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Resumen

El estudio de las relaciones entre fuentes de sustratos y del desarrollo de botones florales de café después de la latencia, ha demostrado que se requiere un área foliar de aproximadamente 4 70 cm² para que una flor normal se abra. La fotosíntesis concurrente, dependiendo del área de la hoja, fue esencial para el proceso y excedió la contribución de las reservas almacenadas, ambas en las hojas y en la madera de las ramas. Los botones florales fueron capaces de utilizar sustrato procedente de hojas alejadas del botón, ya sea en dirección ascendente o descendente.

Introduction

During the formation and initial growth of coffee flower buds, a steady decline in the starch reserves in the leaves and branch wood is observed, indicating a mobilization of carbohydrates (Janardhan *et al.* 12). Following a short period of initial growth, the flower buds pass through a variable period of dormancy (Mes 15, Frederico and Maestri 7), when the metabolic activities are minimal (Gopal and Vasudeva 9). With the onset of the first rains, after a dry period or a sudden drop in the temperature, or both (Browning 2), the flower whorls expand rapidly until anthesis, with a marked rise in

the metabolism of carbohydrates (Croope *et al.* 6, Gopal *et al.* 10, Janardhan *et al.* 13) and with an increase in dry matter of over 500% in relation to the dormant buds (Mes 15, Croope *et al.* 6). Thus, a fast transport of organic substances to the flower buds is necessary at this time.

This paper reports on the contribution of different sources of assimilates for the growth of flower buds, from the break of dormancy to anthesis.

Material and methods

This study was carried out in a greenhouse in Viçosa, Minas Gerais from August through October 1979, using a local selection of the hybrid "Catimor" (*Coffea arabica* L. x *C. canephora* Pierre). The plants, which were approximately three years old and blossoming for the first time, were grown in soil in 20 kg cans. Flower bud dormancy was broken by plentiful re-watering of the soil, following an eight-day period of suspended irrigation. This procedure is considered to mimic the natural conditions (Cramer 5, Alvin 1).

The treatments, which followed a completely randomized design with four replications, were set in place before the re-watering. Basically, these consisted of the isolation of a node or a branch segment of one or a few internodes of a first order

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lateral branch by making one bark girdle above and one below the node or the branch segment under study.

The contribution of the concurrent photosynthesis was estimated by leaving six flower buds and leaves trimmed to areas of approximately 30.00, 22.50, 15.00, 7.50 and 2.75 cm² on each axil of girdle-isolated nodes. Parallel treatments, but with leaves covered with aluminum foil, were made to assess the contribution of assimilate reserves of the leaves (previous photosynthesis). Leafless segments of one, two and four internodes in length, with six flower buds in each axil of a single node, served to estimate the contribution of assimilate reserves in the wood. As controls, ungirdled nodes were left with six flower buds and 30.00 cm² of leaf area per axil, either covered or uncovered.

The attracting ability of floral buds for assimilates from sources located at various distances was measured by taking branch segments having six flower buds per axil of a node and a leaf area of 40.00 cm² per axil either on the node under study, or on the first, second or fourth node, either above or below the flower buds.

A possible lateral transport was investigated by leaving six flower buds on one axil and only a 40.00 cm² leaf on the opposite axil, either of the same node or of the node immediately above. The leaf area needed for the normal development of one bud was determined by leaving a leaf area of approximately 12.50 cm² and two, four and six flower buds on each axil of girdle-isolated nodes.

The competition ability for assimilates by the flower buds and by the apical vegetative bud was studied by taking girdle-isolated segments of first order branches, as comprised of the most mature distal node with six flower buds and the terminal bud, and with one 20.00 cm² leaf per axil, at an intermediate position, left between those two structures. Identical segments, either without flower buds or detipped, completed the treatment series.

Every other day, starting from the re-watering of the plants, the lengths of the flower buds were taken and their dry weight was estimated by the following relation previously established from direct measurements:

$$Y = 1.8541 + 0.3008X + 0.0096X^2$$

where Y is the dry weight, and X is the length.

Results and discussion

Mass transfer to the flower buds after the break of dormancy seemed to be a function of the available leaf area which reached a plateau at a leaf area of 28.80 cm² for six buds. This represented a requirement of an area of 4.70 cm² for the normal expansion of one bud (Figure 1). This should explain why the flower buds did not go on to anthesis when Magalhães and Angelocci (14) removed the leaves of a girdled flowering node. It also explains why Robusta coffee trees bear a larger number of flower per axil than do those of Arabica. In Figure 1, it can be observed that the ability of the flower buds to mobilize reserves from the leaves appeared to saturate from a rather low leaf area of about 15.00 cm². Beyond this value, the mass transfer seemed to be due to the concurrent photosynthesis.

Despite the rather low starch content in the branches of coffee trees (Cooil 4), reserves were readily available to the growth of buds, as shown in Figure 2. The slope of the curve suggests that mobilization ability of the flower buds might go beyond the fourth internode, which could explain Browning's (3) observation that some flower buds open even on defoliated branches.

Four sources of organic nutrients can participate in the final dry weight of flower buds after dormancy break: 1) concurrent photosynthesis in the leaves; 2) branches and 4) original matter of the dormant bud proper. In this study, the average dry weight of the dormant buds was 3.90 ± 0.80 mg and only the

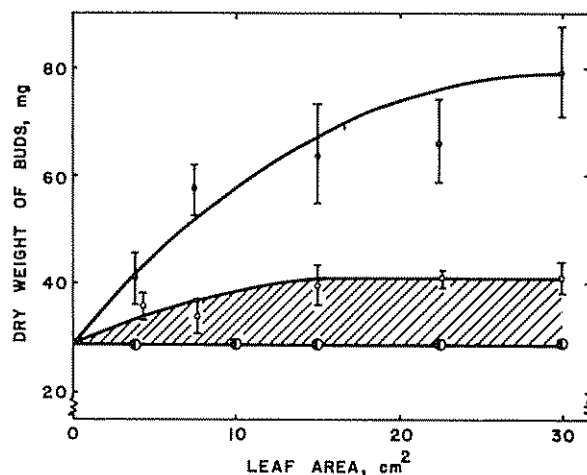


Fig. 1. Dry matter accumulation in six flower buds as a function of the leaf area. Leaves uncovered (●) or covered with aluminum foil (○). (■) dry matter contribution from the dormant bud. The vertical line represents the standard mean deviation in this and in the following figures.

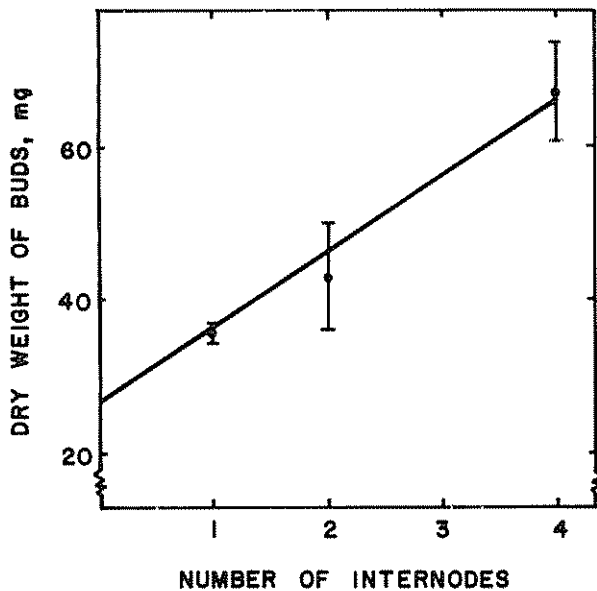


Fig 2. Dry matter transfer from internodes to six flower buds per axil. Dry matter accumulation is taken from the dry weight of the dormant buds as the start.

weight in excess of 4.70 mg, the upper limit of the range (shown in Figures 1-5 and 7 as 28.20 mg for six buds per axil), was considered as mass transfer. Although the chloroplasts of dormant flower buds are able to carry on the Hill reaction, they occur in such small numbers that their contribution is negligible (Janardhan and Gopal 11). Furthermore, after the second day following re-watering, when dry matter accumulation began to accelerate, the flower buds were already of a whitish colour. The contribution of the original matter of the dormant buds to the final weight of the open flowers is shown in Figure 3. This ranged from 100% in the dormant bud to 35% in the open flower. These values are likely affected by varietal and environmental differences as dry weight of the dormant buds can change from approximately 3.00 mg in Minas Gerais, Brazil (Frederico and Maestri 7), to 5.50 and 6.70 mg in different seasons in Southern India (Gopal and Vasudeva 9).

By assuming that the expanding flower buds can drain reserve assimilates from along the length of one internode (half internode lengths above and below the node under study), one internode could supply only 7.00 mg of dry matter for the flowers on one axil of a node, on the twelfth day after the start of re-watering (Figure 3). This accounted for 8.75% of the total dry weight and 13.5% of the mass transfer to six flowers. Considering that the average dry weight of a flower ranges from 13.00 to 15.00 mg, the contribution of one internode seemed to be

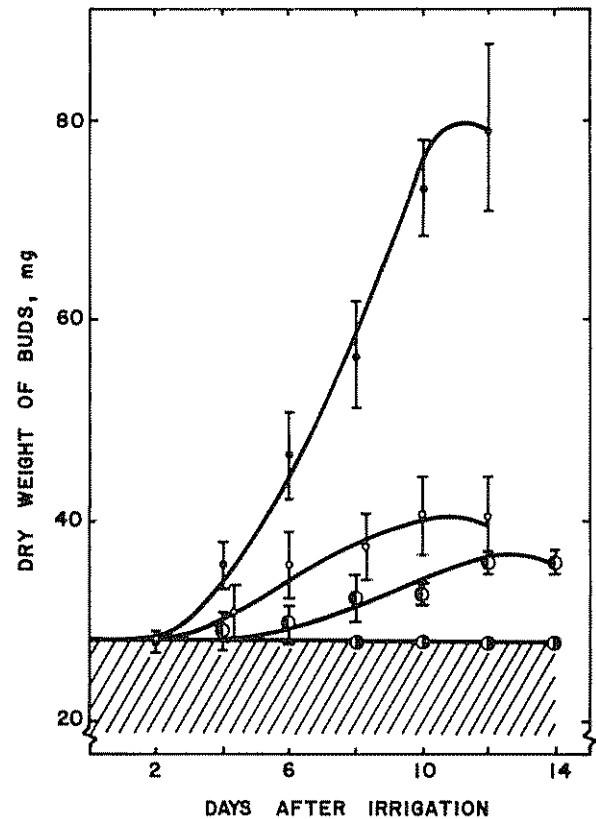


Fig 3. Expansion of six flower buds as a function of the source of assimilates ● - uncovered leaves, ○ - covered leaves, ◐ - internode, ◑ - original organic matter from the dormant bud.

insufficient for the expression of a single open flower (4.70 mg from the dormant bud plus 7.00 mg from the internode). Concerning this, Mes (15) had already observed that the food material from an explant of one node plus one internode was sufficient only for a limited growth of the buds, and these did not reach full anthesis. However, the mass transfer from several internodes to just one internode (Figure 2) could bring about some flower opening, as observed in this study and in the previously mentioned example of Browning (3). Therefore, although the flower buds easily were able to mobilize the reserves from the branches (as shown in Figure 2), the contribution of one internode for the expansion of the flower buds (Figure 3) seemed to be limited by its low storage content (Cooil 4). This is in clear contrast to many temperate woody plants whose flower buds open at the beginning of spring when the plants bear no leaves.

In spite of the high starch content in coffee leaves which can account for as much as 20% of their dry weight (Cooil 4), it seemed that the flower buds attracted only the food material stored in the

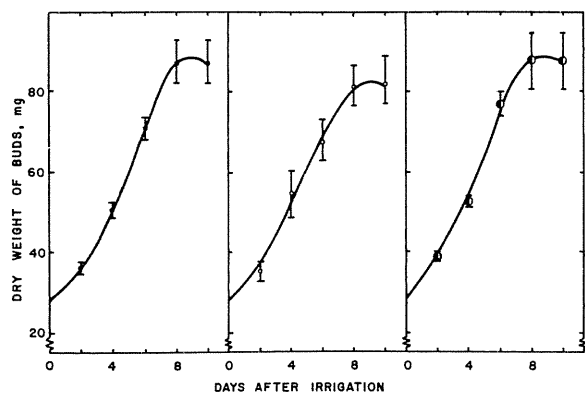


Fig. 4. Growth of six flower buds as a function of a 40.00 cm² leaf area left at each axil of the subtending node (●), two nodes above (○), or two nodes below (○), the buds under study.

proximal parts of leaves, as indicated by the data in Figure 1. This seems to suggest that leaf reserves are not so readily available to flower bud growth as are the branch storages. With saturating leaf area, the contribution of leaf storage for the flowers did not exceed 13.00 mg (Figure 1), which represented 25.0% of the mass transfer and 10.5% of the total dry weight of the six flowers (Figure 3).

On the other hand, concurrent photosynthesis could supply 40.0% of the total dry weight and 61.5% of the mass transfer to the six flowers (Figure 3), and so was the most important source for flower bud growth. The other three sources previously discussed were naturally limited in supplying carbohydrates for flower bud growth. However, as shown in Figure 1, assimilates from concurrent photosynthesis could be transferred to the threshold of the sink capacity of the flower buds (see Figure 6, as well). Since the contributions of the leaf reserves saturated at a low leaf area (Figure 1), the formation of flowers with over 15.00 mg in dry weight, or the maintenance of a greater number of buds per axil, depend basically on an increase in the photosynthesis as obtained through the larger leaf area required for the flower expansion (Figure 1).

No difference was observed in the growth of flower buds on ungirdled axils, whether the subtending leaves were covered or not. Taking into account that the reserves in the leaves (Figure 1) and in one internode (Figures 2 and 3) are well below the threshold value for the opening of six flowers, a transport of assimilates must have occurred from more distant leaves to the flower buds on axils with covered leaves. This hypothesis was tested by taking a 40.00 cm² leaf per axil which either subtended six buds or was located one, two or four internodes

below or above the buds under study. Since there were no differences among the treatments, Figure 4 shows only the results from the control (flower buds on the same node as leaves) and from the flower buds two internodes apart, both above or below the source leaves. It can be seen that the buds attracted assimilates from sources located at some distance, irrespective of whether the flow direction was acropetal or basipetal. Even two days after rewatering, no differences in the growth of the buds were observed. In the case of distant sources, initial growth must have been due to storage reserves in the branches (Figure 2), until a direct connection of the sinks (buds) with the main sources (leaves) was established. Very likely, this occurs in the first growth stages of the buds. These facts would explain why, under natural conditions, open flowers can be seen all along a branch which retains only the most apical two or three leaf pairs. Growth of flower buds also did not differ even when the leaves were located on the opposite side of the same node or on the node immediately above (curves in Figure 5 compared to the curve on the far left in Figure 4). Thus apparently the transport system must be so interconnected, either at the node level or at the internode length, so that a radial flow of assimilates obtains.

Some difference is noted between the growth curves as given in Figure 3 and in Figures 4 and 5. While in the former, growth on the second day was slow, with anthesis occurring on the 10th to 12th day after irrigation, growth in the first two day, as shown

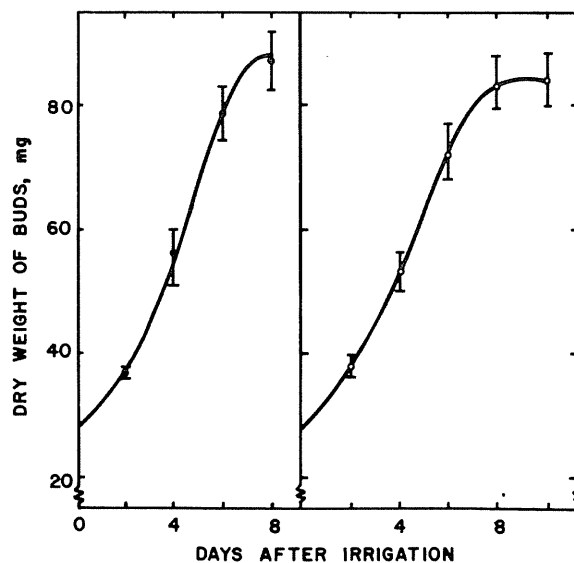


Fig. 5. Growth of six flower buds as a function of a 40.00 cm² leaf area left on the opposite side of the same node (●) or of the node immediately above (○).

in Figures 4 and 5, was already very fast and the flowers opened on the 7th to 8th day after irrigation. Since the growth rate of coffee flower buds is directly related to temperature (Mes 15), it can be assumed that the above differences were due to lower temperatures which prevailed in Viçosa in August, when the data of Figure 3 were collected, than in October, at which time the data for curves of Figures 4 and 5 were taken.

The study on the change in the number of buds with relation to a fixed leaf area of approximately 12.50 cm² has shown that, despite a rise in net assimilation rate with an increase in the quantity of buds, the maximum number of normal open flowers remained at about 2.63 (Figure 6). That is, a leaf area of approximately 4.75 cm² is necessary for the expansion of a normal flower, quite in agreement with the data of Figure 1. Excessive numbers of flower buds per axil resulted in abortion, abscission, or abnormal flowers.

When flower buds and the terminal vegetative bud competed for the assimilates from a common source of 20.00 cm² leaf, which is insufficient to support

the expansion of six flower buds (Figure 1), it was observed that the flower buds grew as well as those on a branch without the terminal vegetative bud (Figure 7). On the other hand, the expansion of the terminal leaves was always much greater in the treatments in which the flower buds were removed than in those which had the competing flower buds. In the latter, the terminal leaves started expanding only after the 10th day, when flower buds had abscised or stopped growing. This indicates a larger sink strength for the flower buds than for the vegetative buds. This also happens in *Monodora tenuifolia* Benth, a tropical tree which bears vegetative and floral buds spatially conjugated and not so distant as the buds under the artificial conditions of the present work. The expansion of flower buds precedes the sprouting of new leaves which, too, points to a higher competitive ability of the flower buds (Njoku 16).

Conclusions

Since the reserves in the internode that were available for the expansion of the flower buds were

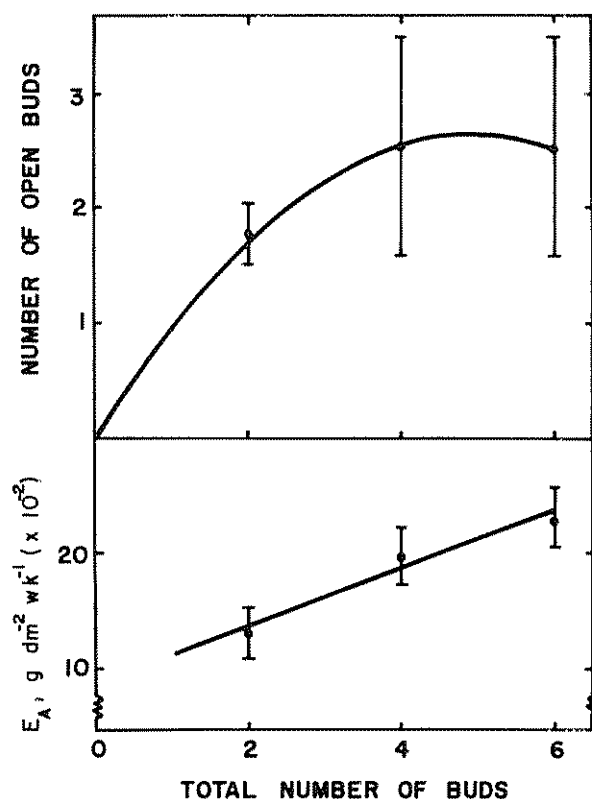


Fig. 6. Number of open flowers and net assimilation rate (E_A) as a function of the number of flowers per axil, with a constant leaf area of approximately 12.50 cm².

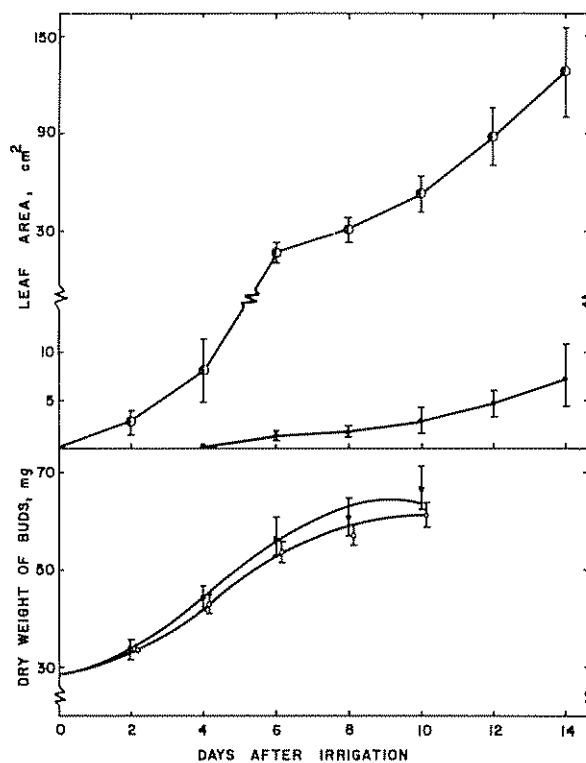


Fig. 7. Mass transfer from a 20.00 cm² leaf area left in an intermediate position between six flower buds and the terminal vegetative bud (O), or under otherwise similar conditions but with either the flower buds (O) or the terminal vegetative bud (O) removed

limited to 7 00 mg per axil (Figure 3), and the supply of reserves from the leaves saturated at a low leaf area (Figure 1) and, in consideration that under natural conditions the number of flower buds per leaf axil is well above six, the number tested in this study, the relative contributions of those sources of assimilates should be lower. Moreover, as a consequence of a higher leaf area, the participation of the concurrent photosynthesis should be higher than that observed in the present work. The information gathered here supports the contention that for the expansion of the flower buds, the contribution of the various sources followed the order: concurrent photosynthesis \gg storage reserves in the leaves $>$ storage reserves in the branch wood, not taking into consideration the dry matter of the dormant bud itself. In addition, concurrent photosynthesis may be the sole source that could be, in part, affected by the sink strength (Figure 6). These facts may explain the higher correlations of the number of normal opened flowers with the number of leaves rather than with branch reserves, as reported by Gopal and Raju (8).

The initial enlargement of the buds, after re-watering, did not differ statistically, whatever the sources of assimilates to which they were connected (Figure 3). If in this stage, the organic nutrients come preferentially from wood reserves in the branches, from reserves in the leaves or from concurrent photosynthesis, or from the two or three sources simultaneously, only further studies on assimilate mobilization can demonstrate this. One needs to explain why, in absolute quantities, the contribution of leaf reserves for the total final dry weight of the bud saturates at so low a leaf area (Figure 1), even though the leaf starch content could be high (Cooil 4).

Detailed anatomic studies of the transport system for assimilates are also needed to explain the reason for the existent up and down flow (Figure 4) and radial flow, as well (Figure 5).

Although the floral buds have potentially a higher competitive ability than the terminal vegetative bud, this may not be, in fact, a true competition, since the leaves subtending the floral buds were removed (Figure 7). Although some competition may be initiated, the processes of enlargement and anthesis in plants with gregarious flowering, such as coffee, occur over such a short time span that the vegetative growth would hardly be impaired; hence, the phenologic pattern of plant growth may not be affected.

Summary

A study of the relationship between sources of assimilates and the growth of flower buds of coffee, after dormancy break, has shown that a leaf area of approximately 4.70 cm² is required for the opening of one normal flower. Concurrent photosynthesis, as dependent on leaf area, was essential for the process and far exceeded the contribution of storage reserves, both in the leaves and in the branch wood. Flower buds were able to draw assimilates from distant source leaves, irrespective of the up or down flow direction. Lateral transport was also observed. Flower buds had a greater sink strength than the terminal vegetative buds of the branch.

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Reseña de libros

IOSHIDA, S. *Fundamentals of rice crop science* 1981. International Rice Research Institute. Los Baños, Philippines. 1981.

Este libro trata sobre aspectos fisiológicos del cultivo del arroz.

La obra consta de 269 páginas e incluye 479 referencias generadas en las últimas 3 décadas sobre la ciencia en el cultivo del arroz, destacándose las investigaciones generadas por el IRRI en estos últimos 20 años.

El libro cubre la mayoría de los aspectos fisiológicos del cultivo del arroz y su relación con otras disciplinas y enfatiza el hecho de que el arroz sigue siendo un alimento vital para más de la mitad de la población del mundo.

El primer capítulo pone en conocimiento del lector, estudiante o productor, todos los aspectos del crecimiento y desarrollo del cultivo. En el capítulo dos el autor muestra en forma práctica como los factores climáticos afectan el crecimiento y desarrollo del cultivo. Los capítulos tres y cuatro cubren todos los aspectos nutricionales, tanto los positivos como los desórdenes de tipo negativo.

Los fundamentos fisiológicos del cultivo adquieren su relevancia cuando se discuten en el capítulo cinco los aspectos de fotosíntesis y respiración siempre relacionados con el crecimiento del arroz. Los índices óptimos de área foliar se discuten en este capítulo y los aspectos bioenergéticos de producción del cultivo.

En el capítulo seis se tratan las características de la planta de arroz y su habilidad productiva; se destacan las nuevas variedades de alta producción adaptada a las condiciones del trópico y su relación con las características de plantas asociadas con el nuevo y viejo concepto del tipo de planta ideal.

El autor termina el libro con los aspectos fisiológicos y su relación con el análisis de rendimiento. Se encuentran y discuten dentro del texto el por qué de las diferencias de rendimiento con diferentes grados de tecnología y el máximo potencial productivo y los factores que actualmente limitan ese máximo productivo. En otras palabras, los capítulos seis y siete el autor discute los componentes y factores que influyen en el rendimiento.

En términos generales el libro está escrito en una forma muy comprensible. En sus 269 páginas incluye un total de 92 cuadros y 123 figuras, más 39 láminas a colores sobre deficiencias y desórdenes nutricionales del arroz. Los cuadros, láminas y figuras hacen muy amena la lectura y facilitan la comprensión de los aspectos fisiológicos del cultivo del arroz.

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