A Study of Leaf Development in Doxantha Unguis-Cati (Rehder).

Dan Richard Sistrunk

Louisiana State University and Agricultural & Mechanical College

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A STUDY OF LEAF DEVELOPMENT IN DOXANTHA UNGUIS-CATI
REHDER.

The Louisiana State University and Agricultural
and Mechanical College, Ph.D., 1972
Botany

University Microfilms, A XEROX Company, Ann Arbor, Michigan
A Study of Leaf Development in *Doxantha unguis-cati* Rehder

A Dissertation

Submitted to the Graduate School of the
Louisiana State University
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Botany

by

Dan Richard Sistrunk
B.S., McNeese State University, 1963
M.S., McNeese State University, 1969
August, 1972
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indistinct print.
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This study was undertaken to provide basic information on the ontogeny and differentiation of leaf tendrils.

Two distinct growth stages of *Doxantha unguis-cati* Rehder (Bignoniaceae) occur. The juvenile form produces simple leaves, and the adult form produces compound leaves. Juvenile and adult apices were studied anatomically and histochemically. A preliminary study indicates that heterophylly in *Doxantha* may be partially controlled by auxins.

The compound leaf of *Doxantha* is composed of two lanceolate leaflets and a terminal tripartite thorn-tendril. Compound leaf primordia are initiated simultaneously in pairs on opposite flanks of the shoot apical meristem by periclinal cell divisions in the outermost layer of the peripheral flank meristem.

A pair of leaflet primordia are the first lateral appendages of the compound leaf primordium. Initiation of a pair of leaflet primordia occurs on the adaxial side of a compound leaf primordium 63-70μ in height. Lamina formation is initiated at the base of a leaflet primordium 70-90μ long and continues acropetally. Mesophyll differentiation occurs late in development of leaflets.

The second pair of lateral appendages of the compound leaf primordium differentiate as tendrils. Initiation of a pair of lateral tendrils occurs on the adaxial side of a primordium approximately 168μ
Acropetal procambialization and vacuolation extend to the apex of tendrils about 112\textmu{} long, restricting the tendril meristem to the adaxial side of the primordium. The tendril meristem is gradually limited to a more basipetal position as elongation of apical cells continues. Sclerification of the tendril apex begins in tendrils approximately 550\textmu{} long and proceeds basipetally. Sclerification extends a greater distance below the apex on the abaxial tendril surface, causing formation of the claw-like thorn-tendril.

Developmentally and morphologically the modified leaflets of *Doxantha* resemble thorns more than tendrils. However, they are closer to tendrils functionally because they are organs of attachment. These structures possibly represent an intermediate class of modified plant organs; thorn-tendrils.
INTRODUCTION

This study was undertaken to provide basic information on the ontogeny and differentiation of leaf tendrils. A study of the indeterminate shoot apical meristem and the determinate leaflet and tendril meristems could elucidate basic changes that occur in the vegetative apex and lateral appendages in many plants.

Very few histological studies have been conducted to determine the fate of determinate vegetative apical meristems. Boke (1959) reported four types of determinate shoot meristems in the Cactaceae, exclusive of floral primordia and the intercalary meristems at the bases of spines. Detailed ontogenetic studies of thorn shoots have been conducted by Blaser (1956), Arnold (1959), and Bieniek and Millington (1967).

Tendrils are defined as modified leaves or portions of leaves, but in some plants such as Vitaceae a modified stem forms a tendril, a slender spirally coiling sensitive organ serving to attach a plant to its support. Tendrils have intrigued plant scientists for many years, as indicated by the works of Darwin (1884), Goebel (1900), and Haberlandt (1901, 1914). Until recent years, very little was known about tendril histology. Detailed studies of tendril ontogeny have been made by Moens (1956), Millington (1965), Tucker and Hoefert (1968), Shah and Dave (1970). A wide range of structures were found to differentiate from the determinate apical meristems of the tendrils studied.
However, the majority of these tendrils are modified stems. *Doxantha unguis-cati* Rehd., a member of the Bignoniaceae, was selected for this study because it produces tendrils that form claw-like structures, unlike any tendril previously studied developmentally. The tendrils of *Doxantha* are clearly modified leaflets. This provides an opportunity to compare differentiation of a leaflet and tendril which are homologous but differ in ontogeny.

The ontogenetic study of compound leaf development is another neglected area of plant anatomy. The works of Foster (1935, 1936, 1949), Tepfer (1960), and Rickson (1969), are notable exceptions. Therefore, another objective of this study was to provide information on the structural changes that occur in the compound leaf primordium as lateral appendages are initiated and differentiated.

The only recent work on *Doxantha* is that by Dobbins (1969, 1971), who correlated the vascular system of *Doxantha* with the anomalous cambial activity in the stem. He reported that the shoot apical meristem consists of a two-layered mantle covering a corpus composed of a mother cell zone and a flanking meristem. He also observed a great deal of variation in the shape of leaves. Other studies of *Doxantha* are morphological rather than anatomical.

The existence of two distinct growth stages of *Doxantha* became apparent very early in this study, stimulating the author's interest in heterophylly. This provided an opportunity to compare the range of genetic expression for leaf development in adult and juvenile shoots.
Vegetative buds and leaves of Doxantha were collected at various times throughout the year from adult and juvenile growth stages. Collections were made from numerous plants which are cultivated on the Louisiana State University campus, Baton Rouge, Louisiana.

Numerous leaves of various ages and several shoot apices were cleared, and their vasculature was stained with safranin (Arnott, 1959).

Shoot apices were killed and fixed in formalin-acetic acid-alcohol (FAA) and chromic-acid acetic-acid formalin (CRAF III), dehydrated in a tertiary butyl alcohol series, and embedded in paraffin (Johansen, 1940). Some apices were killed and fixed by freeze substitution, according to the method of Jensen (1962).

Sections were cut at 7μ on an '820' Spencer rotary microtome, and stained with (1) fast green-safranin (Sass, 1951), (2) Delafield's hematoxylin-safranin (Jensen, 1962), (3) tannic acid-ferric chloride-safranin (Foster, 1934), (4) tannic acid-iron alum-safranin-orange G (Sharman, 1943), or (5) hematoxylin-chlorazol black E (Rickson, 1968) for cytological examination. The following histochemical tests were made: (1) Feulgen test for DNA, (2) methyl green-puronine test after differential extraction of DNA and RNA by the perchloric acid method, (3) potassium iodide-iodine (IKI) test for starch, (4) periodic acid-schiff's (PAS) reaction for total insoluble polysaccharides, (5) differential extraction of cell wall components (Jensen, 1962).
Sections were photographed with a Leitz Orthomat microscope camera with brightfield illumination. Standard photographic techniques were followed. Some specimens were observed and photographed with the aid of a scanning electron microscope, model JSM-2 made by Japanese Electron Optics. Specimens were prepared for SEM study by evaporating gold to less than 100 Å thick on the material. The thickness of the gold was optically determined.

The width of shoot apical meristems was measured on longitudinal sections utilizing an ocular micrometer. Height of shoot apical meristems was determined by counting the number of 7μ-thick transverse sections clearly showing the apical outline. Measurements were obtained from 20 apices in minimum and 20 apices in maximum plastochronic stages.

The rate of leaf production was determined by counting the number of expanded leaves on 20 juvenile and 20 adult shoots. Leaf counts were made every three days for a period of 45 days, beginning February 12, 1971 and ending March 29, 1971. Shoot growth of adult and juvenile plants was measured over the same period of time. Mean internode length was determined by counting the number of internodes and dividing this figure into the total shoot growth.

Leaf prints were made to record leaf shape and venation. A burning candle was held under cardboard which had been coated with lanolin. Carbon deposited on the cardboard was used for making leaf prints. Leaf area per node was determined with a planimeter.

The rooting ability of shoots was observed on cuttings. The apical 10 cm. section was excised from 12 shoots of both adult and juvenile
growth forms. Excised shoots were placed in moist peat and observed at frequent intervals of time, for a period of three weeks.

In growth regulator tests, indole-3-butyric acid, gibberellic acid, and kinetin were diluted to concentrations of 2.5, 5, and 10 ppm by weight, and applied to excised shoots. Hormones were collected from adult and juvenile apices in agar receiver blocks as described by Mitchell and Livingston (1968), and applied to excised shoots also. Plants were placed in a moist chamber for 96 hours, then transferred to a greenhouse after treatments. Responses were determined by comparing the differentiation of axillary shoots on treated plants and on controls.

To construct a graphic representation of comparative meristem size, the following method was used. The limits of a compound leaf primordium meristem were determined by arbitrarily defining the meristem as comprised of cells having a greater affinity for cytoplasmic stains; these cells typically appear less vacuolate than other cells of the primordium. Although arbitrary judgment was made, the results are comparable. The width and height of this primordium meristem were measured with an ocular micrometer on approximately median longitudinal sections. A rectangle of the average height and width of each of the primordia meristems was drawn to scale on graph paper. A median longitudinal section of the meristem forms a hyperbola in outline. The hyperbola was then drawn to the rectangular dimensions (Fig. 77). The rectangle was cut out and weighed. Next, the hyperbola was cut out and weighed. The area of the meristem was determined by the following formula:
Area of meristem = Area of hyperbola =
\[
\frac{\text{wt. hyperbola}}{\text{wt. rectangle}} \times \text{Area of rectangle}
\]

A compound leaf primordium is approximately circular in transverse section; therefore, area increase probably indicates an increase in volume. Numerous measurements revealed that the variation in weight of the graph paper and pencil marks were negligible.
RESULTS

**Morphological Observations:**

Two distinct growth forms occur in *Doxantha*. Adult and juvenile growth forms have been reported for numerous taxa, but not previously for *Doxantha*. The juvenile growth form produces at each node a pair of simple leaves. Juvenile leaves are lanceolate to ovate in shape with entire or irregularly serrate margins, mucronate tips, and cuneate bases (Fig. 1). Juvenile leaves are decussately arranged and range in length from 3 to 6 cm. The basal juvenile leaves commonly undergo abscission after about one year. Some juvenile leaves are evergreen and persist for several years. Seedlings and young shoots possess juvenile characteristics.

The adult form produces a pair of pinnately compound leaves at each node. Each compound leaf is composed of two leaflets and a terminal tripartite tendril (Fig. 3). Leaflets are typically less than 3 cm. long; however, some may attain lengths of 6.5 cm. Leaflets are lanceolate in shape with entire margins, mucronate tips, and cuneate bases. Mature tendrils are approximately 1 cm. in length, and are terminated by a claw-like structure. Adult leaves are evergreen and persist for several years. Adult leaves are initiated in a decussate fashion, but become bilaterally symmetrical due to twisting of alternate internodes below the terminal bud. The adult form, once attained, is essentially permanent and normally irreversible for that shoot.
A comparison of the morphological characteristics of adult and juvenile growth forms of *Doxantha* is given in Table 1. The average rate of shoot growth in adult plants was 1.26 cm. per day. Juvenile shoots increased in height at a rate of 0.16 cm. per day. The mean leaf area per node was 3.84 in.$^2$ for juvenile shoots and 4.84 in.$^2$ for adult shoots. All cuttings developed adventitious roots within three weeks.

The number of pairs of juvenile leaves were counted on 50 plants which had undergone the transition to the adult stage. The average number of nodes bearing juvenile leaves was 3.74 with a range of 2 to 7 among all plants observed. The transition from the juvenile to the adult growth stage is seldom abrupt. In a majority of the plants observed, one finds a transitional node at which leaves showed characters that were intermediate between juvenile and adult foliage types (Fig. 2 A-G). Compound leaves possessing axillary floral buds lack tendrils, and therefore are composed of only two leaflets. Leaf variations in positions other than the transitional node are extremely rare in *Doxantha*.

**Experimental Modification of Form:**

The discovery of heterophyll in *Doxantha* provided an opportunity to try manipulating form of the plant experimentally. Various attempts were made to bring about reversion of the adult to the juvenile growth stage.

**Pruning Experiments:**

Pruning has been reported to induce juvenility in certain plants. The terminal vegetative bud was excised from 30 plants in both growth
stages to determine if this would occur in Doxantha. Branches developed from axillary buds one or two nodes below the excision. In all cases the foliage produced on these branches was of the same type as the parent shoot.

**Hormone Treatments:**

An attempt was made to determine if heterophylly in Doxantha is under hormonal control. The apical 3 to 5 mm. was removed from adult and juvenile shoots. Excised apices were then placed on agar receiver blocks in moist petri dishes for 24 hours. Receiver blocks were next placed on excised adult shoots and left in a moist chamber for 96 hours, then transferred to a greenhouse. Reversion to juvenile foliage production occurred in 8 of 23 plants which were treated with extract from juvenile shoot apices. Two of 14 plants treated with extract from adult shoot apices also produced juvenile foliage. A few reversions also occurred when anhydrous lanolin alone was applied to the axillary buds of adult excised shoots. A more commonly observed response to the lanolin treatment was the absence of tendrils on compound leaves.

**Growth Regulator Treatments:**

Growth regulators were applied in an attempt to determine the hormone or hormones responsible for heterophylly in Doxantha. Gibberellic acid, indole-3-butyric acid, and kinetin were applied to excised shoots; no response was observed by treating intact plants. No reversions were observed in treatments of excised shoots with gibberellic acid or kinetin. Concentrations of 2.5 and 10 ppm. of indole-3-butyric acid were found to be ineffective in producing the desired response.
Transitional shoot apices were identified on the basis of two criteria. The first internode below the shoot apex may become greatly elongate prior to producing transitional foliage (Fig. 6), or transitional apices are dome-shaped but only about one-half the diameter of adult apices (Fig. 7).

**Compound Leaf Development:**

**Early Ontogeny:**

Leaves are initiated simultaneously in pairs on opposite flanks of the shoot apical meristem. Transverse sections of terminal vegetative buds show that leaves are initiated in a decussate phyllotactic arrangement (Fig. 12).

The first indication of leaf initiation is the presence of periclinal cell divisions in the outermost layer of the peripheral flank meristem (Fig. 9). Numerous periclinal cell divisions in this layer of the meristem with concomitant cell enlargement give rise to the two leaf buttresses (Fig. 10, 11). The term leaf buttress signifies a very early stage in leaf formation and is restricted to a primordium only a few μ in height. Periclinal cell divisions begin to occur in the second tunica layer of the meristem after the leaf buttress has attained a height of about 10μ. Derivatives of periclinal cell divisions in the second tunica layer are shown in Fig. 12. The surface layer is continuous with the shoot apical meristem and the leaf buttress because only anticlinal cell divisions occur in that layer. Derivatives of the first and second layers below the protoderm divide predominantly in a plane anticlinal to the surface. These divisions and increased cell size are responsible for initial elongation of the paired compound leaf.
primordia of Doxantha (Fig. 13, 14). Occasional periclinal cell divisions increase the width of the primordium (Fig. 17). The entire leaf primordium appears uniformly meristematic in all stages below 60μ in height. When the compound leaf primordia reach a height of about 60μ, another pair of leaves is initiated on the shoot apex in a plane at right angles to the existing pair.

The shape of the meristem changes during a plastochron from low-convex to a high dome. The apex is circular in transverse section at the time of leaf initiation (Fig. 10). The apex widens preferentially in one plane to become oval in transverse section, as leaf differentiation continues (Fig. 12).

**Initiation and Early Development of Leaflets:**

Leaflets are initiated in the basal region of a compound leaf primordium that has reached a height of about 63μ. Leaflets are initiated by periclinal cell divisions in the third adaxial layer. The paired leaflet primordia arise as small protuberances on the adaxial surface of a compound leaf primordium 70μ in height (Fig. 22). The appearance of a protuberance on the adaxial surface of a primordium is followed by periclinal cell divisions in the second adaxial layer. The leaflet primordium elongates by anticlinal cell divisions in the derivatives of the second and third adaxial layers and by cell enlargement. The entire leaflet primordium is relatively undifferentiated and highly meristematic throughout in early stages of development (Fig. 25).

Apical and sub-apical initials are first apparent in a compound leaf primordium approximately 70μ in height (Fig. 18). When a compound leaf primordium has reached a height of 85μ, it shows a terminal
meristematic region composed of apical and sub-apical initials, and their most recent derivatives. These cells are more isodiametric and less vacuolate than other cells within the primordium (Fig. 19). Prominent vacuolation begins in the basal abaxial side of a compound leaf primordium about 70μ long. Vacuolation proceeds acropetally, and extends to the base of the meristem in a primordium about 85μ long. On a compound leaf primordium approximately 90μ high, leaflet primordia are 20μ high (Fig. 22). When compound leaf primordia reach approximately 136μ in height, cells of the abaxial side undergo extensive vacuolation and enlargement causing curvature of the compound leaf primordium (Fig. 20).

Lamina Development:

Two small protuberances appear on the adaxial surface in the proximal region (20 μ from the base) of a leaflet primordium 90μ in length (Fig. 23). From such protuberances the lamina of a leaflet develops. When the inceptive lamina reaches 30μ in length, marginal and submarginal initials are evident (Fig. 21). A row of marginal initials extends the protoderm, and sub-marginal initials give rise to the three internal layers of the lamina (Fig. 28). The abaxial derivatives of sub-marginal initials contribute frequently to the middle row of cells in the lamina.

Initiation and development of the lamina proceed acropetally. However, lamina formation does not extend to the apex of the leaflet primordium. A transverse section of the apical region of 4 leaflet primordia is shown in Fig. 26, and marginal growth is absent. The apical region of a leaflet primordium in this stage of development is
relatively undifferentiated (Fig. 27). This region of the leaflet becomes increasingly vacuolate as lamina development occurs (Fig. 31). This abaxial vacuolation and cell enlargement later extends into the base of the lamina, causing the lamina to inroll in a complicated fashion.

The growth rates of the rachis and the leaflets are approximately equal in early development. The initial 60 to 70µ height advantage of the compound leaf primordium before leaflets are initiated prevails while leaflets are developing. This condition changes as the rachis exceeds 170µ in height. Figure 61 shows a compound leaf primordium 189µ in height with a leaflet 204µ long. The growth rate of leaflets obviously exceeds that of the rachis at this point in development. Once established, the greater growth rate of leaflets over that of the rachis is maintained throughout development of a compound leaf (Fig. 76).

**Procambial Development:**

Procambium is first present at the base of a compound leaf primordium about 63µ high. This will later become the median vascular bundle of the rachis. Procambial differentiation is continuous from the axis and proceeds acropetally in the rachis at approximately the same rate as height increase of the rachis. Procambium first appears in leaflet primordia when they are about 63µ long. Procambium is not yet present in a leaflet primordium 56µ in height (Fig. 23).

Three separate procambial strands are present basally in a compound leaf primordium approximately 217µ in height (Fig. 30). The median procambial strand differentiates continuously and acropetally
in the central region of the rachis. The two lateral procambial traces also differentiate continuously and acropetally and diverge into the leaflet primordia. The two leaflet bundles differentiate within the central region of the two leaflet primordia and constitute their incipient mid-veins. Procambial differentiation extends to 14μ below the apex of the leaflets at node 5. The nodes are numbered from the apex downward. At the leaf base the two leaflet traces join the vascular cylinder of the stem on either side of the median procambial strand, at approximately the same level, within the first internode below. At this level the vascular cylinder is composed of discrete primary vascular bundles; whereas, a mature stem contains a solid vascular cylinder composed of some secondary vascular tissues.

Lateral procambial strands of the first order branch from the incipient midvein into the lamina. This phenomenon is responsible for the pinnate venation of mature leaflets. Later procambial strands of secondary and tertiary order arise first near the margin slightly below the apex of a leaflet, and differentiate basipetally. The procambial strands of higher orders anastomose to form vein islets and the characteristic netted venation of mature leaflets.

**Differentiation of Vascular Tissues:**

Phloem differentiates before xylem within a compound leaf primordium of *Doxantha* (Fig. 30). Phloem differentiates acropetally and is continuous with pre-existing phloem below. Mature sieve tube elements and companion cells are first observed in the median bundle of a compound leaf primordium 364μ in height approximately 126μ below the leaf tip. Leaflets are about 308μ long when the first row of protophloem
sieve tube elements appears in the proximal region.

Xylem is present but at first discontinuous at the base of the compound leaf primordium. The continuity of xylem seen basally in older primordia is the result of bi-directional differentiation within the intervening procambial areas. The first mature protoxylem vessel elements were observed in a compound leaf primordium 770μ in height 266μ below the tip. Leaflets are about 469μ in length at the time protoxylem differentiates within the incipient midveins of the leaflets.

Axillary Bud Development:

The first axillary buds initiate at node three below the shoot apical meristem (Fig. 39). Periclinal cell divisions occur in the second and third layers below the stem surface in the axil of a compound leaf. A small protuberance appears in the axil of a leaf located at the fourth node (Fig. 40). This recently differentiated meristematic region is approximately 40μ in width, in median longitudinal section. At node four, it is apparent that the two outermost cell layers have divided anticlinally and the cellular derivatives of the third layer have occasionally divided in various planes.

The meristems of axillary buds at the fifth node show a cellular arrangement similar to that of the terminal shoot meristem (Fig. 41). Axillary meristems at this stage in development are approximately 80μ in width in median longitudinal section. Periclinal cell divisions in the third adaxial layer initiate two prophylls in a plane at right angles to the sagittal plane of the subtending leaf. Prophylls are 80 to 100μ in height at node six. Cells in the abaxial side of each prophyll become larger and more vacuolate than cells of the adaxial
side, causing the prophyll to curve inward. The prophylls cover the axillary meristem as they continue to elongate. Procambial traces first appear in the basal region of a prophyll and then differentiate bidirectionally, to connect with the vascular cylinder of the stem.

**Differentiation of Mesophyll:**

Mesophyll is not yet differentiated in leaflets about 2.85 mm. long, at the seventh node below the shoot apical meristem. Blades of these leaflets are composed of 5 layers of relatively undifferentiated cells. The lamina has more cell layers in the area of procambial bundles (Fig. 28, 33).

Mesophyll differentiation begins in leaflets at the ninth node, starting approximately 150 μ below the apex and proceeding basipetally. Anticlinal elongation of the adaxial ground meristem cells begins in the lamina adjacent to the midvein. Enlargement of the cells of the adaxial protoderm and ground meristem layer extends approximately midway to the margin in leaflets at node 10, and has reached the margin of a leaflet at the eleventh node.

The adaxial ground meristem layer is composed of precursory palisade cells. The darker staining quality of the precursory palisade tissue is due to the differentiation of plastids which have an affinity for hematoxylin and other basic stains (Fig. 32, 35).

The lamina changes from a complicate to a parallel orientation when the two adaxial layers of cells in the lamina undergo anticlinal elongation. Periclinal cell divisions produce two tiers of palisade parenchyma and three layers of spongy parenchyma in a leaflet at the twelfth node. Completely differentiated leaflets with three tiers of
palisade and three layers of spongy mesophyll are present at the fourteenth node (Fig. 37). Cells of the spongy mesophyll remain approximately isodiametric throughout development. Plastids differentiate in spongy mesophyll cells but are fewer in number than in palisade cells. Intercellular spaces develop in the palisade and spongy layers as anticlinal elongation of epidermal cells continue after growth has ceased in the mesophyll. The formation of intercellular spaces marks the maturation of mesophyll.

**Differentiation of Epidermis:**

Protoderm is the undifferentiated, meristematic surface layer of cells which divide primarily anticlinally. However, in trichome development periclinal cell divisions are common. The epidermis is derived from the protoderm. Anticlinal cell divisions continue in the abaxial epidermis for a longer time than in the adaxial epidermis. In mature leaflets, adaxial epidermal cells are more vacuolate than abaxial epidermal cells (Fig. 37). Divisions continue in the mesophyll after the epidermal cells have ceased dividing. The epidermal walls in *Doxantha* are covered with a waxy cuticle approximately 1μ thick. Mature epidermal cells typically are elongate parallel to the long axis of the leaflet.

**Specialized Epidermal Cells:**

Two types of specialized epidermal cells are present in *Doxantha*; guard cells and trichomes.

**Guard Cells:**

Guard cells are specialized paired cells which surround a pore in the epidermis. Guard cells in *Doxantha* are restricted to the abaxial
epidermis (Fig. 37). Subsidiary cells are not present; several typical-appearing epidermal cells are irregularly arranged around the guard cells.

Precursory guard cells originate by an unequal cellular division in the protoderm. The smaller, darker staining cell in Figure 35 is a guard cell precursor. Precursor cells enlarge and divide anticlinally to produce two guard cells (Fig. 36). The intercellular substance is broken down and the two guard cells separate to form a pore or stomatal opening. Precursor guard cells appear first in the abaxial epidermis of leaflets at the tenth node. Mature guard cells have differentiated on leaflets at the fourteenth node.

Trichomes:

Trichomes are initiated by periclinal cell divisions in the protoderm. They arise very early in development of leaves with repeated initiations of new hairs throughout ontogeny. Initiation of trichomes seems to be a highly orderly process as they are spaced at regular distances apart.

Three structurally different types of trichomes are present on shoots of *Doxantha* (Fig. 49, 50, 51). Trichome precursors, unlike the precursors of guard cells, do not arise from an unequal division of the cytoplasm. The unicellular, non-secretory trichome shown in Figure 49 results from a single periclinal division followed by extensive vacuolation and expansion of the outer cell.

The two types of secretory trichomes of *Doxantha* (Fig. 50, 51) undergo similar developmental sequences in early ontogeny. The 2-celled stage derived from a trichome precursor is shown in Figure 42. The
outer cell later will also divide in a plane parallel with the leaflet surface. Typically the two cells derived from this division contain unequal amounts of cytoplasmic components (Fig. 43). The cells then undergo enlargement and the apical cell divides in a plane anticlinal to the leaf surface. Each of these two terminal cells next divides anticlinally to produce a 4-celled terminus (Fig. 44, 52). The two types of secretory trichomes diverge in their manner of development at this point.

If the basal cell becomes more vacuolate than adjacent epidermal cells, meristematic activity seems to be restricted to the terminus. Continued anticlinal cellular divisions in the terminus (Fig. 45, 48) followed by anticlinal elongation results in the large peltate trichome or colleteter shown in Figure 51, 53.

Alternately, the basal cell may divide in a plane parallel with the surface after the 4-celled terminus is formed (Fig. 46). Next, the sub-terminal cell enlarges (Fig. 47), and later divides in the same plane as the terminal cell. The derivatives divide likewise to form the type of trichome shown in Figure 50.

The glandular hairs of Doxantha contain large basal or stalk cells. These cells contain a dark staining substance and large vacuoles. Thomson and Liu (1967) referred to cells of this type in Tamarix as collecting cells.

Trichomes differentiate very early in ontogeny of compound leaves. Some are completely differentiated on a compound leaf primordium about 85μ in height (Fig. 18), and on leaflets about the time of early lamina formation (Fig. 31). Trichomes are not restricted to leaflets; they
also occur on the rachis and tendrils (Fig. 54, 55, 57). However, trichomes do not develop on the sclerified tendril tip (Fig. 56).

The number and shape of terminal and stalk cells is quite variable in glandular trichomes. The unicellular, non-glandular trichome shows least variability, although a few two-celled filamentous hairs, similar in appearance to the unicellular trichomes, were observed.

**Differentiation of the Leaflet Pedicel:**

The lamina extends to the base of the rachis primordium in compound leaves of the fourth node. Sections of a compound leaf at the fifth node show that the pedicel is about 21 μ long. Leaflets are approximately 959 μ long at the time pedicel differentiation begins. The pedicel increases in length by intercalary growth of the entire basal region of a leaflet. A pedicel at the sixth node is approximately 140 μ long. A pedicel has reached maturity at the fourteenth node and is about 1 cm. long. The types of tissues present and their arrangements are similar in the stem, rachis, and leaflet pedicel.

**Tendril Development:**

Each leaf bears a tripartite tendril at the tip. Two parts arise laterally, on the rachis while the third is a prolongation of the rachis tip.

**Initiation and Early Ontogeny:**

Early stages of tendril development are shown for the laterals because curvature of the rachis makes median sections difficult to obtain. However, the terminal tendril develops similarly to the laterals.
Lateral tendrils are initiated by periclinal cell divisions in the third adaxial layer of a compound leaf primordium about 168μ in height which also bears two leaflets near the base, each about 100μ high. The initiatory divisions occur about 63-70μ below the apex of the primordium, so are apparently not products of the tip meristem. Compound leaf primordia in this stage of development occur at the third node below the shoot apical meristem.

The lateral tendril primordia appear in transverse section as two protuberances approximately 20μ in length on the adaxial surface of a compound leaf primordium about 180μ tall (Fig. 60). The development of the terminal tendril is delayed initially as laterals increase in size. A frontal section of a slightly later stage is shown in Figure 58. The lateral tendril primordia have attained approximately the size of the median tendril primordium by this stage of development.

Apical and sub-apical initials are present in lateral tendrils soon after they are initiated (Fig. 62, 64). These initials and their derivatives divide predominantly anticlinally. Concomitant cellular enlargement causes the growing tendril to elongate. Occasional periclinal cellular divisions increase the width of the growing tendril.

Procambium differentiates acropetally into the base of a lateral tendril when it is about 70μ long (Fig. 59). Vacuolation of abaxial cells extends above the point of insertion of lateral tendrils in a compound leaf primordium approximately 200μ in height (Fig. 62). Procambium has differentiated to 40μ below the apex at this stage. Vacuolation and procambial differentiation occur about 35μ below the apex in a compound leaf primordium 240μ tall.
**Late Development:**

Late stages of development are shown for the terminal tendril because of difficulty in obtaining suitable sections of laterals.

Vacuolation and procambial differentiation extend to the apex of a compound leaf primordium 320μ long (Fig. 63, 65, 66). The shape of the tendril apex changes from a dome to a sharp cone in a compound leaf primordium about 340μ long (Fig. 67). Several procambial strands extend nearly to the apex in the ground meristem, 4 to 5 cell layers located abaxially and adjacent to the procambium have undergone extensive vacuolation. This restricts the tendril meristem to the adaxial side, somewhat removed from the apex. The tendril is about 112μ long at this stage in development and the meristem is approximately 35μ below the apex. The tendril meristem is gradually limited to a more basipetal position as apical cells elongate. A tendril about 235μ long has a meristem located about 110μ below the apex. Apical cells have become elongate and spindle-shaped (Fig. 68). In a tendril 280μ long, mature sieve tube elements are present at a level 220μ below the apex and mature xylem vessel elements at a level 200μ below the apex.

In all stages of late tendril development, mitotic figures continue to occur in the basipetally displaced meristem of the tendril. However, cellular divisions occur throughout the tendril and with concomitant cell enlargement result in continued tendril elongation in late development. In tendrils about 550μ long, it is impossible to identify the meristem. The tendril meristem is composed of vacuolate parenchyma, which is identical to other cortical parenchyma (Fig. 70).
Spinescence:

Sclerification of the tendril begins at the apex and proceeds basipetally. Tendrils approximately 530μ long have a few apical cells sclerified (Fig. 69). Sclerification extends about 120μ below the apex of a tendril 550μ long (Fig. 70). The leaf rachis, at this stage in development, is about 2 mm. long. Sclerification extends a greater distance along the abaxial side of the tendril (Fig. 71). Adaxial cells remain parenchymatous and capable of cellular enlargement for a longer period of time than abaxial cells. This unequal sclerification results in an adaxially-inclined curvature of the tendril tip, to form the claw-like structure shown in Figure 55.

The base of a sclerified tendril is oblong in shape in transverse section; it is widest in a plane perpendicular to the primary shoot axis (Fig. 72, 73). Cells with darker staining contents occupy primarily the adaxial peripheral regions (Fig. 73). New cells are added to the elongating tendril primarily from these peripheral zones. A transverse section 200μ closer to the apex (Fig. 74) shows that the shape of the tendril is more nearly spherical and the central region and abaxial side are less vacuolate. Protophloem and protoxylem are continuous within the tendril to this height. Protophloem ceases to differentiate about 250μ below the apex of a tendril approximately 550μ long. Approximately 100μ below the apex, the tendril is almost circular in transverse outline (Fig. 75). A single protoxylem vessel element is present near the center of the tendril at this level. Sclerification of the abaxial surface and vacuolation of the adaxial tendril surface are also evident. This pattern of sclerification is
duplicated in the mucronate leaflet tip (Fig. 24).

Elongation of the tendril continues by basal intercalary growth until a length of about 1 cm. is reached. Sclerification of the mature tendril remains restricted to the tip or claw (Fig. 71).

Changes in Meristematic Area of Compound Leaf Primordia with Age:

The area of the terminal rachis meristem, in median longitudinal section, was determined in 30 compound leaf primordia. Measurements were made in three different stages of development: (1) before leaflet initiation, (2) after leaflet initiation and before tendril initiation, (3) after lateral tendril initiation.

A mean cellular area of 1837.2µ² is occupied by the meristem of a compound leaf primordium before leaflets are initiated. The mean cellular area of the meristem increased to 1994.7µ² after leaflets and before tendrils were initiated. The maximum area of 2053.5µ² occurred immediately after initiation of lateral tendrils.
DISCUSSION

In recent years, the shoot apex in seed plants has been the subject of intensive investigation. An excellent recent review of the subject has been written by Gifford and Corson (1971). The vegetative shoot apical meristem in *Doxantha* is composed of a two-layered tunica, a central mother cell zone, and a peripheral flank meristem. Vegetative shoot apices with similar zones are common among Angiosperms.

The meristematic layers from which compound leaf primordia arise seem to be extremely variable. The paired compound leaf primordia in *Doxantha* are initiated by periclinal cell divisions in the outermost cell layer of the peripheral flank meristem. Only after formation of the leaf buttress do periclinal cell divisions occur in the second tunica layer. Foster (1935) found that the primordia of cataphylls and foliage leaves of *Carya buckleyi* arise from periclinal cell divisions in the second tunica and first and second corpus layers. Tepfer (1960) reported that the earliest evidence of leaf initiation in *Clematis ligusticifolium* was periclinal cell divisions in the second tunica layer, followed by periclines in the first corpus layer. Rickson (1969) observed the first periclinal cell divisions associated with leaf initiation in *Acacia cornigera* in the third or fourth tunica layer. These divisions were followed by periclinal cell divisions in the underlying corpus and second tunica layers. The four studies cited represent four different families of Angiosperms. It would be
interesting to find if plants within the same family which produce compound leaves have the same sequence of initiatory divisions.

One of the first indications of specialization within a plant organ is the differentiation of procambium. Procambium first differentiates into the base of a compound leaf primordium of *Clematis* about 40µ high, *Carya* from 50 to 90µ high, and *Acacia* and *Doxantha* at approximately 60µ in height. These measurements fall within the range of observations for procambial development in simple leaves 54 to 70µ high, summarized in the review by Foster (1936). In all histological studies of compound leaves, procambium differentiation within the rachis is acropetal and continuous since successively formed procambium arises in continuity with earlier formed more basipetally located procambium. This course of differentiation has been reported by Esau (1964) to be of general occurrence within the midvein region of simple dicotyledonous leaves.

Apical and sub-apical initials are present very early in the ontogeny of all compound leaf primordia previously studied. Foster (1935) reported that the entire compound leaf primordium of *Carya* consisted of deeply stained, rapidly dividing cells, at stages prior to 90µ high. He found apical and sub-apical initials in primordia 90 to 190µ long. Tepfer (1960) observed in *Clematis* apical and sub-apical initials in a primordium 115µ high. Rickson (1969) reported that in *Acacia* a group of sub-apical initials becomes evident in a compound leaf primordium approximately 60µ in height. The entire compound leaf primordium of *Doxantha* appears uniformly meristematic when 60µ high. An apical meristematic region composed of apical and sub-apical
 initials and their most recent derivatives develops when a compound leaf primordium is about 85\(\mu\) high. A single apical initial does not occur in a leaf primordium of Doxantha; there seem to be a series of them in time.

Acropetal vacuolation is responsible for changing the uniformly meristematic primordium of Doxantha into a structure with localized meristematic regions. Acropetal vacuolation occurs in all compound leaves previously studied, except Acacia. Rickson (1969) observed in Acacia that epidermal and sub-epidermal cells of the abaxial side of a compound leaf primordium develop heavily thickened walls. The development of thick cell walls began at the base and proceeded acropetally. This may be a different manifestation of a developmental phenomenon common in all compound leaf primordia; the establishment of a leaf apical meristem which persists throughout early development.

Vacuolation of the abaxial side of the compound leaf primordium causes curvature of the rachis over the summit of the shoot apical meristem in Doxantha. The shoot apical meristem may gain protection from a hostile environment by the incurring leaves. Tepfer (1960) observed that vacuolation caused curvature of the rachis in Clematis. The illustrations by Foster (1935) and Rickson (1969) also show curvature of the rachis. The different microenvironments in which the abaxial and adaxial sides of the leaf primordium differentiate probably cause the early variations in local vacuolation or lignification.

Branching of the primordium, and apical growth of leaflets in Doxantha occurs at much earlier stages than is known for other plants. Leaflets are initiated in a compound leaf primordium of Doxantha 63 to
70µ tall. Rickson (1969) observed leaflet initiation in a primordium 75µ in height. Foster (1935) noted that a compound leaf primordium was 190 to 500µ high when leaflet primordia differentiate.

Procambial differentiation may be correlated with other phenomena. Tepfer (1960) observed that with differentiation of procambium into the base of a leaf primordium the abaxial cells of the ground meristem become increasingly vacuolate. In Doxantha, vacuolation of the abaxial cells of the ground meristem and the initiation of leaflet primordia seem to be synchronized with the differentiation of procambium into the base of the compound leaf primordium.

According to Troll (1935) cited in Foster (1936) and Hagemann and Kurbs (1971), leaflets may arise in three possible sequences; basipetal, acropetal, or divergent. These studies were based on comparative morphology; the histological aspects of leaf development were ignored. Histological studies of Clematis, Carya, Acacia, and Doxantha indicate that lateral appendages are initiated in an acropetal sequence, on the adaxial side of a compound leaf primordium. A histological study of the palmately compound leaf of Helleborus foetidus, described morphologically by Hagemann and Kurbs (1971) and given as an example of basipetal leaflet development, could help clarify this controversial aspect of compound leaf development.

Leaflets of Doxantha differ from other plants previously studied because lamina differentiation never reaches the apex. Cells at the apex of the leaflet become highly sclerified, eventually forming a spiny claw-like structure, similar to the tendril tip. Otherwise, differentiation of the midrib and blade meristem of leaflet primordia
in *Doxantha* are similar to other compound leaves.

The height of the compound leaf primordium at the time of lateral tendril development, in *Doxantha*, correlates closely with the height of the primordium when leaflet growth rate exceeds that of the rachis. Possibly metabolites necessary for growth are directed into the lateral tendril primordia, as lateral tendrils soon equal the size of the median tendril.

Initiatory divisions and early ontogenetic stages of leaflets and tendrils are comparable. Their ontogeny differs when the lateral primordia are approximately 70\(\mu\) long. Marginal and sub-marginal initials differentiate within leaflets, but not in tendrils. Procambial differentiation and abaxial vacuolation encroach the tendril apex as the primordium elongates. In a tendril 112\(\mu\) long procambial differentiation and abaxial vacuolation extend to the apex. Thus, a second ontogenetic difference becomes evident in the two homologous structures, leaflets and tendrils. The tendril meristem becomes progressively more basipetally located with continued cell elongation at the tip. Consequently, apical growth of tendrils ceases very early in ontogeny in comparison with leaflets.

Throughout development of the compound leaf of *Doxantha*, differentiation occurs earlier than previously found for other compound leaves. The second pair of lateral appendages are initiated in *Doxantha* when the primordium is 168 to 180\(\mu\) high, and in *Clematis* when the primordium is about 273\(\mu\) high. In *Carya* and *Clematis* a terminal leaflet develops from the upper part of the axis of a compound leaf primordium. Topfer (1960) reported that the terminal leaflet is
Initiated in a primordium 460μ high. The tip of the primary rachis, in *Acacia*, differentiates into a Beltian body, a storage structure useful in plant dispersal, when approximately 2000μ long. The fate of the primary rachis apex in *Doxantha* is determined in a compound leaf primordium 320μ high. It develops into a tendril exactly like lateral tendrils. Differentiation of the rachis apex of *Doxantha* at an earlier developmental stage than has been previously found in compound leaves further exemplifies the rapid differentiation occurring in this plant.

Tendril ontogeny in *Doxantha* clearly differs from any tendril previously studied. Moens (1956) studied tendril development in *Ampelopsis, Vitis*, and six genera of the Bignoniaceae family. He found three different tendril types, all of which produce secretory structures. He found that the apical cells of *Ampelopsis* divide and elongate anticlinally upon contact with a support. The internal cells also divide and elongate radially. Development in *Anisostichus capreolata* is similar, but divisions occur less frequently in the epidermal cells than in the underlying cells. In *Glaziovia* the dermatogen is differentiated into haustoria rather than adhesive papillae as found in *Ampelopsis* and *Anisostichus*. Tucker and Hoefert (1968) reported that the activity of the tendril apex of *Vitis vinifera* is brief and its meristem differentiates completely into a hydathode. As the tendril nears maturity the tip undergoes irreversible changes producing a ridge or several lateral appendages. Most of the epidermal cells over the summit enlarge and differentiate, eventually containing a tanniferous material. Depressions containing water pores give the
appearance of a pitted epidermis. Millington (1966) found that the organization of the tendril apex in *Parthenocissus inserta* is similar to the parent shoot apex. He also found that the tendril apex diminishes in volume with each successive appendage produced.

Ontogenetically the tendrils of *Doxantha* more closely resemble thorns than tendrils. Blaser (1956) reported that all of the uppermost cells of the senescent thorn meristem of *Gleditsia* become large and vacuolate. These cells later become sclerenchymatous forming the spiny tip of the mature thorn. In *Gleditsia*, thorns commonly increase 5 to 6 times their initial length after the apical meristem becomes senescent. Bieniek and Millington (1967) studied the differentiation of lateral shoots as thorns in *Ulex europaeus*. The first morphologically detectable change of the meristem during the transition from leafy shoot to thorn shoot is a vertical elongation of the distal rib meristem initials and their immediate derivatives. The apex shifts from a dome to a sharp cone due to elongation which causes the innermost initials to converge to a point. This change is characterized by increased vacuolation and cell enlargement. Sclerification progresses basipetally and represents the final phase of thorn differentiation. Neville (1969) made similar observations in a study of thorn development in *Gleditsia triacanthos*. *Gleditsia* differs from *Ulex* only in late development. Just prior to senescence, an abscission zone differentiates at the base of the thorn shoot in *Gleditsia*. Arnold (1959) studied spine differentiation in *Hymenanthera alpina*. He found that during the final stages of spinescence the periderm completely covers the summit of the thorn, and no trace of the apical meristem remains.
The position once occupied by the apical meristem is the location of a mass of parenchymatous tissue showing no particular organization.

Tendrils of *Doxantha* differ from the thorns previously studied in several ontogenetic aspects. In *Doxantha* the vertical elongation of cells of the rib meristem is initially restricted to the abaxial side of the primordium. Continued elongation of apical cells results in a progressively more basipetally located tendril meristem. In thorns an equal amount of vertical elongation occurs in the rib meristem cells, and the meristem remains in an apical position.

Numerous reports of juvenility have appeared in the literature since 1850 but not previously for *Doxantha*. Schaffalitzky de Muckadell (1954) has reviewed many of the earlier works. Maisenhelder (1969) describes and illustrates 68 species of juvenile seedlings which occur in southern hardwood forests. Many plants commonly undergo transitional changes in leaf shape from juvenile to adult forms. Goebel (1900) observed that *Adlumia cirsosha* and several other plants show transitions from non-tendrillose first foliage leaves to those which form tendrils instead of the leaf. He coined the term heteroblastic, to indicate development of several types of leaves on a single plant. Schaffalitzky de Muckadell (1954) reported that *Fagus sylvatica* has a juvenile stage in which most leaves are retained during the winter. He found that pruning helped retain juvenility, and that scions in the juvenile stage retain their leaves when grafted to an adult stock. Robbins (1960) also noted that heavy pruning of *Hedera helix* resulted in the production of juvenile shoots. Pruning adult plants of *Doxantha* does not cause a reversion to juvenility. However, by continuously
pruning juvenile plants, the juvenile stage may be maintained for an indefinite period of time.

Ashby (1948) reported that heteroblastic development was somewhat dependent upon day-length in some species of *Morus, Kalanchoe, Sedum Gossypium*, and *Sesamum*. Heteroblastic development in *Doxantha* is not affected by the natural variance in daylength which occurs in Baton Rouge, Louisiana. No correlation has been found between heteroblastic development and any external condition in *Doxantha*.

Beakbane (1961) and Goodin (1965) reported that adult shoots of several plants contain more fibers and sclereids than juvenile shoots. The greater ease in rooting juvenile cuttings is attributed to this difference. In *Doxantha* no great differences were observed in the number of fibers produced or the rooting ability of the two growth stages.

Stein and Fosket (1969) reported that juvenile and adult shoot apical meristems of *Hedera* have similar histological structure. They found that cellular area in the apex is one-third greater in juvenile than in adult plants. However, the total apical area is twice as great in the adult as in the juvenile plant. In *Doxantha* also, the total apical area of the juvenile plant is about one-half as great as the adult plant. Juvenile apices in *Doxantha*, however, have slightly smaller cells than adult apices, unlike those of *Hedera*. Stein and Fosket (1969) suggested that the differences in size and shape of adult and juvenile leaves of *Hedera* possibly may be due to slower leaf development and longer plastochrons. The same observations were made in *Doxantha*. The size of the shoot apical meristem seems to be another
causative factor involved in heteroblastic development. These studies suggest that heteroblastic development occurs only in those plants in which the meristematic capital varies greatly in different growth stages. This agrees with the fact that leaf type changes within one internode with just one transitional node. However, this will remain speculation until more comparative studies are made.

In recent years, numerous workers have used histochemical tests in studies of the shoot apical meristem. Gifford and Tepper (1962) used histochemical and autoradiographic techniques to characterize the vegetative and inflorescence apices in Chenopodium album. As far as I am aware, no histochemical studies have previously been made of juvenile and adult shoot apical meristems. No histochemical differences were detected in the apices of the two growth stages of Doxantha, but how frequently adult and juvenile apices have similar histochemistry will have to await future studies.

Gibberellic acid has been reported to bring about the reversal of adult to the juvenile stage; in Hedera canariensis by Robbins (1957), and Goodin and Stoutemyer (1961), in Ipomoea caerulea by Njoke (1958), and in Hedera helix by Robbins (1960). Gibberellic acid did not bring about the reversion of adult to juvenile shoots in Doxantha.

De Zeeuw and Leopold (1955) found that application of auxin prior to cold treatments resulted in flowering, an adult characteristic, of otherwise juvenile plants in 60 percent of the cases in Brassica oleracea var. gemmifera. Contrary to their findings, application of auxin to Doxantha induced juvenile characteristics. Although only a preliminary study was made of the effects of growth regulators on adult
and juvenile shoots of *Doxantha*, the results indicate that heteroblastic development may be partially controlled by auxins.

Leaves located adjacent to axillary floral buds are composed of two leaflets and tendrils are not present (Fig. 78). Leaves of this type were induced on adult shoots by application of anhydrous lanolin to axillary buds prior to their development into lateral branches. Although no attempt was made to study the reproductive phase of *Doxantha*, this information should be of value in future work. To propose a suggestion for the suppression of tendrils at this time would be entirely speculative.

Usually trichomes are not present on meristematic tissue, but in *Doxantha* they cover embryonic leaves. Trichomes are not initiated on mature leaves and their function seems to be the secretion of a material which protects the embryonic organs. In some of the trichome Figures, the stalk and basal cells appear to be plasmolyzed. This could be the result of plasmolysis during fixation, dehydration and embedding. However, Thomson and Liu (1967) made similar observations in salt glands of *Tamarix aphylla* and reported that the high osmotic concentrations in cells comprising glands was a causative factor for this appearance.

Developmentally and morphologically the modified leaflets of *Doxantha* resemble thorns more than tendrils. However, they are closer to tendrils functionally because they are organs of attachment. These structures possibly represent an intermediate class of modified plant organs; thorn-tendrils. Many terms are encountered: shoot-tendrils, thorn-shoots, leaf-tendrils, root-thorns, etc., presently are used.
Confusing terminology such as leaf-thorn-tendril is absurd, yet required if present definitions are utilized. Possibly their function should be ignored and thorns defined as modified plant organs in which the tip becomes sclerified, and tendrils modified plant organs in which the tip does not become sclerified.
LITERATURE CITED


Sharman, B. C. 1943. Tannic acid and iron alum with safranin and orange-G in studies of the shoot apex. Stain Tech. 18: 105-111.


Table 1. A morphological comparison of adult and juvenile growth forms of D. unguis-cati.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Juvenile</th>
<th>Adult</th>
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<tr>
<td>Growth habit</td>
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<td>Decussate</td>
<td>Distichous</td>
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<td>Present</td>
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<tr>
<td>Flowers</td>
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<td>Present</td>
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<tr>
<td>Rooting ability</td>
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<td>Good</td>
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<tr>
<td>Aerial roots</td>
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Table 2. A cytological comparison of adult and juvenile shoot apical meristems.

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<th>Cellular dimensions</th>
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<td>Mean cell height</td>
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<tr>
<td>Mean cellular area</td>
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<td>76.46 µ²</td>
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</table>
PLATE LEGENDS

Fig. 1-3. Leaf Prints.

Fig. 1. Juvenile leaf.

Fig. 2. (A-G). Transitional leaves showing various degrees of transition from juvenile to adult foliage.

Fig. 3. Adult leaf.
Fig. 4. Juvenile shoot apex in longitudinal median section. X 110.

Fig. 5. Juvenile shoot apex in longitudinal median section. X 660.

Fig. 6. Transitional shoot apex to be compared with adult and juvenile apices for the amount of internode elongation present. Longitudinal median section. X 110.

Fig. 7. Transitional shoot apex of about the size of a juvenile apex but dome-shaped. Longitudinal median section. X 110.

Fig. 8. Adult shoot apex in longitudinal median section. X 110.

Fig. 9. Adult shoot apical meristem with a mitotic figure (arrow) in the outermost layer of the peripheral flank meristem. Longitudinal median section.
Fig. 10. Adult shoot apical meristem (SAM) circular in outline in transverse section. X 620.

Fig. 11. Adult shoot apical meristem showing the first ($T_1$) and second ($T_2$) tunica layers, the central mother cell zone (MCZ) and the peripheral flank meristem (PFM) in longitudinal median section. X 690.

Fig. 12. Terminal vegetative bud showing the shoot apical meristem (SAM) and four pairs of decussately arranged compound leaves, labeled $L_1-L_4$. X 70.
Fig. 13. Shoot apex with a pair of protuberances (Leaf buttresses) B, on opposite flanks of the meristem. Longitudinal median section. X 85.

Fig. 14. Shoot apical meristem with a mitotic figure (arrow) in the second layer of the peripheral flank meristem. The leaf buttresses are about 20μ high. Longitudinal median section. X 380.

Fig. 15. Shoot apical meristem showing that derivatives of the second tunica layer produced by periclinal cell divisions (arrow) widen the leaf buttress. Longitudinal median section. X 555.

Fig. 16. Shoot apical meristem showing that the shape of the meristem has become more convex. Longitudinal median section. X 450.
Fig. 17. Compound leaf primordium approximately 40μ high which appears uniformly meristematic. Occasional periclinal divisions increase the width of the primordium. The shoot apex is at the right. Longitudinal median section. X 900.

Fig. 18. Compound leaf primordium in which procambium extends to the base of the terminal meristem. A leaflet (LF) primordium is present near the base of the compound leaf primordium. Longitudinal median section. X 1000.

Fig. 19. Compound leaf primordium showing the sub-apical initial (SAI) a central procambial strand (PC). The small protuberance on the adaxial side of the primordium adjacent the shoot apical meristem (SAM) is a developing leaflet primordium. Longitudinal median section. X 400.

Fig. 20. Compound leaf primordium showing the terminal meristematic region composed of apical and sub-apical initials and their most recent derivatives. Longitudinal median section. X 1000.
Fig. 21. Compound leaf primordium just prior to leaflet initiation. Leaflets are initiated by periclinal cell divisions in the regions indicated by an arrow. Transverse section. X 375.

Fig. 22. Leaflet primordium in longitudinal median section. X 1000.

Fig. 23. Compound leaf primordium showing two adaxially located leaflet primordia (LF). R, rachis; SAM, shoot apical meristem. Transverse section. X 550.

Fig. 24. Leaf clearing to show the sclerified tip of a leaflet. X 50.

Fig. 25. Two leaflet primordia in longitudinal section. X 300.

Fig. 26. The apical region of 4 leaflet primordia in transverse section. X 215.

Fig. 27. The apical region of a leaflet primordium prior to development of the sclerified tip in longitudinal section. X 225.
Fig. 28. Leaflet lamina showing a marginal initial (MI), a sub-marginal initial (SMI) and a procambial strand (PC). Transverse section. X 950.

Fig. 29. Leaflet primordium showing lamina initiation encroaching upon the leaflet tip. Transverse section. X 355.

Fig. 30. Compound leaf primordium showing 3 procambial traces. The two laterals diverge into the leaflets and the median trace remains in the rachis. Phloem (P) is present at this stage. Transverse section. X 600.
Fig. 31. Leaflet primordium 90μ high with marginal and submarginal initials (L₃). The first leaf (L₁) is relatively undifferentiated. Transverse section. X 665.

Fig. 32. Leaflet undergoing differentiation of palisade parenchyma in transverse section. X 240.

Fig. 33. An immature leaflet with 5 relatively undifferentiated layers of cells in transverse section. ABX, abaxial; ADX, adaxial. X 300.

Fig. 34. A mature leaflet in transverse section. X 240.

Fig. 35. Leaflet showing precursor guard cell (PGC). Transverse section. X 665.

Fig. 36. Leaflet showing the two derivatives (immature guard cells) resulting from the division of a precursor. Transverse section. X 665.

Fig. 37. Mature leaflet showing 3 rows of palisade and 3 rows of spongy mesophyll in transverse section. X 700.

Fig. 38. Guard cells with ledges of wall thickening on both the lower and upper surfaces in transverse section. X 1750.
Fig. 39. Nodal region of stem in an early stage of axillary bud development in longitudinal section. This stage occurs at the third node below the shoot apical meristem. X 745.

Fig. 40. A later stage in axillary bud development at the fourth node below the shoot apical meristem. Longitudinal section. X 1330.

Fig. 41. An axillary bud at a stage just prior to prophyll initiation in longitudinal section. X 830.
Fig. 42, 43. Early ontogenetic stages in development of glandular hairs.

Fig. 44, 45, 48, 51. Developmental stages of the large peltate colleter.

Fig. 46, 47, 50. Developmental states of the club-shaped colleter.

Fig. 42. A 2-celled stage derived from a trichome precursor. Longitudinal median section. X 1750.

Fig. 43. An unequal cytoplasmic division has occurred in the outermost cell. Longitudinal median section. X 1750.

Fig. 44. A trichome composed of a vacuolate basal cell, a stalk cell, and a 4-celled terminus. Longitudinal median section. X 875.

Fig. 45. A trichome with a 6-celled terminus. Longitudinal median section. X 875.

Fig. 46. A trichome in which a second periclinal division had occurred in the basal cell. Longitudinal median section. X 1750.

Fig. 47. A trichome in which the two stalk cells have become vacuolate. Longitudinal median section. X 875.

Fig. 48. A trichome with an 8-10-celled terminus. Longitudinal median section. X 875.

Fig. 49. A unicellular non-secretory trichome in longitudinal median section. X 675.

Fig. 50. A club-shaped secretory trichome or colleter in longitudinal median section. X 500.

Fig. 51. A peltate secretory trichome or colleter in longitudinal median section. X 500.

Fig. 52. A 4-celled terminus of a trichome such as shown in Figure 50. Transverse section. X 1000.

Fig. 53. Two multicellular termini, one in a plane more basipetally located than the other, of the peltate type of trichome shown in Figure 51. Transverse section. X 1000.
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Fig. 55. SEM photograph of a tendril. X 76.

Fig. 56. SEM photograph of a sclerified tendril tip. X 152.

Fig. 57. SEM photograph of that portion of a tendril immediately below the sclerified tendril tip. X 228.
Fig. 58. Tripartite tendril showing the median and two lateral tendril primordia in frontal section. X 800.

Fig. 59. Lateral tendril primordium showing procambial development into the base in longitudinal median section. X 570.

Fig. 60. Compound leaf primordium showing two lateral tendril primordia. The structures located adjacent the primordium are leaflets. Transverse section. X 1000.

Fig. 61. Compound leaf primordium showing the rachis (R) and an attached leaflet (LF). The length of the leaflet exceeds that of the rachis. Longitudinal section. X 420.
Fig. 62. Compound leaf primordium showing that abaxial vacuolation extends above the point of insertion of lateral tendrils (LT). V, vacuolation; MT, median tendril. Longitudinal median section. X 500.

Fig. 63. Lateral tendril after vacuolation extends to the apex. The rachis is out of the plane of section. SAI, sub-apical initial. Longitudinal section. X 460.

Fig. 64. Lateral tendril primordium showing apical and sub-apical initials. ABX, abaxial; ADX, adaxial. Longitudinal section. X 500.

Fig. 65. Rachis showing abaxial vacuolation extending to the apex in longitudinal section. L₂, leaf No. 2; L₄, leaf No. 4. X 345.
Fig. 66. Tendril apex showing that acropetal procambialization and abaxial vacuolation have confined the meristem to the adaxial side of the tendril. M, meristem; PC, procambium. Longitudinal median section. X 660.

Fig. 67. Tendril apex showing that the apical shape has changed from a dome to sharply conical in longitudinal median section. X 345.

Fig. 68. A tendril with the meristem located about 110μ below the apex in longitudinal section. X 365.

Fig. 69. A tendril at the beginning of sclerification (S). Longitudinal section. X 700.

Fig. 70. A tendril showing that the meristem remnant (M) appears similar to other cortical cells. Longitudinal section. X 200.

Fig. 71. Tendril tip after curvature of the spine in longitudinal section. X 143.
Fig. 72. Basal region of a tripartite tendril-spine in transverse section. X 150.

Fig. 73. Basal region of the median tendril about 550μ long showing the dark staining peripheral regions. Transverse section. X 450.

Fig. 74. A tendril about 550μ long sectioned transversely approximately 300μ below the apex. X, xylem; P, phloem. X 450.

Fig. 75. A tendril about 550μ long sectioned transversely approximately 100μ below the apex. X 900.

The adaxial side is up in all Figures.
Fig. 76. Relative growth rates of the rachis and leaflets at successive stages. A, early; B, late.

Fig. 77. Determination of the meristematic area of a compound leaf primordium.
Fig. 78. Leaf variation in developmental stages of Doxantha.
REPRODUCTIVE

ADULT
75+ NODES

TRANSITIONAL
1 NODE

JUVENILE
2–7 NODES
VITA

Dan Richard Sistrunk was born in Converse, Louisiana, May 25, 1939; son of Floyd N. Sistrunk and Buna V. Sistrunk. He attended public schools in Converse, Louisiana and graduated from Converse High School in 1957. He served two years in the U. S. Marine Corps, and was honorably discharged in 1963. He entered McNeese State University, Lake Charles, Louisiana, in 1959, and received the Bachelor of Science degree in biological science education in May, 1963.

He was employed by Mobile Oil Company, Morgan City, Louisiana, as a geophysical helper, for one year. He then taught for one year at Byrd High School, Shreveport, Louisiana. He worked as a roughneck and an electrician's helper in 1965. In 1966, he taught at Zwolle High School, Zwolle, Louisiana.

He entered graduate school at McNeese State University, and received the Master of Science degree in biology in May, 1969. Graduate studies were continued at Louisiana State University, Baton Rouge, Louisiana, where he is presently a candidate for the Doctor of Philosophy degree in botany.

He is married to Frances Mayo Sistrunk, and they have one child, William Nathan, age two.
EXAMINATION AND THESIS REPORT

Candidate: Dan Richard Sistrunk

Major Field: Botany

Title of Thesis: A Study of Leaf Development in *Doxantha unguis-cati* Rehder.

Approved:

\[\text{Signature}\]
Major Professor and Chairman

\[\text{Signature}\]
Dean of the Graduate School

EXAMINING COMMITTEE:

\[\text{Signature}\]
William J. Blackmer

\[\text{Signature}\]
Charles A. Shiverud

\[\text{Signature}\]
James E. Gossett

Date of Examination:

July 14, 1972