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# Growth and flowering of cacao under controlled atmospheric relative humidities

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SUMMARY

Young clonal cacao trees have been grown for 390 days in controlled environment rooms, either continuously at relative humidity levels of 50–60% (low), 70–80% (medium) or 90–95% (high), or alternated between any two of these levels at 109-day intervals. The temperature was 80 ± 1 °F. (26·7 °C.) throughout, and the plants were watered frequently to keep the soil near to field capacity.

Plants at the low humidity flushed before the others, but thereafter the period between flushes was rather longer at low and medium than at high humidity. There was little difference in numbers of leaves expanded, but the area of each expanded leaf was consistently least during periods of high humidity and, overall, greatest during periods of low humidity. Leaf weight per unit area was greatest at high humidity. Total dry weight increase per plant was greatest under alternating humidities, particularly when one of the periods was at high humidity. At constant high humidity both net leaf area and total dry weight were least of all. Stem length was significantly greater at high humidity than at low.

Flowering was good in all treatments and usually particularly profuse following the transfer of plants from a low or medium to a high humidity.

CACAO (*Theobroma cacao* L.) is native to the tropical rain forests of the Amazon basin where, growing as an under-storey tree, it is normally subjected to high atmospheric relative humidities. Traditionally, cultivated cacao is also grown under shade trees, but the results of an experiment started by Evans and Murray (1953) in Trinidad, and since confirmed by other workers, showed that under favourable conditions, on soils of high nutrient status, the greatest yields of cacao may be obtained in the absence of shade. The removal of shade trees may affect not only light intensity but also other environmental factors such as air movement and humidity and air and soil temperatures, and under some conditions shade trees are considered to provide an essential buffering action against the deleterious effects of sudden and extreme environmental fluctuations. Most cacao-growing regions have fairly distinct dry and wet seasons, and McDonald (1932), comparing high- and low-yielding cacao plots, found the latter to be characterized by marked fluctuations in soil and atmospheric moisture which occurred particularly under windy conditions in the dry season.

In the field, the levels of the climatic factors are often interdependent, and it may be difficult to distinguish the effects of one from those of another. The construction of con-

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trolled environment growth rooms in Trinidad has helped to overcome this problem, and in the work reported here growth and flowering of cacao have been studied when the relative humidity of the atmosphere was the only variable environmental factor.

## METHODS

The three growth rooms used were described previously (Sale, 1968). The temperature in each room was maintained at 80 ± 1 °F. (26·7 °C.) day and night, a temperature which the previous work had shown to be favourable for growth and flowering of cacao. The light intensity at the plant tops, 3 ft. from the fluorescent tubes, averaged 31,600 ergs/cm.$^2$/sec. The lights were switched to give an 18-hour day, and the plants therefore received 50% more total light energy than those given a 12-hour day in the previous work. Piringer and Downs (1960) found that the only morphological difference in cacao seedlings grown at these two photoperiods was a rather longer stem and slightly earlier jorquetting (branching) at an 18-hour day, and Alvim and Grangier (1965) showed that cacao did not have a specific photoperiodic requirement for flower initiation.

Dehumidification in these growth rooms is achieved by use of the air conditioner unit which also controls temperature. In this experiment, the lowest relative humidity range, measured by a thermohygrograph which was checked frequently against a whirling hygrometer, was 50–60%, the fluctuations occurring every few minutes as the compressor cut in and out. The higher humidities, obtained with centrifugal humidifiers controlled through paper humidistats, were 70–80% (medium) and 90–95% (high), fluctuations within each range again occurring every few minutes. Occasionally at the medium or high humidities the range of fluctuation would drift to a maximum of an additional ± 5%. Rain water was used to supply the humidifier reservoirs so as to avoid any possible growth effects from minerals dissolved in the mains water.

Cuttings of the cacao clone ICS 95, taken in August 1966, were potted up in April 1967 into galvanized containers, size 12 in. × 12 in. × 18 in. deep, using a compost of shredded soil and rotted manure. The plants were grown in a glasshouse until 26th September 1967, when, following a vigorous leaf flush on all the plants, all the older leaves which showed any sign of senescence were removed and each of the others tagged with a leaf and plant number, and its length measured. Eighteen plants were then placed in each of the growth rooms and a further six left in the glasshouse. All the plants were thereafter watered frequently, thereby maintaining the soil close to field capacity at all times, to try and avoid any effects due to soil moisture stress. The plants were given liquid fertilizer once a month and sprayed against pests whenever necessary.

Detailed growth measurements were made on each plant throughout the experiment. Once a week the numbers of new flushes were counted, the length of every leaf that had expanded and started to harden during the previous week was measured, and the leaf tagged to record its number and date of expansion. The area of each leaf was subsequently calculated by means of a formula derived according to the method of Asomaning and Lockard (1963). Any abscissed leaves were collected daily and recorded, and their dry weights determined. Every week the number of active flowering cushions (those bearing at least a visible bud) were counted, as were the total numbers of flowers open on each plant and the numbers which had opened and abscissed during the week.



After about 100 days the plants at the three humidities were showing marked differences in their patterns of growth, and on day 109, shortly after most plants had flushed, of the eighteen plants at each level of relative humidity, six were moved to each of the other two levels of humidity while the remaining six were not moved. The first 109 days will be referred to as the first period. After a further 109 days (second period) the plants which had been moved were restored to their original humidity level and, finally, after yet another 109 days (third period), moved back to their second position where they spent 60 days (fourth period) before being harvested. Thus, there were nine growth room treatments, each with six replicated plants, in which plants were either grown constantly at one level of relative humidity or alternated between any two of the levels at 109-day intervals. At the end of the experiment the dry weights of roots, stems and leaves were determined separately, and the total stem length measured.

To determine the relative transpiration rates at each humidity level, four plants and their containers in each growth-room were weighed daily for three weeks, starting on day 180, and known amounts of water were added after weighing to keep the soil near to field capacity. Evaporation from the soil surface was prevented by tying sheets of polythene round the plant stems and sides of the containers.

## RESULTS

To reduce the considerable volume of data resulting from this experiment, values for the various parameters measured are sometimes given in the Tables below as means for each treatment over the whole experimental period; only where differences were highly significant are values given for the four periods separately. Values are given for the glasshouse plants for comparison, but are not included in the statistical analyses.

### *Flushing*

In the first two periods, plants at low and medium humidities produced rather more flushes than those at the high humidity, but the opposite was true for the last two periods. Differences were generally not significant as standard errors were fairly high, and there were no significant differences in the total numbers of flushes over the whole period (Table I). There was very little axillary flushing. A marked difference in time of flushing which occurred at the beginning of the experiment can be seen from the data for numbers of leaves expanded (Fig. 1). All the plants at the low humidity produced five to seven flushes per plant at about 20 days and again at 50 and 100 days from the beginning of the experiment, with a few flushes at 70 days. At the high humidity there were three to five flushes per plant after 20 and 70 days, but a vigorous flush (13–20 per plant) at 105 days (the end of the first period). At the medium humidity there were four to six flushes per plant at about 20 and 50 days, followed by eight to fourteen per plant at 105 days. Thereafter flushing behaviour settled into a steadier pattern. Plants kept continuously at the low or medium humidity tended to produce several flushes about every 30 days, while those continuously at the high humidity produced rather fewer flushes about every 20 days. Within each treatment the six plants usually flushed in phase, though any one plant would quite often miss a flush. The transference of plants from one humidity to another had no consistent effect

TABLE I

*Flush and leaf numbers and leaf areas for cacao grown at low, medium or high relative humidity, either constantly or alternating between two humidity levels at 109-day intervals. Values are means for the whole experiment, except for mean areas per leaf which are also given for each period separately*

| Relative humidity | | | | Total number of flushes per plant | Mean numbers of leaves per flush | Mean leaf area expanded per plant, dm.² | Mean leaf area per plant during experiment dm.² | Mean area per leaf, cm.² | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 2 | 3 | 4 | | | | | Overall | 1 | 2 | 3 | 4 |
| Low | Low | Low | Low | 105 | 1·89 | 445 | 187 | 219 | 192 | 232 | 231 | 235 |
| Low | Medium | Low | Medium | 117 | 1·89 | 509 | 195 | 226 | 196 | 265 | 216 | 219 |
| Low | High | Low | High | 127 | 1·98 | 451 | 189 | 188 | 200 | 210 | 200 | 171 |
| Medium | Low | Medium | Low | 106 | 1·86 | 395 | 152 | 212 | 171 | 232 | 254 | 221 |
| Medium | Medium | Medium | Medium | 123 | 1·65 | 400 | 143 | 188 | 157 | 163 | 246 | 256 |
| Medium | High | Medium | High | 99 | 1·87 | 351 | 161 | 188 | 172 | 163 | 201 | 250 |
| High | Low | High | Low | 116 | 1·84 | 395 | 155 | 187 | 124 | 188 | 201 | 197 |
| High | Medium | High | Medium | 126 | 1·84 | 417 | 179 | 164 | 115 | 175 | 176 | 240 |
| High | High | High | High | 105 | 1·66 | 298 | 102 | 149 | 137 | 121 | 157 | 207 |
| s.e. (treatments) (45 d.f.) | | | | ±16·6 | ±0·084 | ±46·8 | ±16·4 | ±11·3 | ±18·8 | ±16·6 | ±20·0 | ±28·1 |
| Means† | (a) | Low | | 116 | 1·92 | 468 | 190 | 211 | (c) 196 | 217 | 216 | 218 |
| | | Medium | | 109 | 1·79 | 382 | 152 | 196 | 167 | 201 | 234 | 241 |
| | | High | | 116 | 1·78 | 370 | 145 | 166 | 126 | 165 | 178 | 209 |
| | (b) | Low | | 109 | 1·86 | 412 | 165 | 206 | | | | |
| | | Medium | | 122 | 1·79 | 442 | 172 | 193 | | | | |
| | | High | | 110 | 1·84 | 367 | 151 | 175 | | | | |
| s.e. (means) (45 d.f.) | | | | ±9·6 | ±0·049 | ±27·0 | ±9·1 | ±6·5 | ±10·7 | ±9·6 | ±11·6 | ±16·3 |
| Glasshouse plants | | | | 60 | 3·68 | 454 | 259 | 209 | 194 | 229 | 200 | 178 |

†Mean (a) is for the level of humidity given during periods 1 and 3, mean (b) for that during periods 2 and 4. Mean (c) is for all plants at each level of humidity during the current period, and values are therefore for different plants in 1 and 3 compared with 2 and 4.



on flushing behaviour. Thus, although there was a vigorous flushing shortly after the final transfer from low humidity to medium or high humidity in the low-medium-low-medium and low-high-low-high treatments, there was no similar effect after the second transfer in the medium-low-medium-low and high-low-high-low treatments.

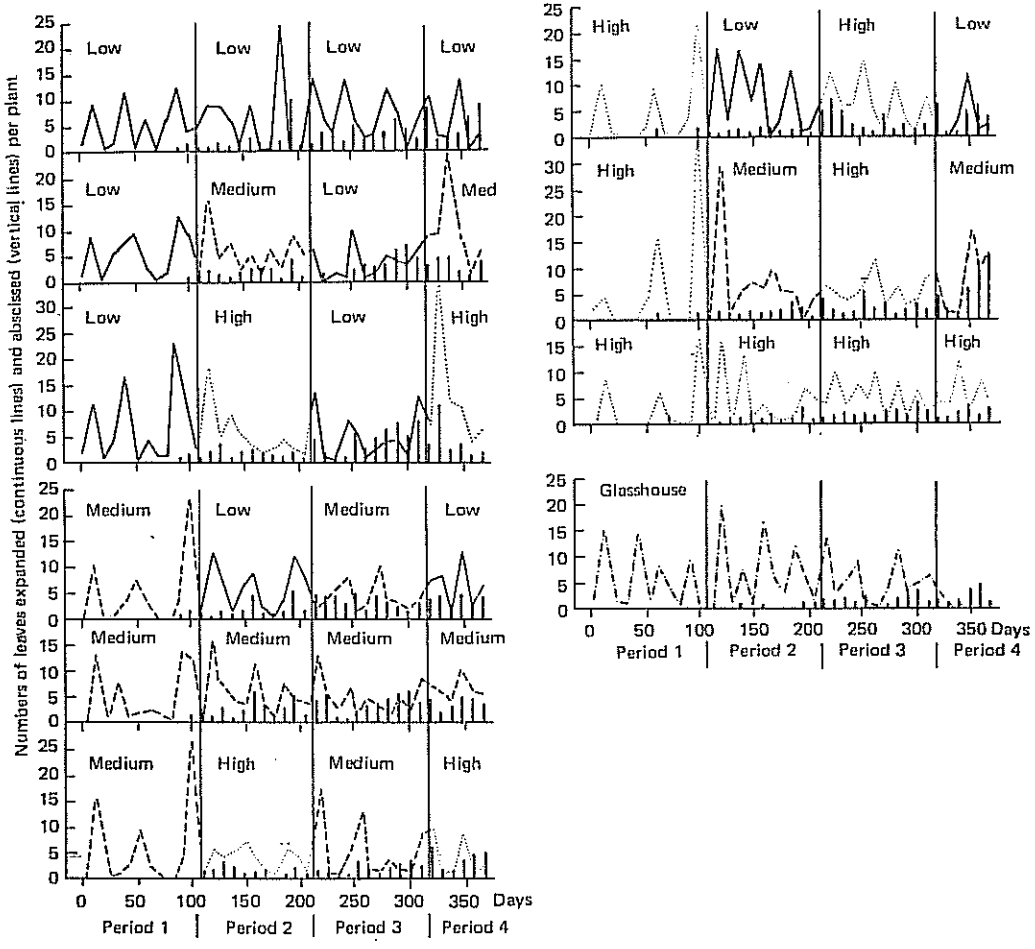


FIG. 1

Numbers of leaves expanded (continuous lines) and abscissed (vertical lines) for cacao grown at low (solid continuous lines), medium (dashed lines) or high (dotted lines) relative humidities either constantly or alternating between two humidity levels at 109-day intervals. Values for glasshouse plants are also shown. The abscission of leaves which expanded before the treatments were started is not included. Values are means for six replicates.

*Leaf growth*

Over the whole experimental period, the numbers of leaves expanded per flush were significantly less ($P < 5\%$) on plants at the continuously high or continuously medium humidity than on plants given any of the other treatments (Table I). This effect was not sufficiently large to result in any significant difference in the total numbers of leaves expanded per plant. Although the glasshouse plants produced only about half as many flushes as growth-room plants each flush expanded about twice as many leaves, resulting in a similar total leaf number.

There was a marked effect of humidity on the expanded area of each leaf, and values are given in Table I for each period separately. The mean leaf size for all plants currently at each humidity level was always significantly the smallest ($P < 0{\cdot}1\%$) at the high humidity. In periods 1 and 2, leaves expanded at the low humidity were larger than those at medium humidity ($P < 1\%$ and $< 5\%$, respectively); however, in periods 3 and 4, this order was reversed, though differences were not significant. Averaged over the whole experiment, leaves at the low humidity were significantly the largest ($P < 5\%$).

This effect on the area of each leaf resulted in significant differences in total area of all new leaves expanded per plant in each treatment, although the standard errors for this parameter were rather high. In period 1, the new expanded area at low humidity was greater than that at medium humidity, which in turn was greater than at high humidity (both differences significant at $P < 0{\cdot}1\%$). In period 2, the total new expanded area was again least ($P < 0{\cdot}1\%$) at high humidity, but the difference between medium and low humidities was not significant. In the third and fourth periods, when rather more leaves were expanded on plants at the high humidity, differences were smaller and not significant. Overall, the greatest total area of expanded leaf occurred in the low-medium-low-medium humidity plants (significant at $P < 5\%$ over all the others) (Table I), while the least was at constant high humidity (significantly less at $P < 5\%$ than all except the medium-high treatment).

The net leaf area per plant depends not only on numbers and size of leaves expanded but also on leaf duration. This was very variable in all the treatments and values are not given, for although many leaves abscissed during the experiment a considerable number which expanded when the treatments started were still on the plants at the end. However, some of these first leaves began to abscise about 120 days after expansion (Fig. 1) and, as the experiment progressed, there was a tendency for more to abscise on plants currently at the low humidity than at the high. The effect of this on net leaf area per plant (Fig. 2) was partly to offset the greater area per leaf at low humidity. In Figs. 1 and 2 only those leaves which expanded after the beginning of the growth-room treatments are taken into account. Thus, for the plants grown at constant humidities, although the net leaf area was always greatest at low and least at high humidity, most of the difference arose during the first period and early part of the second before the greater size per leaf was balanced by the rather greater abscission and slightly fewer new leaves expanded at the low humidity. The result of these effects was also seen in plants receiving alternating humidities. Thus, while in the second period there was a marked increase in net leaf area where low or medium followed high humidity, and a decrease in rate where high followed low or medium, in the latter half of the third period the effect of leaf abscission became increasingly marked, and there was a slight change in the relative numbers of new leaves expanded, resulting in a small



decrease in net leaf area where low had followed high or medium humidity. There was no decrease at medium or high humidity in this period. The response in the fourth period was similar. Overall, the mean net leaf area per plant throughout the experiment (Table I) was significantly less at the continuously high humidity than in any of the other treatments ($P < 5\%$ or better), while plants which had a low humidity during the first period had the greatest leaf area.

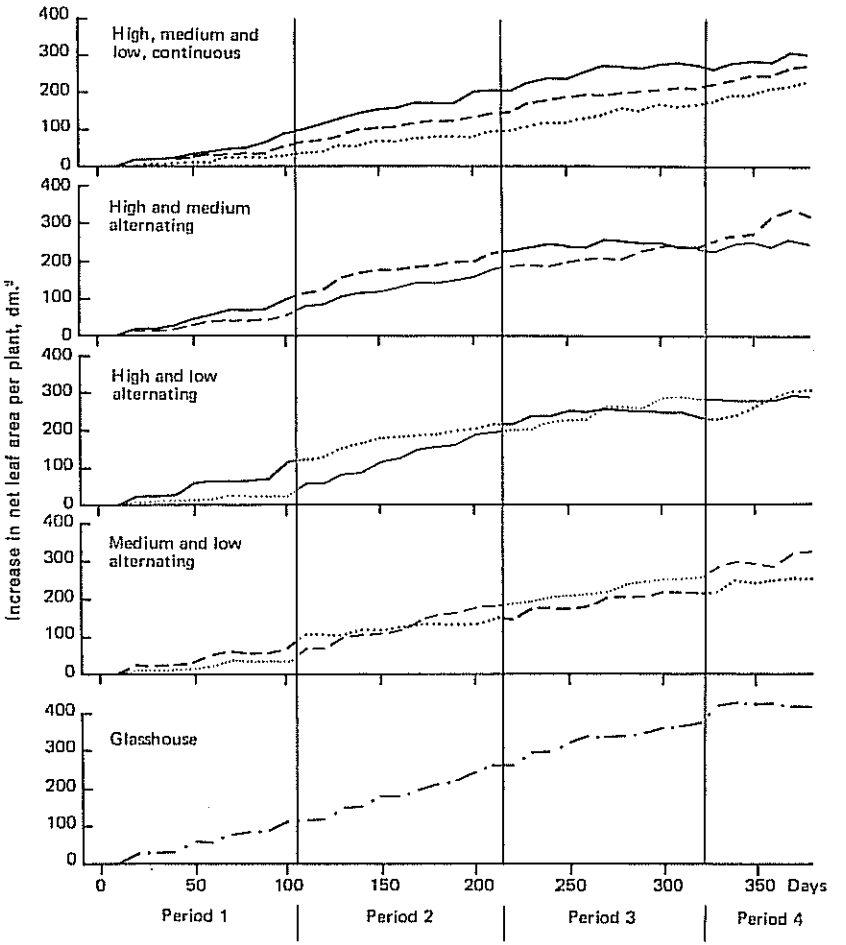


FIG. 2
Increase in net leaf areas per plant (dm.²) for cacao given relative humidity treatments as described in Fig. 1.

TABLE II

*Dry weights and stem length of cacao plants harvested after growing for 378 days at low, medium or high relative humidity, either constantly or alternating between two humidity levels at 109-day intervals. The total dry weight gain during this period (see text) and dry weight ratios are also given*

| Relative humidity | | | | Dry weights at harvest, g. | | | | Dry weight gain in experiment, g. | Total weight gain per unit mean leaf area g./dm.² | Leaf weight per unit area g./dm.² | Ratio total leaf weight to total plant weight | Stem length at harvest cm. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 2 | 3 | 4 | Root | Stem | Leaf | Total | | | | | |
| Low | Low | Low | Low | 19 | 87 | 109 | 215 | 240 | 1·22 | 0·346 | 0·654 | 572 |
| Low | Medium | Low | Medium | 25 | 85 | 123 | 233 | 265 | 1·24 | 0·334 | 0·666 | 737 |
| Low | High | Low | High | 31 | 111 | 133 | 275 | 310 | 1·52 | 0·430 | 0·620 | 821 |
| Medium | Low | Medium | Low | 23 | 69 | 95 | 187 | 207 | 1·29 | 0·365 | 0·698 | 572 |
| Medium | Medium | Medium | Medium | 15 | 68 | 97 | 180 | 191 | 1·27 | 0·343 | 0·726 | 645 |
| Medium | High | Medium | High | 36 | 93 | 128 | 257 | 267 | 1·56 | 0·480 | 0·603 | 825 |
| High | Low | High | Low | 22 | 90 | 129 | 241 | 236 | 1·50 | 0·418 | 0·634 | 732 |
| High | Medium | High | Medium | 35 | 117 | 163 | 315 | 330 | 1·75 | 0·468 | 0·615 | 963 |
| High | High | High | High | 15 | 58 | 88 | 161 | 156 | 1·47 | 0·382 | 0·675 | 757 |
| s.e. (treatments) (45 d.f.) | | | | ±3·6 | ±8·5 | ±13·6 | ±22·4 | ±26·6 | ±0·144 | ±0·0208 | ±0·030 | ±75·8 |
| Means† | (a) | Low | | 25 | 94 | 122 | 241 | 271 | 1·32 | 0·370 | 0·647 | 710 |
| | | Medium | | 25 | 77 | 107 | 208 | 222 | 1·38 | 0·396 | 0·676 | 680 |
| | | High | | 24 | 88 | 127 | 239 | 241 | 1·58 | 0·423 | 0·642 | 817 |
| | (b) | Low | | 21 | 82 | 111 | 214 | 228 | 1·34 | 0·376 | 0·662 | 625 |
| | | Medium | | 25 | 90 | 128 | 243 | 262 | 1·42 | 0·382 | 0·669 | 781 |
| | | High | | 27 | 87 | 116 | 231 | 244 | 1·52 | 0·431 | 0·633 | 801 |
| s.e. (means) (45 d.f.) | | | | ±2·1 | ±5·1 | ±7·8 | ±12·9 | ±15·3 | ±0·066 | ±0·0120 | ±0·017 | ±43·7 |
| Glasshouse plants | | | | 120 | 303 | 260 | 683 | 679 | 2·37 | 0·582 | 0·429 | 775 |

†Mean (a) is for the level of humidity given during periods 1 and 3, mean (b) for that during periods 2 and 4.



### *Dry weights*

Table II gives the dry weights at harvest and also the total dry-weight gain during the experimental period. The latter values include all the abscissed experimental leaves and assume an initial dry weight per plant of 51 g., which was the mean for six plants sampled at the beginning of the treatments. For each parameter, the smallest dry weight increase was in plants grown at constant high humidity ($P < 5\%$ or better) and the next smallest in those at constant medium humidity. In contrast, the greatest increase occurred in the high-medium-high-medium plants, followed by those given low-high-low-high and medium-high-medium-high humidities. In general, an alternating humidity appeared to be favourable for dry weight increase, particularly when part of the time was spent at high humidity.

This order of response is different from that of humidity on net leaf area, and Table II shows that the increase in weight per unit mean net leaf area was significantly greater ($P < 5\%$) for all those plants which had periods at high humidity than for those which did not, while in the high-medium-high-medium treatment it was greatest of all. Similarly, although area per leaf was greatest at low humidity, the mean leaf weight per unit area over the whole period (Table II) was significantly greater in plants given a high humidity, especially when it alternated with periods at low or medium humidity. The latter plants also had the greatest total leaf weight to total plant weight ratio.

### *Water loss*

The total water losses per day, averaged over a three-week period starting on day 180, were 489, 347 and 163 g. per plant at the low, medium and high humidities respectively. There was considerably less difference when loss was related to the leaf area of the plants, the values then being 2·27, 2·16 and 1·04 g./dm.² net leaf area/day, a ratio of 1:0·95:0·46.

### *Flowering*

Flowering cushions were beginning to appear on all the plants when the growth-room treatments started, and a differential response to humidity soon developed. The rate of increase in flowering was most rapid at the high humidity, reaching a peak for the first period of six to ten cushions per plant after 50 days (Fig. 3). At the medium and low humidities flowering increased more slowly, reaching a peak of six to eight cushions per plant after 90 days. Flowering declined again in all the treatments towards the end of the first period. Two to three weeks after the beginning of the second period flowering became profuse in plants which were moved from low or medium to high humidity, and did not decrease again until the plants were moved back to medium or, especially, low humidity in the third period. There was a smaller increase in the fourth period when the plants were moved back to high humidity. The same effect was found when plants were moved from medium to high humidity in the high-medium-high-medium treatment, though here flowering continued to increase markedly in the fourth period. In contrast, there was no marked increase following the change to high humidity in the high-low-high-low plants, and here, as in the plants alternated between medium and low humidities, flowering was fairly steady but much less, with no marked response to change in treatment except for temporary decrease following transference to low humidity in period 4. All the plants grown at one

of the humidities continuously also flowered fairly steadily with no very marked fluctuations, though there was a general decline in cushion numbers during the third and fourth periods in the constant low and constant high humidity treatments.

Humidity also had an effect on the numbers of flowers which opened per cushion per week. Numbers were least at low humidity in each period (Table III) and, except in period 3, greatest at the high humidity. Over the whole experimental period the treatments which produced the most cushions per plant also resulted in the most flowers per cushion. Very few cherelles set on any except the glasshouse-grown plants.

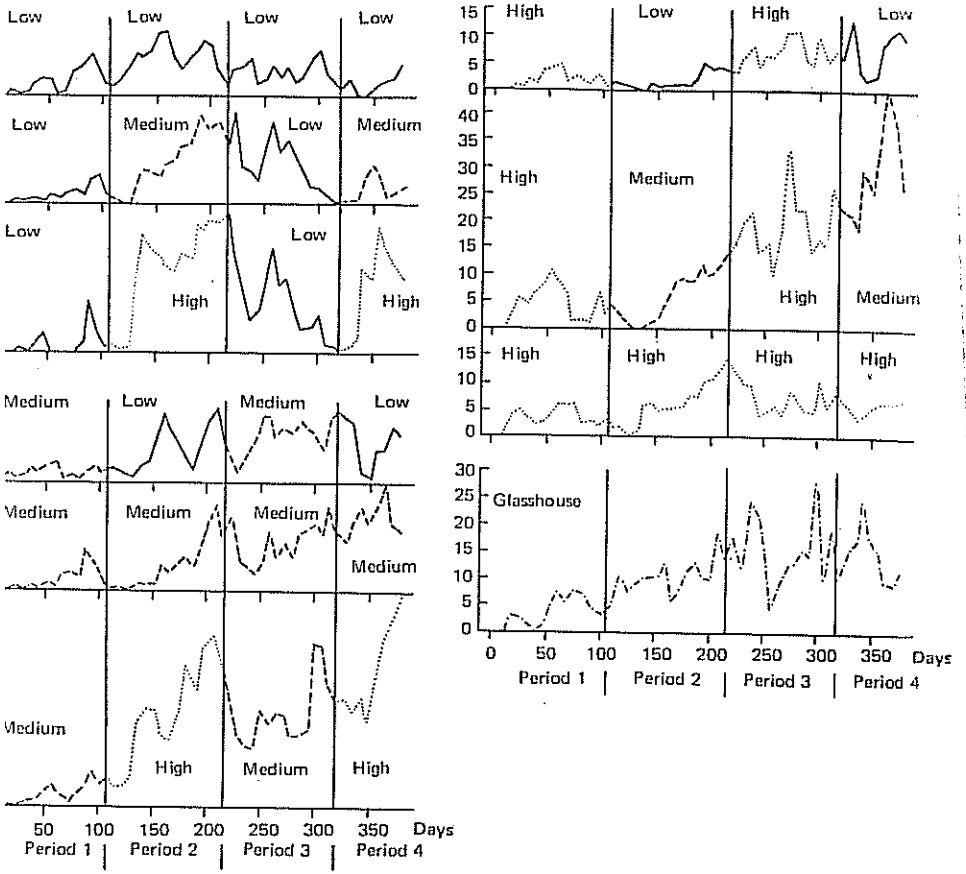


FIG. 3
Numbers of flowering cushions per plant per week for cacao given relative humidity treatments as described in Fig. 1.



TABLE III
*Numbers of flowering cushions per plant per week (means for whole experiment) and numbers of flowers produced per cushion per week (for separate periods) for cacao grown at low, medium or high relative humidity, either constantly or alternating between two humidity levels at 109-day intervals*

| Relative humidity | | | | Mean number of flowering cushions per plant per week | Numbers of flowers per cushion per week | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 2 | 3 | 4 | | Overall | 1 | 2 | 3 | 4 |
| Low | Low | Low | Low | 5·93 | 0·95 | 0·50 | 1·23 | 1·00 | 0·82 |
| Low | Medium | Low | Medium | 4·94 | 1·02 | 0·31 | 1·13 | 1·00 | 1·01 |
| Low | High | Low | High | 10·41 | 1·26 | 0·26 | 1·41 | 1·39 | 1·20 |
| Medium | Low | Medium | Low | 6·61 | 1·01 | 0·57 | 0·89 | 1·07 | 1·44 |
| Medium | Medium | Medium | Medium | 6·66 | 1·29 | 0·51 | 1·05 | 1·35 | 1·67 |
| Medium | High | Medium | High | 16·02 | 1·84 | 0·44 | 1·71 | 1·93 | 2·32 |
| High | Low | High | Low | 4·47 | 1·01 | 1·13 | 0·34 | 1·05 | 1·16 |
| High | Medium | High | Medium | 14·73 | 1·43 | 1·06 | 1·03 | 1·52 | 1·64 |
| High | High | High | High | 4·63 | 1·33 | 0·90 | 1·20 | 1·33 | 1·81 |
| s.e. (treatments) (45 d.f.) | | | | ±1·63 | ±0·121 | ±0·180 | ±0·219 | ±0·172 | ±0·272 |
| Means† (a) | | | | Low | 7·10 | 1·08 | 0·36 | 0·82 | 1·13 | 1·14 |
| | | | | Medium | 9·76 | 1·38 | (c) 0·51 | 1·07 | 1·45 | 1·44 |
| | | | | High | 7·95 | 1·25 | 1·03 | 1·44 | 1·30 | 1·78 |
| Means† (b) | | | | Low | 5·67 | 0·99 | | | | |
| | | | | Medium | 8·78 | 1·25 | | | | |
| | | | | High | 10·35 | 1·47 | | | | |
| s.e. (means) (45 d.f.) | | | | ±0·95 | ±0·070 | ±0·104 | ±0·127 | ±0·099 | ±0·157 |
| Glasshouse plants | | | | 10·29 | 1·28 | 0·91 | 1·45 | 1·37 | 0·96 |

†Mean (a) is for the level of humidity given during periods 1 and 3, mean (b) for that during periods 2 and 4. Mean (c) is for all plants at each level of humidity during the current period, and values are therefore for different plants in 1 and 3 compared with 2 and 4.

Thus the treatments which produced the best vegetative growth—high humidity alternating with periods at a lower humidity—also resulted in the most profuse flowering of the plants, except that flowering was relatively poor on plants given high-low-high-low humidities. The reason for this exception is not apparent.

There was no apparent relationship between the times of flowering and leaf flushing in this experiment.

## DISCUSSION

In the study of plant growth and development in relation to changes in environmental factors, only a few investigations have been made into the effects of the relative humidity of the atmosphere. Of these, the majority are confined to studies of the importance of atmospheric humidity on internal water balance under variable soil moisture conditions. In the present work the plants were always kept well watered and therefore it is unlikely that the water stress within any of the plants was very great. It is certainly improbable that any small differences in soil moisture which may have arisen affected transpiration, for a previous

glasshouse experiment (Sale, 1970) showed that even when the available soil water fell to 50% of the maximum there was little effect on the rate of leaf water loss. This was just over 2 g./dm.$^2$ net leaf area/day, and very similar to the rate of loss from the growth-room plants at medium and high humidities in the present experiment. The small difference in transpiration rate between plants at low and medium humidities was unexpected, and the rate at high humidity, although half that at low, was surprisingly great. This suggests that the leaves were possibly heated above air temperature by the absorption of radiant heat from the lamps, thereby increasing the vapour pressure deficit between leaves and the atmosphere, but no such effect could be detected by thermocouples placed on the undersides of the leaves. However, a comparison of transpiration rates per unit leaf area is possibly misleading, for Kramer (1959) has pointed out that small plants may transpire more rapidly than large ones on this basis, and in the growth-room plants at this time there were considerable differences in net leaf area and in total transpiration per plant.

Few morphological differences attributable to varying relative humidities have been recorded. Early experiments, reviewed by Wangermann (1961), showed that leaf-cell size and consequently area per leaf were often smaller at low than at high humidities. The opposite effect was found in the present experiment: leaves were consistently largest at the low humidity and smallest at the high, and differences were highly significant. On the other hand, the weight per unit leaf area was significantly greater at high humidity, suggesting a greater leaf thickness. This difference in leaf expansion again suggests that there was little water stress within the plants, for any such stress would presumably have been greatest at low humidity—and previous work (Sale, 1970) showed that a water stress imposed by varying soil moisture markedly decreased leaf size.

An increase in relative humidity, when soil moisture was not limiting, has been found to give slightly increased stem length in tomato (Went, 1944) and *Impatiens* (Hughes, 1966). The same effect has been found here in cacao. The figures in Table II are for the total length of all the branches on each plant. Although the standard error is rather high, the stem length of all plants which spent part of their life at the high humidity is generally significantly greater than that of the other plants.

The overall effect of humidity levels on vegetative growth was to increase the net leaf area of plants at low compared to high humidities, especially early in the experiment before the abscissional effect became marked, whereas dry weight gain was greatest when a period of high humidity alternated with one of a lower humidity. There is no obvious explanation of these dry weight differences. Several workers have found photosynthesis to be greater at high than at low humidities (e.g. Nátr and Kousalová, 1965) but only under conditions of low soil moisture where the humidity had a direct effect on increasing the period of stomatal opening. Moreover, continuous high humidity in the present work resulted in the smallest leaf area and dry weight gain of all. Went (1957) mentions that coffee plants were larger when grown at a low relative humidity (20%) day and night than at a constant high (80%) or alternating humidity, though he does not specify whether his plants were compared on a leaf area or dry weight basis.

A marked difference between the growth-room and the glasshouse plants occurred in the proportion of root dry weight to total dry weight at harvest. Roots formed about 10% of the total in growth-room plants but nearly 18% in the glasshouse plants. This



indicates that the former might not have been able to meet any very high transpirational demands even if in soil near to field capacity, but, as pointed out above, the results suggest that the roots were sufficiently developed to ensure that there was little moisture stress within the plants.

Flowering occurred in all the growth-rooms plants, but was particularly heavy in three out of the four treatments where high humidity alternated with periods at a lower humidity. These were also the treatments where dry weight increase was greatest, but the marked flowering response which sometimes occurred after moving the plants from low to high humidity suggests that there was also a more direct relationship between the two. In previous work where temperature (Sale, 1969) or soil moisture (Sale, 1970) was the variable factor the results also suggested some relationship between plant size and number of flowers, but again there were much greater differences in flowering behaviour attributable more directly to variations in these factors. None of these experimental results has indicated that a growth check is necessary before flowering can occur.

In the glasshouse-grown plants, which gained the greatest dry weight of all, flowering was not exceptionally heavy but neither was it less than that of most of the growth-room plants, as had been found before (Sale, 1969). The suggestion was then made that the difference may have been due to lower atmospheric humidities in the glasshouse during an exceptionally severe dry season. The present results indicate that such a difference was unlikely to have been more than a contributory factor.

In Trinidad, the relative humidity usually rises to about 100% at night throughout the year and falls to about 70–80% in the wet season or to as low as 50% in the dry season, when potential evapo-transpiration may also be increased by winds. However, the effects of the different levels of atmospheric humidity reported here are probably not sufficiently great to have much importance in the field as long as soil moisture is adequate, and they may be masked by the effects due to variations in other factors such as temperature and light intensity. The marked flowering response to a change in humidity suggests that the increase in flowering which is often associated with the onset of the wet season (e.g. Hurd and Cunningham, 1961) may be due partly to an increase in atmospheric humidity as well as to alleviation of soil moisture deficit. This experiment has been confined to the effect of relative humidity in the absence of soil moisture stress. The importance of the effect of humidity on the water balance of the plant when soil moisture is deficient needs further investigation.

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# Some aspects of developmental physiology of the mango fruit

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SUMMARY

The studies relate to mangoes of the Alphonso variety harvested in a Mysore orchard in 1965 and 1966. The fruit reached harvest maturity in 16 weeks after fruit-set. The weight continued to increase until harvest. The growth of fruit in terms of length, diameter and weight slowed between 9 and 14 weeks, at the time of the development of the stone. The moisture content of the fruit at maturity was about 80%.

Acidity reached a peak around the 7th week but had decreased at harvest. The astringency, rather pronounced to start with, decreased towards maturity.

Sugar content declined throughout the period of growth; reducing sugars were present in higher concentration than non-reducing sugars. Accumulation of starch continued to increase with growth and development.

Protein nitrogen formed the bulk of the total nitrogen; it decreased for about 9 weeks from the time of fruit-set and thereafter remained steady.

Respiration showed a peak during growth, corresponding to the growth climacteric. The pattern of respiration of whole fruit was corroborated by the study of tissue slices.

MANGO (*Mangifera indica* L.), native to India, is a popular fruit of the tropics and is prominent among the fruits of the world. The Alphonso mango grown in Maharashtra, Gujarat, Mysore, Madras, Kerala and Andhra Pradesh is excellent for dessert purposes and for processing. In recent times it has become important in the export trade and therefore its preservation in a fresh state for extended periods without loss of quality has become an urgent problem. Effective preservation in the fresh state is governed by several factors such as stage of maturity at harvest, handling conditions and period of storage. Biochemical and physiological changes occurring during growth and development of the fruit have been studied by Leley *et al.* (1943), Mukerjee (1959), Singh *et al.* (1937). These authors observed that the mango fruit took about 90 days for complete development, and physical increase in size and weight stopped 4–5 weeks before harvest maturity. The respiratory climacteric was also reached a few weeks before harvest (Mukerjee, 1959). A respiratory climacteric during the early stages of fruit development has also been reported in mango (Singh *et al.*, 1937), peaches and plums (Roux, 1940) and apples (Kidd and West, 1945).

It was considered necessary to carry out systematic studies to obtain an understanding of the developmental physiology of the mango fruit.