Tropical Agricultural Research Vol. 16: 223-241 (2004)

Cuscuta Species in the Lowlands of Sri Lanka, their Host Range and Host-Parasite Association

C. Jayasinghe, D.S.A. Wijesundara[1], K.U. Tennekoon[2] and B. Marambe[3]

Postgraduate Institute of Agriculture
University of Peradeniya
Peradeniya, Sri Lanka.

ABSTRACT. *The study included current distribution, host range, taxonomy and anatomy of the host-parasite association. The lowland Cuscuta spp. identified in the present study was different to Cuscuta chinensis as previously reported but similar to Cuscuta campestris.*

It was observed that Cuscuta is widely distributed in the dry areas such as Anuradhapura, Polonnaruwa and Hambantota in Sri Lanka. However, it was also found in scattered patches in the low country wet zone. In the dry zone, it was found frequently along the banks of irrigation channels, agricultural land and roadside vegetation. In the coastal areas Cuscuta was distributed mostly along the railway tracks, roadsides and wastelands. About 161 host plant spp., including rice, belonging to 59 families and 139 genera were observed as the host plants of this holo-parasite. Mikania cordata and Wedelia trilobata appear to be the primary hosts to the lowland Cuscuta.

Haustorial penetration was observed in the different host plants, including rice. However, in the rice plant, haustorial penetration was observed only on the midrib of the leaves. Haustoria of lowland Cuscuta did not show complex anatomical differentiations, but penetration distance depends on location of the host vascular system. However, some host plants showed resistance against the penetration of haustoria.

INTRODUCTION

Angiosperm parasites in primary habitats are an integral part of the ecosystem. They behave as "prudent predators" and are adapted to the life cycle of their principal hosts. Approximately 3,900 species of parasitic plants have been recorded (Nickrent, 2002), amounting to more than 1% of the flowering plants. Almost half the total can be attributed to the family Scrophulariaceae.

Cuscuta is a parasitic angiosperm genus belonging to the family Convolvulaceae, but some scientists classify the genus as a member of a separate family Cuscutaceae. Weber (1986) divided the family Cuscutaceae into two genera *i.e. Cuscuta* and *Grammica,* based on the shape of the stigma. Some species of *Cuscuta* are considered as noxious, invasive weeds. It is commonly known as "agamula-nethi-wela" in Sinhala and "kaskutta" in Tamil. The other common names of this parasite include "love vine",

1 Royal Botanic Gardens, Peradeniya, Sri Lanka.

2 Department of Botany, Faculty of Science, University of Peradeniya, Sri Lanka.

3 Department of Crop Science, Faculty of Agriculture, University of Peradeniya, Sri Lanka.

"strangleweed", "devil's-guts", "goldthread", "pull-down", "devil's-ringlet", "hellbine", "hairweed", "devil's-hair" and "hailweed".

In Sri Lanka two species of *Cuscuta* have been recorded, namely *Cuscuta chinensis* Lam. distributed in the low country and *Cuscuta reflexa* Roxb. found in the montane zone (Trimen, 1895; Austin, 1980) *Cuscuta* spp. has been reported as problematic parasitic weed to crop plants in agricultural systems in semi-humid and semi-arid areas of Africa and Asia (Dawson *et al.*, 1994). Significant crop losses have been reported due to infestation with *Cuscuta* in many crops (Kondap and Kumar, 1993; Dawson and ARS, 1989; Jeschke *et al.*, 1994; Sadler *et al.*, 1997; Marambe *et al.*, 2002). Pulses in general have been seriously infested while cereals have never been reported to be infested by the parasite irrespective of seasonal conditions (Kumar and Mohan, 1994; Dawson *et al.*, 1994). However, according to Rao *et al.* (1991) the susceptibility of pulse crops to infestation with *Cuscuta* could vary with the variety. *Cuscuta* produces a dense and shady barrier or canopy, which drastically reduces the growth and vigor of the host plant (Lawrance, 1966). Eppler (1992), Zhang *et al.* (1991) and Marcone *et al.* (1999) reported that *Cuscuta* could also be a transmitter of viral diseases in crops.

The invasive characteristics of *Cuscuta* spp. could be detrimental to the cultivation of many economically important crops. It could also affect the natural ecological balance and floristic composition in natural ecosystems. Some *Cuscuta* spp. have important medicinal, pharmacological, and edible values while others are a threat to the natural ecosystems and agricultural crops. Some *Cuscuta* spp. have been reported to show resistance to herbicides such as Glyphosate (Hassar and Rubin, 2003). Being a parasitic plant connected to a host plant renders *Cuscuta* difficult to control by using herbicides.

The present study was conducted to determine the current extent of distribution, host range, host-parasite association, and the taxonomy of *Cuscuta* spp. found in selected agro-ecological regions of Sri Lanka.

MATERIALS AND METHODS

Field Collections

Site visits were made randomly to collect *Cuscuta* samples where the branching pattern, colour, twining pattern around the host plant and flowers of the *Cuscuta* spp. were observed. Reproductive parts of the *Cuscuta* spp. were collected from five different places each in the midcountry wet zone (WM 3; Kandy), low country wet zone (WL 2; Galle and Kalutara and WL 4; Colombo), low country dry zone (DL1; Anuradahapura, Polonnaruwa) and low country intermediate zone (IL1; Badulla) of Sri Lanka for taxonomic studies. The coordinates of the locations of occurrence of *Cuscuta* were recorded using a Global Position System (GPS 76 Garmin, USA). By using the above data and DIVA GIS Package a distribution map was developed for *Cuscuta* spp. in the lowlands of Sri Lanka. In this study, the lowlands were considered as the area above 1000m amsl.

Taxonomical Studies

Line diagrams of the floral parts were made with the help of a dissecting and light microscope. These diagrams were compared with the published diagrams, photographs and herbarium specimens of different *Cuscuta* spp. Assistance was sought from staff of the National Herbarium of Royal Botanic Gardens, Peradeniya, Sri Lanka for identification of the collected species. Yuncker's (1932) key on most common *Cuscuta* spp. in the world was modified using the information collected during the present study.

Anatomical Studies

Representative stem cuttings of the host at the point of the host-parasite association, where the haustorium is connected to the host shoot system, were taken from different areas and preserved in Formalin Acetic Acid (FAA) for subsequent anatomical studies. Preserved herbarium specimens of different host plants were prepared for identification. Collected haustorial samples were soaked in flowing water overnight under room temperature (26±2°C) to remove the preservatives. The samples were then passed through an alcohol-xylene series and embedded in paraffin wax using the method described by Berlyn and Miksche (1976).

The wax-embedded samples were used to obtain transverse sections (15 µm thick) with a rotary microtome. Sections were mounted on microscope slides using Glycerine-Albumen as an adhesive. Sections were stained using 10% Toluidine Blue, mounted in Canada balsam to prepare permanent slides, and the anatomy of the host-parasite interface was examined under the light microscope. Photomicrographs were taken using an Olympus BH2 camera to show the haustorial penetration in different host plants.

RESULTS AND DISCUSSION

Taxonomy of lowland *Cuscuta*

The *Cuscuta* spp. found in the low country (below 1000 m altitude) are slender, thread-like creepers showing anti-clockwise twining. The stem color of these plants varied from pale green to yellow or bright orange although *Cuscuta* spp. growing in shady areas is somewhat green in colour. Furthermore, *Cuscuta* found in the lowland shows an opposite branching habit. They are either leafless or having a small, scale-like triangular leaves of about 0.1 cm in length. The inflorescence is usually cymose cluster, flowers actinomorphic, 3-4 mm long, bisexual, white, orange or yellow in colour. Calyx deeply 5 lobed, lobes orbicular, corolla as long as (1.4-3.9 mm) the corolla tube, slightly overlapping, thick at base of sinuses, broadly triangular, acute, spreading with erect or inflexed tips, stamens 5, slightly shorter than corolla lobes, filaments as long as or longer than anthers, inserted on corolla below the sinuses, styles 2, as long as depressed globose ovary. Stigmas globose. Capsule round, very much exposed and with an indentation between the two styles. depressed, globose. Capsule 1.2-3.1 mm in diameter, infrastaminal scales exserted, fimbriate, and not bifid. However, in the specimens collected from Kalutara district, the capsule was not as exposed as in specimens collected from elsewhere.

Austin (1998) reported only two species of *Cuscuta* from Sri Lanka, namely *C. chinensis* and *C. reflexa*. However, the characteristics of the *Cuscuta* spp. collected in the

present study from the lowland areas of the country did not match with the records available on those two species. Lowland *Cuscuta* showed a more exposed capsule than that of *C. chinensis*. According to Yuncker (1932), *C. chinensis* capsules split around the circumference, which is not always easy to detect. Yuncker (1932) also developed a taxonomical key to separate the *Cuscuta* spp. According to that key, the *Cuscuta* spp. of the low country is similar to *C. campestris* (Fig. 1). Most probably the *C. chinensis* is a misidentification. A modified version of Yuncker's (1932) key is given in Table 1. *Cuscuta* found in the upcountry region in this study is taxonomically similar to *C. reflexa* as recorded by Austin (1980).

Eco-geographical distribution and host range has made *C. campestris* among one of the most damaging parasites worldwide, causing severe damage to carrot, alfalfa, sugarbeet, onion, legumes and other crops (Parker and Riches, 1993; Dawson *et al.*, 1994). Unlike root parasites, *C. campestris* seeds do not require a specific stimulant to induce germination. Mechanical or chemical scarification of the seed coat is sufficient to facilitate germination (Hutchison and Ashton, 1980), thus helping *C. campestris* spread very rapidly. *C. campestris* also has a highly efficient absorption pattern of resources from the host tissues (Tsivion, 1978). Recent reports from Israel indicate that *C. campestris* is resistant to the non-selective systemic herbicide, Glyphosate (Hassar and Rubin, 2003)

Host range and Current distribution of lowland *Cuscuta*

The field investigations revealed that *Cuscuta* is widely distributed in Polonnaruwa and Anuradhapura areas associated with irrigation systems that were established during the last few decades. This indicates that *Cuscuta* dispersal has been enhanced due to increased farming systems or intensive agricultural development programmes in the country (Fig. 2).

Cuscuta fruits have papery walls and a low weight when dry and are capable of floating on water. This can lead to long distance dispersal along canals and rivers. On the other hand, wind may also be playing a role in the dispersal of these light weight fruits. The above factors may have contributed to the increase in *Cuscuta* populations in the dry zone of Sri Lanka. In WL4 zone, most of the *Cuscuta* stands were found along the railway track in the west coastal belt.

Elderly farmers in the Randenigala area (Central Province) reported that they first saw *Cuscuta* in their region about 18 years ago. Trimen (1895) reported that *C. chinensis* was very rare and only found in the suburbs of Colombo, parasitizing on grass, low herbs and shrubs. Recent studies (Arulandhy and Padmasiri 1997; Jayakody, 1997) and the present study suggest that there is an increase in the incidence of *Cuscuta* infestation during the past century. This could be due to the subsequent entry of a new strain of *Cuscuta* into the island or an environmental change that has occurred during the recent past. Austin (1980) claimed that *Cuscuta* seeds have been introduced to the country with the rice seeds imported from China. On the other hand many other types of raw foods such as dhal and onions are imported from various countries, which do not undergo the rigorous quarantine checks to which planting materials are subjected. Importation of such material contaminated with *Cuscuta* propagules could also have contributed to the sudden increase of the *Cuscuta* population in the recent past.

Host plants identified in the present study include 161 species belonging to 59 families and 139 genera (Annex 1). The host range of the parasite comprised of 27 crops,

22 weeds and 60 medicinal plants. Of the recorded hosts 24 were trees, 42 were shrubs, 12 were creepers and 83 were herbs, while 18 were monocots and 144 were dicots. Of the identified hosts 59 were exotic plants and 85 indigenous plants.

Mikania cordata and *Wedelia trilobata* were observed as the most preferred host plants of the parasite. Field investigations showed that rice and other grass species can also be parasitized by *Cuscuta*. In lowland areas, *Cuscuta* appears to have recognized primary and secondary hosts. Primary hosts are those on which *Cuscuta* can establish and develop from the seedling stage. Secondary hosts are those on which the parasite is apparently unable to establish from the seedling stage but on which it is able to make attachment and sink effective haustoria after it is well established on a primary host. *M. cordata* and *W. trilobata* can be considered as primary hosts of the lowland *Cuscuta*.

Table 1. **Key to the most common *Cuscuta* spp. (modified from Yuncker, 1932).**

1- **One style** ..... (Section Monogyna)

2- **Style shorter than the stigmas,**
Flowers 6-8 mm long, white with purplish rim. Calyx very short, Capsule conical 5-8 mm long , seeds 3-3.5 mm, Mainly to East Asia
.....*C. reflexa*

2 – **Style as long as stigmas or longer**

3- **Style as much as long as stigmas**
Flowers 3-4 mm, calyx with broad fleshy lobes, almost equaling corolla tube, capsule elongated, cone shaped, 6 mm long, seeds 3-3.5 mm. Mainly in the Middle East.
.....*C. monogyna*

3- Style longer than stigmas

4 - **Style twice longer than stigmas**
Flowers 3-5 mm long, in elongated clusters, some times red spotted, calyx much shorter than corolla, the lobes narrower than, Seeds 2-3 mm long, mainly in Europe
.....*C. lupuliformis*

4 - **Style more than twice as long as stigma**
Style much longer than short stigmas, flowers 3-4 mm long in elongated clusters, Seed about 3 mm long, Mainly in East Asia
.....*C. japonica*

1- **Two styles** ..... (Section *Cuscuta*)

5-**Stigmas linear , without knobs**

6- **Perianth mostly of 4-parts**

7- **Flowers In loose heads of 3-8 flowers**
Flowers 2-3 mm, pedicelled, Stigmas subsessile, capsule , closely enclosed by corolla. Seed about 1.25mm, Mainly West and Central Asia .....*C. pedicellata*

7- Very small heads
Flowers 1.5-2 mm, sessile in very small heads 4-6 mm across, corolla lobes with erect hooded tips. Seed about 1 mm, Mainly eastern Mediterranea.....*C. palaestina*

6- **Perianth mostly of 5-parts**

8- Calyx lobes fleshy at least at the tip
Flowers 1.5-2.5 mm, sessile in heads 5-6 mm across. Capsule round, enveloped in corolla. Seeds about 1mm. Widespread .....*C. planiflora*

8- Calyx lobes membranous

9- Stem slender reddish
Flowers 3-4 mm in dense heads 7-10 mm across, style plus stigmas slightly longer than ovary Mainly Europe .....*C. epithymum*

9-Stem not slender and reddish
Flowers 3 mm long in heads 10-15 mm across, Styles plus stigmas shorter than the ovary. Capsule roughly round. Seed about 1.2 mm. Only in flax and linseed fields. Widespread.....*C. epilinum*

5-Stigmas capitate, with knobs

10-Flowers granulate
Covered with minute protuberances 2-2.5 mm long on distinct pedicels. Seed about 1.5 mm. Mainly north and Central America and Caribbean ..... *C. indicora*

10- Flowers not granulate

11- Capsule enclosed in corolla

12- Flowers in a loose head , lobes deflexed
Flowers 2-4 mm long , some what glandular, corolla persisting as a cap on the capsule, seeds 1.5 mm. Mainly North America .....*C. gronovii*

12- Dense heads. Corolla lobes fleshy at the tip
Flowers 2-3.5 mm Capsule 3-4 mm across, enclosed tightly by corolla, circumscissile. Seeds about 1.2 mm. Mainly in East Asia. .....*C. chinensis*

11- Capsule exposed

13- Corolla lobes obtuse Infra staminal scales bifids

Flowers about 2 mm in compact heads,. Seeds about 1.5 mm, Some times reddish–glandular on capsule. Distinct crater between styles. Widespread through the Europe and Asia. .....*C. australis*

13- Corolla lobes acute, often flexed upwards., Infra-staminal scales exerted fimbriate, not bifid
Flowers 2-3 mm, in compact heads 10-12 mm across. Capsule round, 2-3 mm across, not concealed by corolla. seeds 1-1.5 mm, Almost worldwide
.....*C. campestris*

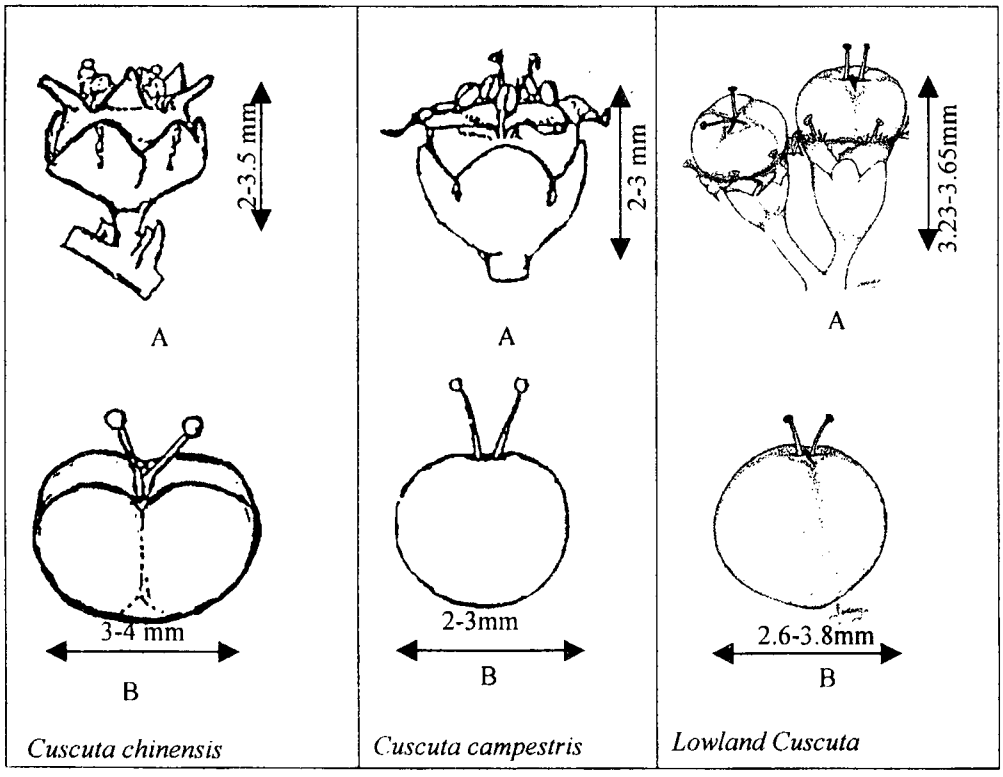

Fig. 1. Taxonomical comparison of *Cuscuta chinensis* and *C. campestris* (adopted from Yuncker, 1932), and lowland *Cuscuta* observed in the present study. (A) line drawing of *Cuscuta* flower; (B) line drawing of *Cuscuta* capsule.

It was observed that *Cuscuta* plants tend to parasitize shrubs and herbs. When they parasitize tree species, saplings and juvenile stages of the trees were preferred. However, the present study did not observe *Cuscuta* parasitizing an adult tree. In the saplings and seedlings of the tree species the resistance to penetration of *Cuscuta* haustoria may be weaker than that of mature woody plants.

The present study also revealed that *Cuscuta* parasitizes several monocotyledons including rice and some other grasses. Haustoria formation in grass plants occurred only along the veins of the leaves. However, those haustoria were easily detachable. No haustoria formation was found on stems of the grasses.

In *Alocasia cuculata* and *Musa paradisaca* haustoria formation was through the leaf petioles. However, those haustoria are also easily detachable. In monocotyledonous

plants vascular bundles are distributed randomly and close to the epidermis. Therefore, *Cuscuta* haustoria may not penetrate deep into the stem and the associations were easily broken by a small mechanical force. It was observed that some host plants such as *Cyperus* spp. act as a bridge for the parasite to spread further and find preferred host plants. These plants act as a pseudo-hosts and only help to anchor the parasite.

Cuscuta was found on various crops and wild plants, and was found to be a serious problem in the agriculture research plots in the Horticultural Research and Development Institute, Gannoruwa, Sri Lanka (mid country wet zone), where outdoor experiments on leafy vegetables are conducted.

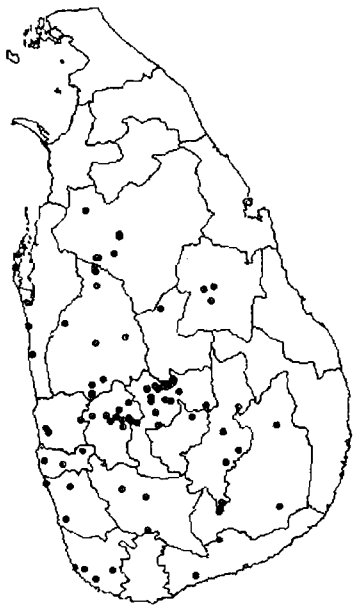

Fig. 2. Distribution of *Cuscuta* in lowland of Sri Lanka (dots indicate the location of specimens collected).

Anatomy of Haustoria and the Host-parasite association

Haustoria of *Cuscuta* have no distinct shape and they originate from the axial part of the vein. Some haustoria show a globose body with a haustorial neck. In most other parasitic plants, haustoria show clear differentiations of epidermis or peridermis cortex and the central vascular system (Riopel and Timko, 1995). However, haustoria of *Cuscuta* do not show differentiation but the stem cells are globular and haustorial cells are elongated.

The present study indicated that the shape of *Cuscuta* haustoria is variable. In hard stems (e.g. *Justicia adhathoda*) they show globose or irregular shape (Plate 1), while in most fleshy stems (e.g. *Basella* spp.) *Cuscuta* haustoria show a conical shape (Plate 2). Therefore, it can be assumed that the shape of the *Cuscuta* haustoria is related to the hardness of the host stem or penetrated depth of the haustoria. Haustoria having a spherical shape may offer the parasite more contact points with the host vascular bundles than those with conical shape.

Kuo *et al.* (1990) reported that an increased number of parenchyma cells in the haustorium could increase the absorption of nutrients by the parasite, and branching of haustoria increases the absorption area of the host-parasite interphase. Hence, it can be assumed that the production of irregular shaped, branched haustoria may be a strategy for increase in the absorption of nutrients by this holo-parasite.

According to the present investigations, the length of haustoria differs from host to host and place of infection within the host (Plates 1, 2, 3,4). If host vascular bundles are placed close to the epidermis, the haustoria appear to be shorter than in those hosts with vascular bundles located away from the epidermis. This was clearly evident in haustoria that penetrate monocots such as rice (Plate 3). As the majority of the vascular bundles are scattered closer to the epidermis, when *Cuscuta* parasitizes monocot plants, haustoria need to penetrate only a short distance. Such shorter haustoria tend to detach even with a small mechanical force.

Some plant species, such as cabbage and beans, are capable of preventing haustorial penetration and development. In these plants, when the haustoria have penetrated, the cells around the developing haustorium die due to a necrosis reaction or hypersensitivity reaction, thus preventing further development of the haustoria (Plate 4). This incompatibility may be correlated with the formation of mechanical barriers such as impenetrable boundary tissues or chemical barriers (Capdepon *et al.*, 1985). There are a few reports of resistance to parasitic plants from crop populations (Lane *et al.*, 1993; Cubero *et al.*, 1994), but studies on host parasitic associations of natural populations of parasitic and host plants are scarce.

The chemical resistance against haustoria penetration can be observed after the haustoria have penetrated some distance into the host cortex. Beans and cabbage plants clearly showed resistance after haustoria penetrated some distance within the cortex. Parenchyma cells of the host cortex around the haustoria in the infested stems turned black in colour. It can be assumed that the black (dead or necrotic) cell layer behaves as a barrier to haustoria penetration. Similar reports about resistance against *Cuscuta* penetration are given by Capdepon *et al.* (1985). Resistance to haustoria penetration may be correlated with impermeable boundary tissues or chemical resistance. Formation of a secondary tissue leads to the expulsion of already differentiated haustoria in *Gossypium hirsutum* and *Hisbiscus rosa sinensis* (Capdepon *et al.*, 1985). However, necrosis could also occur following microbial pathogen attack or wounding. Induction of cell elongation is characteristic of *C. reflexa* infection (Ihl *et al.*, 1988).

Any resistance mechanism should start at the early stages of the haustorial development or before the haustoria reach the vascular bundles of the host plant. This reaction mechanism is indicated by a blackish resistance cell layer produced around the haustoria before it reaches the vascular bundle. Due to the production of chemicals in the parenchyma cells blackish death cells are observed. A similar reaction was reported by Ihi *et al.* (1988). The resistance reaction may also be a hypersensitive response to counteract *Cuscuta* haustoria. The hypersensitive response (HR) is the most well-studied cell death process in plants. As a result of interactions of plants and incompatible pathogens, a rapid collapse of the infected tissue would occur leading to resistance. Programmed cell death (PCD) is involved in the HR, as shown by genetic, biochemical, and cell biological studies (Dangl *et al.*, 1996; Greenberg, 1997). Cell death is often a feature of disease symptoms during the susceptible interaction between plants and necrotrophic pathogens. Usually, the cells are killed by the action of pathogen-derived toxins or else die at a late stage after infection. However, cell death is not well understood in most cases. It may be a necrosis reaction or PCD reaction. Therefore, to confirm that

the resistance process occurs due to PCD more studies on morphological and biochemical processes are needed.

Any type of resistance or tolerance to parasites and pathogens may be energy-wise costly and lead to reduced allocation of limited resources to growth and reproduction (Goater and Holmes, 1997). Therefore, if a host is resistant or susceptible to the parasite, its fitness and the yield will be affected. On the other hand when the plant develops resistant mechanisms against a parasite, different toxic, hemistichal compounds need to be produced at the expense of growth and development of the host plant. Therefore, it may be advantageous to prevent field infection by *Cuscuta*.

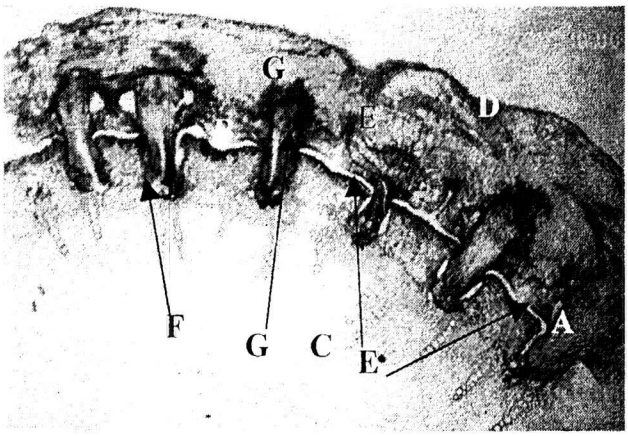

Plate 1. A transverse section of *Justicia adhathoda* stem showing haustorial penetration: (A) Endophyte, (B) Haustorium, (C) Host pith, (D) Parasite tissues, (E) Host xylem vessels (F) Host phloem, (G) Host epidermis (Magnification 10X10).

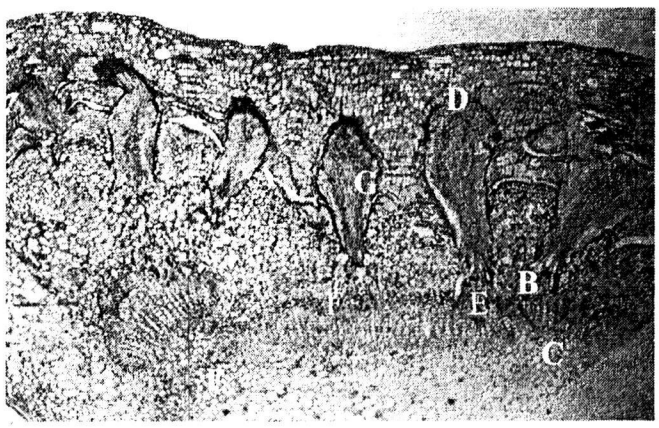

Plate 2. A transverse section of *Basella alba* stem showing haustorial penetration: (A) Endophyte, (B) Haustorium, (C) Host pith, (D) Parasite tissues, (E) Host xylem vessels (F) Host Phloem, (G) Host epidermis (Magnification 10X10).

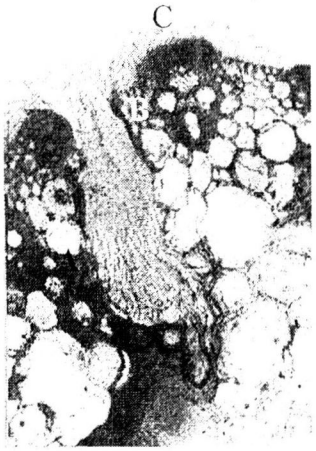

Plate 3. A transverse section of mid-rib of *Oryza sativa* showing haustorial penetration: (A) Haustorium, (B) Vascular bundle of host , (C) Parasite tissues (Magnification 10x10).

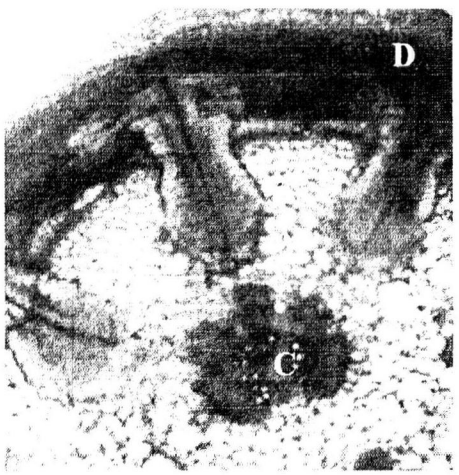

Plate 4. A transverse section of *Brassica oleraceae* leaf stem showing resistance reactions against haustorial penetration: (A) Haustorium, (B) Host vascular system, (C) Necrosis cell area, (D) Parasite tissues (Magnification 10x10).

CONCLUSIONS

Cuscuta is widely distributed in lowlands of the country. Investigations revealed that lowland *Cuscuta* spp. found in Sri Lanka is not *C. chinensis* or *C. reflxa* as previously recorded. It is more similar to the problematic parasitic weed *C. campestris*. However, the possibility of differentiation of a naturalized *Cuscuta* spp. to a new strain could not be ruled out.

Most of the *Cuscuta* populations are distributed in agricultural areas (mainly in the dry zone) along the irrigation channels, abandoned lands and in roadside vegetations.

As *Cuscuta* is found on banks of irrigation channels there is a possibility of further infestation in agricultural fields. In the dry zone, irrigation channels could be a major dispersal medium of *Cuscuta*. Furthermore, *Cuscuta* has a broad host range that also includes rice. *Cuscuta* also parasitizes many important medicinal plants. Thus, precautionary measures should be adopted to prevent infestation of agricultural fields by this holo-parasite.

Haustoria of *Cuscuta* do not show complex anatomical differentiations, but penetration distance depends on location of the host vascular system. However, some host plants show resistance to the penetration of haustoria, where the resistance mechanism could be mechanical or chemical. Mechanical forms of resistance could be by development of epidermal hairs and multicellular epidermis, whereas the chemical methods would be a hypersensitive reaction or programmed cell death. However, further studies are suggested for clear understanding about resistance mechanisms of the hosts to the parasite.

REFERENCES

Arulandhy, V. and Padmasiri, I.S. (1987). Threat of *Cuscuta* parasite in Chili. Krushi. 10:52-54.

Austin, D. F. (1980). Convolvulaceae. pp. 305-307. *In*: Dassanayake, M.D. and Fosberg F.R. (Eds.), Revised Hand Book to the flora of Ceylon. Amerind publishing Co. Pvt. Ltd., New Delhi.

Austin, D. F. (1998). Parallel and convergent evolution in the Convolvulaceae. pp. 201-234. *In:* Biodiversity and taxonomy of tropical flowering plants. Mentor Books.

Berlyn, G. and Miksche, P. (1976). Botanical Micro Techniques and Cytochemistry. Second Edition, The Iowa University Press, Ames, Iowa.

Capdepon, M., Fer, A. and Ozenda, P. (1985). Sur un Systeme inedit de reject d'un parasite: example de la Cuscute sur Cotonnier (*C. lupiliformis* Krock.Sur *Gossypium hirsutum* L.) C R Acad. Sci. Paris. 300 (Abstract).

Cubero, J.I., Pieterse. A.H., Khalil, S.A. and Sauerbon, J. (1994). Screening techniques and sources of resistance to parasitic angiosperms. Euphytica 73:51-58.

Eppler, R.E. and Norris, R. (1995) Control of Parasitic Weed Parasitic Plants. pp. 225-272. In: Press, C. and Graves, J.D. (Eds) Chapman and Hall, London.

Dangl, J.L., Dietrich, R.A. and Richberg, M.H. (1996). Death don't have no mercy: Cell death programs in plant–microbe interactions. Plant Cell 8:1793-1807.

Dawson, J. H. (1989). Dodder (*Cuscuta* spp.) control in established alfalfa (*Medicago sativa*) with glyphosate and SC-0224. Weed Technol. 3: 552-559.

Dawson, J. H., Musselman, L. J., Wolswinkel, P. and Dorr, 1. (1994). Biology and control of *Cuscuta*. Review Weed Science 6:265-317.

Goater, C.P and Holmes, J.C. (1997). Parasite –mediated natural selection. pp. 11-29. *In*: D.H.Clayton and J.Moore. Ed). Host Parasite Evolution. General Principle and Avian Models,Oxford University Press, Oxford.

Greenberg, J.T. (1997). Programmed cell death in plant–pathogen interactions. Annu. Rev. Plant Physical. Plant Mol. Biol 48:525-545.

Hassar, N.T and Rubin, B. (2003). Natural tolerance of *Cuscuta campestris* to herbicides inhibiting amino acid biosynthesis. Weed Research 43: 341-345

Hutchison, J.M. and Ashton, F.M. (1980). Germination of field dodder (*Cuscuta campestris).* Weed Sci. 28:330-333.

Ihl. B., Hagen, A., Jacob, F. (1988). Studien an *Cuscuta reflexa* Roxb. VII *Zum Abwehrmechanisums* von *Lycoppersicon esculentum* Mill. Flora. 181: 383-393.

Jayakody, D.P.P. (1995). Some biological aspects of *Cuscuta chinensis* Lam. Paper presented at the 2nd Weed Science Congress, Weed Science Society of Sri Lanka, Peradeniya, Sri Lanka (Abstract).

Jeschke, W. D., Rath, W., Baumel, P., Czygan, F.C., and Proksch, P. (1994). Modelling the flow and partitioning of carbon and nitrogen in the holoparasite *Cuscula reflexa* Roxb. and its host *Lupinus albus* L.I. Methods for estimating net flows. J. Exp. Bot. 45: 801-812.

Kondap, S.M. and Kumar, R.M. (1993). Management of *Cuscuta* in croplands and fallows: Integrated weed management for sustainable agriculture. Proceedings of the International Symposium (Hisar, India, 18-20 November). Indian Society of Weed Science 407-411.

Kuo, J., Pate, J.S. and Davidson, N.J.(1990). Ultra structure of haustorial interphone and apoplastic connection between host and the root hemiparasite *Olax phyllanthi* (Labill) R.Br.(Olacaceae). Protoplasma 150:27-30.

Kumar, R. and Mohan, J. (1994). Transmission of lentil Mosaic Virus. Legume Research 17:217-221.

Lane, J.A., Bailey, J.A., Butler, C. R., and Terry, P.J. (1993). Resistance of cowpea (*Vigna unguiculata* (L) Walp.) to *Striga gesnerioides* (Willd.) Vatke, a parasitic angiosperm. New Phytol. 125: 405-412.

Lawrance, J.K (1966) Weed of the world. Interscience Publisher. Inc. pp. 44-45.

Marambe, B., Wijesundara, S., Tennakoon, K., Pindeniya, D. and Jayasinghe, C. (2002). Growth and development of *Cuscuta chinensis* Lam. and its impacton selected crops. Weed Biology and Management 2:79-81.

Marcone, C., Hergenhahn, F., Ragozzino, A. and Seemüller, E. (1999). Dodder, Transmission of Pear Decline, European Stone Fruit Yellows, Rubus Stunt, *Picris echioides* Yellows and Cotton Phyllody Phytoplasmas to Periwinkle. Journal of Phytopathology 147:183 -187.

Nickrent, D. L. (2002). Chapter 3. Phylogenetic Origins of Parasitic Plants.Lopez-Saez, J.A., Catalan, P. and Saez, L. (Eds). Parasitic Plants of the Iberian Peninsula and Balearic Islands. Mundi-Prensa, Madrid. Pp. 29-56.

Parker, C. and Riches, C.R. (1993). Parasitic weeds of the world: Biology and control. Parker, C. and Riches, C. R. (Eds), Allingford, CAB International. pp. 331-332.

Rao K.N., Rao, R.S.N., Ransom, J.K., Musselman, L.J., Worsham, A.D. and Parker, C. (1991). Evaluation of herbicides to control *Cuscuta* spp. in rice fallow black gram. Proceedings of the 5th international symposium of parasitic weeds, Nairobi, Kenya. 164-169.

Riopel, J.L. and Timko, M.P. (1995). Haustorial initiation and differentiation. Parasitic Plant. In:Press, M.C. and Graves, J.D. (Eds). Chapmn and Hall, London. pp. 39-75.

Sadler, H.A., Else, M..J. and Sutherland. M. (1997). Application of sand for inhibition of swamp Dodder (*Cuscuta gronovii)* seedling emergence and survival on Cranberry *(Vaccinium macrocarpon)* Bogs. Weed Technology 11: 318-325.

Trimen, H. (1895). Handbook to the Flora of Ceylon. Dulau and Co., Soho, London. 3: 229.

Tsivion, Y. (1978) Loading of assimilates and some sugars into the translocation system of *Cuscuta.* Aust. J. Plant Physiol. 5 : 851-857.

Weber, W.A. (1986). Colorado Flora: Western Slope. Colorado Associated University Press, Boulder.

Yuncker, T.G. (1932). The Genus *Cuscuta.* Memoirs of the Torrey Botanical Club.18(2):250.

Zhang, X. C. (1991). Studies on the infection of MLO of jujube witches'-broom disease to periwinkle, *Vinca rosea.* Tropical Plant Diseases 9:251-256

Annex 1. Host-range of lowland *Cuscuta* spp. recorded in Sri Lanka during the study. Cr=creeper; Hb=herb; Sh=shrub; Tr=tree; Hab=Habit; Cr=Crop; Ex=Exotic plant; In=Indigenous plant; We=Weed Me=Medicinal plant; M/D =Monocot or Dicot plant; * indicates representation of the category.

	Family	Name	Hab	Cr	Ex	In	We	Me	M/D
1	Fabaceae	*Abrus melanospermus*	Cr			*	*	*	D
2	Malvaceaee	*Abutilon indicum*	Hb			*	*	*	D
3	Euphorbiaceae	*Acalypha indica*	Sh			*	*		D
4	Euphorbiaceae	*Acalypha wilkesiana* cv. Macrophylla	Sh		*				D
5	Euphorbiaceae	*Acalypha wilkesiana* cv. Macafena	Sh		*				D
6	Amaranthaceae	*Achyranthes aspera*	Hb			*			D
7	Amaranthaceae	*Aerva lanata*	Hb						D
8	Amaranthaceae	*Ageratum conyzoides*	Hb			*	*	*	D
9	Arecaceae	*Alocasia cuculata*	Sh		*			*	M
10	Amaranthaceae	*Amaranthus dubius*	Hb			*			D
11	Amaranthaceae	*Amaranthus spinosus*	Hb			*		*	D
12	Amaranthaceae	*Amaranthus tricolor*	Hb	*	*				D
13	Amaranthaceae	*Amaranthus viridis*	Hb			*		*	D
14	Araceae	*Amorphophallus paeoniifolius*	Hb			*		*	D
15	Polygonaceae	*Antigonon leptopus*	Cr			*			D
16	Convolvulaceae	*Argyreia populifolia*	Cr			*		*	D
17	Meliaceae	*Azadirachta indica*	Tr			*		*	D
18	Euphorbiaceae	*Barringtonia racemosa*	Tr			*		*	D
19	Basellaceae	*Basella alba*	Hb	*	*				D
20	Begoniaceae	*Begonia ulmifolia*	Hb			*			D
21	Nyctaginaceae	*Boerhavia diffusa*	Hb			*			D
22	Clusiaceae	*Calophyllum inophyllum*	Tr			*			D
23	Asclepiadaceae	*Calotropis gigantea*	Tr			*		*	D
24	Theaceae	*Camelia sinensis*	Sh	*					D
25	Cannaceae	*Canna indica*	Sh		*				M
26	Solanaceae	*Capsicum annuum*	Hb	*		*			D
27	Sapindaceae	*Cardiospermum halicacabum*	Hb			*		*	D

28	Caricaceae	*Carica papaya*	Tr	*		*		*	D
29	Apiaceae	*Catharanthus roseus*	Hb		*			*	D
30	Bombacaceae	*Ceiba pentandra*	Tr		*				D
31	Amaranthaceae	*Celosia argentea*	Hb		*				D
32	Apiaceae	*Centella asiatica*	Hb	*		*		*	D
33	Apocynaceae	*Cerbera manghas*	Tr			*		*	D
34	Poaceae	*Chloris barbata*	Hb				*		M
35	Asteraceaee	*Chrysanthemum morefolium*	Hb		*				D
36	Poaceae	*Chrysopogon aciculatus*	Hb			*	*		M
37	Rutaceae	*Citrus aurantifolia*	Tr	*				*	D
38	Capparaceae	*Cleome viscosa*	Hb			*			D
39	Urticaceae	*Clerodendrum paniculatum*	Tr		*			*	D
40	Fabaceae	*Clitoria ternatea*	Cr			*			D
41	Crassulaceae	*Coccinia grandis*	Hb			*			D
42	Euphorbiaceae	*Codiaeum variegatum*	Sb		*				D
43	Labiatae	*Coleus blumeii*	Hb		*				D
44	Araceae	*Colocasia esculenta*	Hb	*				*	M
45	Commelinaceae	*Commelina benghalensis*	Hb			*			D
46	Tiliaceae	*Corchorus aestuans*	Hb			*			D
47	Fabaceae	*Crotalaria juncea*	Hb		*				D
48	Cucurbitaceae	*Cucurbita maxima*	Cr	*		*			D
49	Thelypteridaceae	*Cyclosorus interruptus*	Sh			*			D
50	Poaceae	*Cymbopogon nadus*	Hb			*			M
51	Poaceae	*Cynodon dactylon*	Hb			*			M
52	Asteraceaee	*Dahlia variabilis*	Hb		*				D
53	Solanaceae	*Datura metel*	Sh			*		*	D
54	Apiaceae	*Daucus carota*	Hb	*					D
55	Fabaceae	*Desmodium heterophyllum*	Hb			*		*	D
56	Fabaceae	*Desmodium heterocarpum*	Hb			*		*	D
57	Fabaceae	*Dichrostachys cinerea*	Hb			*		*	D
58	Verbenaceae	*Duranta repens*	Sh		*				D
59	Poaceae	*Echinochloa crusgalli*	Hb		*		*		M
60	Poaceae	*Eichhornia crassipes*	Hb		*		*		M
61	Fabaceae	*Erythrina indica*	Tr			*		*	D

62	Euphorbiaceae	*Euphorbia heterophylla*	Hb				*	*	D
63	Euphorbiaceae	*Euphorbia hirta*	Hb			*			D
64	Moraceae	*Ficus racemosa*	Tr			*			D
65	Acanthaceae	*Fittonia verschaffeltii*	Sh		*				D
66	Urticaceae	*Fleurya interrupta*	Hb			*			D
67	Rubiaceae	*Gardenia latifolia*	Sb		*				D
68	Asteraceaee	*Gerbera jamesonii*	Hb		*				D
69	Fabaceae	*Gliricidia sepium*	Tr		*	*		*	D
70	Tiliaceae	*Grewia orientalis*	Tr			*			D
71	Malvaceaee	*Hedyotis neesiana*	Hb			*			D
72	Heliconiaceae	*Heliconia spp*	Sh		*				D
73	Periplocaceae	*Hemidesmus indicus*	Hb			*		*	D
74	Malvaceaee	*Hibiscus furcatus*	Hb			*			D
75	Malvaceaee	*Hibiscus rosasinensis*	Hb		*				D
76	Malvaceaee	*Hibiscus surattensis*	Hb		*				D
77	Malvaceaee	*Hibiscus vitifolius*	Hb			*			D
78	Malpighiaceae	*Hiptage benghalensis*	Cr			*		*	D
79	Apocynaceae	*Ichnocarpus frutescens*	Sh			*		*	D
80	Poaceae	*Imperata cylindrica*	Hb		*		*		M
81	Convolvulaceae	*Ipomoea aquatica*	Hb	*					D
82	Convolvulaceae	*Ipomoea palmata*	Hb			*			D
83	Convolvulaceae	*Ipomoea batatas*	Hb	*					D
84	Convolvulaceae	*Ipomoea mauritiana*	Hb			*			D
85	Convolvulaceae	*Ipomoea pes-caprae*	Hb			*		*	D
86	Rutaceae	*Ixora coccinea*	Sh			*		*	D
87	Olacaceae	*Jasminum angustifolium*	Sh			*			D
88	Euphorbiaceae	*Jatropha curcas*	Sh		*			*	D
89	Euphorbiaceae	*Justicia adhathoda*	Sh			*			D
90	Verbenaceae	*Lantana camara*	Sh		*			*	D
91	Araceae	*Lasia spinosa*	Sh	*					M
92	Fabaceae	*Leucaena leucocephala*	Tr		*			*	D
93	Lamiaceae	*Leucas zeylanica*	Hb			*		*	D
94	Onagraceae	*Ludwigia decurrens*	Hb			*			D
95	Onagraceae	*Ludwigia perennis*	Hb			*			D

96	Solanaceae	*Lycopersicon esculentum*	Sh	*					D
97	Fabaceae	*Macroptilium atropurpureum*	Hb	*				*	D
98	Fabaceae	*Macroptilium lathyroides*	Hb	*	*				D
99	Euphorbiaceae	*Manihot esculenta*	Sh	*	*				D
100	Euphorbiaceae	*Manihot glaziovii*	Sh			*			D
101	Asteraceae	*Mikania cordata*	Cr		*		*		D
102	Fabaceae	*Mimosa pudica*	Hb				*	*	D
103	Fabaceae	*Mimosa invisa*	Sh		*		*		D
104	Fabaceae	*Mimosa pigra*	Sh		*		*		D
105	Araceae	*Monstera oblique* cv. *expilata*	Hb		*				M
106	Moringaceae	*Moringa olefera*	Tr	*				*	D
107	Tiliaceae	*Muntingia calabura*	Tr		*			*	D
108	Musaceae	*Musa paradisaca*	Sh	*					M
109	Apocynaceaea	*Nerium oleander*	Sh		*			*	D
110	Lamiaceae	*Ocimum tenuiflorum*	Sh			*		*	D
111	Rubiaceae	*Oldenlandia biflora*	Sh		*				D
112	Poaceae	*Oryza sativa*	Sh	*					D
113	Oxalidaceae	*Oxalis corniculata*	Hb		*	*		*	D
114	Pandanaceae	*Pandanus amaryllifolius*	Sh			*			M
115	Poaceae	*Panicum maximum*	Hb		*		*		M
116	Apocynaceae	*Parsonsia laevigata*	Cr			*			D
117	Poaceae	*Paspalidium flavidium*	Hb		*		*		M
118	Passifloraceae	*Passiflora foetida*	Cr			*			D
119	Euphorbiaceae	*Pedilanthus tithymaloides*	Hb		*				D
120	Lauraceae	*Persea americna*	Tr	*				*	D
121	Fabaceae	*Phaseolus lunatus*	Cr	*		*			D
122	Verbenaceae	*Phyla nodiflora*	Hb			*		*	D
123	Euphorbiaceae	*Phyllanthus urinaria*	Hb					*	D
124	Apocynaceae	*Plumeria obtusa*	Tr		*			*	D
125	Apocynaceae	*Plumeria rubra*	Tr		*			*	D
126	Araliaceae	*Polycias scutellaria*	Sh		*				D
127	Polygonaceae	*Polygonum crispus*	Sh			*			D
128	Araceae	*Pothos scandens*	Cr			*			M
129	Myrtaceae	*Psidium guajava*	Tr	*					D

130	Combretaceae	*Quisqualis indica*	Sh		*				D
131	Euphorbiaceae	*Ricinus communis*	Sh			*		*	D
132	Phytolaccaceae	*Rivina humilis*	Hb				*		D
133	Rosaceae	*Rosa indica*	Sh		*	*			D
134	Malvaceaee	*Sida mysorensis*	Hb		*	*		*	D
135	Malvaceaee	*Sida rhombifolia*	Hb		*	*		*	D
136	Malvaceaee	*Sida acuta*	Hb		*	*		*	D
137	Malvaceaee	*Sida retusa*	Hb	*				*	D
138	Solanaceae	*Solanum macrocarpon*	Hb	*				*	D
139	Solanaceae	*Solanum melongena*	Hb						D
140	Acanthaceae	*Spilanthes paniculata*	Hb			*			D
141	Anacardiaceae	*Spondias pinnata*	Tr	*		*		*	D
142	Verbenaceae	*Stachytarpheta indica*	Hb		*	*			D
143	Verbenaceae	*Stachytarpheta jamaicensis*	Hb		*		*		D
144	Verbenaceae	*Stachytarpheta urticaefolia*	Hb			*			D
145	Apocynaceae	*Tabernaemontana divaricata*	Sh			*			D
146	Fabaceae	*Tephrosia purpurea*	Hb			*			D
147	Combretaceae	*Terminalia catappa*	Tr					*	D
148	Malvaceaee	*Thespesia populnea*	Tr		*			*	D
149	Acanthaceae	*Thunbergia alata*	Sh		*				D
150	Acanthaceae	*Thunbergia erecta*	Sh		*				D
151	Asteraceae	*Tithonia diversifolia*	Sh			*	*		D
152	Asteraceae	*Trianthema decandra*	Sh		*				D
153	Asteraceae	*Tridax procumbens*	Hb				*	*	D
154	Malvaceae	*Urena sinuata*	Hb			*	*		D
155	Malvaceae	*Urena lobata*	Hb			*	*		D
156	Asteraceae	*Vernonia cinerea*	Hb			*		*	D
157	Verbenaceae	*Vitex trifolia*	Sh			*			D
158	Asteraceae	*Wedelia trilobata*	Cr		*		*		D
159	Fabaceae	*Xanthium indicum*	Hb		*		*		D
160	Zingiberaceae	*Zingiber officinale*	Hb	*	*			*	M
161	Rhamnaceae.	*Ziziphus lucida*	Sh			*		*	D