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Cyanogenesis in the Euphorbiaceae

Lucinda L. Horton
Eastern Illinois University

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CYANOGENESIS

IN THE EUPHORBIACEAE

(TITLE)

BY

LUCINDA L. HORTON

B. S., Eastern Illinois University

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

Master of Science

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY
CHARLESTON, ILLINOIS

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CYANOGENESIS IN THE EUPHORBIACEAE

BY

LUCINDA L. HORTON

B. S., Eastern Illinois University

ABSTRACT OF A THESIS

Submitted in partial fulfillment of the requirements for the degree of Master of Science at the Graduate School of Eastern Illinois University

CHARLESTON, ILLINOIS

1989

ABSTRACT

Fresh samples of nine species included in the family Euphorbiaceae, Acalypha gracilens, Acalypha ostryaefolia, Acalypha rhomboidea, Acalypha virginica, Chamaesyce maculata, Chamaesyce supina, Cnidoscolus stimulosus, Euphorbia corollata, and Poinsettia dentata, were tested for the production of cyanide using the Feigl-Anger technique. Two of these taxa were tested for polymorphism of cyanogenesis by repeated testing of the same individuals within a population. Two of these nine species, Acalypha ostryaefolia and Cnidoscolus stimulosis, gave positive results, although not every individual tested was positive. One of the species tested for polymorphism, Acalypha ostryaefolia, proved to be polymorphic for the production of cyanogenic compounds. Euphorbia corollata was not found to be positive for hydrogen cyanide liberation. Dried material from 624 specimens, representing 105 species, in the Stover Herbarium at Eastern Illinois University, were also tested for cyanide production. Twelve species representing five tribes of the Euphorbiaceae in the herbarium were found to be cyanogenic. Ninety-five species of the family Euphorbiaceae, representing 20 tribes, have previously been reported as cyanogenic. Literature dealing with these reports is reviewed, emphasizing the plant parts tested and cyanogenic compounds which have been isolated.

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INTRODUCTION

Many plants synthesize compounds which liberate hydrogen cyanide upon enzymatic hydrolysis, a phenomenon known as cyanogenesis. Cyanogenesis has been reported in bacteria, lichens, fungi, ferns, fern allies, gymnosperms, and at least 2050 species representing more than 110 families of angiosperms (Gibbs, 1974; Hegnauer, 1959; Seigler, 1976; Tjon Sie Fat, 1979). Cyanogenesis results from the hydrolysis of cyanoglucosides or cyanolipids, which yields one or more sugars, fatty acids, aldehydes, ketones, or hydrogen cyanide. The amount of hydrogen cyanide liberated depends on intrinsic (genetics, plant organ, age of plant, and even sex of the plant) and extrinsic factors (climate, available moisture, soil fertility, and frost damage) (Seigler, 1976; Hegnauer, 1959). Although numerous plants have been reported to be cyanogenic, little information is available concerning the extent of cyanogenesis in natural populations. Previous works, however, indicate a high degree of polymorphism, a characteristic which requires repeated testing. Cyanogenesis is important to systematists who utilize chemosystematics to support phenetic relationships by chemical similarities, and ecologists studying evolutionary selection. Cyanogenic glycosides may also serve as storage compounds for nitrogen accumulated in conditions favorable for rapid nitrogen cycling, such as the warm, wet conditions of early spring (Dement and Mooney, 1974). These nitrogen stores are later utilized by plants when nitrogen becomes limiting. It has also been shown that cyanogenic compounds afford some protection against herbivores (Jones, 1972; Jones, 1978).

Several major reviews of cyanogenesis in plants have been published including Dunstan and Henry, 1906; Greshoff, 1906a,b, 1909; Rosenthaler, 1919, 1929; Gibbs, 1974; Seigler, 1977; Tjon Sie Fat, 1979; Conn, 1981; Hegnauer, 1986. The relationship between cyanogenesis and systematics has also been reviewed (Hegnauer 1962-1973, 1971, 1977, 1986).

Recent studies of taxa included in the Euphorbiaceae indicate that cyanogenesis is common in this family (van Valen, 1978; Gibbs, 1974). The present study was undertaken to determine if cyanogenesis is associated with particular subfamilies or sections of the Euphorbiaceae as classified by Webster (1989). Population studies of several common taxa were also undertaken to determine if cyanogenesis is a polymorphic trait within the Euphorbiaceae.

Results from many early cyanide tests are questionable (Herbert, 1922; Juliano, 1923, 1933; Juliano and Guerrero, 1935; Kalaw and Sacay, 1925; de Peralta, 1928; and Quisumbing, 1951). A modified procedure proposed by Herbert (1922) which involved immersing the test samples into a sodium picrate solution containing chloroform, was used. The efficacy of the method is not discussed and the positive results from these studies in many cases have not been confirmed. As such, the workers and methods involved must be taken into consideration when published reports are critically reviewed.

Reports of cyanogenic species in the Euphorbiaceae are recorded in Table 1. Synonyms of names are given in parenthesis in Table 1 for convenience in cross-referencing in older literature.

MATERIALS AND METHODS

A total of 624 specimens (105 species) from the Stover Herbarium at Eastern Illinois University were tested for the presence of hydrogen cyanide. In addition, 1170 specimens (9 species) obtained from natural populations, mostly from east central and southern Illinois were also tested. In two of the nine taxa tested from natural populations, thirty individuals were marked with numbered nursery tags to assay fluctuations in cyanide production over a period of several weeks. Samples were tested for cyanide production using the Feigl-Anger technique (Feigl and Anger, 1966; Tantisewie, 1969). 200 mg of leaf tissue was crushed and placed in a 1 dram (15mm x 45mm) vial with 4-5 drops of distilled water. A strip of filter paper impregnated with copper ethylacetoacetate and tetra base (4,4-tetramethyldiamino-diphenylmethane) was suspended with a dry cork over the sample, taking care to avoid contact with the leaf-water mixture. The test samples were read and recorded after 24 hours at room temperature. A light blue color on the lower part of the test strip indicated a weakly positive reaction. A moderate reaction was indicated if most of the paper turned light blue, and a strong reaction when the paper turned dark blue throughout. Although a quantitative determination of cyanide production was not made, the intensity of the color change gives some indication of the amount of hydrogen cyanide released (Dickenmann, 1982). A weak reaction indicates about 2-20 mg of hydrogen cyanide per kg fresh weight, a moderate reaction indicates 21-50 mg of hydrogen cyanide per kg fresh weight, and the strong reaction exceeds 50 mg of hydrogen cyanide per kg of fresh weight. Negative results are not included in this study. While negative results usually indicate that cyanide is lacking, improper sample preparation, excessive heat, bacteria, and fungi may adversely affect the ability of cyanogenic compounds and hydrolytic enzymes to liberate hydrogen cyanide.

RESULTS

Taxa tested and the results obtained from the Feigl-Anger tests are recorded in Table 1 according to Webster's (1989) classification of the Euphorbiaceae . Literature citations of previously published positive results are also included in Table 1, along with the plant part tested. Results of this study listed in Table 1 are from samples for which hydrogen cyanide had not been previously reported. A summary of the findings pertaining to cyanide production in the Euphorbiaceae, based on an evaluation of the literature available, is presented in the discussion.

DISCUSSION

The results from Table 1 demonstrate the first reports of cyanogenesis from eight species, *Acalypha ostryaefolia*, *Chamaesyce supina*, *Cnidoscolus multilobus*, *Cnidoscolus urens*, *Cnidoscolus variegatum*, *Croton punctatus*, *Croton lobatus*, and *Euphorbia hexagona*. These taxa are, however, in genera which contain additional cyanogenic taxa. Fresh specimens of *Acalypha ostryaefolia* and *Cnidoscolus stimulosus* were positive when tested for cyanogenesis. All 60 of the randomly chosen samples of *C. stimulosus* from natural populations in South Carolina were found to be cyanogenic. In three marked populations of *A. ostryaefolia*, a rather short lived, weedy annual which germinates late in the summer, cyanogenic polymorphism was demonstrated (Table 2). The testing period was shortened somewhat in this study due to the very dry conditions, however, the young plants demonstrated a higher frequency of positive tests and stronger reactions. When tested weekly for polymorphism of cyanide production, five individuals gave positive reactions throughout the test period and eleven individuals were positive for two consecutive weeks.

Five populations of thirty individuals each of *Acalypha gracilens*, *A. rhomboidea*, *Chamaesyce maculata*, *C. supina*, and *Poinsettia dentata* randomly chosen from habitats in the southern half of Illinois were also tested for cyanogenesis over a period of several weeks. No positive reactions resulted from these tests. Three populations of 30 individuals of *Euphorbia corollata* were marked and tested on a weekly basis for cyanogenesis. No positive tests were recorded for these populations.

The ability to release cyanide upon hydrolysis has been reported in four of the five subfamilies of the Euphorbiaceae; Phyllanthoideae, Acalyphoideae, Crotonoideae, and Euphorbioideae. Five of the eleven tribes in the Phyllanthoideae - Bridelieae, Andrachneae, Antidesmeae, Phyllantheae, and Bischofieae have been reported to be cyanogenic. Triglochinine has been isolated from members of the tribes Bridelieae, Andrachneae, and Phyllantheae (van Valen, 1978). In addition, dhurrin has been found in taxa belonging to Bridelieae and taxiphyllin has been isolated from members of the Phyllantheae (van Valen, 1978; Tjon Sie Fat, 1979). Cyanogenesis has not been found in the tribes Weilandieae, Amanoeae, Drypeteae, Aporuseae, Hymenocardieae, or Uapaceae.

Four tribes, Chrozophoreae, Alchornieae, Acalypheae and Plukenetieae in the subfamily Acalyphoideae are reported to include cyanogenic taxa. The only cyanogenic compound isolated from the tribe Acalypheae, acalyphin, was found in Acalypha indica. Cyanide has not been reported in tribes Clutieae, Pogonoporeae, Chaetocarpeae, Pereae, Dicoelieae, Galearieae, Erismantheae, Ampereae, Agrostistachydeae, Caryodendreae, Pycnocomeae, Bernardieae, Epiprineae, and Omphaleae. Cyanogenesis is more widespread in the subfamily Crotonoideae, with eight of thirteen tribes represented by cyanogenic species. Linamarin and lotaustralin have been isolated from plants of the tribes Micandreae and Manihoteae.

Although taxa which are reportedly cyanogenic are included in the tribes Elateriospermeae, Codiaeae, Ricinocarpeae, Crotoneae, and Aleuritideae, no compounds have been isolated. The tribes Adenoclineae, Trigonostemoneae, Joannesieae, and Neoboutonieae apparently lack cyanogenic compounds. In the subfamily Euphorbioideae, the ability to release hydrogen cyanide upon hydrolysis is reported in the Hippomaneae, Hureae, and Euphorbieae but not in the Stomatocalyceae or Pachystromateae. A summary of literature reports of cyanogenesis in the Euphorbiaceae is presented below.

SUBFAMILY PHYLLANTHOIDEAE

Tribe Bridelieae

All cyanogenic species known in this tribe belong to the genus *Bridelia*. Dhurrin and triglochinin have been isolated from one species, *Bridelia monoica* (van Valen, 1978).

Tribe Andrachneae

Several taxa included in the genera *Andrachne* and *Poranthera* have been reported to be cyanogenic and triglochinine has been isolated from both genera (van Valen, 1978). Leaves, bark, and flowers of *Andrachne colchica* produced strong cyanide reactions (van Valen, 1978) and the leaves of two species of *Poranthera* are reported as cyanogenic (Gibbs, 1974).

Tribe Antidesmeae

Although the leaves and bark of *Antidesma bunias* were reported to give positive tests (Juliano and Guerrero, 1935), more recent tests have yielded only negative results (Gibbs, 1974). No cyanogenic glycoside has been identified.

Tribe Phyllantheae

Three species of Securinega give positive results and triglochinine has been isolated from S. suffruticosa (van Valen, 1978). One species of Breynia is listed as being cyanogenic, however, field tests were not performed and the cyanogenic glycoside has not been identified. Five species of Phyllanthus have been reported to contain cyanide in the leaves. Taxiphylline (formerly known as phyllanthin) has been isolated from Phyllanthus gasstroemii (Tjon Sie Fat, 1979).

Tribe Bischofeae

The leaves of Bischofia javavica, have been reported to be cyanogenic (Herbert, 1922), although no cyanogenic glycoside was isolated.

SUBFAMILY ACALYPHOIDEAE

Tribe Chrozophoreae

The leaves and stems of Melanopsis multiglandulosa have been reported to be cyanogenic (Juliano, 1933), although no cyanogenic glycoside has been identified.

Tribe Alchornieae

The leaves of two species in the genus Alchornea are reported to be cyanogenic (Gibbs, 1974), although no cyanogenic glycoside has been isolated.

Tribe Acalypheae

Several genera in this tribe include cyanogenic taxa (Ricinus, Homonoia, Mercurialis, Macaranga, Claoxylon, *Acalypha, Mallotus*) (Gibbs, 1974; Tjon Sie Fat, 1979). The only cyanogenic compounds isolated has been acalyphin from *Acalypha indica* (Rimington and Roets, 1937). During this study, herbarium specimens and fresh samples of *Acalypha ostryaefolia* gave positive cyanide tests.

Tribe Plukenetieae

Specimens of *Dalechampia micromeria* are reported to be cyanogenic (Kaplan et al., 1983), although no cyanogenic glycoside has been isolated.

SUBFAMILY CROTONOIDEAE

Tribe Micandreae

The genus *Hevea* has been shown to contain several cyanogenic taxa with cyanogenis compounds most common in stems and leaves, and less common in flowers, seeds, and roots. Linamarin and lotaustralin have been isolated from several species (Leiberei et al., 1985, 1986). In *Hevea brasiliensis*, the distribution of linamarin in seeds has been investigated. All seeds tested contained some degree of cyanide, although the cyanide content dropped during germination and plantlet development. Newly formed primary leaves have only 4% of the cyanide capabilities of young leaves of an adult plant. In *H. brasiliensis*, cyanogenic glycosides seem to function as a storage compounds for protein synthesis (Lieberei et al., 1985, 1986).

Tribe Manihoteae

Several species of *Manihot* and *Cnidoscolus* are strongly cyanogenic. Both linamarin and lotaustralin have been isolated from *Manihot* (Butler, 1965), while only linamarin has been isolated in Cnidoscolus (Seigler and Bloomfield, 1969). In this study Cnidoscolus multilobus, C. urens, and C. variegatum were found to be cyanogenic taxa for the first time. Manihot esculenta, commonly known as cassava, is an important food crop in which the production of cyanogenic compounds creates a nutritional problem. Global production has doubled in the last three decades and is now estimated at 100 million tons annually (Cooke and Coursey, 1977). High yields, disease, drought, and insect resistance, and the high food/energy input ratio makes Manihot very important to the subsistence sector of the economy where most of this production takes place. The root is the part of Manihot most often eaten, although the leaves may be used as a protein source in some parts of the world (Rogers and Milner, 1963). Manihot provides a food staple for 200 - 300 million people in the tropical areas of the world (Coursey and Haynes, 1970; Nestel, 1973). The toxicity of Manihot was reported as early as 1601. Various processing methods such as sun drying, leaching, soaking, and roasting have been employed to remove the toxin and transform the perishable root into a stable product. The toxin has been identified as linamarin (Conn, 1969). More recently, small amounts (10%) of lotaustralin have been shown to be present (Cooke and Coursey, 1977). All parts of the plant with the possible exception of the seeds have been shown to contain these cyanogenic glucosides, however, there is a wide range of cyanide concentrations among cultivars, ranging from a few parts per million to 1000 parts per million. Cyanide concentration may vary within roots of the same plant (Cooke et al., 1978b). Fatalities caused by acute poisonings are uncommon, however, long term toxic effects such as ataxic neuropathy, goiter, and cretinism may be attributed to diets high in cassava.

Tribe Jatropheae

Seven species in the genus Jatropha have been shown to be cyanogenic (van Valen, 1978), although no cyanogenic glycoside has been reported.

Tribe Elateriospermeae

Leaves and seeds of Elateriospermum tapos have been shown to be cyanogenic (Greshoff, 1906a; Tjon Sie Fat, 1979), although no cyanogenic glycoside has been isolated.

Tribe Codiaeae

Bark and leaves of Codiaeum variegatum are cyanogenic (Seigler, 1976a), although no cyanogenic glycosides have been isolated.

Tribe Ricinocarpeae

Leaves of Beyeria leschenaultii have been reported to be cyanogenic (van Valen, 1978), although no cyanogenic glycoside has been identified.

Tribe Crotoneae

Croton scouleri has been reported to be slightly cyanogenic (Adserson et al, 1988), and herbarium material of C. punctatus, and C. lobatus gave positive cyanide results in this study. No cyanogenic glycoside has been identified.

Tribe Aleuritideae

Two species of Aleurites have been shown to be cyanogenic, although no cyanogenic glycoside has been identified. In

Aleurites trisperma, the roots, bark, leaves, flowers, fruit and wood were reported to be cyanogenic (Peralta, 1928).

SUBFAMILY EUPHORBIOIDEAE

Tribe Hippomaneae

The genera Colliguaja, Gymnanthes, Sapium, and Stillingia contain cyanogenic species (Gibbs, 1974; Tjon Sie Fat, 1979), although no cyanogenic compounds from these genera have been isolated.

Tribe Hureae

The bark and leaves of Hura crepitans have a positive cyanide reaction (Juliano, 1933), although a cyanogenic glycoside has not been identified.

Tribe Euphorbieae

Several taxa in the genera Euphorbia and Chamaesyce are cyanogenic (Tjon Sie Fat, 1979; Adserson et al., 1988), with several of the Euphorbia species implicated in livestock deaths (Finnemore and Cox, 1928; Shore and Drummond, 1965). Herbarium material of Chamaesyce supina gave positive test results in this study. To date, a cyanogenic glycoside has not been identified in this tribe.

Table 1. Reports of cyanogenic plants from the Euphorbiaceae. Plant part tested: b = bark, f = fruit, fl = flower, l = leaves, r = root, rh = rhizome, s = stem, se = seed.

SUBFAMILY I. PHYLLANTHOIDEAE

TRIBE 1. WEILANDIEAE

TRIBE 2.AMANOEAE

TRIBE 3.BRIDELIEAE

Bridelia exaltata s,l	Gibbs, 1974: Everist, 1964: van Valen, 1978; Tjon Sie Fat, 1979; Smith and White, 1918
Bridelia mollis	Shore and Drummond, 1965
Bridelia monoica s,l	Tjon Sie Fat, 1979; van Valen 1978
Bridelia ovata l	Gibbs, 1974; Gardner and Bennetts, 1956; Greshoff, 1906a, 1906b, 1907; Rosenthaler, 1919; Tjon Sie Fat, 1979; van Valen, 1978; Treub, 1907; van Romburgh, 1899b
Bridelia tomentosa l	Gibbs, 1974; Tjon Sie Fat, 1979; Rosenthaler, 1919; van Valen, 1978; Treub, 1907

TRIBE 4.ANDRACHNEAE

Poranthera corymbosa l	Gibbs, 1974; van Valen, 1978; Tjon Sie Fat, 1979; Finnemore

and Cox, 1928

Poranthera microphylla — Gibbs, 1974; Everist 1964;
1 — Gardner and Bennett, 1956; Tjon Sie Fat, 1979; van Valen, 1978

Andrachne colchica — Gibbs, 1974; Greshoff, 1909,
b,l,f — 1910; Rosenthaler, 1919; Pammel, 1910; Tjon Sie Fat, 1979; van Valen, 1978

Andrachne decaisnei — Gibbs, 1974; Everist, 1964; van Valen, 1978; Tjon Sie Fat, 1979; Shaw et al., 1959

TRIBE 5. DRYPETEAE

TRIBE 6. APORUSEAE

TRIBE 7. ANTIDESMEAE

Antidesma bunias — Gibbs, 1974; Juliano and
l,b,s — Guerrero, 1935

TRIBE 8. PHYLLANTHEAE

Securinega ramiflora — Gibbs, 1974; Greshoff, 1909, 1910; Pammel, 1911; Rosenthaler, 1919

Securinega suffruticosa — Tjon Sie Fat, 1979; van
l,b — Valen, 1978;

Securinega virosa — Shore and Drummond, 1965

Breynia oblongifolia — Everist, 1964

Phyllanthus acuminatus — Tjon Sie Fat, 1979; Seigler
l — et al., 1979

Phyllanthus gasstroemii — Gibbs, 1974; Everist, 1964;

1	Gardner and Bennetts, 1956; van Valen, 1978; Tjon Sie Fat, 1979; Finnemore et al., 1936; Webb, 1949
Phyllanthus lacunarius 1	Gibbs, 1974; Everist, 1964; van Valen, 1978; Tjon Sie Fat, 1979; Hurst, 1942
Phyllanthus niruri	Gibbs, 1974; Siegler, 1976b
Phyllanthus speciosus 1	Gibbs, 1974; Tjon Sie Fat, 1979; van Valen, 1978

TRIBE 9. HYMENOCARDIEAE

TRIBE 10. UAPACEAE

TRIBE 11. BISCHOFIEAE

Bischofia javavica 1	Gibbs, 1974; Herbert, 1922

TRIBE 1. HYAENANCHEAE

TRIBE 2. PICRODENDREAE

TRIBE 3. CALETIEAE

SUBFAMILY III.ACALYPHOIDEAE

TRIBE 1. CLUTIEAE

TRIBE 2. POGONOPHOREAE

TRIBE 3. CHAETOCARPEAE

TRIBE 4. PEREAE

TRIBE 5. DICOELIEAE

TRIBE 6. GALEARIEAE

TRIBE 7. ERISMANTHEAE

TRIBE 8. AMPEREAE

TRIBE 9. CHROZOPHOREAE

Melanopsis multiglandulosa Gibbs, 1974; Juliano, 1933

l,s

TRIBE 10. AGROSTISTACHYDEAE

TRIBE 11. CARYODENDREAE

TRIBE 12. PYCNOCOMEAE

TRIBE 13. BERNARDIEAE

TRIBE 14. EPIPRINEAE

TRIBE 15. ALCHORNIEAE

Alchornea parviflora l	Gibbs, 1974
Alchornea sicca l	Gibbs, 1974; Kalaw and Sacay, 1925

TRIBE 16. ACALYPHEAE

Ricinus communis sd,r,b,l,w	Gibbs, 1974; Greshoff, 1906a, 1906b, 1907; Seigler, 1976b; Wokes and Willimott, 1951; Hegnauer, 1959b, 1961; Peralta, 1928; Pammel, 1911
Homonoia riparia b	Gibbs, 1974; Juliano and Guerrero, 1935
Mercurialis annua r	Gibbs, 1974; van Valen, 1978; Tjon Sie Fat, 1979; Friese, 1937
Mercurialis perennis r	Tjon Sie Fat, 1979; Friese, 1937
Macaranga grandiflora r	Gibbs, 1979; Juliano, 1933
Macaranga tanarius s,l,r,b	Gibbs, 1974; Juliano, 1933; Juliano and Guerrero, 1935

Claoxylon elongatum	Gibbs, 1974; Juliano, 1933
l,s,r	
Acalypha indica	Gibbs, 1974; Steyn, 1937; Tjon Sie Fat, 1979; van Valen, 1978; Rimington and Roets, 1937
s,l	
Acalypha ostryaefolia	This study
l	
Acalypha tricolor	Gibbs, 1974
Acalypha wilkesiana	Juliano, 1933
l,s	
Mallotus phillippinensis	Gibbs, 1974; Peralta, 1928
r,s,l	
Mallotus ricinoides	Gibbs, 1974; Peralta, 1928
r,l,w	

TRIBE 17. PLUKENETIEAE

Dalechampia micromeria	Kaplan et al., 1983

TRIBE 18. OMPHALEAE

SUBFAMILY IV. CROTONOIDEAE

TRIBE 1. MICANDREAE

Hevea benthamiana	Lieberei et al, 1986
l	
Hevea brasiliensis	Gibbs, 1974; Butler, 1965; Greshoff, 1906a, 1906b, 1907; Tjon Sie Fat, 1979; Lieberei et al., 1985, 1986; van Valen, 1978; Wokes and Willimott, 1951; Rosenthaler, 1919; van Romburgh, 1899a; Gorter, 1912; Kerbosch,
s,l,fl	

	1915; Treub, 1907
Hevea camargoana	Lieberei et al., 1986
Hevea ceara	Wokes and Willimott, 1951
se	
Hevea confusa	Wildeman, 1939; Lieberei et al., 1986
l	
Hevea guianensis	Lieberei et al., 1986
s,l	
Hevea pauciflora	Wildeman, 1939; Lieberei et al., 1986
l	
Hevea pauciflora X Hevea guianensis	Lieberei et al., 1986
Hevea spruceana	Gibbs, 1974; Greshoffff, 1906a, 1906b, 1907; Leiberei et al., 1986; Tjon Sie Fat, 1979; van Valen, 1978; Rosenthaler, 1919; Treub, 1907; van Romburgh, 1893
l	
Hevea viridis	Lieberei et al., 1986
s,l	

TRIBE 2. ADENOCLINEAE

TRIBE 3. MANIHOTEAE

Manihot aipi	Tjon Sie Fat, 1979
r	
Manihot bankensis	Gibbs, 1974; Greshoff, 1906a, 1906b, 1907; Tjon Sie Fat, 1979; Rosenthaler, 1919; Greshoff, 1892, 1898

Manihot carthaginensis r	Gibbs, 1974; Butler, 1965; van Valen, 1978; Tjon Sie Fat, 1979
Manihot esculenta (utilissima)	Kingsbury, 1964; Shore and Drummond, 1965
Manihot flabellifolia l	Abiusso, 1966; Seigler et al., 1979; Tjon Sie Fat, 1979
Manihot glaziovii r,l,se,b	Gibbs, 1974; Greshoff, 1906a, 1906b, 1907; Tjon Sie Fat, 1979; Juliano and Guerrero, 1935; van Valen, 1978; Rosenthaler, 1919; van Romburgh, 1899; Greshoff, 1892
Manihot palmata (aipi) r,l	Gibbs, 1974; Clark, 1936; Greshoff, 1906a, 1906b, 1907; Rosenthaler, 1919; Treub, 1907; van Valen, 1978; Henry and Boutron-Charland, 1836; Dunstan, Henry and Auld, 1906; Francis, 1870
Manihot tweediana	Gibbs, 1974; Wildeman, 1939
Manihot utilissima r,l	Gibbs, 1974; Clark, 1936, Greshoff, 1906a, 1906b, 1907; Juliano, 1923; Rosenthaler, 1919; van Valen, 1978; Pammel, 1911; Tjon Sie Fat, 1979; Dunstan et al., 1906; Kalaw and Sacay, 1925; Treub, 1907
Manihot walkerae	Seigler, 1976b; Rogers and Appan,

	1973; Correll and Johnston, 1970
Cnidoscolus angustidens rh	Gibbs, 1974
Cnidoscolus cnicodendron l	Tjon Sie Fat, 1979; Seigler et al., 1979
Cnidoscolus loasoides l	Tjon Sie Fat, 1979; Seigler et al., 1979
Cnidoscolus stimulosis sd,r	Tjon Sie Fat, 1979; van Valen, 1978; Seigler and Bloomfield, 1969
Cnidoscolus texanus r,se	Gibbs, 1974; Seigler, 1976; van Valen, 1978; Tjon Sie Fat, 1979; Seigler and Bloomfield, 1969
Cnidoscolus multilobus l	This study
Cnidoscolus urens l	This study
Cnidoscolus variegatum l	This study

TRIBE 4. GELONIEAE

TRIBE 5. JATROPHEAE

Jatropha angustidens rh	Greshoff, 1906a, 1906b, 1907; Tjon Sie Fat, 1979; Rosenthaler, 1919; van Valen, 1978; Heyl, 1902
Jatropha capensis l	Gibbs, 1974; Tjon Sie Fat, 1979; van Valen, 1978; van der Walt and

	Steyn, 1940
Jatropha curcas l,b,r,f,w	Gibbs, 1974; Peralta, 1928
Jatropha gossypifol	Wokes and Willimott, 1951
Jatropha hieronymii l	Tjon Sie Fat, 1979; Seigler et al., 1979
Jatropha macrocarpa l	Tjon Sie Fat, 1979; Seigler et al., 1979
Jatropha multifida r,s,l	Gibbs, 1974; Peralta, 1928; Wokes and Willimott, 1951
TRIBE 6. ELATERIOSPERMEAE	
Elateriospermum tapos l,se	Gibbs, 1974; Greshoff, 1906a, 1906b, 1907; Rosenthaler, 1919; van Valen, 1978; Tjon Sie Fat, 1979; van Romburgh, 1899
	van Valen, 1978
TRIBE 7. CODIAEAE	
Codiaeum variegatum b,l	Gibbs, 1974; Herbert, 1922; Seigler, 1976b
TRIBE 8. TRIGONOSTEMONEAE	
TRIBE 9. RICINOCARPEAE	
Beyeria leschenaultii l	Gibbs, 1974; Tjon Sie Fat, 1979; van Valen, 1978
TRIBE 10. CROTONEAE	
Croton scouleri	Adserson et al., 1988
Croton punctatus l	This study
Croton lobatus	This study

l

TRIBE 11. JOANNESIEAE

TRIBE 12. ALEURITIDEAE

Aleurites moluccana	Gibbs, 1974; Peralta, 1928
s,l,f	
Aleurites trisperma	Gibbs, 1974; Peralta, 1928
r,b,l,fl,f,w	

TRIBE 13. NEOBOUTONINAE

SUBFAMILY V.EUPHORBIOIDEAE

TRIBE 1. STOMATOCALYCEAE

TRIBE 2. HIPPOMANEAE

Colliguaja integerrima	Gibbs, 1974; van Valen, 1978
Gymnanthes lucida	Gibbs, 1974; Tjon Sie Fat, 1979;
l	van Valen, 1978
Sapium haematospermum	Tson Sie Fat, 1979; Seigler et
l,fl	al., 1979
Sapium luzonicum	Gibbs, 1974; Juliano and
l,b	Guerrero, 1935
Sapium sebiferum	Seigler, 1976b
Stillingia dentata	Gibbs, 1974; Kingsbury, 1964;
l	Moran et al., 1940; Seigler,
	1976b
Stillingia texana	Seigler, 1976b

TRIBE 3. PACHYSTROMATEAE

TRIBE 4. HUREAE

Hura crepitans	Gibbs, 1974; Juliano, 1933
b,l	

TRIBE 5. EUPHORBIEAE

Euphorbia hexagona	This study
Euphorbia boophthona	Tjon Sie Fat, 1979; van Valen, 1978; Gardner and Bennetts, 1956
Euphorbia clutioides	Tjon Sie Fat, 1979; van Valen, 1978; Gardner and Bennetts, 1956
Euphorbia drummondii	Gibbs, 1974; Hurst, 1942; Everist, 1964; Hegnauer, 1959b; van Valen, 1978; Tjon Sie Fat, 1979; Finnemore and Cox, 1928; Webb, 1949; Shore and Drummond, 1965
Euphorbia eylesii	Shore and Drummond, 1965
Euphorbia hirta r,s,l	Gibbs, 1974; Juliano, 1923; Seigler, 1976a, 1976b
Euphorbia lupatensis	Shore and Drummond, 1965
Euphorbia peplus	Gibbs, 1974; van Valen, 1978
Euphorbia pilulifera r,s,l	Quisumbing, 1951; Juliano, 1923
Euphorbia prostrata	Everist, 1964
Euphorbia trigona l,b,r,s	Gibbs, 1974; Peralta, 1928
Chamaesyce abdita	Adserson, 1988
Chamaesyce galapageia	Adserson, 1988
Chamaesyce recurva	Adserson, 1988
Chamaesyce viminea	Adserson, 1988
Chamaesyce supina l	This study

Table 2. Cyanogenesis in three natural populations of *Acalypha ostryaefolia*.

	Population #1			Population #2			Population #3		
	9/14	9/23	9/30	9/14	9/23	9/30	9/14	9/23	9/30
1	–	–	–	+++	–	–	+	–	–
2	–	–	–	++	–	–	+	–	–
3	–	–	–	++	–	–	+	–	–
4	–	–	–	+	–	–	+	–	–
5	+	–	–	+++	–	–	+	+	–
6	–	–	–	–	+	+	++	–	–
7	+	+	–	–	–	–	++	–	–
8	+	+	+	–	–	–	–	–	+
9	++	+	+	–	–	–	–	–	–
10	–	–	–	–	+	+	++	+	–
11	+	–	–	+	–	+	–	–	–
12	+	+	+	++	–	–	–	–	–
13	–	–	+	+	+	–	–	–	–
14	+	–	–	–	–	–	–	–	–
15	+++	–	–	–	–	–	–	+	–
16	+++	–	–	+++	–	–	–	–	–
17	–	–	–	+	–	–	–	–	–
18	+	+	–	+	+	+	–	+	–
19	+	+	–	+	–	–	–	–	–
20	++	–	–	–	–	–	+	–	–
21	+++	+	+	–	–	+	+	–	–
22	+++	–	–	–	–	–	–	–	–
23	+	–	+	–	–	–	+	+	–
24	++	–	–	–	–	–	–	–	–
25	+++	–	–	+++	+	–	+	+	–
26	–	–	–	+++	–	–	+++	–	–
27	–	–	–	–	–	–	+	–	++
28	++	–	–	+	–	–	+	–	–
29	–	–	–	++	–	–	+++	–	–
30	–	–	–	++	–	–	++	–	–

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