Branch formation in cocoa (**Theobroma cacao** L., Sterculiaceae)* ——— DAVID WHEAT**

COMPENDIO

Los dos botones que quedan en las axilas de las hojas del cacao tienen poten-
cialidades morfogenéticas distintas; empero, la diferencia entre ambas clases de boto-
nes no es la fuente de la diferenciación del eje.

El botón distal es más grande, se forma antes que el otro, y recibe la deno-
minación de "botón principal". El botón más pequeño, que se forma más tarde, es
llamado "botón subordinado".

El botón principal puede originar una rama siléptica y plagiotrópica, con filo-
taxis dística, en el desarrollo de la horqueta. Tal rama tiene una conexión primaria
amplia con el sistema vascular del tronco que la sostiene.

Un botón principal que no se desarrolla silépticamente, puede formar más
tarde una rama proléptica. Tal rama proléptica puede desarrollar de dos maneras; la
primera, consiste en formar una rama ortotrópica con filotaxis espiral, generalmente
sobre el eje ortotrópico del tronco. En cambio, conforme a la segunda posibilidad, los
botones prolépticos pueden engendrar ramas plagiotrópicas con filotaxis dística, gene-
ralmente sobre otras ramas laterales plagiotrópicas. Una rama proléptica tiene una
conexión primaria angosta con el sistema vascular secundario del eje que la sostiene.

El botón subordinado se forma sobre el botón principal, y jamás lo hace
silépticamente. Si el botón principal y el eje son dañados, el botón subordinado puede
formar una rama proléptica, tal como lo hace un botón principal proléptico. Por lo
general, el botón subordinado se desarrolla en una inflorescencia.

En esencia, puede afirmarse, por el momento, que la diferencia entre ramas
plagiotrópicas y ortotrópicas nada tiene que ver con el tipo de botón que las haya
originado, ni tampoco al hecho de que su origen sea por silepsis o por prolepsis.

Introduction

THEOBROMA cacao has an unusual and distinc-
tive pattern of growth, categorized as Noze-
ran's model by Halle and Oldeman (9) and
described by Hallé and Oldeman (9), Hallé et al.
(10), Vogel (16), Greathouse and Laetsch (7),
Brooks and Guard (1), and Cuatrecasas (5). The
young seedling (which has epigeous germination ac-
cording to Cuatrecasas, (5)) forms an orthotropic un-
branched axis with spiral phyllotaxis. After reaching
a height of 100-150 cm (according to Hallé and Ol-
deman (9) and Vogel (16)) the apical meristem loses
its meristematic character and disappears. Hallé and
Oldeman (9) state that this disappearance occurs dur-
ing a period of rapid growth, i.e., during one of the
flushes of the shoot. The loss of the apical meristem
is preceded immediately by the appearance of three to
six sylleptic lateral branches at successive congested
nodes near the tip of the now-terminated orthotropic
axis. (The terms "'syllepsis" and "prolepsis" are used
in the sense of Hallé et al. (10)). Thus a "pseudo-
whorl" of sylleptic branches (the "orqueta" or "jor-
quette") is formed. These branches grow out horizon-
tally (i.e., they are plagiotropic) and have distichous
phyllotaxis. There is a leaf dimorphism in that the
petioles of the leaves on the plagiotropic lateral branches
(which are called "fan branches") are markedly shorter
than those of the spirally-arranged leaves of the ortho-
tropic shoot.

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The plagiotropy of the lateral branches is quite strongly determined and a plagiotropic branch will not turn upward to form an orthotropic shoot. This is true both on the intact tree and on rooted cuttings from such branches (see Cheeseman (2); discussion in Fisher (6)). Usually the lateral buds of the plagiotropic branches only give rise to further plagiotropic branches, although rarely and under unusual circumstances an orthotropic shoot may arise from one of these buds (2, 5, 16); see the comments by Alvim in the discussion of Fisher (6).

Normally the tree resumes growth in height by replacement of the lost orthotropic apical meristem with a new orthotropic shoot developed by prolepsis from a resting bud on the parent shoot somewhere below the newly-formed tier of horizontal branches. This replacement shoot ("chupon") bears leaves in spiral phyllotaxis and repeats the development of its parent axis, eventually ceasing extension growth and giving rise to another pseudowhorl of lateral branches in the manner just described.

Thus the trunk of the tree is sympodial, made up of a succession of replacement shoots, each originating below a whorl of sylleptic lateral branches. All of the first-order lateral plagiotropic branches are sylleptic and are borne near the tip of a trunk unit All of the shoots which make up the trunk are proleptic, except the initial seedling axis Flowers and fruits are borne laterally on the older wood of the branches and trunk on specialized axillary short-shoot systems called "flowering cushions" (see Lent (13))

Growth is "rhythmic", with flushes of shoot extension and leaf expansion separated in time by periods of relative quiescence of the apical bud when there is no stem elongation or leaf production. Greathouse et al. (8) found that new leaf primordia were produced on the orthotropic shoot apex at the same rate that the leaves expand. Thus the number of leaf primordia in the bud at the apex of the main shoot remains more or less constant. Iserentant (12) studied the relative lengths of the periods of growth and rest and concluded that the newly produced leaves of each flush had an inhibitory efect on the growth of the apex of the branch which bore them, imposing upon it a period of quiescence.

The strict correlation between syllepsis, plagiotropy, and distichy of the lateral branches in contrast to the prolepsis, orthotropy and spiral phyllotaxis of the branches which make up the trunk, together with rhythmic growth, is also seen in the other trees conforming to this architectural model (10, p. 178 ff.). Tomlinson (15) stated "This correlation between length of rest and subsequent symmetry of shoots seems common in tropical trees and needs emphasis, as its may depend on contrasted methods of anatomical attachment resulting from contrasting developmental procedures".

Theobroma cacao has two buds in the axils of most of its leaves. Multiple buds in one leaf axil is a common situation in tropical woody plants. (One recent sampling at the Fairchild Tropical Gardens found multiple buds in 37 per cent of the woody dicots examined; (14)). The varied potential of the different buds in an axil is part of the cause of the complex vegetative and reproductive development patterns seen in evergreen tropical trees.

In *T. cacao* the two buds differ in their size and in their potential. There are three possible fates for an axillary meristem: it may produce a sylleptic vegetative branch, or a proleptic vegetative branch, or an inflorescence. Lent (13) has shown that the cauliflorous inflorescences of *T. cacao* are the products of axillary buds which have remained dormant in the outer layers of the stem Where inflorescences develop on younger twigs, Lent found that they always arise from the smaller of the two axillary buds which he called the "subordinate bud". The "subordinate bud" is always found below the larger so-called "principal" bud.

Greathouse and Laetsch (7) state "It is possible that the subordinate buds can offer an explanation of branch dimorphism. Subordinate buds on orthotropic shoots might give rise to plagiotropic shoots while principal buds always give rise to orthotropic shoots". These authors also reported that the phyllotaxis of the principal bud always matched that of the shoot which bore it This differs from the observations of Brooks and Guard (1) that all of the principal buds had distichous phyllotaxis, whether on orthotropic or plagiotropic shoots. Greathouse and Laetsch attribute this discrepancy to the possibility that Brooks and Guard observed only very young axillary buds on orthotropic shoots.

None of the studies which appeared before that of Hallé et al (10) correlated the well-known branch dimorphism of this tree with the developmental distinction between prolepsis and syllepsis The branches of the orqueta form by syllepsis while the replacement orthotropic shoot develops from a resting bud by prolepsis According to Cook (3), sylleptic branching is apparently possible on the plagiotropic lateral branches as well, again giving rise to plagiotropic branches, at least in *Theobroma bicolor* H. & B. (Cook Reported that early branching sometimes took place on lateral branches, and that "the development of this bud appears to be almost simultaneous with that of the terminal"). Commonly the plagiotropic lateral branches form further plagiotropic branches by prolepsis from their axillary resting buds. Only in very rare cases and by unusual treatments can the resting buds of plagiotropic branches give rise to orthotropic shoots. Greathouse and Laetsch (7) and recently Vogel (16) have demonstrated that it is possible to produce plagiotropic lateral branches by prolepsis from resting buds on the orthotropic shoot, by pruning. Although Lent (13) found that the subordinate bud usually formed an inflorescence he and also Vogel (16) were able to cause it to grow out as a vegetative branch by decapitating the shoot and destroying the principal bud.

Table 1 —Type of Branch Produced by Axillary Meristems in *Theobroma cacao*

Bud Position and Development	Parent Shoot Type	
	Orthotropic	*Plagiotropic*
Subordinate Bud (*proleptic*)	Inflorescence	Inflorescence
Principal Bud (*sylleptic*)	Plagiotropic Branch	Plagiotropic Branch
Principal Bud (*proleptic*)	Orthotropic Branch (rarely plagiotropic branch)	Plagiotropic Branch (rarely orthotropic branch)

These complex relationship between buds and branches are set forth in Table 1. This table shows that there is only one combination which normally produces an orthotropic shoot with spiral phyllotaxis, i.e. the proleptic development of a resting bud on an orthotropic shoot. All of the other types and sites of principal bud development result in the formation of a plagiotropic branch.

Materials and Methods

Material of *Theobroma cacao* L. was collected by Dr. P. B. Tomlinson at Finca La Selva, Puerto Viejo, Costa Rica (PBT 1-II-78). This material was fixed in FAA for later study in Cambridge, Massachussetts.

Herbarium specimens in the Gray and Arnold Arboretum Herbaria in Cambridge (G and A) were checked for comparative information on other *Theobroma* species.

Many of the observations reported here are based on dissections and hand-sectioning techniques. In addition, paraffin-embedded serial sections were prepared by the usual methods. The cinematographic methods of Zimmermann and Tomlinson (19) were used for analysis of the vasculature of the orqueta.

Observations

Buds

On the older portions of plagiotropic branches (about 5 mm in diameter) two buds are visible in each leaf axil. On orthotropic shoots and on the younger parts of plagiotropic branches the principal bud was always visible to the naked eye and the smaller subordinate bud was sometimes visible and was always found upon dissection, even though superficially obscured by the dense indumentum of the stem. This

subordinate bud is located in a depression in the stem between the principal bud and the leaf base and often is further surrounded by and embedded in the base of the petiole of the subtending leaf. The petiole base may form a pocket hiding the subordinate bud until after leaf fall.

The principal bud has two outer scales and three to five leaf primordia. Axillary buds can be found in the axils of these primordia although there may be one bud in the axils of the prophylls, rather than the normal pair of buds. In many cases the leaves and primordia of the principal bud showed distichous phyllotaxis above the level of the prophylls, on both orthotropic and plagiotropic shoots. There was an angle of about 30° between the plane of insertion of the prophylls (which is perpendicular to the plane of the subtending leaf axis and the parent stem axis) and the plane of distichy of the remaining leaves of the bud (Fig 1). Principal buds were often up to 3-4 mm long from the base to the tips of the bud scales.

The subordinate buds have two enclosing scales and two or three primordia enclosed within those scales. The enclosed scales are more or less at right angles to the prophylls. Because of the small number of appendages it is difficult to mawe any definite statement about the phyllotaxis of the small subordinate buds (see Fig. 2).

Theobroma cacao has trilacunar nodes. The median leaf trace enters the petiole directly. Each of the lateral traces sends about five parallel veins into the stipule above it, as it passes horizontally toward the leaf base, before entering the petiole. The vascular connections of the axillary buds arise from the sides of the median leaf gap. The principal bud is first distinguishable in the axil of P-3 or P-4. It develops directly from detached residual meristem adjacent to the subtending leaf primordium In the axil of P-4 (Fig 3), the fourth youngest leaf primordium of the shoot, the axillary meristem is distinguishable only as a region of densely-staining meristematic tissue. It does not project into the axil. It has at this stage a two-layered tunica and a corpus region below. No shell zone was seen at this stage.

The axillary meristem in the axil of P-5 (Fig. 4) protrudes slightly into the axil as the corpus enlarges and divisions within the lower part of the meristematic region begin to form a rib meristem. At this stage no appendages are visible. The older developing bud in the axil of P-6 has two opposite prophyll primordia (Fig. 5). In this figure of the principal bud in the axil of P-6 the shell zone of the subordinate bud may be seen.

The subordinate bud appears at the stage of the axillary meristem subtended by P-7 as a protuberance of meristematic tissue between the base of the principal bud and the base of the subtending leaf (Fig. 6, 7). The subordinate bud is inserted well below the level of the prophylls of the principal bud and is not in the plane of the prophylls. Rather it is near the plane containing the axis of the subtending leaf and
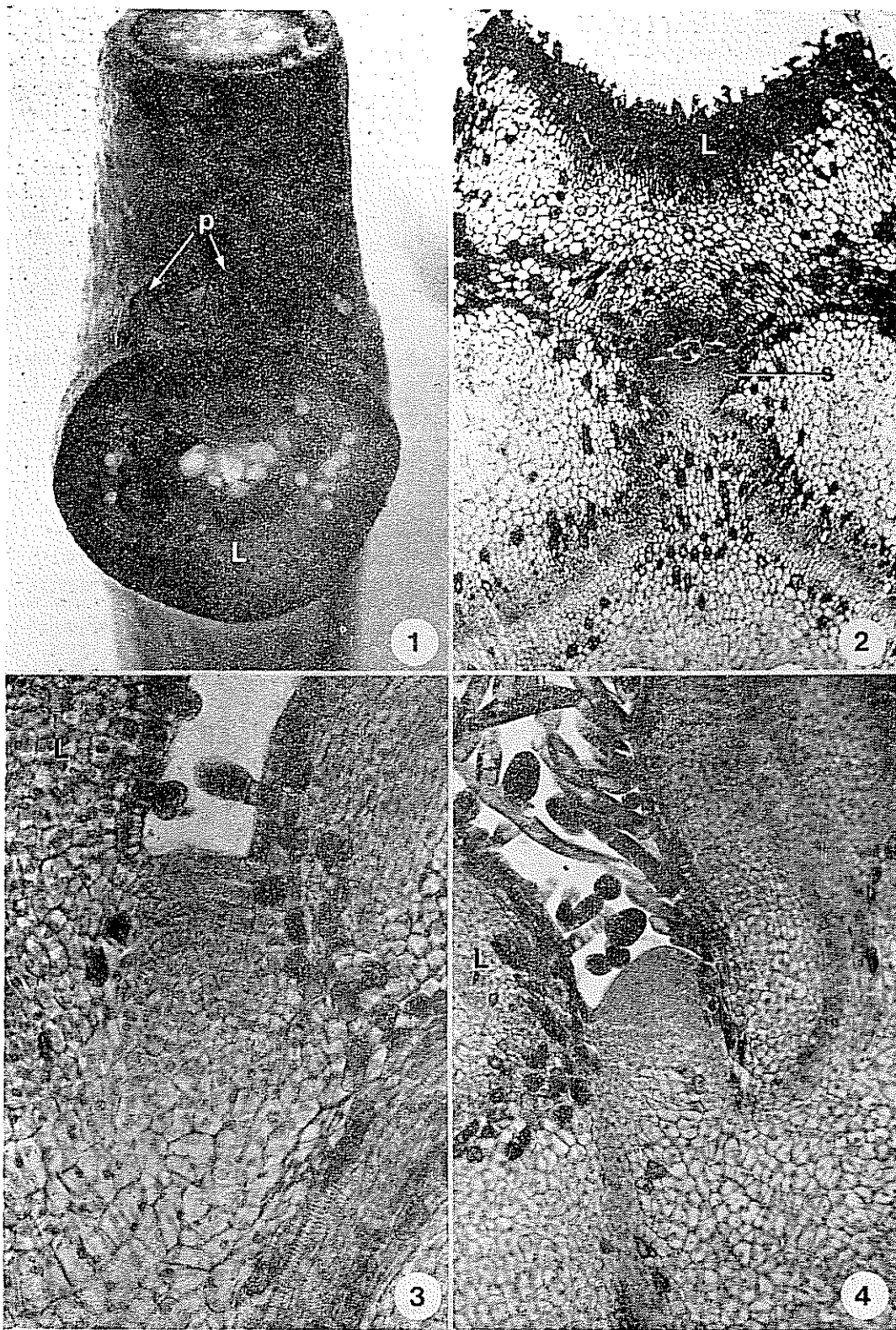
Fig. 1-4.—Thechroma cacao. Fig. 1. Principal bud on plagiotropic lateral branch, dissected to show arrangement of bud scales and primordia. x 10. Fig. 2. Transection showing subordinate bud and vascular cylinders of principal bud and main stem. x 30. Fig. 3. Longitudinal section of axil of leaf P-4 of a plagiotropic lateral shoot showing developing principal bud. About x 450. Fig. 4. Longitudinal section of axil of leaf P-5 of shoot shown in Fig. 3, showing developing principal bud. About x 450. L, leaf base. P, prophyll. s, subordinate bud.
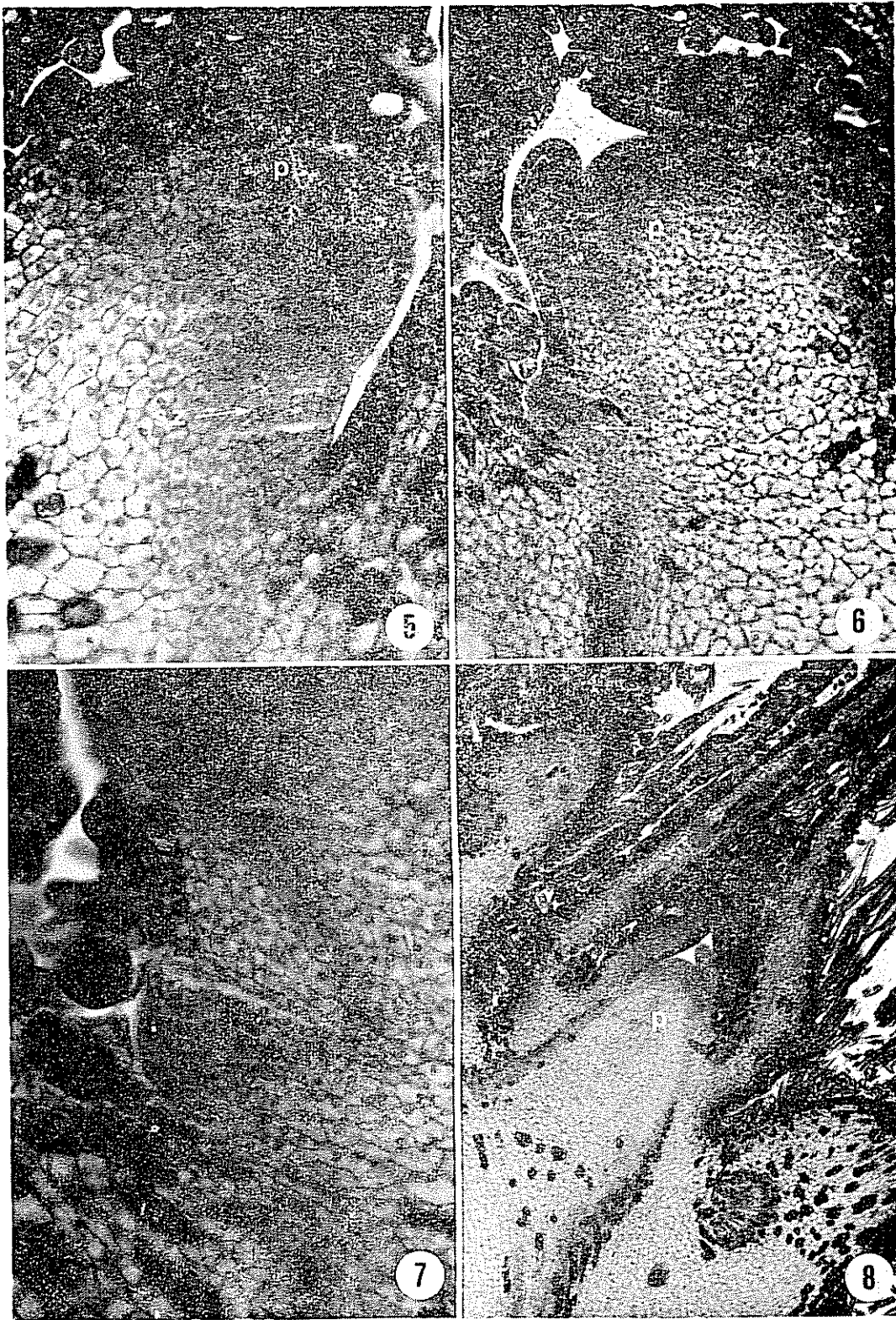
Fig. 5-8—Theobroma cacao, plagiotropic lateral branch. Fig. 5, Longitudinal section of principal bud in the axil of leaf P-6. x 200 Fig. 6, Longitudinal section of principal bud in the axil of P-7. x 100 Fig. 7, Longitudinal section of subordinate bud in the axil of leaf P-7. x 450 Fig. 8, Median longitudinal section of principal bud in the axil of leaf P-8. x 30 P, principal bud; s, subordinate bud; sz, shell zone.

the parent axis. There is a noticeable bud gap in the developing vascular cylinder of the principal bud opposite the insertion of the subordinate bud. The principal bud in the axil of P-8 is seen in Figure 8. No appendages develop in the subordinate bud until much later, after the stage when it is subtended by P-10. If the principal bud elongates to form a sylleptic branch the subordinate bud is usually left behind in the axil of the subtending leaf.

Orthotropic branches have both principal and subordinate buds developed and arranged as described above for plagiotropic branches. The principal buds on plagiotropic branches were usually larger and more conspicuous than those on ortotropic shoots, but in other respects the axillary buds of the two types of axes differed little.

Both orthotropic and plagiotropic branches appear to arise from principal buds. The leaves which subtend the branches of the orqueta all have small resting buds in their axils between the base of the subtended branch and the petiole or leaf scar (Fig 9). From serial transections it can be clearly seen that this resting bud is the subordinate bud and that the principal bud has grown out to form the branch.

In the proleptic development of replacement shoots on a decapitated orthotropic shoot such renewal shoots arose from the principal resting bud at one or more nodes below the cut (Fig 10). The resting subordinate bud could still be found between the developing principal bud and the base of the subtending leaf

The Orqueta

The normal structure of the orqueta is quite consistent. Judging by the spacing of the nodes the orqueta appears to form during a flush of growth of the shoot, but I have not been able to observe this event in living material. Hallé and Oldeman (9) state that the apex aborts during a period of rapid growth. Brooks and Guard (1) say that marked lack of internodal elongation is the first sign that an orqueta is forming. Normally the orqueta consists of a series of four or five branches developed from principal buds by syllepsis. The morphology of the last, distal branch differs from that of the others as its subtending leaf is apparently adnate to the branch. Therefore, this ultimate branch is not subtended by a foliage leaf (Fig 11).

The last branch bears the scars of a foliage leaf and its two stipules about 1 cm above the base on the abaxial side as its first appendage. The foliage leaf it bears subtends a small bud. The prophyll of a sylleptic branch in T. cacao is usually a reduced unitary structure, rather than a leaf and pair of stipules (see below). Therefore I interpret this reduced leaf and pair of normal stipules on the ultimate branch as the subtending leaf of that branch, which has been carried up on the side of the hypopodium.

The cessation of meristematic activity and differentiation of the apical meristem of the shoot coincides with the unusual elogation of the ultimate branch.

Often there is a small leaflike structure, without stipules, or merely a small bump, on the otherwise bare dome left where the apical meristem of the shoot has disappeared.

Below, or occasionally among, the branches of the orqueta one or two structures may sometimes be found which might be classed as large buds or short branches (Fig 12). They have the features of aborted sylleptic branches. There may be a short hypopodium, 1-3 mm long, with no scales at the base. Its prophylls and subsequent foliage leaves are similar in structure to those of young sylleptic branches.

These aborted branches look like the very young branches of a young orqueta. They have the distichous phyllotaxis characteristic of the branches of the orqueta. As the branches of the orqueta undergo secondary growth any such arrested branches soon wither and are lost. A groove in the stem may be seen below such an arrested branch as secondary growth is initially concentrated below the fully-developed branches of the orqueta. This groove disappears as the stem grows in thickness and any such arrested branches die

Proleptic Branches

I was unable to study the formation of the proleptic "chupon" branches, which were very rare in my material. On a decapitated orthotropic shoot one or more resting buds develop by prolepsis to form replacement orthotropic shoots. Such branches have scales at the base and a transition from scales to foliage leaves is accomplished over the first few millimeters of the branch base (Fig 10). There are about five scales or their scars within the first millimeter of the base of the branch. Above these the internodes are longer and reduced stipulate leaves are formed, grading into normal foliage leaves through a short transitional series. A change from the distichous phyllotaxis of the foliage leaves is made in this region of transition. There is a small subordinate bud at the base of such a branch, between the branch base and the subtending leaf. Therefore such a proleptic branch is developed from a principal bud.

Proleptic branches were seen on distichous plagiotropic branches as well. The scars of the subopposite prophyll were visible close together (the intervening internode was less than 2 mm long) at the base of the daughter branch. The internodes beyond the second prophylls were much longer (about 1 cm or more). The transitional series of gradually longer internodes is lacking. Since the leaves had abscised from my material I cannot say whether the transition in leaf form from the prophylls to the foliage leaves was abrupt or gradual.

Where the vascular cylinder of the proleptic branch connects to that of the plagiotropic axis which bears it the pith of the branch is very narrow. The size and cross-sectional shape of the pith of a proleptic branch at its base are the same as those of a principal resting bud similar to the one from which the proleptic branch
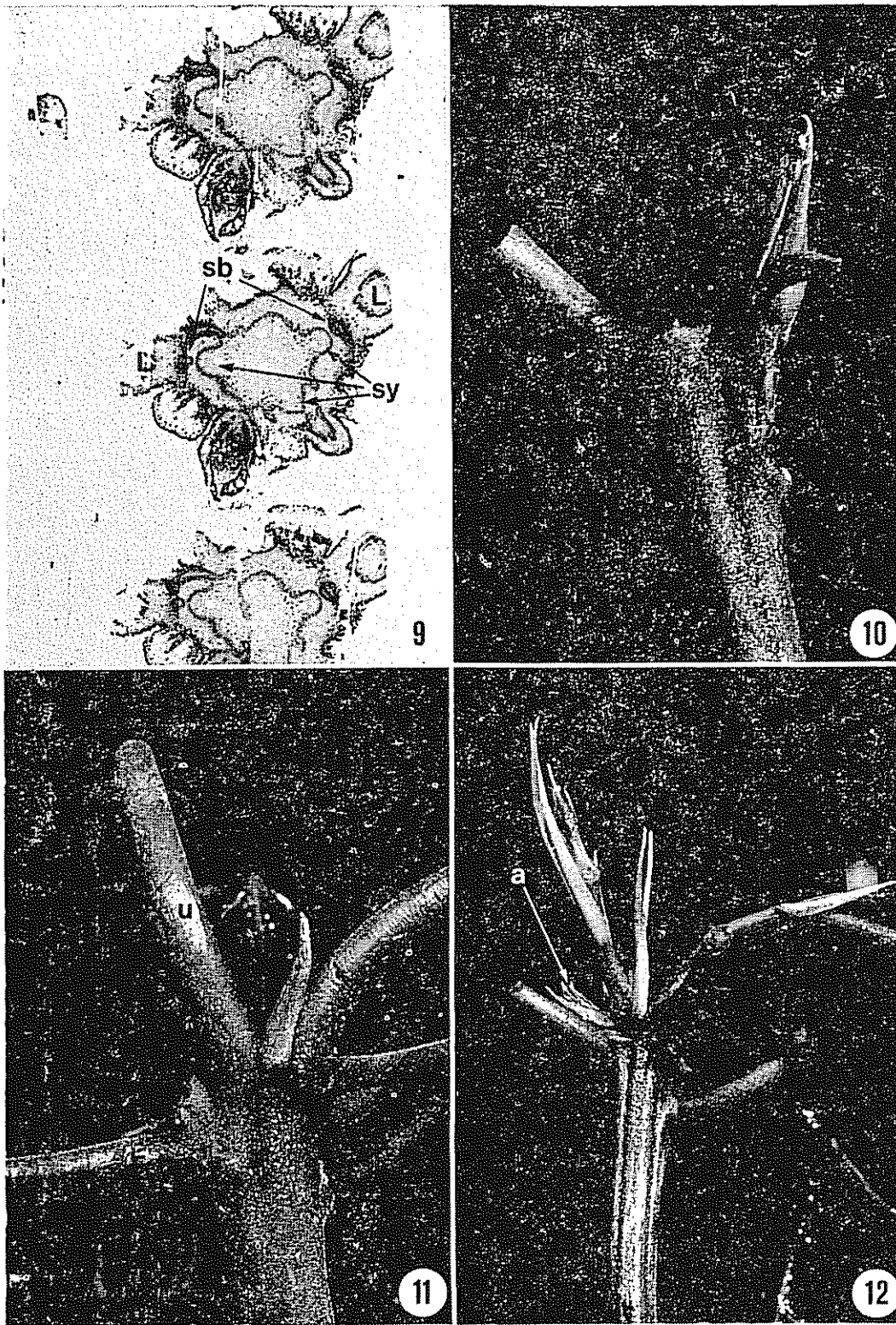
Fig 9-12.—Theobroma cacao *Fig. 9 Transection below a young orqueta, showing subordinate buds and bases of sylleptic branches, x 10. Fig. 10, Proleptic branch x 3 Fig 11. Ultimate branch of a young orqueta, x 3. Fig. 12. Young orqueta, x 2. a, aborted branch; L, leaf base, sb, subordinate bud, sy, vascular cylinder of sylleptic branch, u, ultimate branch.*

grew. The vascular cylinder of a principal resting bud is oval in cross-section. The oval is elongated perpendicular to the axis of the branch which bears the bud. The traces to the prophylls are prominent at the ends of the elongate oval. The pith is about 1.5 mm along its long axis and 1 mm along its short axis, as seen in cross-section where it emerges from the stem.

In herbarium material of *T. cacao* I observed what appeared to be sylleptic lateral branches on plagiotropic distichous shoots. These sylleptic daughter branches are also plagiotropic and have distichous phyllotaxis. I also found examples of proleptic development of plagiotropic, distichous daughter branches on plagiotropic shoots on herbarium specimens. Inflorescences, when seen on herbarium material, were always axillary to leaves or at the bases of proleptic lateral branches, where they were probably axillary to the bud scales of such branches.

Discussion

The results reported here support the observations of Lent (13), who stated that the inflorescence arises from the subordinate bud, not from the principal bud. The near-universal presence of two axillary buds in each axil reported by Lent and Vogel (16) is also borne out by my studies. All of the vegetative branches I examined arose from the principal bud and none of them from the subordinate. Lent (13) stated that '. . . a subordinate bud can form a vegetative branch if the branch on which it is borne is decapitated and the principal bud to which it is adjacent is removed. Normally a subordinate bud will remain dormant, elongating very little, until the branch which bears it has become older". Also according to Lent and to Greathouse and Laetsch (7) principal buds which do not give rise to vegetative branches abort after a time. But subordinate buds persist to give rise to inflorescences or "flowering cushions" on older wood. The behavior of subordinate buds in *T. cacao* is thus very similar to that seen in *Eucalyptus regans* F. Muell. by Cremer (4).

So the hope expressed by Greathouse and Laetsch (7) that "Subordinate buds on orthotropic shoots might give rise to plagiotropic shoots while the principal buds always give rise to other orthotropic shoots", is not fulfilled. On the contray all branches, both sylleptic and proleptic and both orthotropic and plagiotropic, arise from the principal buds.

The hypothesis raised by Greathouse and Laetsch (7) that the phyllotaxis, and presumably the geotropic response, of a resting bud are fixed early and duplicate that of the stem which bears the bud was not supported by my observations. I was unable to confirm the statement of Greathouse and Laetsch (7) that ". . . the buds show the phyllotaxis of the parent shoot". The principal buds showed a wide range of form based on degree of development. But I am inclined to support the statement of Brooks and Guard (1) that all of the well-developed buds have distichous phyllotaxis initially.

It is not possible, however, to say anything about the determination of geotropic response on the basis of bud structure.

The development of branches with distichous phyllotaxis initially. It is not possible, however, to say anything about the determination of geotropic response on the basis of bud structure.

The development of branches with distichous phyllotaxis would require the least re-arrangement of the pattern of leaf production already established in most buds. But the characteristics of the meristem which make the shoot plagiotropic and produce short-petioled leaves may be determined in some other way. The development of a shoot with spiral phyllotaxis requires a change in the phyllotaxis of the shoot from that found in the bud to that of the branch stage. Perhaps in *T. cacao* this is only possible with the intervention of a period of relative quiescence and slow development of the meristem entailed by proleptic development. This would explain why orthotropic renewal shoots are produced only from resting buds.

The reverse is not always true in *Theobroma cacao*, for as I have observed on lateral branches and as was shown in pruning experiments by Greathouse and Laetsch (7) and Vogel (16), plagiotropic distichous branches may arise by prolepsis. A similar but more restricted situation was reported by Fisher (see discussion following Fisher (6)), for *Terminalia catappa*: "If lateral buds undergo prolonged rest in *Terminalia* they can never be plagiotropic branches". They can be released by decapitation of the shoot tip but always grow out as orthotropic shoots.

According to my observations of *Theobroma*, the transition from scale-like leaves with distichous phyllotaxis at the base of a proleptic orthotropic shoot to normal foliage leaves with spiral phyllotaxis only begins with the formation of new leaves as the bud apical meristem resumes growth. The prophylls and the primordia already formed before the bud's resting phase are not rearranged.

This may explain to some extent the more rapid transition to longer internode length seen in proleptic branches on plagiotropic laterals. Here there is no change in phyllotaxis from bud to the branch. It may also be that these branches, though proleptic, were formed on younger stems after a shorter period of rest of the bud, and perhaps the bud had more complete vascular connections with the conducting system of the parent axis at the time the bud began to grow out than do most resting buds.

Tomlinson (15) discussed "meristem differentiation". He defined primary differentiation of shoot meristems as the phenomenon in which each primary meristem of the shoot shows a preferred symmetry and orientation from its inception. Noting that in trees with such primary meristem differentiation the plagiotropic shoots are usually sylleptic while the orthotropic ones are proleptic he stated "This correlation between length of rest and subsequent symmetry of shoots seems common in tropical trees and needs emphasis, as it

may depend on contrasted methods of anatomical attachment resulting from contrasting developmental procedures".

In *T. cacao* sylleptic branches are predictably found only in the orqueta at the top of the stem axis, where the development of conducting tissues is much modified. The anatomy of the bases of sylleptic and proleptic branches of equivalent size in *T. cacao* were therefore different from each other, but it is difficult to compare them. The base of a branch of the orqueta has a wide pith, and its vascular cylinder is essentially a primary part of the vascular cylinder of the suuporting stem. In the orqueta the bases of the sylleptic branches comprise most of the vascular cylinder of the trunk apex, and relatively little is made up of vascular tissue that is not part of a sylleptic branch base. The base of a proleptic branch has a narrow pith and its vascular cylinder is developed contemporaneously with and connected to the secondary vascular cylinder of the stem. Brooks and Guard (1) reported that the mature stem anatomy of plagiotropic and orthotropic branches in *T. cacao* is similar in terms of the distribution of pith, provascular, cortical, and epidermal tissues, and in the occurrence and distribution of lysigenous mucilage cavities.

If the anatomy of the branch connection influences the determination of the type of branch to be produced it must do so at a very early stage. The number of features involved in meristem differentiation in *T. cacao* (viz., phyllotaxis, petiole length, geotropic response) argue for a complex cause or combination of causes. Also one must keep in mind that plagiotropic second order branches develop on plagiotropic lateral branches by prolepsis or, as described by Cook (3) for *Theobroma bicolor* H. & B. *(Tribroma bicolor* (H. & B.) Cook), in some cases apparently by syllepsis. In addition Greathouse and Laetsch (7) showed that plagiotropic branches can develop by prolepsis if the trunk of *T. cacao* is decapitated just below the orqueta. These facts argue against the hypothesis stated by Tomlinson (15), cited above, at least as it applies to *T. cacao*.

If there is an influence of developmental procedure on meristem differentiation I believe it may have to do with the slow development of the proleptic branch, associated with its gradual transition from the resting to the growing state, the need to re-establish vascular connection with the cambium if secondary growth in thickness of the supporting stem has begun, and the concomitant gradual increase in the rate of extension growth of the branch.

The strongly plagiotropic, pagoda-like habit of *T. cacao*, and indeed of many similar trees with all branches strongly plagiotropic from their inception, deserves some comment as an "ecological strategy". *T. cacao* is an understory tree of the tropical rain forest. Its spreading branches with distichous leaves probably capture more light with less mutual shading than would orthotropic branches with spirally arranged leaves. Growth in height, unless it leads to a place in the canopy, may confer little advantage in the low-light

environment of the understory of a dense rain forest. *Theobroma* seems to have adapted to a strategy of efficient light capture, rather than one of waiting for an opportunity for canopy penetration depending on rapid growth in height. Cook (3) emphasized the suitability of the habit of *T. cacao* for growth in the understory. According to the theories of Horn (11) the structure of an understory tree in the wet tropical evergreen forest should approach a monolayer. This is what he found in the forests he studied in Costa Rica. I do not know whether *T. cacao* conforms to this prediction.

The dimorphism in petiole length in *T. cacao* may represent an additional economy, as long petioles on the two-ranked leaves of plagiotropic branches would confer no advantage. Presumably the mutual shading of leaves on the orthotropic shoot is minimized by re-adjustments of position made possible by a longer petiole with pulvini at either end, such as *T. cacao* has.

The adaptive value of the peculiar method of forming the pseudowhorl of plagiotropic branches exhibited by *T. cacao* is not evident. Its essential features are parenchymatization of the apex (not its loss due to terminal flowering, as in some modes of growth) and the formation of the orqueta of sylleptic branches. An alternative pattern often observed is the intermittent formation of a tier of sylleptic lateral branches on a continuous monopodial trunk, as in *Myrsine floridana* (17) or *Diospyros*. Perhaps the loss of the apical meristem of the trunk allows more efficient allocation of resources to the lateral branches. If the findings of Zimmermann (18) that there is a bottleneck in the leaf-specific conductivity of the xylem path at the base of a branch, compared to the path in the stem, hold true for sylleptic as well as proleptic branches, then the loss of the apex might well change the hydraulic structure of the tree. The branches of the orqueta would not, when young, be competing with the growing trunk above, as the trunk does not extend above the orqueta. Later a trunk relay axis is formed from a resting bud below the orqueta: the trunk itself morphologically and anatomically, at least initially, is a branch. Thus when young this part of the trunk itself would confront the same bottleneck effect. Under drought stress the young plagiotropic branches might then have an advantage over the young trunk above in terms of water availability and susceptibility to drought. Later still, after a period of secondary growth, the trunk would possibly acquire the advantage of a preferential water pathway seen in temperate trees.

Summary

The two buds present in the leaf axils of cocoa have different morphogenetic potential, but the distinction between the two types of buds is not the source of the axis differentiation characteristic of the plant.

The larger, distal, first-formed "principal bud" may give rise to a sylleptic, plagiotropic branch with distichous phyllotaxis in the formation of the orqueta.

Such a sylleptic branch has a broad primary connection with the vascular systems of the axis which bears it. A principal bud which does not develop by syllepsis may form a proleptic branch later. Such a proleptic branch may be orthotropic with spiral phyllotaxis (generally on the orthotropic axis of the trunk) or plagiotropic with distichous phyllotaxis (generally on plagiotropic lateral branches). Such a proleptic branch has a narrow initial connection with the secondary vascular system of its parent axis.

The smaller, later-formed "subordinate bud" is formed abaxially on the principal bud. It never develops by syllepsis. If the principal bud and the axis above are damaged the subordinate bud may form a proleptic branch, in the manner of a resting principal bud. Normally the subordinate bud develops into an inflorescence.

The distinction between plagiotropic and orthotropic branches is not due to their origin from different types of buds, nor to their origin by syllepsis or prolepsis.

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Notas y Comentarios

Reunión sobre subproductos del café

Se ha anunciado la realización en la ciudad de Guatemala de la Segunda Reunión Internacional sobre "La utilización integral de los subproductos del café", que tendrá lugar del 3 al 5 de diciembre de 1979.

La reunión tiene por objeto dar a conocer los avances logrados desde la primera reunión que tuvo lugar en el CATIE, Turrialba, Costa Rica, en 1974. Además, se ocupará de las tendencias en este asunto; de las modificaciones que deben hacerse a los sistemas de beneficios del café para un mejor aprovechamiento de los subproductos; y buscar una coordinación entre los centros que tienen proyectos similares

La reunión está auspiciada por el Instituto Centroamericano de Investigación y Tecnología Industrial (ICAITI) y la Organización de los Estados Americanos (OEA), en colaboración con la Asociación Nacional del Café (ANACAFE, Guatemala). La dirección es Apartado Postal 1552, Guatemala.