Twin Raphides in the Vitaceae and Araceae and a Model for Their Growth

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Abstract
Several optical tests were employed to demonstrate twinning in raphides from 10 species in the family Vitaceae and one species in the Araceae. Scanning electron microscopy revealed that twin raphides differ from the reported shape of twin styloids and that raphides of the Vitaceae are "barbed" along two sides. A model is proposed to describe in vivo raphide production under saturated to supersaturated conditions of directional nutrient flow.

Disciplines
Botany | Other Plant Sciences | Plant Biology | Plant Breeding and Genetics

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TWIN RAPHIDES IN THE VITACEAE AND ARACEAE AND
A MODEL FOR THEIR GROWTH

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Several optical tests were employed to demonstrate twinning in raphides from 10 species in the family Vitaceae and one species in the Araceae. Scanning electron microscopy revealed that twin raphides differ from the reported shape of twin styloids and that raphides of the Vitaceae are “barbed” along two sides. A model is proposed to describe in vivo raphide production under saturated to supersaturated conditions of directional nutrient flow.

Introduction

Arrow-shaped raphides in the leaves and wood of various members of the grape family (Vitaceae) have been noted (SOLEREDER 1899; GARD 1900; SOLENDER and MEYER 1928; METCALFE and CHALK 1950). ESAU (1965, figs. 9B, 33A) observed the raphides of Vitis as four-sided in section. METCALFE and CHALK (1950) described leaf raphide sacs in the Vitaceae as “of variable lengths and often containing mucilage... the individual raphides [being] pointed at one end but bidentate at the other in Cissus and Vitis.” GARD (1900) found similar raphides in Ampelopsis and compared them with twin gypsum crystals collected at Montmarte, France.

KOLLBECK, GOLDSCHMIDT, and SCHRÖDER (1914) used optical analysis with polarized light to determine that arrow-shaped styloids from Iris pseudacorus were twin crystals. FREY (1925) and ARNOTT (1981) suspected that forked raphides also might be twin crystals because they possessed a dovetailed reentrant angle at one end of each crystal and because of the apparent morphological similarity of raphides to Iris styloids.

Until we found unusually large raphides in the petioles of Cissus rotundifolia, the small size of raphides and their complex optical behavior impeded an understanding of their crystallographic nature. Scanning electron microscopy, optical crystallographic techniques, and X-ray diffraction analysis were employed to study them and raphides from nine other species in five genera of the family Vitaceae and from Xanthosoma sagittifolium in the family Araceae.

Material and methods

Sample collection

Cissus rotundifolia (Forsk.) Vahl., C. discolor Blume, C. quadrangularis L., C. rhombifolia Planch., Rhoicissus capensis (Burm f.) Planch., Tetrastigma voinierianum (Baltét) Pierre ex Gagnep., Vitis vinifera var. Concordia, and Xanthosoma sagittifolium (L.) Schott. were collected in the Bessey Hall Greenhouse; Parthenocissus quinqufolia (L.) Planch., P. tricuspidata (Sieb. & Zucc.) Planch., P. vitacea (Knerr) Hitchc., and Vitis riparia Michx. were collected on the Iowa State University Campus, Ames. Raphide crystals were extracted from fresh plant material so that the effects of secondary physical or chemical alteration of the crystals would be negligible. Raphides from the petioles were chosen for study because they appeared to be largest and, therefore, more amenable to optical study.

Scanning electron microscopy (SEM)

Fresh longitudinal and transverse hand sections of petioles were mounted on brass disks with conductive silver paste, coated with Au-Pd in a Polaron E5100 sputter coating unit, and examined at 15 kV with a JEOL JSM 35 SEM.

Individual raphides were extracted by dicing transversely cut petioles with a razor blade and then touching the fragments to a piece of cover glass. The crystals were allowed to settle for 1 min before the preparation was flooded with methanol, which was then drawn off with filter paper. This procedure was repeated several times to remove extraneous plant material. An examination of methanol-washed and nonwashed crystals showed that the fine surface features of calcium oxalate monohydrate (COM), which is insoluble in alcohol, were not affected by the washing. Cover glass fragments with crystals were mounted on brass disks with silver conductive paste and sputter coated in the same manner as fresh petiole sections. To reduce SEM beam penetration, an operating voltage of 15 kV was used; in most instances, a sample tilt of 50° was advantageous.

Optical microscopy

Single raphides were removed by macerating transversely cut petioles and touching them to mi-
croscope slides. After the crystals had settled, the slide was rinsed with a pipetted stream of methanol to remove excess plant material. Raphide total length and width at center point were measured at X 400 with a calibrated eyepiece. For each species, 50 unbroken raphides were measured. A petrographic microscope with a rotating stage was used to examine raphides at X 500 in optical index oils in transmitted light and between crossed polarizers. A quartz plate compensator was also used with crossed polarizers to verify twinning.

**X-ray Diffraction**

Entire petioles were processed in methanol in a high-speed blender. Excess plant material was removed from the suspension with a separatory funnel where the heavier crystals settled to the bottom. Crystals were repeatedly suspended and allowed to settle before most of the alcohol remaining with the crystal fraction was evaporated. The mixtures were mounted on glass microscope slides and air-dried. Removal of all plant material was not necessary. Samples were analyzed in a Phillips X-ray diffractometer using CuKα radiation, 40 kV, 20 mA, and 2°/min scan speed between 10° and 52° 20. Patterns were indexed with ASTM Powder Diffraction File cards 20-231 Whewellite and 17-541 Weddellite.

**Results**

In one view, SEM (fig. 1, vertical crystal) revealed that raphide crystals of the Vitaceae were sharply pointed at one end and blunt at the other. Crystals extinguished between crossed polarizers when their greatest lengths were parallel to either polarizer, indicating that the crystals were oriented parallel to the crystallographic plane (101). The long sides of the crystal in this view appeared smooth.

When turned 90° to the (101) view, crystals were sharply pointed at one end and bidentate (forked) at the other. The long sides of the crystals in this view were irregular or barbed. On some crystals, the barbs occurred only near the sharply pointed end (fig. 2), while on others they were found along the entire length of the crystal (figs. 3, 4).

When a crystal in the bidentate view was rotated between crossed polarizers, the entire crystal showed birefringent illumination (fig. 5) that extinguished at a different angle in each elongate half of the raphide (figs. 6, 7). These images indicated the twin nature of the crystals. Crystals in this view never were completely extinguished during 360° rotation, a further proof of twinning. The twin plane appeared perfectly planar along the entire crystal length (figs. 6, 7), while the outer surfaces of the crystal were irregular but in optical continuity with their twins. Because of the need for high magnification and the narrow width of the crystals, measurement of the angle between extinctions could not be accurate. The values 15.3°, 15.2°, and 15.1° were obtained for different crystals and were reasonably close to the 14.7° accurately measured in large heart-shaped COM twins on (101) found in Bavarian coal mines (KOLLMICKE et al. 1914).

During rotation, the dark line of the twin plane (fig. 8) moved across the width of the crystal, indicating that the twin plane was being viewed at an angle rather than in normal cross section. The lateral extent of movement was proportional to the deviation of the twin plane from vertical (fig. 9).

When a quartz plate compensator was used with crossed polarizers, light passing through the twin was retarded to a greater extent when the principal optical axis or direction of greatest light retardation of a crystal (double arrow, fig. 10) was aligned more closely with the principal optical axis of the quartz plate. Greater light retardation resulted in higher-order colors, so that one-half of the raphide appeared as a first-order red-orange, and the other half, as a second-order blue.

When crystals were examined with SEM at ca. X 10,000 and at a tilt angle of 50° with respect to the primary beam axis, a shadowing effect accentuated crystal surface relief. At high tilt, the mirror plane of crystal symmetry (in the bidentate view) bisected the crest of a peak (stereopair; fig. 11) rather than a flat (010) face as it does in styloids from Iris pseudacorus (KOLLMECKE et al. 1914; ARNOTT 1981). The former situation was true for raphides from Tetrastigma (fig. 12), Rhoicissus (figs. 13, 14), and the other seven species in the Vitaceae. The [100] axis of each crystal also intersected a peak (fig. 10) to give a four-sided appearance to the crystal cross section (fig. 15).

Fractured raphide bundles showed that nearly all crystals, with a few exceptions (arrow, fig. 16), were oriented in one direction. The raphides were four-sided but not crowded, indicating that their general shape was crystallographically determined and not the result of close packing of crystals in the bundle.

The edges near the sharply pointed ends of crystals were barbed (fig. 17), like the sides of crystals from the aroids Xanthosoma, Colocasia, and Alo-casia (SAKAI and HANSON 1974). The barbs pointed away from the sharply pointed end of each crystal, and they were slightly hooked at their tips. The barbs alternated along opposite sides of a crystal, giving a false helical appearance. Grooves were not observed along the sides of any crystals from the Vitaceae.

Because of their grooves (arrow, fig. 18), crystals from the aroid Xanthosoma sagittifolium were 1+4.

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1 The Miller indices of a plane represent the inverse of the coordinates from the center of a crystal to the center of that plane. A bar above a number refers to the plane being on the negative number end of an axis. See WHITTAKER (1981) for further explanation.
FIGS. 1-8.—Light and scanning electron micrographs of twin raphide crystals from Vitaceae. Fig. 1, Cissus discolor raphide oriented parallel to (101), showing pointed terminations. Bar = 10 μm. Fig. 2, Cissus rotundifolia raphide oriented parallel to (010), showing barbed sides and sharply pointed and forked ends. Bar = 10 μm. Fig. 3, Cissus quadrangularis raphide barbed along its entire length. Bar = 10 μm. Fig. 4, Rhoicissus capensis raphides with barbs directed away from their sharply pointed ends. Bar = 2.5 μm. Fig. 5, Cissus rotundifolia raphide showing full birefringent illumination. Bar = 10 μm. Fig. 6, Raphide in fig. 5 showing extinction of right half. Note smooth trace of twin plane and rough, barbed outer surface. Bar = 10 μm. Fig. 7, Raphide in fig. 5 showing extinction of left half. Barbs are in optical continuity with their crystal half. Bar = 10 μm. Fig. 8, Dark line showing trace of twin plane through center of crystal during rotation between crossed polarizers. Bar = 10 μm.
shaped in cross section (fig. 19). Like the raphides of the Vitaceae, they were sharply pointed at one end and blunt at the other (figs. 20, 21). Grooves traversed the length of the crystals except at their centers (figs. 21, 22, 24) and possibly at their tips (figs. 22, 23, 25). The centers of crystals did not crack or appear to distort when the electron beam was concentrated on them for 1 min at 30 kV. When extracted, isolated crystals were viewed between crossed polarizers (fig. 26); a twin plane was observed in the groove of each. Crystals in the proper orientations also showed half (fig. 27) or full illumination (fig. 28).

When length/width ratios of raphides from the Vitaceae were computed (fig. 29), the greatest ratios occurred in Cissus and Rhoicissus, with C. quadrangularis exhibiting a maximum ratio. Species with greater raphide length/width ratios were also those with the most pronounced barbs, and length/width ratios of species of the same genus appeared clustered. When raphides of the aroid Xanthosoma were measured by the same method, their average length/width ratio was 92.2.

The X-ray diffraction analyses (table 1) revealed that crystals in the 10 species of the Vitaceae and the one species in the Araceae were monoclinic calcium oxalate monohydrate (COM; Whewellite).

Discussion

Twin raphides with barbed sides are characteristic for 10 species from five genera of the Vitaceae and one genus of the Araceae. Twinning, the production of barbs, and the biological factors that lead to this type of crystal, however, must be understood in reference to an overall view of raphide growth in plants rather than as isolated incidents with no connection.

Atoms and molecules in solution are in continuous motion. Statistically, the arrangement of dissolved atoms is completely random over a period of time. At any given moment, however, some of the atoms may have the configuration they would in a crystal structure. This arrangement is called a “cluster.” Because of random motion of the atoms, clusters rapidly break up with the same energetic ease with which they form. When the solution is cooled below equilibrium temperature, or the saturation level of dissolved atoms is increased, clusters may continue to grow in size and form crystal nuclei. In plant vacuoles, increased saturation is probably the factor responsible for nucleation. There, the rate of saturation is controlled by plant metabolism, which determines the rate of production of materials necessary for crystal growth.

To continue growth, crystal nuclei must reach a “critical size” where their free energy is less than that of the solution and they are the stable phase. If this does not occur, the nuclei redissolve. Under certain conditions, one nucleus may grow, depleting the solution of ions and causing nearby pre-critical nuclei to redissolve. This mechanism could prevent the further growth of more than one crystal per chamber and/or vacuole.

TILLER (1963) showed that thermal transport and solute transport were quantitatively described by the same differential equation and the same kind of boundary conditions in the vapor phase and in melts of metals. Contours of temperature distribution and solute distribution also were shown to have the same shape around dendritic crystals. This information was applied validly to solution growth and is applied here to the growth of crystals within plant vacuoles, where the predominant phase is generally a liquid or the liquid part of a sol (FREY-WYSSLING 1948).

Early vapor-phase studies in metals showed that, at equilibrium vapor pressure, atoms could move
FIGS. 11–19.—Light and scanning electron micrographs of twin raphide crystals from Vitaceae and Araceae. Fig. 11, Stereopair of forked end of Cissus rotundifolia raphide. Faces meet to form an edge along twin plane. Bar = 1 μm. Fig. 12, Tetrastigma raphide with mirror plane of symmetry bisecting crest of a peak. Bar = 1 μm. Fig. 13, Rhoicissus capensis raphides. Bar = 2 μm. Fig. 14, Rhoicissus raphide viewed parallel to (101). Arrow indicates crystalline material deposited during raphide growth. Bar = 1 μm. Fig. 15, Broken Tetrastigma raphide showing four-sided cross section. Bar = 0.5 μm. Fig. 16, Rhoicissus capensis raphide bundle with nearly all crystals oriented with pointed ends in one direction. Arrow indicates an exception. Bar = 2 μm. Fig. 17, Barbs on raphides from Cissus quadrangularis. Hand section of fresh plant material. Bar = 1 μm. Fig. 18, Grooved raphide from aroid Xanthosoma. Bar = 1 μm. Fig. 19, H-shaped cross section showing grooves in Xanthosoma raphides. Bar = 0.5 μm.
FIGS. 20–28.—Raphide crystals from *Xanthosoma sagittifolium* (Araceae). Fig. 20, Crystals showing preferred orientation on sides flattened parallel to plane (101). Note blunt and sharply pointed terminations. Bar = 5 μm. Fig. 21, Crystals from fig. 20 rotated and tilted 50° to reveal lateral grooves. Arrows indicate central area where groove appears absent. Bar = 1 μm. Fig. 22, Raphide viewed in (010) plane. Bar = 5 μm. Fig. 23, Enlargement of blunt raphide tip in fig. 22. Bar = 1 μm. Fig. 24, Enlargement of central region of raphide in fig. 22. Note termination of groove. Bar = 1 μm. Fig. 25, Sharply pointed tip of raphide in fig. 22. Bar = 1 μm. Fig. 26, Trace of twin plane seen in raphides oriented in (010) plane and rotated between crossed polarizers. Bar = 5 μm. Fig. 27, Raphide in fig. 26 rotated to show extinction in one-half of crystal. Bar = 5 μm. Fig. 28, Raphide in fig. 26 rotated to show full birefringent illumination. Bar = 5 μm.
back and forth between the vapor phase and the surface of the crystal. The degree of supersaturation required for growth was also found to be ca. 50 times less than its calculated value. Frank (1949) determined that this occurred because crystal faces were not perfectly planar but contained minute steps and structural defects. If the layers of atoms in a growing crystal are represented by cubes (fig. 30), an atom coming in contact with a planar surface (fig. 30A) will be bound by a force from only one side, and this may not be sufficient to keep it bound to the crystal. Atoms added along steps (fig. 30B) are bound from two directions, while those added in corners (fig. 30C) are bound from three sides. The latter situation liberates the most energy in atom deposition (Kossel 1927, pp. 135-143), and the atoms are more likely to remain on the crystal and contribute to its growth. Edge dislocations and screw dislocations produced surface imperfections necessary for more rapid growth, as did twinning (Burton, Cabrera, and Frank 1951).

The reentrant groove at the bidentate end of a twin crystal provides the ideal growth interface for the stabilized addition of atomic planes because atoms deposited there are bound from two to three sides. Most raphides observed in our study showed an irregular deposit in the notched region, and this was interpreted as the initiation of new growth layers (arrow, fig. 14). Direct application of Frank's concepts to COM was presented by Nancollas and Gardner (1974), who derived experimental evidence that the kinetic rate equation of COM formation at low supersaturations was consistent with the Burton-Cabrera-Frank model of crystal growth (Burton et al. 1951).

In figure 31, twin growth also proceeds perpendicular to the plane of the diagram to produce crystals like those shown in this study. Little, if any, growth occurs at the pointed end of the crystal, where atoms would be less readily bound by forces from only one direction (Hamilton 1965). This factor is of special significance to twin raphides in bundles where most of the crystals appear oriented in one direction (fig. 16). Because twin raphide crystals appear to grow mainly from the bidentate end, their growth must have begun at one end of the developing raphide bundle—perhaps through specific sites of nucleation on the inside of membrane chambers in a vacuole or in crystal chambers associated with paracrystalline bodies such as those in Capsicum annuum (Horner and Wagner 1980; Horner, Kausch, and Wagner 1981).

In the growth of a single crystal, successive layers of atoms are stacked on its surface and occupy the lowest available energy positions (fig. 32, lines A, B, and C; Whittaker 1981). If an alternate position of only slightly higher energy is available (fig. 32, line D), an atom may occupy that position (a stacking error) without being unstable, and successive layers of atoms deposited in the most stable configuration give rise to a simple contact twin.2 In heart-shaped COM twins, the composition plane

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2 Phillips and Phillips (1980, p. 241) stated: "Crystals composed of two individual parts which have definite structural relation to one another are said to be simple twins. If the two parts of a simple twin are separated by a definite surface, it is described as a contact twin and the surface along which individuals are united is called the composition plane."
### TABLE 1

**X-ray diffraction analyses of crystals from 10 species of the family Vitaceae and the aroid Xanthosoma sagittifolium**

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<thead>
<tr>
<th>ASTM</th>
<th>Cissus rotundifolia</th>
<th>Cissus discolor</th>
<th>Cissus quadrangularis</th>
<th>Cissus rhombifolia</th>
<th>Parthenocissus quinquefolia</th>
<th>Parthenocissus tricuspidata</th>
<th>Parthenocissus vitacea</th>
<th>Rhoicissus capensis</th>
<th>Tetragastigma voignieri</th>
<th>Vitis riparia</th>
<th>Xanthosoma sagittifolium</th>
</tr>
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<tbody>
<tr>
<td>100</td>
<td>6.18</td>
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<td>−</td>
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<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
</tr>
</tbody>
</table>

**NOTE:** +, peak observed; −, peak not observed.
is (101) (Kollbeck et al. 1914). When the energy difference between two possible atomic positions is great, twinning occurs rarely, but if it is small, twinning will be common, as it is in many plant crystals (Arnott 1981).

Even though the potential for twinning may be inherent in a material, twinning will not occur unless conditions are right. Experimental evidence (Goss and Weintraub 1951) showed that the conditions for monocrystalline growth are satisfied by slow rates of growth and no supercooling. In plants, the equivalent of supercooling would be a rise in concentration above equilibrium concentration. The two terms will be used here to mean the same thing.

Bolling, Tiller, and Rutter (1956) studied the occurrence of growth twins in germanium and found that, in every case, nucleation of a twin could be related to supercooling during solidification. The same results occurred whether supercooling was absolute (the concentration of ions increased) or constitutional (foreign ions raised the supersaturation). Nancollas and Gardner (1974) found that the rate constant of COM crystallization did indeed increase and became appreciably greater as calcium concentration increased beyond stochiometric proportions. When this is considered in reference to plants, it becomes apparent that twin raphides will be formed under conditions of greater supersaturation or calcium influx into an oxalate environment than will single raphides. Because supersaturation is controlled by plant metabolism, which in turn is genetically controlled, it is reasonable to accept a specific crystal shape as characteristic for a particular plant species or family (Franceschi and Horner 1980).

Single crystals grow slowly under conditions close to equilibrium saturation by the regular addition of ions to their surfaces. Faces that grow most rapidly are those having the greatest roughness in atomic lattice structure (Bunn 1964), thereby offering more stable sites for addition of ions (fig. 30). When the nutrient supply for a growing crystal is directional and parallel to a zone axis, it may promote the growth of elongate, acicular crystals (Whittaker 1981). In COM raphides, elongation occurs parallel to the axis of the zone including the face (101) (Frey-Wyssling 1981).

In a twin crystal, the reentrant angle eliminates the need for surface nucleation by constantly providing a site for the stabilized addition of new layers of atoms. Metallurgical studies have shown that isothermal and isocentration lines around a growing twin crystal (fig. 30) curve inward toward the notch of the twin (Hamilton 1965). Because growth is more rapid at the notch, the solution interface nearest it becomes depleted, and a concentration and heat flow gradient develops so that ions actually flow toward the notch faster than they could in a single crystal. This results in growth of the twin face (fig. 31). The growth of the twin face is often accompanied by a zone of work-hardened material at the original growth face, which may cause deformation of the host crystal (fig. 32).

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**Fig. 30.—** Idealized view of three possible sites for atomic addition during crystal growth: A, on a plane; B, along an edge; C, in a corner. Redrawn from Frank (1949).

**Fig. 31.—** Two-dimensional view of growth of a twin crystal by more stable addition of new material (dashed blocks) at reentrant notch. Dotted lines indicate equal solution concentration with a higher gradient at notched end of crystal. Redrawn with changes from Hamilton (1965).

**Fig. 32.—** Contact twin resulting from error in atomic stacking. Simplified and redrawn from Whittaker (1981) and Burgers (1963).
do to other parts of the crystal. In studying twinning in germanium and silicon, BILLIG (1954) found that twin crystals grew when their twin planes were aligned as parallel to the direction of maximum heat flow and concentration gradient as was possible. Assuming that this is true for crystals growing in plant twin raphide chambers, we may conclude that crystal-growth nutrients would have to be enriched at the notched end of the chamber for growth to occur.

FREY-WYSSLING (1935, 1981) speculated that calcium ions were fed into the needle tip ends of nontwinned raphide bundles through the caps of cytoplasm that cover them. RUBIN (1982) described calcium “gates” or “channels” in membranes, and evidence for their existence in other biological membranes comes from electrophysiological ion-conductance studies. Calcium gates have not yet been isolated and identified. It is still not known whether such gates could be clustered about the tip(s) of a raphide crystal chamber or could be positioned throughout the chamber and turned off or closed in relay as the raphide grows into the chamber, thus maintaining a greater calcium concentration at the growth front.

The general directions of barb growth are undoubtedly controlled by crystal structure because they reflect the monoclinic atomic structure of the mineral (Cocci 1961). If a straight edge is held against the long side of a crystal (fig. 17), all barbs and crystal surfaces end along a straight line, presumably the position of the membranous sheath (chamber) around the raphide. If calcium could enter along all the membrane throughout all stages of crystal growth, the sides of the crystal would continue to grow until the embayments within the barbs were grown in. If calcium migrated from the bidentate end and then along the sides of the crystal (or the calcium gates along the side of the crystal were closed), growth would have continued until the channel was closed and all the calcium in the “embayment” was used up. Curving of the barbs up into the embayment suggests that termination of nutrient source may have occurred.

It is also apparent, from the way that the natural monoclinic crystal form of the barbs is truncated (fig. 17), that their further growth was in some way inhibited by the chamber membrane. ARNOTT (1966) suggested that some crystal chambers may act as “boules” in molding the shape of crystals. The physical strength of membranes, however, would not be sufficient to contain the forces resulting from crystal growth. The action of the chambers as rigid molds or “boules” does not seem probable. The COM crystals growing in solutions, as well as the calcium and oxalate ions that form them, are coated with hydration layers (NANCOLLAS and GARDNER 1974). It seems more likely that these polar layers of water may be repelled by polar proteins and/or hydrophobic lipids of the chamber membrane.

The aspects of dendritic (treelike or snowflake) crystal growth have been studied in great detail by metallurgists (GRUBEL 1961). The main ribs or branches of dendrites were single or multiple twin crystals with twin planes parallel to the long axes of the crystals. The production of a reentrant notch through twinning accounted for the rapid growth of crystals by eliminating the necessity of surface nucleation, and the rate at which dendrites grew depended on the degree of supersaturation (BOLLING et al. 1956). The radius of curvature (ρ) of a twin dendrite tip growing into a melt was governed by freezing velocity, atomic kinetics, and material parameters (BOLLING et al. 1956; BOLLING and TILLER 1961) and could be expressed in its simplest form by the equation

\[
ρ = P \left( \frac{[e^{xE_1(-x)}]^2}{x[e^{xE_1(-x)}]^2 - \frac{c}{\Delta H} \Delta T} \right)
\]

where \( x = V_{max}(\rho/2a_c) \), \( a_c = \) thermal diffusivity of the liquid, \( E_1 = \) exponential integral function, \( C = \) specific heat of the solid, \( \Delta T = \) bath supercooling, and \( P = \) a constant (TILLER 1963). Earlier
in this paper we showed that the equivalent of $\Delta T$
in raphide growth was the concentration gradient
at the solid-liquid interface. The equation therefore
shows that, as concentration increases, the radius
of curvature of the dendritic tip decreases, and the
length/width ratio of the resulting crystal increases.
Concentration increase, whether absolute or con-
stitutional, would account for the production of
raphides with greater length/width ratios.

The synthetic dendrite growth experiments con-
ducted by HOLMES (1961) showed that dendritic
crystals followed a developmental sequence (fig.
33). Twin crystals with somewhat rounded cross
sections developed into twins with four-sided cross
sections, like twin raphides of the Vitaceae. If su-
sersaturation in the liquid still existed after for-
mation of the initial elongate crystal, growth along
preferred crystal directions could occur, and “growth
hillocks” could be produced along certain sides of
the crystal (HOLMES 1961). These hillocks would
be in continuity with their twin lattices and show
optical continuity with them, like the barbs of
raphides from the Vitaceae. Further development
produced oriented growth along the sides of the
hillocks (BOLLING and TILLER 1961) and resulted
in twin crystals with $\text{H}$-shaped cross sections, like
the cross sections of raphides from Xanthosoma,
Colocasia, and Alocasia (SAKAI and HANSON 1974),
Lemna (ARNOTT 1966; ARNOTT and PAUTARD
1970), and Spirodela (LEDBETTER and PORTER

TABLE 2
SUMMARY OF RAPHIDE TYPES IN HIGHER PLANTS

<table>
<thead>
<tr>
<th>Raphide type*</th>
<th>Single/twin</th>
<th>Mucilage*</th>
<th>Taxon</th>
<th>Author(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Four-sided crystals with pointed ends .................</td>
<td>Single</td>
<td>No</td>
<td><em>Psychotria</em></td>
<td>HORNER and WHITMOYER (1972)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Oenothera</em></td>
<td>SCHÖTZ, DIERS, and BATHELT (1970)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Morinda</em></td>
<td>SCURFIELD, MICHELL, and SILVA (1973)</td>
</tr>
<tr>
<td>Four-sided crystals with one pointed end and one blunt bidentate end ..........</td>
<td>Twin</td>
<td>Yes</td>
<td><em>Cissus</em></td>
<td>CODY and HORNER (this study)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Parthenocissus</em></td>
<td>CODY and HORNER (this study)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Tetragastrigma</em></td>
<td>CODY and HORNER (this study)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Vitis</em></td>
<td>CODY and HORNER (this study)</td>
</tr>
<tr>
<td>Six- and eight-sided crystals with pointed ends ..........</td>
<td>Single</td>
<td>Yes</td>
<td><em>Agave</em></td>
<td>WATTENDORFF (1976)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Typha</em></td>
<td>HORNER et al. (1981)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Ornithogalum</em></td>
<td>TILTON and HORNER (1980)</td>
</tr>
<tr>
<td>Crystals with $\text{H}$-shaped cross sections, one pointed end, and one bluntly pointed end ........</td>
<td>Twin</td>
<td>Yes</td>
<td><em>Monstera</em></td>
<td>RAKOVÁN, KORVÁČS, and SZUJKÓ-LACZA (1973)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Xanthosoma</em></td>
<td>SAKAI and HANSON (1974)</td>
</tr>
<tr>
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<td></td>
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<td><em>Colocasia</em></td>
<td>CODY and HORNER (this study)</td>
</tr>
<tr>
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<td><em>Lemna</em></td>
<td>SAKAI and HANSON (1974)</td>
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<td></td>
<td><em>Spirodela</em></td>
<td>ARNOTT (1966)</td>
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<td></td>
<td></td>
<td></td>
<td>ARNOTT and PAUTARD (1970)</td>
</tr>
</tbody>
</table>

* Conditions observed at maturity.

b WATTENDORFF (1976) listed *Vitis* as having four sides and, like ESAU (1965), did not mention a
bidentate end.

c Author who published first summary and listed raphides of *Agave* as six-sided (see also HORNER et al. 1981).
1970). The H-arm bars grow in a preferred direction determined by the crystal lattice and would give rise to extensions equivalent to the barbs of aroid raphides (fig. 33). The periodicity and shape of the barbs would again depend on the lattice structure of the material and the degree of saturation in the liquid.

Growth of the H-arm bars in a highly developed dendrite often results in a crystal that is flattened parallel to its twin plane, making the optical analysis of twinning difficult. The trace of a twin plane was observed, however, in excised raphides from Xanthosoma sagittifolium (figs. 26–28), confirming the postulated twin nature of its raphides.

WATTENDORFF (1976) described three morphological raphide types: four-sided single, six-sided single, and H-shaped. This study adds four-sided twins, shows H-shaped crystals to be twins, and brings the number of raphide types to four (table 2). An attempt is made to tie the taxonomic value of plant crystals to their growth dynamics which, in turn, are controlled by plant metabolism. Crystal morphology reflects the environment within a living plant, and crystallographic study offers an important key to discerning this environment. Plant crystal studies can progress from being purely descriptive to being interpretive only when the finest crystal details are considered.

**Acknowledgments**

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**LITERATURE CITED**


