total amounts of rubber and minerals per plant (shoot plus root). Concentration values are means derived for the top storey leaves sampled in July, September and February and are expressed either as a % or ppm of dry matter. The total values (mg/plant) were derived from the February sampling (14-months old plants) and are each based on analysis of a total of 8 plants

Treatment	Cu_1	Cu_2	Cu_3	Cu_4	Min. 5% Sig. Diff.
Concentration values					
Cu . . . . ppm	2.8	3.6	11.8	13.7	2.03
Rubber (laminae) . . %	0.50	0.45	0.39	0.39	0.19
Rubber (petioles) . . %	1.85	1.08	1.09	1.02	0.89
Chlorophyll . . . . %	0.96	0.94	1.04	1.05	.054
N . . . . %	5.12	4.46	4.52	4.64	0.21
P . . . . %	0.56	0.34	0.34	0.34	.034
Mg . . . . %	0.31	0.27	0.26	0.26	.035
K . . . . %	1.44	1.28	1.40	1.38	0.29
Ca . . . . %	0.38	0.33	0.30	0.36	0.14
Fe . . . . ppm	110	108	110	106	34
Mn . . . . ppm	56	31	30	39	4.3
Total values (mg/plant)					
Cu	0.3	1.8	9.8	49.9	
Rubber	632	1644	2455	2191	
N	3324	9291	13302	13726	
P	735	1512	1879	1950	
Mg	318	1197	1818	1916	
K	1099	3905	6777	6534	
Ca	575	1639	2871	2732	
Fe	36	167	476	457	
Mn	8.1	12.6	18.3	16.8	

storey laminae (Table II). This difference in copper concentration was frequently not significant. Conclusive data could not be collected for the Cu_1 plants as during the time when symptoms were present, second and third storey leaves were not available for sampling. There was a clear indication that, for the Cu_3 and Cu_4 plants, top storey laminae possessed a higher concentration of copper than the older second and third storey laminae.

In the early sampling of March 1955 when symptoms of copper deficiency were not marked the top storey laminae of the Cu_1 plants possessed a copper concentration of as much as 9 ppm. As the symptoms developed and became established this concentration fell to between 2 to 3 ppm of copper. The concentration of copper in the corresponding Cu_2 laminae at about this time was consistently higher, and ranged between 3 to 5 ppm. Healthy top storey laminae of the Cu_3 plants possessed a copper concentration of at least 10 ppm (Table I).

TABLE II

Distribution of copper in laminae, according to storey position. Values based on September and February samplings and expressed as ppm of dry matter of laminae

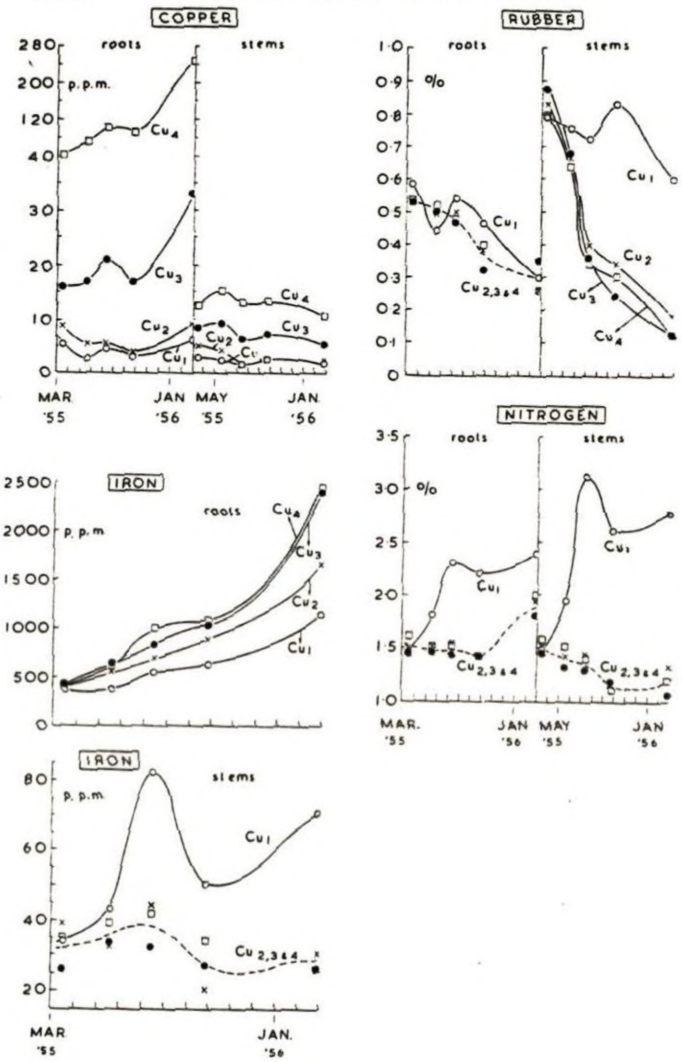
Storey \ Treatment	Cu_2	Cu_3	Cu_4
Top (youngest laminae)	3.2	11.5	13.8
2nd	3.0	10.2	12.5
3rd (oldest laminae) . .	4.2	10.1	11.6
Min. 5% sig. diff. . . .	1.1	1.3	1.3

For both roots and stems the *rubber* concentration was higher in the Cu_1 plants than in plants grown at other copper levels; this difference was slight for the roots but well marked for the stems (Fig. 2). In addition, for the stems, it was found that the Cu_2 plants possessed a higher rubber concentration than the Cu_3 and Cu_4 plants, but albeit much lower than that of the Cu_1 plants. The concentration of rubber within the petioles was much higher in the Cu_1 plants than for all other treatments; a similar, but less obvious effect, was noted for the laminae (Table I). For the roots and stems there was evidence of a decline in rubber concentration as the plants grew older; such a trend was not noted for the petioles.

The concentration of chlorophyll within the top storey laminae of the Cu_1 and Cu_2 plants was less than found for the higher copper levels (Table I). This effect, although significant, was much more strongly evident in the laminae of the second and third storeys, and seemed to indicate that the positive effect of extra copper supply on chlorophyll concentration was more marked in the older laminea. For the earlier samplings, the chlorophyll concentration of the Cu_2 laminae was of the same order as that of the Cu_3 but later, when mild copper-deficiency symptoms became apparent, the concentration fell to that of the Cu_1 laminae. The full data are not presented here.

The concentrations of nitrogen in the roots and stems of the Cu_1 plants were much higher than for plants of other treatments (Fig. 2). It increased progressively with the inception and increasing severity of the copper-deficiency symptoms; this increase did not cease until copper was supplied to the plants in July. The laminae,

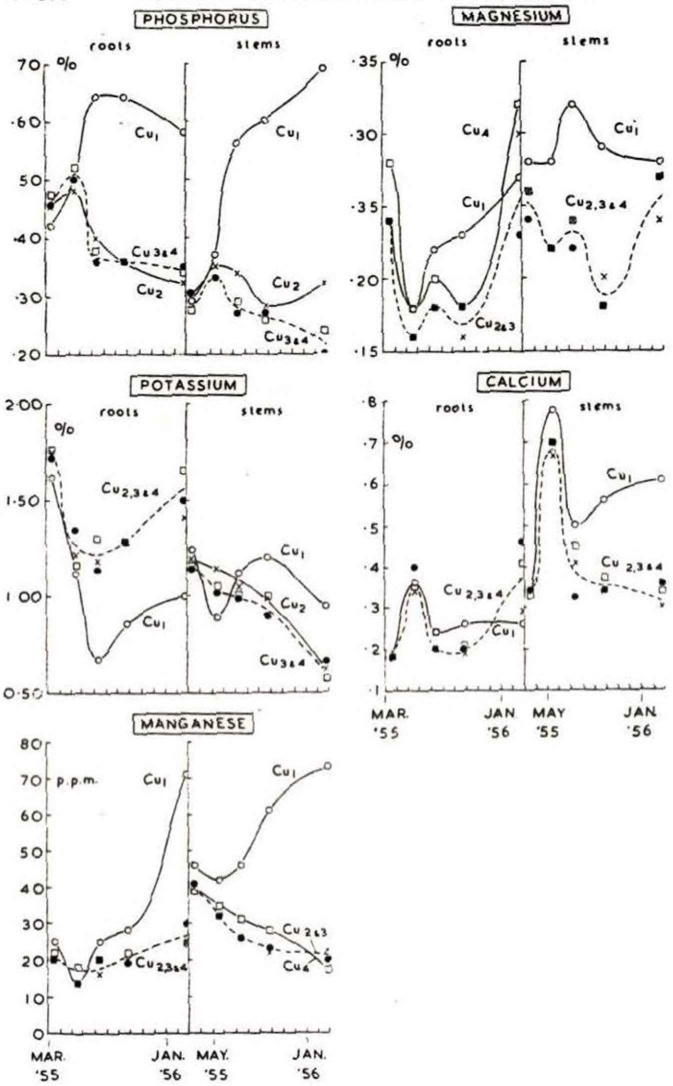
FIG. 2 CONCENTRATION IN DRY MATTER



also, of the Cu_2, Cu_3 and Cu_4 plants contained a smaller concentration of nitrogen than did those of the Cu_1 plants (Table I).

As for nitrogen, the concentrations of phosphorus in the roots, stems and laminae were much greater in the Cu_1 plants than in those of all other treatments (Fig. 3, Table I). The stems of the Cu_2

FIG. 3 NUTRIENT CONCENTRATION IN DRY MATTER



plants usually contained a higher concentration than did those of the Cu_3 and Cu_4 plants and thus showed some parallel to the variation observed for rubber.

The concentration of magnesium in the stem tissues was much higher for the Cu_1 plants than for those of other treatments; no consistent difference was observed between the Cu_2, Cu_3 and Cu_4 stem concentrations of magnesium (Fig. 3). The root tissue did not show a consistent effect of copper level on magnesium concentration which for all treatments showed a sharp initial decline in May to be followed by marked increase towards the end of the experiment. Increased copper supply significantly decreased the magnesium concentration of the laminae but this effect was generally not as well marked as the similar ones noted on nitrogen and phosphorus concentrations (Table I).

A deficiency of copper decreased the concentration of potassium found in the roots (Fig. 3); this effect was in marked contrast to those noted above and is similar for the one noted on iron concentration. For the stems, however, there were indications that the Cu_1 plants possessed a higher potassium concentration than found in healthy plants (Fig. 3). A significant and consistent effect of copper level on the concentration of potassium found in the laminae was not detected (Table I).

The calcium concentrations of both roots and laminae did not vary consistently with copper supply but the stems of the Cu_1 plants possessed a higher concentration of calcium than did those of other treatments (Fig. 3, Table I).

The level of copper supply affected the concentration of iron in the roots (Fig. 2); the iron concentration was lowest for the Cu_1 plants and usually increased with copper level. However, the stems of the Cu_1 plants contained a higher concentration of iron than did plants of other treatments (Fig. 2). A significant effect of copper level on iron concentration of laminae was not obtained (Table I).

The concentrations of manganese found in the root and stem tissues were consistently higher for the Cu_1 plants than for plants of other treatments (Fig. 3). Increased copper supply also significantly decreased the concentration of manganese found in the laminae (Table I).

The relative distribution of rubber and nutrient elements in the plant

The total amount of rubber and of each nutrient element present per plant at the February 1956 sampling is given in Table I. It is clear that the differences in tissue concentrations reported above were insufficient to overcome the overriding beneficial effect of copper on dry weight per plant. Therefore, as the copper level increased so did the amounts of rubber and nutrients found in each plant, despite the frequently elevated concentrations of these substances found in the tissues of the Cu_1 plants. It was noteworthy that whereas the Cu_4 plants contained only about 2 to 6 times as much of nitrogen, phosphorus, magnesium, potassium, calcium and manganese as did the Cu_1 plants, this ratio was many times higher in regard to iron (15 times) and copper (160 times).

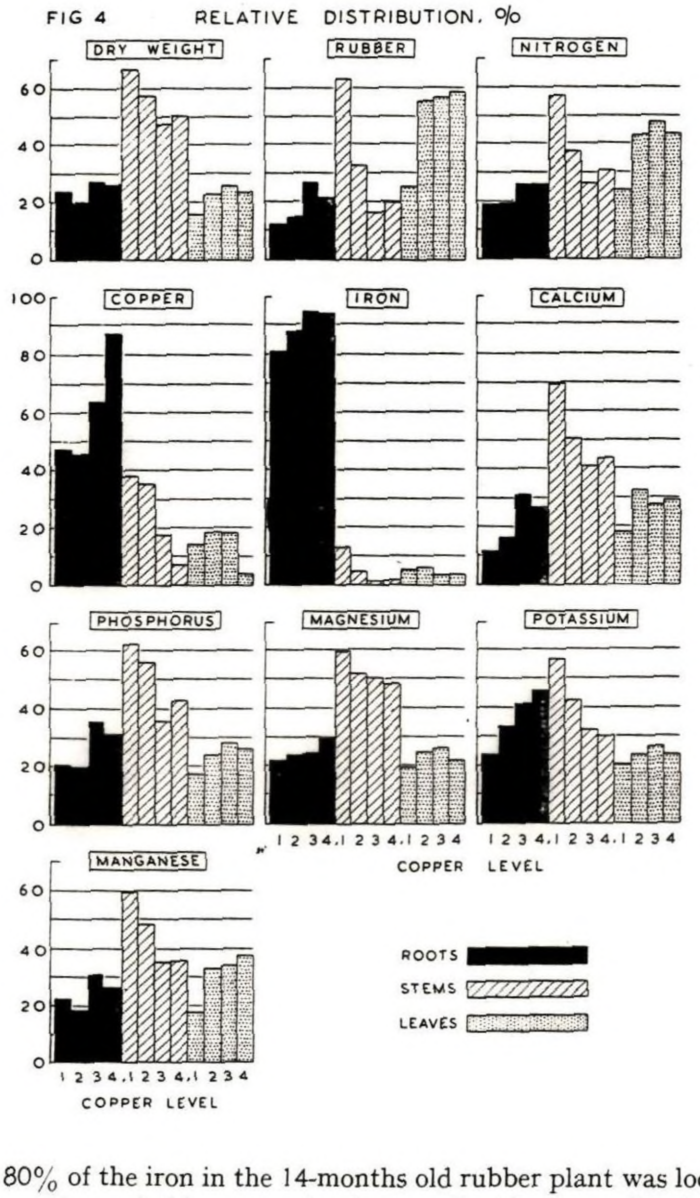
It is not intended to present here the full data on the distribution of nutrient elements, as affected by level of copper supply. The distribution, as a percentage of the total per plant, for any one variable showed certain trends which were best illustrated in the 1956, February sampling; these are described below and are illustrated in Figure 4. Earlier samplings showed the same trends, but were not developed to such a marked degree.

About half of the dry weight of each plant, for the February sampling, was contributed by the stems. The proportion of stem dry weight slightly decreased with increased copper level but that of leaves (laminae plus petioles) increased, while it had no consistent effect on the proportion of dry weight accounted for by the roots. The distribution of minerals did not necessarily follow this pattern and was usually strongly influenced by the copper status of the plant.

Increased copper level increased the proportion of copper distributed to the roots while it decreased that found in stems. These effects were very marked and clearly indicated the retentive influence of roots when a high level of copper was supplied to the plant.

Increased copper supply also reduced the proportion of rubber found in the stems but increased the proportions found in leaves and roots. Here, again, the effect of increased copper level was to decrease the stem/root distribution ratio; for copper, this effect was largely gained by an increase in the proportion found in the roots but for rubber, the decrease in the proportion found in the stems mainly accounted for the decreased ratio.

For the other elements examined (N, P, Mg, K, Ca, Fe and Mn) the distribution, with increased copper level, generally showed a diminution in the proportion found in the stems but increased proportions for roots and leaves. Frequently the proportion of any element distributed to the Cu_4 leaves would be less than for the Cu_3 plants but this was not adjudged to be of great importance. More



than 80% of the iron in the 14-months old rubber plant was located in the roots, and this proportion increased with copper level.

DISCUSSION

The results indicated, beyond reasonable doubt, the essentiality of copper as a nutrient element, for *Hevea brasiliensis*. An obvious similarity existed between the copper-deficiency symptoms, here described for *Hevea*, and the symptoms of dieback and exanthema reported for fruit trees (see Stiles [16] and Gilbert [11]); all were characterised by some apical defoliation and severe dieback of the branch tips. These symptoms were highly characteristic and have not been observed, in *Hevea*, under conditions of any other mineral deficiency. The inception and development of the symptoms were accompanied by a decrease in the chlorophyll concentration within the laminae as has also been noted for some other crops (see Gilbert [11]). It was noteworthy that for most of the tree crops studied (Bould, Nicholas, Tolhurst and Potter [8], Drossdoff and Dickey [10], and Stiles [16]), the threshold copper value associated with the appearance of deficiency symptoms fell within the range of 2–5 ppm of copper (in dried leaves), as compared with the 2–3 ppm. range reported here for *Hevea*. The results of the present experiment, in which plants were grown in sand, suggested that healthy laminae of *Hevea brasiliensis* should contain at least 10 ppm of copper, when expressed on a dry matter basis. Laminae of field-grown rubber plants which have been analysed in the course of advisory work fully confirmed this suggestion and gave copper values which usually ranged between 10 to 20 ppm, although some fell as low as 7 ppm.

Bould *et al* [8]. have indicated that the response of apple trees to copper application, was not always accompanied by an increase in the copper concentration of leaves when expressed as a percentage of dry matter. The present experiment showed that the concentration of copper found in the roots reflected the available supply of copper to the plant better than that found in the laminae which, in turn, furnished a slightly better index than the stems. It appeared that analysis of roots might be useful for field diagnostic purposes if the problem of soil contamination of samples could be overcome.

A significant and important fact which arose from the present experiment was that rubber plants may suffer from a mild deficiency of copper which can cause a marked reduction in dry weight of the plant (Fig. 1) but be insufficiently severe to give rise to diagnostic foliar copper-deficiency symptoms. This was so for some of the Cu_2 plants and emphasised the possibility that many Malayan rubber trees may be suffering from a mild deficiency of copper, especially those grown in peat soils, and lent credence to the claims of rubber production increases, in response to soil applications of copper salts, made by Compagnon and Beaufils [9]. A severe deficiency of copper will certainly reduce the height of the rubber plant but, in general, girth and leaflet number are better indices of the plant's copper status (Fig. I). As leaflet count proves difficult in trees, girth, the traditional index of the rubber tree's health and well-being, may be employed to measure the tree's response to copper addition. The tolerance of *Hevea* to the relatively high concentration of copper (0.5 ppm) supplied in the nutrient to the Cu_4 plants and their improvement in vigour, in relation to the Cu_3 plants, towards the end of the experiment suggested that the rubber plant has a high requirement for copper. In part, this high demand may have been stimulated by the high levels of ammonium and iron ions supplied in the nutrient solution but the possibility that the rubber tree may possess a higher requirement than usually ascribed to temperate-climate plants, should not be overlooked.

Severely copper-deficient plants can only be resuscitated with difficulty; it required a six weeks period, with daily application of Cu_2 nutrient to allow the Cu_1 plants to regain some semblance of vigour. If severe copper deficiency is ever encountered under Malayan conditions it may prove a more successful curative procedure to supply repeated dosages of small amounts of copper salts rather than application of one large dosage.

A deficiency of copper reduced the concentration of potassium found in the roots (Fig. 3); a similar, and perhaps more consistent, effect was found for iron concentration (Fig. 2). This behaviour was in contrast to the accumulation of some other nutrient elements and suggested that copper status played a role in the absorption and retention of both potassium and iron by the roots. The lowest level of copper supply promoted increases in both the potassium and iron concentrations of the stem tissue as compared with plants grown at a higher level of copper supply; these increased concentrations were similar to those recorded for nitrogen, phosphorus and other elements (see Figs 2 and 3). Little evidence was available to show that the reduction, at the Cu_1 level of the total amount of potassium contained per plant was of any greater significance than, for example the reduction in the total amounts of nitrogen or phosphorus per plant (Table I). All effects can readily be explained in terms of the growth reduction suffered at the Cu_1 level rather than to any specific relationship of potassium absorption to copper status as claimed by Beaufils and Compagnon [2 4 9]. It is, however, conceivable that once rubber trees are in tapping the drain on potassium reserves, removed in the latex, may elevate the effect of the plants copper status, as an influencing factor in the absorption of potassium by the roots, to one of controlling importance. It could then be feasibly expected that, unless copper was available in sufficient supply, the addition of potassium to the soil would be insufficient, in itself, to raise the potassium concentration of the roots to a favourable level; once this situation arose the absorption ability of the roots could become detrimentally affected.

A deficiency of copper usually: increased the concentration of nitrogen, phosphorus and manganese found in the roots; increased the stem concentrations of rubber, nitrogen, phosphorus, magnesium, potassium, calcium, iron and manganese; and increased the laminar concentrations of nitrogen, phosphorus, magnesium and manganese. These increased concentrations may be ascribed to the restrictive effect of copper deficiency on the growth of the plant which has consequently accumulated more of these elements than required for growth purposes. Therefore, these inflated values do not imply a greater absorption of these elements by copper-deficient plants which, in fact, contained much less of these nutrients, per plant, than did the healthy Cu_3 plants (Table I). The increased concentrations of many of these elements in the laminae must not be regarded as a specific attribute of copper deficiency as it is well established that a deficiency of any one of the essential nutrient elements will cause accumulation of others; for example a deficiency of nitrogen may cause an increased concentration of potassium and a deficiency of magnesium may promote the accumulation of manganese in the laminae of the rubber plant (Bolle-Jones [6 7]). However, the decreased concentration of potassium and iron in the roots of copper-deficient plants suggested a direct effect of copper status on the accumulation of those elements within the roots.

The parallelism between the increased tissue concentration of these various nutrient elements and that of rubber did not necessarily signify a direct role of these elements in rubber formation. Graphs, which are not presented here, showed that with increased stem concentrations of nitrogen, phosphorus, potassium, iron and manganese, the corresponding rubber concentration also increased. Such relationships, however, seem to be incidental and do not possess any value unless it can be shown that, without large variations in total dry weight of plant, an increase in these elements would also increase the concentration of rubber. The present data did not provide such a comparison, as these increased concentrations of mineral elements and of rubber were accompanied by a marked diminution in growth and dry weight of plant under conditions of copper deficiency: that is, conditions which tend to give an inflationary influence to any values expressed in terms of concentration. Neither was there any evidence to suggest that an increased level of copper supply increased the concentration of rubber within the tissues; in fact, the opposite effect was obtained and there were no grounds whatever for assuming that copper had a major, or an exceptional, role to play in rubber synthesis.

The distribution of rubber and of nutrient elements within the plant were markedly influenced by the level of copper supply. Increased copper usually increased the proportion of rubber and of nutrients distributed to the roots; this root accumulation was most marked for copper, itself, potassium and calcium. The decline in the proportion of rubber and mineral found in the stems, as the copper supply increased, was also most striking and was well marked for most of the variables but was least noticeable for magnesium and iron. Increases in the amounts of rubber and minerals found in the leaves (laminae plus petioles) were recorded with increased copper level but the proportion of total dry weight recorded as leaves also increased with increasing copper level. However, it can be asserted with confidence, that allowing for this parallel increase in dry weight, the proportion of rubber, nitrogen, and manganese found in the leaves increased with copper level. It was also of great interest that increased copper supply could cause such a marked uptake of iron (Table I) most of which was retained in the roots.

SUMMARY AND CONCLUSIONS

1. Rubber seedlings were grown in sand for a fourteen-month period and were supplied with four levels of copper which ranged from a very low to a high nutrient copper concentration.

2. Seedlings grown at the lowest level of copper supply (Cu_1 treatment) exhibited symptoms of copper deficiency which included extensive apical defoliation, severe dieback and marked stunting. The number of leaflets per plant or a measurement of stem girth proved a better and more sensitive index to copper status than did height.

3. Copper-deficient laminae possessed 2 to 3 ppm of copper, as expressed on an oven-dry basis, and were characterised by much higher concentrations of nitrogen, phosphorus, magnesium and manganese and a lower concentration of chlorophyll as compared with laminae produced at a normal level of copper (Cu_3 treatment). It was suggested that the concentration of copper in roots provided a better guide to copper status than that of laminae.

4. Although the decreased concentration of potassium in the roots of the copper-deficient plants suggested a direct effect of copper status on the accumulation of potassium within the roots, this was insufficient reason to attribute the decreased gross potassium content per Cu_1 plant (as compared with a Cu_3 plant) to a specific effect of copper on potassium absorption, as this same effect of copper status was noted on the gross, contents of all other nutrient elements examined. However, it is pointed out that, for tapped mature trees, copper may well exert a major influence on potassium absorption, as claimed by Beaufils.

5. Increased copper supply increased greatly the amount of iron taken up by the seedlings and the proportion of iron which was distributed to the roots.

6. The distribution of rubber and of nutrient elements within the plant were markedly influenced by the level of copper supply. In general, increased copper increased the proportions of rubber and minerals distributed to the roots but decreased the proportion found in the stems. These effects were relatively less well marked for magnesium. The proportions of the total rubber, nitrogen and manganese contents, per plant, distributed to the leaves increased with copper level.

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THE DISAPPEARANCE OF LEAF LITTER UNDER DIFFERENT WOODLAND CONDITIONS *

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FOREWORD

Roudsea Wood is one of the most varied woodlands in the British Isles. It lies in the south of the English Lake District and is about five miles west of Grange-over-Sands. The main part of the wood is situated on two parallel ridges, one of Carboniferous limestone, the other of Silurian slate. The crest and scarp of the limestone ridge are dominated by yew, whilst the eastern dip slope supports coppiced ash-oak woodland; the slate ridge, on the other hand, carries high oak-wood and coppice in which oak and birch predominate. Between the ridges there is a small tarn, now almost filled and surrounded by a fen community. On its seaward side Roudsea slopes down to the salt marshes fringing Morecambe Bay whilst to the landward lie the Holker mosses, a large area of acid peat.

The wood has long been known to naturalists and valued by them for its wide range of native woodland plants. Since its declaration as a National Nature Reserve in 1955 Roudsea Wood has become one of the main sites of intensive study on the ecology of woodlands for the Nature Conservancy's Research Station at Grange-over-Sands. The research effort is being concentrated initially on the biological and chemical processes occurring in the soil and litter, although attention is also being given to the problem of natural regeneration of woodland. It is hoped that a concerted study of the woodland ecosystem by botanists, microbiologists and zoologists will prove particularly fruitful.

INTRODUCTION

Studies on the fate of selected quantities of leaf litter are difficult to carry out under natural conditions because it is impossible to maintain the identity of experimental samples while allowing the full range of environmental factors to operate. In some previous

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