

**HOST PLANTS AND THE HAUSTORIUM OF
CUSCUTA JAPONICA CHOISY VAR.
FORMOSA (HAY.) YUNKER
(CONVOLVULACEAE)**

CHANG-SHENG KUOH⁽¹⁾ and SU-HWA TSAI CHIANG⁽²⁾

(Manuscript received 30 November 1988; revised version accepted 15 March 1989)

Abstracts: *Cuscuta* (dodder) are parasitic plants that attack many commercial crops and orchards. There are two species in Taiwan; i. e., *C. australis* R. Brown and *C. Japonica* Choisy var. *formosana* (Hay.) Yunker. In this report we present the work on the host plants and the haustorium of the latter species.

Field studies indicate that at least 36 host plants are attacked by this dodder including fruit trees, naturally occurring woody species, many herbaceous annual and perennial plants. The spiral growth of this dodder uniformly shows the directions to right, counterclockwise.

Two types of hyphae including intercellular and intracellular type are found which variable with host plants. The penetration of the tip of the haustorium is also under the influence of internal structure of the host. The presence of prehaustorium, brush like structure and granulated cells in the tip of haustorium are a general feature of this dodder.

INTRODUCTION

Dodder (*Cuscuta* spp.) are parasitic plants with slender thread like stems coil on and fasten to their host plants with haustoria and are noxious weeds of many crops, orchards, naturally occurring woody plants and even many herbaceous weedy species (Kuijt, 1969, Division of Agricultural Science University of California, 1976). Dodder reduces the yields of host crop plants, and transmits the plant disease (Yang, 1983). Plant pathologists have often used training dodder to transfer a pathogen from one host to another (Yang, 1983). So the host parasite relationship becomes one of the basic knowledge for controlling dodder. Krohn (1934) has reported that not all plants are susceptible to parasitism from dodder. Gaertner (1950) has reviewed the literature on host species and concluded that data on species parasites by dodder are generally lacking.

Some published results concerning the coiling habit of dodder are contradictory; a clockwise growth direction has been reported (Singh, 1933), but Kuijt (1969) found that the counterclockwise direction is uniformly existed.

The dodder haustorium has been intensely studied. Peruse (1893) recognized an ephemeral organ called "prehaustoria" before the formation of the actual haustorium but Kuijt (1969) thought that it may not be a general feature. There are several changes of the haustorium after its intrusive growth into the host

(1) 郭長生, Department of Biology, National Cheng Kung University, Tainan, Taiwan, ROC.

(2) 江蔡淑華, Department of Botany, National Taiwan University, Taipei, Taiwan, ROC.

body (Thomson, 1925, Bennett, 1944 and Truscott, 1958) and Kujit (1969) points out that the organization and differentiation of dodder haustoria can be influenced by the host species invaded.

Two species of dodder, *C. australis* and *C. japonica* var *formosana* are found in Taiwan (Chang, 1978) in this report, we present the work on the host plants and the haustorium of the latter species, i. e. Formosan dodder.

Field studies indicate that at least 36 host plants were attacked by this dodder including fruit trees, naturally occurring woody species, many annual and perennial herbaceous plants. The coiling direction is to the right, counterclockwise.

The haustoria of this dodder in 25 different hosts are studied. Three types of hyphae including intercellular, intracellular and contact type are found and are diverse with host plants. The penetration of the tip of the haustorium is under the influence of the internal structure of the host. The prehaustorium, brush like structure and tannin cells in the tip of haustorium is a general feature of this dodder.

MATERIALS AND METHODS

I. Host plants and Coiling habit

The plants attacked by Formosan dodder were collected in the field; the herbarium specimens were made and deposited at NCKU herbarium as voucher specimens (Table 1).

II. Internal structure

The organ penetrated by haustoria of the dodder was excised for histological preparations. It was fixed in formalin-acetic acid alcohol, dehydrated in a tertiary butyl alcohol series, embedded in paraffin and sectioned on a rotary microtome at 10 μ m. A simple stain of Delafield's hematoxylin gave good result (Chiang, 1975). Micrographs of internal structure were taken with a Nikon Labophot microscope.

RESULTS AND DISCUSSION

I. Habits of host

36 host species attacked by Formosan dodder are recorded with their vouchers and habits listed in Table 1. Hosts of this dodder include fruit trees (Plate 1-2, 1-3 and 2-2), naturally occurring woody species (Pl. 2-1), and many annual and perennial herbaceous plants (Pl. 1-1 and 2-3). All the hosts belong to vascular plants including ferns, dicots and monocots.

II. Coiling habits

A clockwise coiling habit has been reported by Singh (1933), but we find that the counterclockwise direction is uniformly present in Formosan dodder (Pl. 1, Pl. 2. indicated by arrowheads). This agrees with Kujit's report (1969).

III. The formation of haustoria

1. Prehaustorium

A prehaustoria stage before true haustorial formation has been reported by

Table 1. The host of Formosan dodder

Family	Species	Voucher	Habit
Caprifoliaceae	<i>Sambucus formosana</i>	c45	herb
Caryophyllaceae	<i>Drymaria cordata</i>	c57	herb
Commelinaceae	<i>Commelina</i> sp.	41	herb
Compositae	<i>Ageratum houstonianum</i>	c42	herb
Compositae	<i>Bidens</i> sp.	c33	herb
Compositae	<i>Crassocephalum rabens</i>	c35	herb
Compositae	<i>Elephantopus mollis</i>	c25	herb
Compositae	<i>Synedrella nodiflora</i>	s. n.	herb
Convolvulaceae	<i>Cuscuta japonica formosana</i>	c14, c21	vine
Convolvulaceae	<i>Ipomoea batatas</i>	c38	herb
Convolvulaceae	<i>Ipomoea</i> sp.	c44, c13	vine
Dennstaedtiaceae	<i>Dennstaedtia</i> sp.	c31	herb
Ebenaceae	<i>Diospyros kaki</i>	c48	tree
Euphorbiaceae	<i>Aleurites montana</i>	c50	tree
Euphorbiaceae	<i>Macaranga tanarius</i>	c15, c30	tree
Euphorbiaceae	<i>Ricinus communis</i>	c54	shrub
Labiatae	<i>Hyptis rhomboides</i>	c37	herb
Leguminosae	<i>Mimosa invisa</i>	c43	herb
Leguminosae	<i>Pueraria montana</i>	c22	vine
Leguminosae	<i>Sesbania roxburghii</i>	c28	shrub
Malvaceae	<i>Urena lobata</i>	c53	shrub
Poaceae	<i>Cynodon dactylon</i>	c59	herb
Poaceae	<i>Cyrtococcum accrescense</i>	c32	herb
Poaceae	<i>Oplismenus compositus</i>	c34	herb
Poaceae	<i>Papalum conjugatum</i>	c46	herb
Poaceae	<i>Pennisetum purpureum</i>	c56	herb
Polygonaceae	<i>Polygonum chinense</i>	c51	herb
Ranunculaceae	<i>Clematis</i> sp. 1	c55	vine
Ranunculaceae	<i>Clematis</i> sp. 2	c52	vine
Rubiaceae	<i>Paederia scandens</i>	c27, c24	vine
Rutaceae	<i>Citrus grandis</i>	c49	tree
Sapindaceae	<i>Euphoria longana</i>	c58	tree
Stemonaceae	<i>Stemona tuberosa</i>	c23	vine
Urticaceae	<i>Boehmeria nivea</i>	c36	shrub
Verbenaceae	<i>Clerodendron paniculatum</i>	c16	shrub
Verbenaceae	<i>Lantana camara</i>	39	shrub

Peruse (1893). Kuijt (1969) suggested that it may not be a general feature because it has rarely been mentioned in the scientific literature. In our observations, three to four subepidermal layers of cells are compactly arranged in the cortex of Formosan dodder, with isodiametric cells formed and ephemeral zone prior to the formation of haustorium (Pl. 3, Pl. 4 and Pl. 7-3). This prehaustorial stage is common in Formosan dodder. When contacted with the host organ, the epidermal cells of dodder become elongated at the contact area. The tips constitute of granulated cells which are full of granules and easily stained substance. A tooth like protrusion of the outer periclinal wall of the epidermal cell well matches the sunken surface of the host, forming a key lock feature (Pl. 3, Pl. 4, Pl. 8 and Table 2).

Table 2. The haustoria of Formosan dodder variable with the Host

Family	Species	Ke.	Ta.	Br.	Zo.	Hy.	Tr.
Caprifoliaceae	<i>Sambucus formosana</i>	+	+	+	+		
Caryophyllaceae	<i>Drymaria cordata</i>	+		+	+	+	+
Commelinaceae	<i>Commelina sp.</i>	+	+	+	+	+	+
Compositae	<i>Ageratum houstonianum</i>	+	+	+	+		
Compositae	<i>Elephantopus mollis</i>	+	+	+			
Compositae	<i>Synedrella nodiflora</i>	+	+	+	+	+	+
Convolvulaceae	<i>Ipomoea batatas</i>	+	+	+	+	+	+
Convolvulaceae	<i>Ipomoea sp.</i>	+	+	+	+		
Ebenaceae	<i>Diospyros kaki</i>	+	+	+	+	+	+
Euphorbiaceae	<i>Macaranga tanarius</i>	+	+	+	+	+	
Labiatae	<i>Hyptis rhomboides</i>	+	+	+			
Leguminosae	<i>Mimosa invisa</i>	+	+	+			
Leguminosae	<i>Sesbania roxburghii</i>	+	+	+	+		
Malvaceae	<i>Urena lobata</i>	+	+	+	+	+	+
Poaceae	<i>Cynodon dactylon</i>	+	+	+	+		
Poaceae	<i>Cyrtocaccum accrescense</i>	+	+	+	+		
Poaceae	<i>Papalum conjugatum</i>	+	+	+	+		
Poaceae	<i>Pennisetum purpureum</i>	+	+	+	+	+	
Polygonaceae	<i>Polygonum chinense</i>	+	+	+	+	+	
Ranunculaceae	<i>Clematis sp. 1</i>	+	+	+	+	+	
Ranunculaceae	<i>Clematis sp. 2</i>	+	+	+			
Rubiaceae	<i>Paederia scandens</i>	+	+	+	+	+	+

Note: Ke.—Key and lock connection between the host and the dodder.

Ta.—Tannin-like granules.

Br.—Brush-like structure of dodder's epidermis.

Zo.—Prehaustorial zone in cortex of the dodder.

Hy.—Hypha structure in the tip of the haustorium.

Tr.—Tracheary elements or xylem bridge of the haustorium.

"+"—Observed with microscopy.

2. Haustorial primordium

The origin of haustorium seems to be variable with different dodders, an endogenous nature similar to adventitious root has been reported by Peruse (1893) and a cortex derived pattern has been mentioned by Fahn (1982). However, we find that the haustorial primordium of Formosan dodder is differentiated from interfascicular cambium (Pl. 7-3).

IV. Structure of haustoria

1. Basic structure

The haustorium is originated from a small group of meristematic cells, some of them begin to divide and elongate, penetrate into the host tissue, finally the haustorial tip gives rise to a branching filament like structure. The cells of this hyphal structure under go a series of cell divisions during the process of invasion (Pl. 6-1, 7-1, 7-2, 9-1 and 9-2). Fahn (1982) has revised and mentioned three types of hyphal structure, namely, intercellular hyphae, intracellular hyphae and contact hyphae.

In our observations, two of the above types or states of hyphae are found. The intercellular hyphae constitute a pack of filamentous cells pressing the host tissue (Pl. 9-3, 10-2 and 11-1).

The intracellular hyphae together with the filamentous intercellular hyphae penetrate into the host cell (Pl. 7-1, 11-2 and 11-3). The hyphae change in structures and contents from the time of penetration to the time it begins to conduct food to the external dooder plant (Kuijt, 1969). Therefore, the various stages in the same hypha have been found.

2. Penetration and Host

The penetration of the tip of the haustorium is under the influence of internal structure of the host (10-1 and 10-3). Some haustoria are well connected with the vascular bundles of host (Pl. 5-1, 5-3, 6-2 and 6-3), but some others may pass through the interfascicular region of the host (Pl. 4-1 and Pl. 7-1).

The mature structure of haustoria of different dodders were reviewed and described by Kuijt (1979). He concluded that the possibility of structural variability of haustoria can be influenced by the host species. Kindermann (1928) pointed out that the presence of hyphae and/or tracheary bridges are the characters of a normal haustorium. In our study, at least 9 species of hosts are connected to the haustoria by a xylem bridge (Pl. 6-2, 7-1, 9-3, 11-2 and Table 2).

The development and maturation of the haustorium of the Formosan dodder in 25 host species are examined. It is concluded that the presence of prehaustorium, brush like structure and granulated cells in the tip of haustorium is a general feature during the development (Table 2), and the penetration of the tip is influenced by the host habit and its internal structure as well.

ACKNOWLEDGMENT

This work was a part of a project supported by the National Science Council of the Republic of China. Thanks are also due to Miss H. Y. Chang the research assistant of this project for her painstaking work on preparation of the anatomical sections.

LITERATURES CITED

- BENNETT, C. W. 1944. Studies of dodder transmission of plant viruses. *Phytopath.* **34**: 905-932.
- CHANG, C. E. 1978. Convolvulaceae in Flora of Taiwan, Vol. IV. Editorial Committee of Flora of Taiwan ed. Epoch. Publ. Co., Taipei, Taiwan.
- DIVISION OF AGRICULTURAL SCIENCES UNIVERSITY OF CALIFORNIA. 1976. *Cuscuta* spp. (Dodder): A literature review of its biology and control. Univ. of California Press, Berkeley, USA.
- FAHN, A. 1982. Plant anatomy. 3rd ed. Pergamon Press Inc., New York.
- GAERTNER, E. E. 1950. Studies of seed germination, seed identification and host relationships in dodders, *Cuscuta* sp. Cornell Univ. Agr. Expt. Sta. Mem. 294 (Cited from Kuijt, J. 1969).
- KINDERMANN, A. 1928. Haustorialstudien an *Cuscuta*-Arten. *Planta* **5**: 769-783.
- KROHN, V. 1934. Kurzer Bericht über *Cuscuta halophyta* Fries. *Phytopath. Zeitschr.* **7**: 505-14.
- KUIJT, J. 1969. The biology of parasitic flowering plants. Univ. of California Press, Berkeley and Los Angeles, California, USA.
- PERUSE, G. J. 1893. On the structure of haustoria of some phanerogamic parasites. *Ann. Bot.* **7**: 291-327.
- SINGH, J. C. N. 1933. *Cuscuta* as a parasite on a fern. *Ann. Bot.* **47**: 423-425.
- THOMSON, J. 1925. Studies in irregular nutrition. No. 1. The parasitism of *Cuscuta reflexa* (Roxb.) *Trans. Roy. Soc. Edinb.* **54**: 343-356. (Cited from Kuijt, J. 1969).
- TRUSCOTT, F. H. 1958. On the regeneration of new shoot from isolated dodder haustoria. *Amer. J. Bot.* **45**: 169-177.
- CHIANG, TSAI S. H. 1975. A technical manual for plant anatomy. World Book Co., Taipei, Taiwan.
- YANG, I. L. 1983. Dodder transmission and microscopic observations of peanut witches broom disease. *NSC monthly, ROC.* **11**(9): 821-826. *Natl. Sci. Council, Taipei, ROC.*

PLATE 1

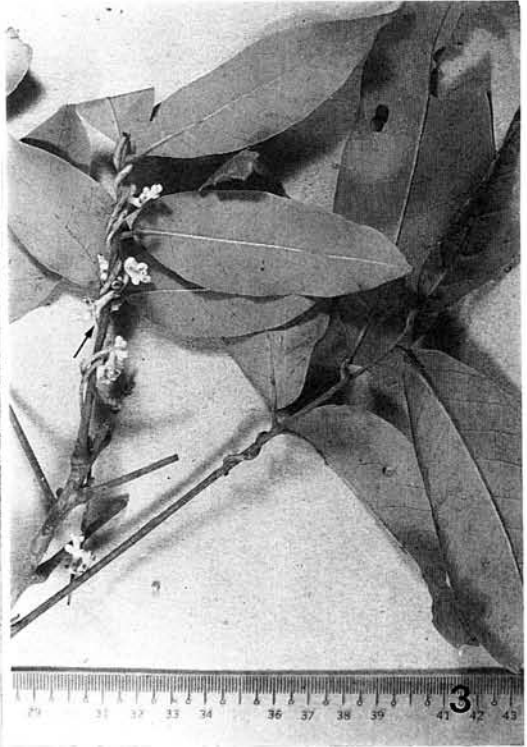
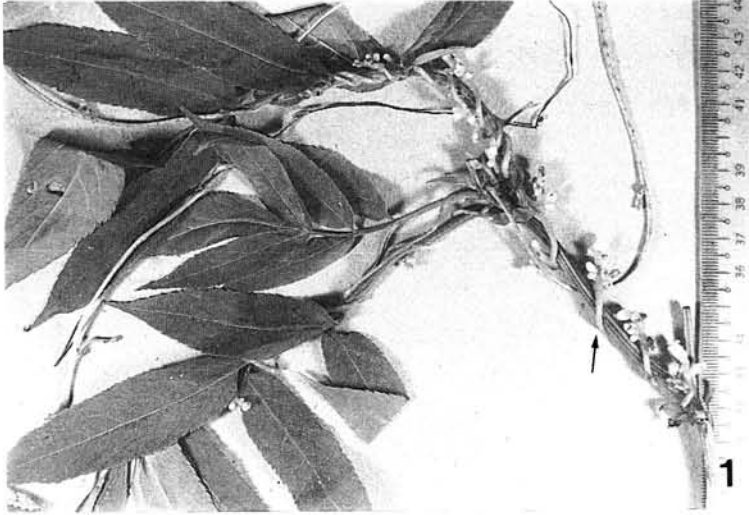


Plate 1. Host plant and the coiling habits, arrowhead showing the anticlockwise growth direction.

1. *Hyptis rhomboides* (c37), a herbaceous dicots.
2. *Diospyros kaki* (c48), a woody fruit tree of dicots.
3. *Euphoria longana* (c58), a woody fruit tree of dicots.

PLATE 2

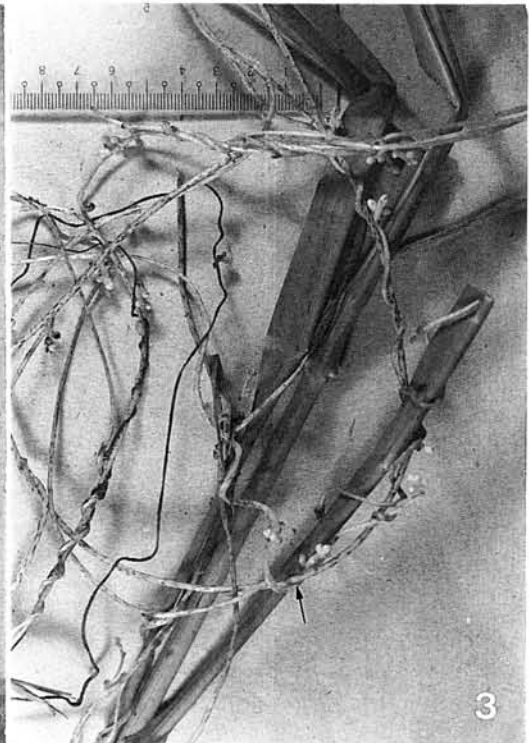
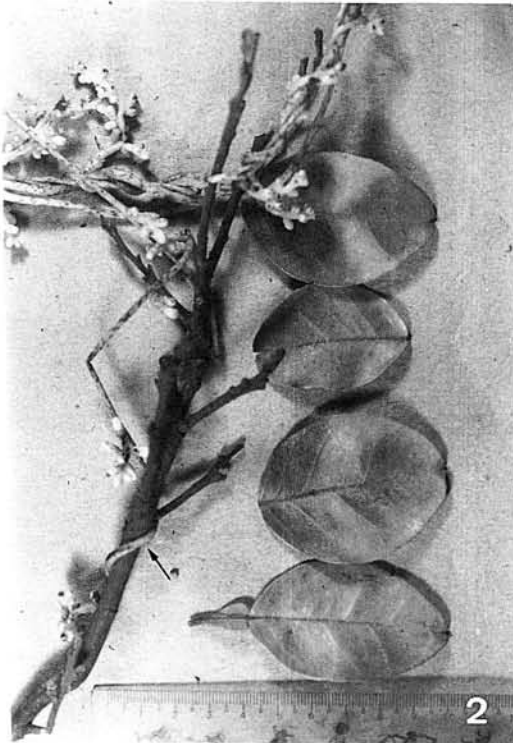
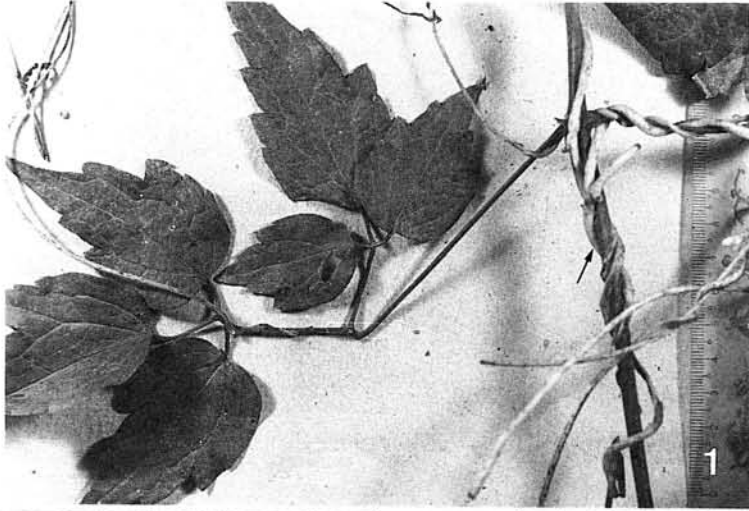


Plate 2. The spiral directions on host plants are uniformly anticlockwise (arrowhead).

1. *Clematis* sp. 1(c55), a vine of dicots.
2. *Citrus grandis* (c49), a woody fruit tree of dicots.
3. *Pennisetum purpureum* (c56), a herbaceous monocots.

PLATE 3

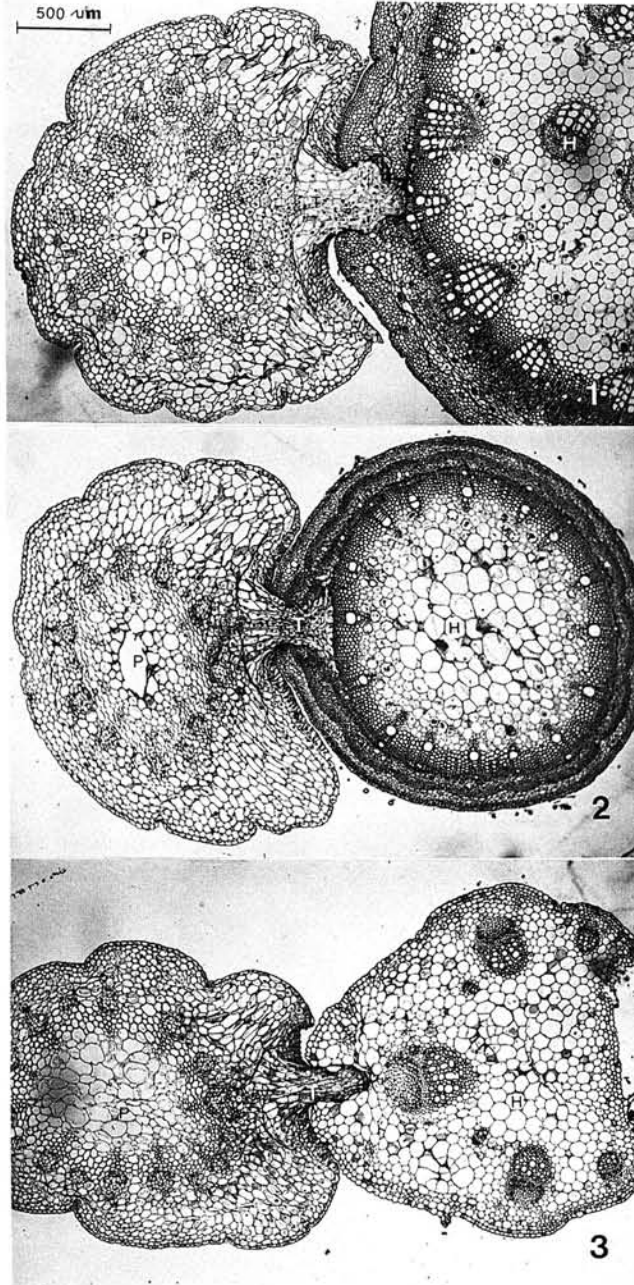


Plate 3. The transverse sections of stems of dodder (left) and host (right), the former with eustele having pith (P) at center, the haustorium (T) invading into the host (H) of following species.

1. *Aleurites montana* (c50), a woody dicots.
2. *Pueraria montana* (c22), a climbing dicots.
3. *Cyrtococcum accrescense* (c32), a herbaceous monocots.

PLATE 4

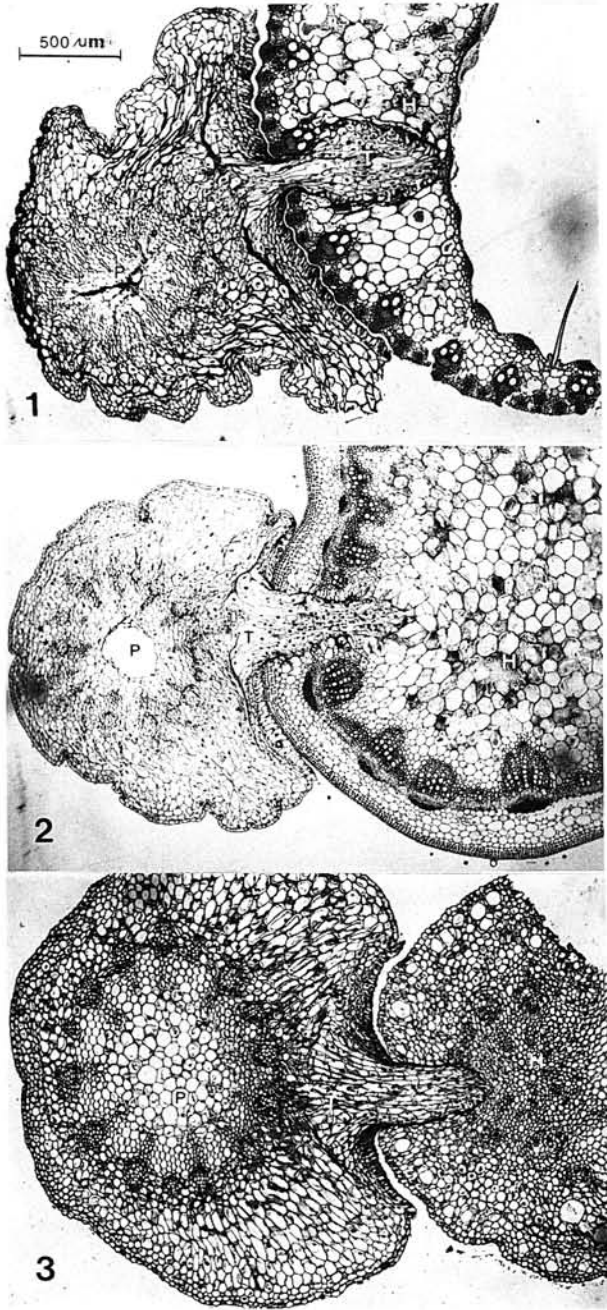


Plate 4. The transverse sections of stem of dodder and the the host (H), herbaceous hosts are penetrated by he haustoria (T) more easily than woody hosts.

1. *Pennisetum purpureum* (c56), a herbaceous grass.
2. *Synedrella nodiflora* (s.n.), a herbaceous dicot.
3. *Ipomea* sp. (c13), a dicot vine.

PLATE 5

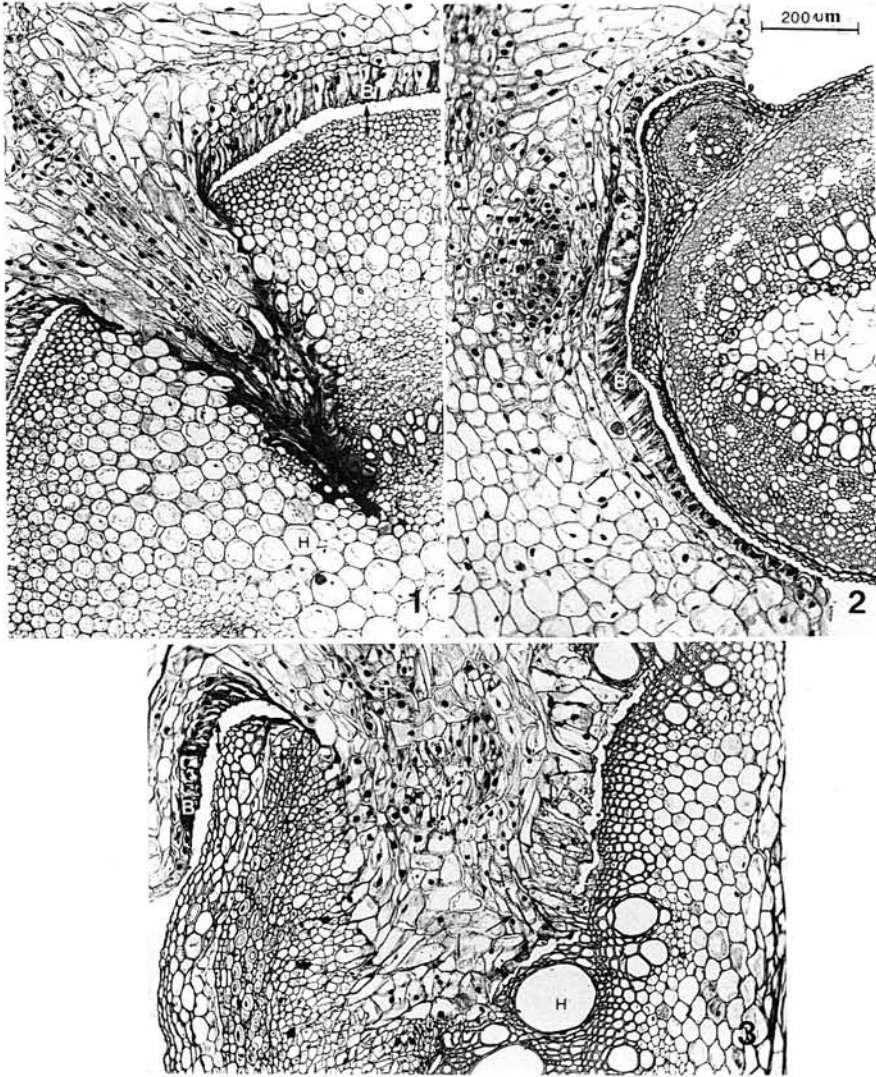


Plate 5. The transverse sections of stem of dodder and the host (H), epidermal cells of dodder differentiated into brush-like structure (B) at contacting part with host epidermis in a key and lock pattern (double arrowhead).

1. A dodder (upper left corner) attack the stem of *Stemonea tuberosa* (c23), a climbing monocots, tip of haustorium contacting a vascular bundle of the host.
2. A dodder (left) contacting the stem of *Sesbania roxburghii* (c28), an annual legume, the haustorial primodium (M) initiated from interfascicular region and becoming elongated.
3. The haustorium differentiated into a xylem bridge (arrowhead) connecting with vascular bundle of the host *Paederia scandens* (c27), a climbing dicots.

PLATE 6

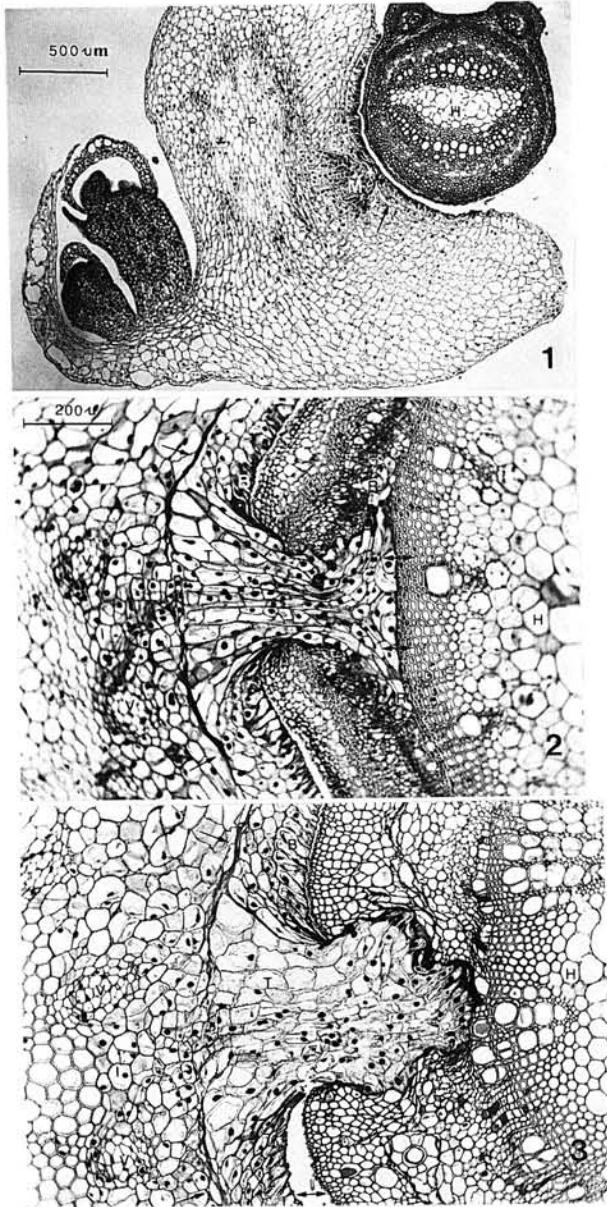
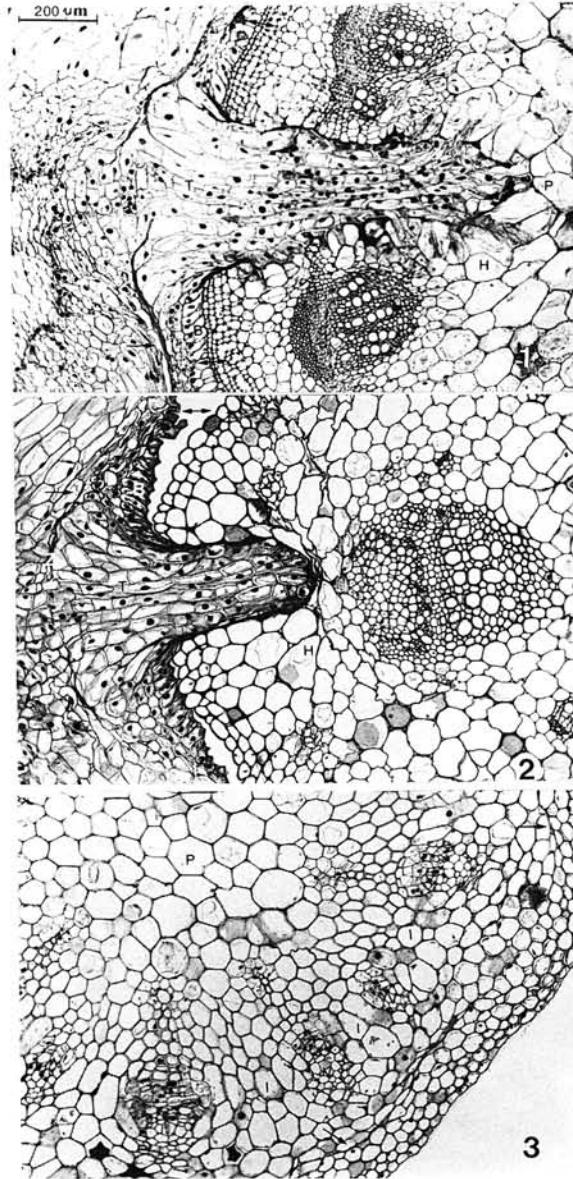


Plate 6. The transverse sections of stem of dodder and host (H).
 1. The haustorial primordium (M) of dodder at inter-fascicular region, brush-like structure at contacting part of epidermis of dodder. (stem of *Sesbania roxburghii*, c28).
 2. The tip of haustorium with hypha attached the vascular bundle of the host, *Pueraria montana* (c22).
 3. The hypha structure from the tip of haustorium (T) connecting the vascular bundle and cortex of the host, *Macaranga tanarius* (c30).

PLATE 7



- Plate 7-1.** A haustorium with numerous hyphae connected with the cortex, the vascular bundles and the pith of the host, *Synedrella nodiflora* (s. n.).
- 7-2.** A haustorium just invading into the cortex of the host, *Cyrtococcum accrescense* (c32), hyphae or xylem bridge not yet organized, the tip of the haustorium becoming straightly forward to one of the vascular bundles.
- 7-3.** The transverse section of stem of *Cuscuta japonica* var. *formosana* (c21), three to four layers of cells constituting the prehaustorial zone (arrowhead) beneath the epidermis.

PLATE 8

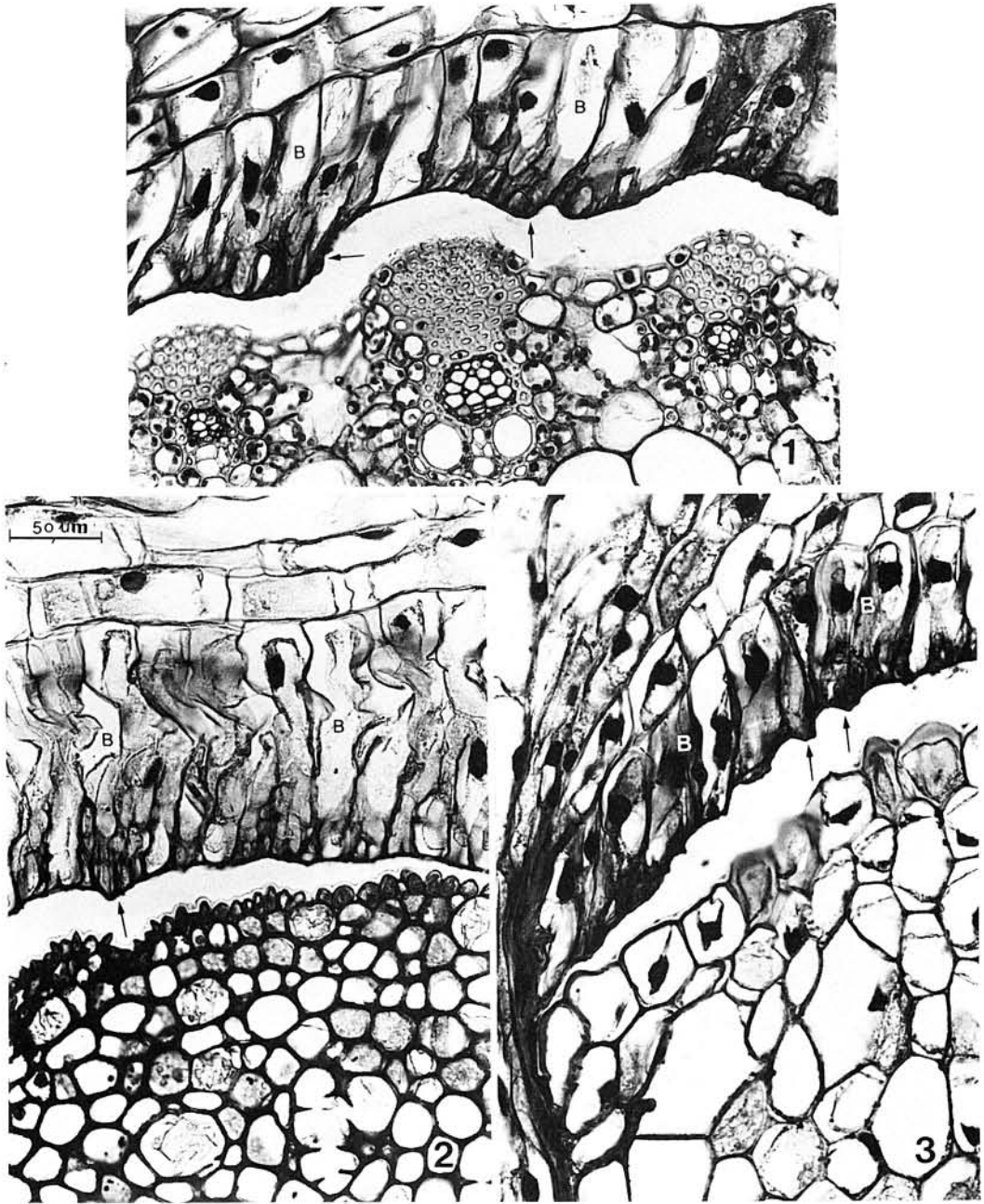
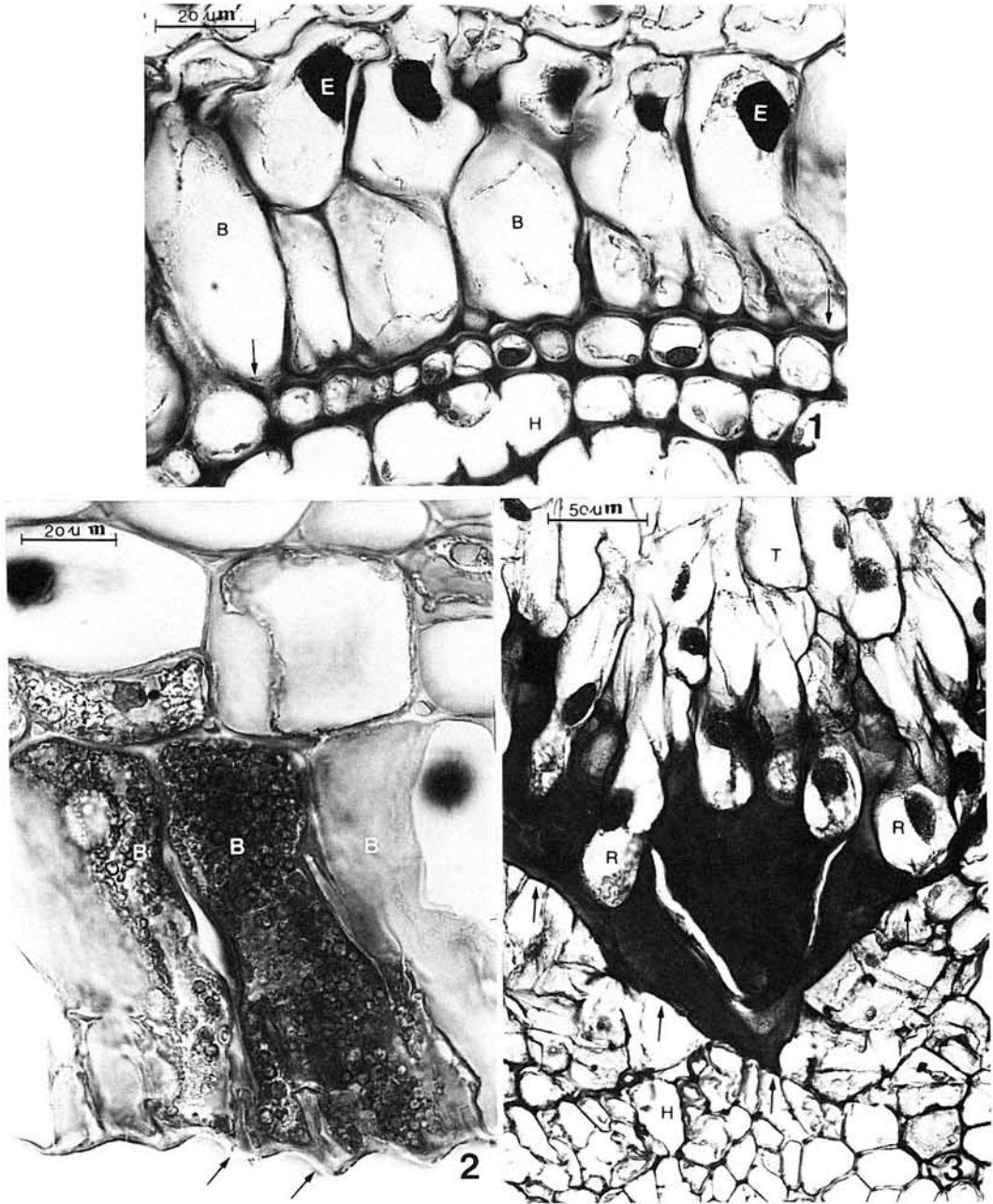


Plate 8. Transverse sections of dodder (upper) and host stem (lower).
1. *Pennisetum purpureum* (c56), a herbaceous grass.
2. *Macaranga tanarius* (c30), a woody dicot.
3. *Ipomea* sp. (c13), a dicot vine.

PLATE 9



- Plate 9-1.** The epidermal cells of dodder (c21) with large nucleus (E) and some cells branching at outer periclinal wall right side (arrowhead).
- 9-2.** The elongated cells of epidermis of the dodder (c21) full of tannin-like granules in cell lumen (B) and protrusion of outer periclinal wall.
- 9-3.** The filamentous branchelets (R) of the haustorial tip invading through the cortex of the host (H), *Stemonea tuberosa* (c23).

PLATE 10

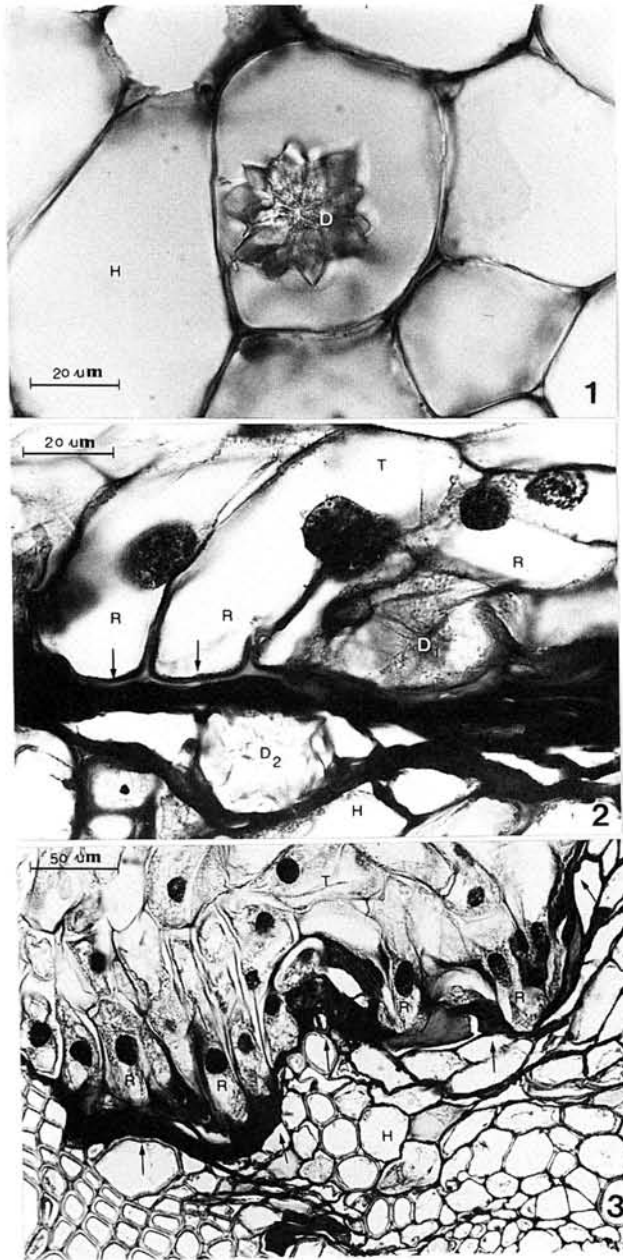


Plate 10. The internal structure of the host, *Macaranga tanarius* (c30), as a barrier from the attack of the parasite:

1. Normal parenchyma cells of the host, one of them contain a druces (D).
2. The druces (D₁ and D₂) as the obstacle the hyphae (R) to branching forward.
3. The vessel members with lignified wall (arrowhead) as an obstacle of the invading of the hyphae (R).

PLATE 11



Plate 11. The transverse sections of stem of the host and the hyphae of the dodder:

1. The hyphae press some parenchymatous (double arrowhead) for invading toward the vascular bundle of the host, *Cyrtococcum accrescense* (c32).
2. The filamentous hypha branchlets (R) entering some tracheary elements of the host *Paederia scandens* (c27) and then differentiate a xylem bridge (arrowhead) for connecting the vascular bundle of the dodder itself.
3. The cell of rhizopodial hypha (R) with large nucleus (E) intruding into the of the phloem cell (double arrowhead) of the host, *Pueraria montana* (c22).

臺灣菟絲子的吸器與寄主

郭長生 江蔡淑華

摘 要

菟絲子類屬寄生性植物，為害許多經濟作物。臺灣產有二種；一為菟絲子 (*Cuscuta australis* R. Brown) 另一為臺灣菟絲子 (*C. japonica* Choisy var. *formosana* (Hay.) Yunker)。本次報告針對臺灣菟絲子之寄主及吸器進行研究。

野外調查可知至少有 36 種寄主；包括果樹、野生木本植物和一年生或多年生草本植物。又知纏繞寄主之方向性全為逆時針方向。

有關吸器之探討、初步瞭解；有二種類型；一為細胞間型，一為細胞內型；隨寄主而定。吸器先端之入侵也受寄主內部構造影響。具前吸器及刷狀構造並有類似單寧細胞在先端等，是臺灣菟絲子常見特徵。