Calcium oxalate crystals in some aquatic angiosperms of Taiwan

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Abstract: We studied crystals in the leaves and stems of 56 species (23 families) of aquatic flowering plants in Taiwan. In the most-studied plant types—emerged, submerged with floating leaves, and floating in water—five types of calcium oxalate crystals were found. The crystals are frequently associated with aerenchyma tissue in the plants. The five types are mostly specific to the plant’s genera and families. Crystals were not found in submerged species. The presence or absence of crystals is probably associated with the aquatic environment, and may useful in the taxonomic analysis of aquatic plants.

Keywords: Aquatic angiosperms; Calcium oxalate crystals.

Introduction

Calcification and the formation of calcium crystals are common phenomena in many plant species under ordinary conditions (Arnott and Pautard, 1970). In angiosperms, calcium oxalate is the predominant deposited calcium salt, and the most commonly encountered shapes are druses, raphides, styloides, prisms, and crystal sands (Fahn, 1990). They may be located in specific tissues and organs (Scott, 1941; Fahn, 1990), or may be distributed sporadically in all plant organs (Genua and Hillson, 1985; Chiang and Huang, 1983). Many studies have been made of the formation of calcium oxalate crystals in the terrestrial plants (Franceschi and Horner, 1980; Doaigey, 1991). Borowitzka (1984) investigated calcification in aquatic plants, primarily the deposition of calcium carbonate in algae. There have been only a few reports on calcium oxalate crystals in aquatic angiosperms (Franceschi, 1987; Kuo-Huang, 1990). The aquatic higher plants are defined as plants that may germinate under normal conditions, and grow with at least their base in the water (Fassett, 1940). In general, they conform to one growth habit through most of their life cycle—emerged, floating, submerged with floating leaves, or submerged in water (Yang, 1987).

This paper reports our attempt to study the specific distributions of different shapes of calcium oxalate crystals in the leaves and stems of 56 species of aquatic angiosperms growing in Taiwan. We make special reference to the possible relationship between occurrence of calcium oxalate crystals and specific aquatic growth habit.

Materials and Methods

Fifty-six species of freshwater angiosperms were selected from 23 families (Table 1) and collected between April and September (1990–1992). The species of plants were determined according to Yang (1987) and ‘Flora of Taiwan’ (Li et al., 1979). Voucher specimens are deposited in the herbarium or the anatomical laboratory of the Department of Botany, National Taiwan University. For light microscopy, the leaves and stem segments were fixed in formalin-acetic acid-alcohol (FAA), dehydrated in a tertiary butyl alcohol series, embedded in paraffin, sectioned on a rotary microtome (at 12 μm), and stained with modified Delafields technique used to specifically locate the calcium oxalate crystals in the plant tissues. Micrographs were made with a Nikon Optiphot or a Leica Diaplan microscope. The materials for scanning electron microscopy (SEM) were fixed in 2.5% glutaraldehyde followed by 1% OsO₄; or in FAA and then dehydrated in an ethanol-acetone series, dried with a Hitachi Critical Point Dryer (HCP-1), coated with an IB-2 ion coater (Dawes, 1979), and examined with a Hitachi S-550 SEM.

Results

Five types of calcium oxalate crystals were identified—druses, raphides, styloides, prisms, and crystal sands (Table 2, Figures 1–3). They were observed in the leaves and stems from 29 of the 56 species of freshwater angiosperms studied (Tables 1 and 2).
Druse crystals

Druses occur as crystal idioblasts in the leaves and stems of Rotala indica, R. rotundifolia, and R. hippociris (Figure 1A and B) and Polygonum hydropiper (Figure 1E). Druses were also seen in the normal parenchymatous cells in the leaves and stems of Linnophila aromatica, L. indica, L. sessiliflora (Figure 1F and G), and Rotala wallichii (Figure 1C and D). The shape and location of druses in the emerged and submerged leaves are similar. In the lamina of emerged leaves of Nelumbo lutea and N. nucifera (Figure 1H and J), druses are distributed in the cells of spongy tissue. In the petiole, they are formed in the cells around the large air channels or in the diaphragms. Druses were also observed in the floating leaves and stolons of Trapa bispinosa (Figure 1L and M), and in the leaves of Victoria cruziana (Figure 1J and K) and Pistia stratiotes (Figure 2B and D). In the leaves, druses are mostly distributed along the veins, and occasionally in the intercostal lamina.

Raphide crystals

These crystal were observed as idioblasts. They are spindle-form and larger than neighboring parenchymatous cells. These crystal idioblasts are especially abundant around the leaf veins (Figure 2E). In the intercostal lamina, they are distributed sporadically. Generally, their axes are parallel to the leaf veins. Raphides occur in the leaves and stems of Ludwigia ascendens, L. octovalvis, L. peploides (Figure 2E and F), and Monochoria vaginalis (Figure 2I and J). In the floating leaves of Spirodela polyrhiza, S. punctata, Lemna aequinoctialis (Figure 2G and H), Pistia stratiotes (Figure 2A, C, and D), and Eichhornia crassipes (Figure 3A and B) raphides are scattered in the mesophyl or they are located in the diaphragms and extend their ends into the air channels of the leaf petioles.

Styloides

The styloid idioblasts are distributed sporadically between the mesophyllous cells in the aerenchyma of the floating leaves of Eichhornia crassipes (Figure 3A) and in the emerged leaves of Phylidiun lanuginosum (Figure 3C and D) and Sparganium fallax. These crystals were found to be covered with wall materials and to extend their ends into air spaces.

Prismatic crystals

In Nymphaea tetragona, N. mexicana, N. lotus (Figure 3E, F, and K), Nuphar luteum (Figure 3G and H), Euryale ferox, and Victoria cruziana (Figure 3I and J), prismatic crystals were found in the cell walls of the sclereids. These sclereid idioblasts are dispersed in the parenchymatous tissue. In the spongy tissue or around the air channel of the petiole they are astro sclereids (Figure 3E–J).

Crystal Sands

These crystal aggregates were observed in parenchymatous tissue of the midrib and intercostal lamina of the leaf, and in the stem cortex of Linnophila sp. (Figure 3L and M).

No crystals were observed in any of the studied species that are submerged in water during their life cycle—Sagittaria pygmea, Blyxa spp., Hydriella verticillata, Hydrocharis dubia, Ottelia alismoides, Vallisneria americana, Ulricularia exoleta, Najas sp. and Potamogeton spp.

Calcium crystals were not found in the species of Nymphoides coreana, N. aurantiacum, and Brasenia schreberi, which are submerged with floating leaves, nor in the emergent species Caldesia grandis, Hygrophila lancea, Sagittaria trifolia, Cyperus sp., Eleocharis dulcis, Schoenoplectus mucronatus, Ericaulon nantense, Sphaerocaryum malaccense, Typha orientalis, and Pogostemon stellatus.

Discussion

Calcium oxalate crystals occur in the plant bodies of 29 species (11 families) of the 56 species (23 families) investigated (Tables 1 and 2). All generally encountered shapes were observed. Most plants contain only one crystal type, except Pistia stratiotes, Victoria cruziana, Eichhornia crassipes, Linnophila sp., and Sparganium fallax, in which two or three crystal types were observed (Table 2).

Crystals of different morphology may occur in the same plant (Figures 2D and 3A). Various shapes of calcium oxalate crystals were found in individual plants of Ricinus (Scott, 1941), Chenopodium album, Datura sp., Nerium, and Rumex (Doigey, 1991). This raises the question of the causes of the different shapes. Scurfeld et al. (1973) suggested that impurities may be a factor in the formation of different crystal types. Franceschi and Horner (1980) reported that various physical and chemical parameters such as temperature, pressure, pH, and ion concentration affect crystal growth, habit, and properties. The actual mechanism controlling shape is unknown. The restricted penetration of light and air into water creates a specific growth condition for aquatic angiosperms (Fassett, 1940). In the aquatic leaves and stems there exists an extensive system of aerenchyma, and a reduced xylem system (Fahn, 1990). The crystal idioblasts observed in the plant bodies of aquatic angiosperms are frequently associated with the aerenchyma (Table 2), and they may contain a large single styloid, a druse, or a bundle of raphides. The ends of these crystals generally protrude into the air spaces (Figure 3E–K). In the studied species of Nymphaea, Nuphar, Victoria, and Euryale, the prismatic crystals are
Figure 2. A) SEM photograph of the petiole section of *Pistia stratiotes* showing raphide idioblasts (→) in the aerenchyma. Bar = 250 µm. B) SEM photograph of druse in the leaf of *P. stratiotes*. Bar = 10 µm. C) SEM photograph of raphide idioblast in *P. stratiotes*. Bar = 15 µm. D) Leaf of *P. stratiotes* showing druses (→) and raphide in the mesophyll. Bar = 250 µm. E) Leaf of *Ludwigia adscendens* showing raphides (→) in midrib region. Bar = 150 µm. F) SEM photograph of the stem section of *L. adscendens* showing raphides in the cortex. Bar = 30 µm. G) SEM photograph of the leaf section of *Lemma aequinoctialis* showing raphides in mesophyll. Bar = 100 µm. H) Enlargement of G. Bar = 20 µm. I) SEM photograph of the petiole section of *Monochoria vaginalis* showing raphide idioblasts (→) in the diaphragm. Bar = 50 µm. J) SEM photograph of the leaf section of *Monochoria vaginalis* showing the raphide idioblast. Bar = 10 µm.
Figure 3. A) SEM photograph of *Eichhornia crassipes* petiole section showing raphide (→) and stylloid crystals in the cortex or around the air channel. Bar = 125 μm. B) Enlargement of A. Bar = 25 μm. C) SEM photograph of stem section of *Phyllium lanuginosum* showing the stylloids (→). Bar = 150 μm. D) Enlargement of C. Bar = 30 μm. E) SEM photograph of petiole section of *Nymphaea mexicana* showing the astrosclereids around the air channel. Bar = 500 μm. F) Enlargement of E showing the prismatic on the sclereid. Bar = 50 μm. G) SEM photograph of petiole section of *Nuphar shima* showing the astrosclereids (→) around the air channel. Bar = 300 μm. H) Enlargement of G showing the prismatic on the sclereid. Bar = 30 μm. I) SEM photograph of leaf section of *Victoria cruziana* showing the astrosclereids around the air channel. Bar = 100 μm. J) Enlargement of I. Bar = 10 μm. K) Enlargement of F showing the prismatic crystals (→). Bar = 5 μm. L) Cleared leaf of *Limnophila* sp. showing the crystal sands (→) in mesophyll. Bar = 10 μm. M) SEM photograph of crystal sands in *Limnophila* sp. Bar = 5 μm.
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<td><em>Trapa bispinosa</em> Roxb.</td>
<td>E</td>
<td>Shung-lien-pi, Ilan</td>
<td>Kuo-Huang 55</td>
</tr>
<tr>
<td>var. <em>inumai</em> Nakano</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Typhaceae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Typha orientalis</em> Presl.</td>
<td>E</td>
<td>Lung-tan, Taoyuan</td>
<td>Kuo-Huang 56</td>
</tr>
</tbody>
</table>
Table 2. Location and shape of calcium oxalate crystals within some aquatic angiosperms in Taiwan (D, druses; P, prisms; R, raphides; S, styloides; CS, crystal sands)

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Crystal type</th>
<th>Specific location</th>
<th>Habit</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Araceae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Pistia stratiotes</em></td>
<td>D, R</td>
<td>leaf aerenchyma and stolonous air channel</td>
<td>F</td>
</tr>
<tr>
<td><strong>Lemnaceae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Lemna aequinoctialis</em></td>
<td>R</td>
<td>fundamental parenchyma</td>
<td>F</td>
</tr>
<tr>
<td><em>Spirodea polyrhiza</em></td>
<td>R</td>
<td>&quot;</td>
<td>F</td>
</tr>
<tr>
<td><em>Spirodea punctata</em></td>
<td>R</td>
<td>&quot;</td>
<td>F</td>
</tr>
<tr>
<td><strong>Lythraceae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Rotala hippuris</em></td>
<td>D</td>
<td>spongy tissues and fundamental parenchyma</td>
<td>E</td>
</tr>
<tr>
<td><em>Rotala indica</em></td>
<td>D</td>
<td>&quot;</td>
<td>E</td>
</tr>
<tr>
<td><em>Rotala rotundifolia</em></td>
<td>D</td>
<td>&quot;</td>
<td>E</td>
</tr>
<tr>
<td><em>Rotala wallichii</em></td>
<td>D</td>
<td>&quot;</td>
<td>E</td>
</tr>
<tr>
<td><strong>Nymphaeaceae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Euryale ferox</em></td>
<td>P</td>
<td>astrosclerid</td>
<td>S/F</td>
</tr>
<tr>
<td><em>Nelumbo lutea</em></td>
<td>D</td>
<td>leaf aerenchyma</td>
<td>E</td>
</tr>
<tr>
<td><em>Nelumbo nucifera</em></td>
<td>D</td>
<td>&quot;</td>
<td>E</td>
</tr>
<tr>
<td><em>Nuphar shimadai</em></td>
<td>P</td>
<td>astrosclerid</td>
<td>S/F</td>
</tr>
<tr>
<td><em>Nymphaea lotus</em></td>
<td>P</td>
<td>&quot;</td>
<td>E</td>
</tr>
<tr>
<td><em>Nymphaea mexicana</em></td>
<td>P</td>
<td>&quot;</td>
<td>S/F</td>
</tr>
<tr>
<td><em>Nymphaea tetragona</em></td>
<td>P</td>
<td>&quot;</td>
<td>S/F</td>
</tr>
<tr>
<td><em>Victoria cruziana</em></td>
<td>P, D</td>
<td>&quot;</td>
<td>S/F</td>
</tr>
<tr>
<td><strong>Onagraceae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ludwigia adscendens</em></td>
<td>R</td>
<td>mesophyll</td>
<td>E</td>
</tr>
<tr>
<td><em>Ludwigia octovalvis</em></td>
<td>R</td>
<td>fundamental parenchyma</td>
<td>E</td>
</tr>
<tr>
<td><strong>Philydraceae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Philydrum lanuginosum</em></td>
<td>S</td>
<td>aerenchyma</td>
<td>E</td>
</tr>
<tr>
<td><strong>Polygonaceae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Polygonum hydropiper</em></td>
<td>D</td>
<td>mesophyll</td>
<td>E</td>
</tr>
<tr>
<td><strong>Pontederiaceae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Eichhornia crassipes</em></td>
<td>S, R</td>
<td>aerenchyma</td>
<td>F</td>
</tr>
<tr>
<td><em>Monochoria vaginalis</em></td>
<td>R</td>
<td>&quot;</td>
<td>E</td>
</tr>
<tr>
<td><em>Monochoria sp.</em></td>
<td>R</td>
<td>&quot;</td>
<td>E</td>
</tr>
<tr>
<td><strong>Scrophulariaceae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Limnophila aromatica</em></td>
<td>D</td>
<td>mesophyll and fundamental parenchyma</td>
<td>E</td>
</tr>
<tr>
<td><em>Limnophila indica</em></td>
<td>D</td>
<td>&quot;</td>
<td>E</td>
</tr>
<tr>
<td><em>Limnophila sessiliflora</em></td>
<td>D</td>
<td>&quot;</td>
<td>E</td>
</tr>
<tr>
<td><em>Limnophila sp.</em></td>
<td>D, CS</td>
<td>&quot;</td>
<td>E</td>
</tr>
<tr>
<td><strong>Sparganiaceae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Sparganium fallax</em></td>
<td>S, D</td>
<td>aerenchyma</td>
<td>E</td>
</tr>
<tr>
<td><strong>Trapaceae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Trapa bispinosa</em></td>
<td>D</td>
<td>leaf aerenchyma</td>
<td>E</td>
</tr>
</tbody>
</table>
located between the plasmalemma and the primary cell walls of the sclereids. These sclereids are distributed mostly around the air channels (Chiang and Huang, 1983; Kuo-Huang and Chiang, 1992). Hence, the formation of calcium oxalate crystals in plants may be linked to evaporation of water (Franceschi and Horner, 1980) or air circulation in the air channels of some aquatic angiosperms (Mevi-Schutz and Grosse, 1988).

The formation of crystal idioblasts is a complex process involving changes in the development of cells and the formation of specific crystal structures. Factors which control oxalate synthesis and cellular calcium uptake and mobility may affect crystal induction and formation (Frank, 1972; Borchert, 1986; Franceschi, 1987). It is interesting to note that no crystals were observed in any of the studied species which grow submerged in water (Table 1).

The presence of crystals in plant bodies is certainly not detrimental to the plant itself. The presence or absence of crystals is an important character for understanding the evolutionary relationships of plant species (Franceschi and Horner, 1980). The specific distribution and shape of the crystals in the aquatic angiosperms we studied demonstrate that the physiological and genetic parameters controlling them are consistent. The characters of calcium crystals may be family, or even genus, specific (Table 1). The observation of calcium oxalate crystals in 29 out of the 56 species we studied indicates that the occurrence and shapes of crystals can be useful in the taxonomic analysis of aquatic plants. It is likely that a fine relationship exists between an absence of calcium oxalate crystals and the submerged growth habit of some of the angiosperms.

**Literature Cited**


Frank, E. 1972. The formation of crystal idioblasts in *Canavalia ensiformis* DC. at different levels of calcium supply. *Z. Pflanzenphysiol.* **67**: 350–358.


台灣水生被子植物的草酸鈣結晶

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本文以光學與掃描式電子顯微鏡觀察 56 種（23 科）台灣水生被子植物體，計有 29 種（11 科）植物有草酸鈣結晶體之分佈，其中包括挺水性，浮葉性及漂浮性植物，而沉水性植物體內並未發現草酸鈣結晶。觀察到的結晶型為：晶簇狀，針束狀，柱狀，多面體型及結晶砂。葉與莖都可發現有草酸鈣結晶的存在，但以葉部為多。觀察結果顯示，水生被子植物體內草酸鈣結晶的分佈與形態為特定的，可做為分類之依據。

關鍵詞：水生被子植物；草酸鈣結晶。