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Dodder Overwintering as Haustorial Tissues within *Cuscuta*-induced Galls

By H. L. DEAN

INTRODUCTION

All species of *Cuscuta* in temperate zones are commonly described as annuals, although certain members of this genus have been reported as frequently and perhaps characteristically perennial in these regions. Perennial species of dodder are supposedly restricted to tropical regions, and of these *Cuscuta reflexa* Roxb. is often cited as an example. Details as to the mode of perennation of tropical dodders are often lacking or incompletely presented.

Kuhn (1868) reported *Cuscuta epithymum* Murr. as commonly perennial on clover and alfalfa in Germany, and in a later paper (1900) he characterized the supposedly annual habit of clover dodder as one of those errors which, even in the realm of science, are sometimes held to with remarkable tenacity. Uloth (1881) recorded 61 instances where dodder (presumably *C. epithymum*) overwintered in fields of clover and alfalfa plants. During the summer he labeled easily recognized plants in private fields, enabling him to relocate them the following winter and spring. Sorauer (1886) reversed a previously held opinion and stated that dodder is not annual but perennial, and that on perennial plants it perpetuates itself more often by the further growth of the previous year's dodder than by the germination of seeds. Stewart (1906), Stewart, et al. (1908) and Stewart and French (1909) reported observations and experiments showing that *C. epithymum* in New York State is characteristically perennial in alfalfa fields as masses of twisted stems on the underside of the crowns of alfalfa, yellow trefoil, dandelion and daisy fleabane. They found that seeds of this dodder were rarely produced in New York alfalfa fields. Lloyd (1908, 1909) briefly described an unidentified species of dodder found near Zacatecas, Mexico, as living overwinter in a semi-dormant condition on various woody shrubs, including guayule, hojosen and others not named. Fulton (1912) found that *C. epithymum* survived the winters in Central Pennsylvania as strands of dodder twisted around the protected parts of the crowns of clover plants. Rao (1939) reported the common perennation of *C. reflexa*, during the dry season in India, by means of haustorial fragments

surviving within the stems of *Strobilanthes gossypinus* and *S. canaricus* host plants. During the dry season all external dodder stems coiled about the host plants were dead and dried. Early in the rainy season living haustorial tissues within the host stems gave rise to new shoots of dodder, with as many as 8-10 new stems emerging from a single haustorial wound. No germinating seeds or young dodder seedlings were found at the beginning of the rainy season when these new shoots appeared. Graham (1942) described galls induced by *C. reflexa* on various hosts in India, especially large ones (one inch in diameter) occurring on *Hibiscus Rosa-sinensis*. He believed that less than 2% of these galls regenerated new dodder stems. Knorr (1949) found aerial dodder developing abundantly from haustorial fragments within galls induced by *C. americana* L. on Tahiti lime trees growing in Florida. Regeneration of aerial shoots occurred even when this dodder had been removed mechanically from the host, in some cases by scraping down the tissues flush with the bark by a fingernail. This dodder had propagated itself from haustorial fragments within the tissues of successive lime tree hosts for a period of 5 years, despite the systematic and complete removal of all external dodder stems every 10-20 days throughout the season. The writer, Dean (1937a, 1937b, 1938) previously described *Cuscuta*-induced galls and the habits of *Cuscuta* with reference to the fact that new stems of the parasite often developed from haustorial tissues within such galls. The present note reports observations and experiments by the writer on the growth of new stems from, and the overwintering of dodder as, living haustorial tissues within *Cuscuta*-induced galls.

EXPERIMENTAL PROCEDURES AND RESULTS

The first *Cuscuta*-induced gall found by the writer to develop new stems from haustorial tissues within it was on a squash (*Cucurbita Pepo*) plant infested by *C. Gronovii* Willd. in a greenhouse of the State University of Iowa. This gall (Fig. 1) was ninety days old when harvested February 5, 1931, and by that date the new growth had formed a cluster of flowers. Similar such occurrences were found at successively later intervals in different lots of galls formed on squash plants infested by *C. Gronovii* and *C. glomerata* Choisy. During these several experiments, 28 *Cuscuta*-induced galls were formed on squash plants and 9 of this number developed new stems from haustorial tissues contained within them. This number could possibly have been larger since quantities of these galls were necessarily collected at earlier intervals for preservation and/or sectioning.

Similarly, two additional herbaceous host plants (*Fagopyrum esculentum* and *Helianthus annuus*) were found to form *Cuscuta*-induced galls and to develop new stems from haustorial tissues within them. The early greenhouse observations on herbaceous hosts prompted a series of experiments outdoors to determine if new dodder stems would also develop from haustorial tissues within *Cuscuta*-induced galls on a woody host (willow), and to learn if dodder would live overwinter as haustorial tissues within such galls. Host plants grown in the greenhouse were hand infested, using seedlings obtained by germinating dodder seeds on wet filter paper in Petri dishes. Willow host plants (*Salix nigra* and *S. longifolia*) were infested naturally by *Cuscuta* seedlings from seeds germinating on the ground.

The total number of *Cuscuta*-induced galls recorded by the writer as giving rise to new stems of the dodder (overwintering in willow), the host plants affected and the one or more species of *Cuscuta* involved are as follows: 9 on squash plants infested by *C. Gronovii* and *C. glomerata*; 10 on buckwheat plants infested by *C. Gronovii* and *C. glomerata*; 28 on sunflower plants infested by *C. Gronovii*, *C. glomerata* and *C. polygonorum* Engelm. and 49 on willow plants outdoors infested by *C. polygonorum*.

As a *Cuscuta*-induced gall enlarges, the tightly encircling stem of the parasite about it may be broken into short, isolated, segments of dodder stem, each attached by means of one or more haustoria. These attached pieces of dodder stem may proliferate new shoots, but with continued enlargement of a gall they sometimes die and only dried, dead segments of dodder stem remain. These dried segments of stem often drop off and if the attached haustoria also rot they leave cavities where decay may continue. Frequently, however, these haustorial tissues remain alive and continue to grow within the gall (Fig. 4). These living haustorial tissues within a gall may originate new growing points of dodder stems (Fig. 5) which produce new shoots of the parasite (Figs. 2, 3) capable of attacking the same or adjacent host plants. Dodder can readily propagate itself in this manner during the summer on both woody and herbaceous hosts, or it may live overwinter as haustorial tissues within galls on woody plants and not form new shoots until the following spring.

The great numbers of young willow plants on the banks of the Iowa River near Iowa City, Iowa, and the abundant infestation of them by *C. polygonorum* (Fig. 6) provided a wealth of naturally growing materials for outdoor experiments concerning over-

wintering of dodder as haustorial tissues within galls on willow induced by this species of *Cuscuta*.

Galls formed outdoors on willow plants during a given spring

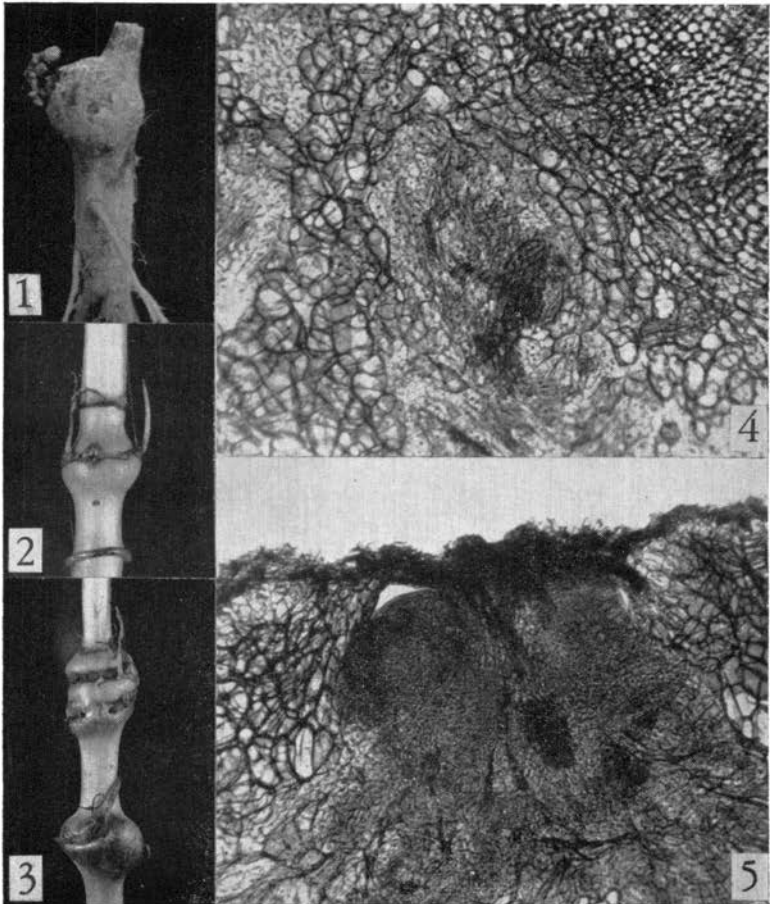


PLATE I

LEGENDS FOR FIGURES

- Fig. 1. Gall 90 days old on squash. Note cluster of flowers on stem developed earlier from haustorial tissues within gall.
- Fig. 2. Gall 43 days old on sunflower. Young dodder stems 11 days old arising on each side of gall. Note cavity near center of gall left by decayed haustorium.
- Fig. 3. Gall 55 days old on sunflower. Young dodder shoot 8 days old growing from upper right hand portion of top (secondary) gall.
- Fig. 4. Freehand cross section of gall 65 days old on sunflower. Living haustorial branches of *Cuscuta* are surrounded by host tissues. Note prominent nuclei in dodder cells.
- Fig. 5. Freehand cross section of gall 65 days old on sunflower. Two new growing points (one partly obscured by dead tissues) of dodder are shown.

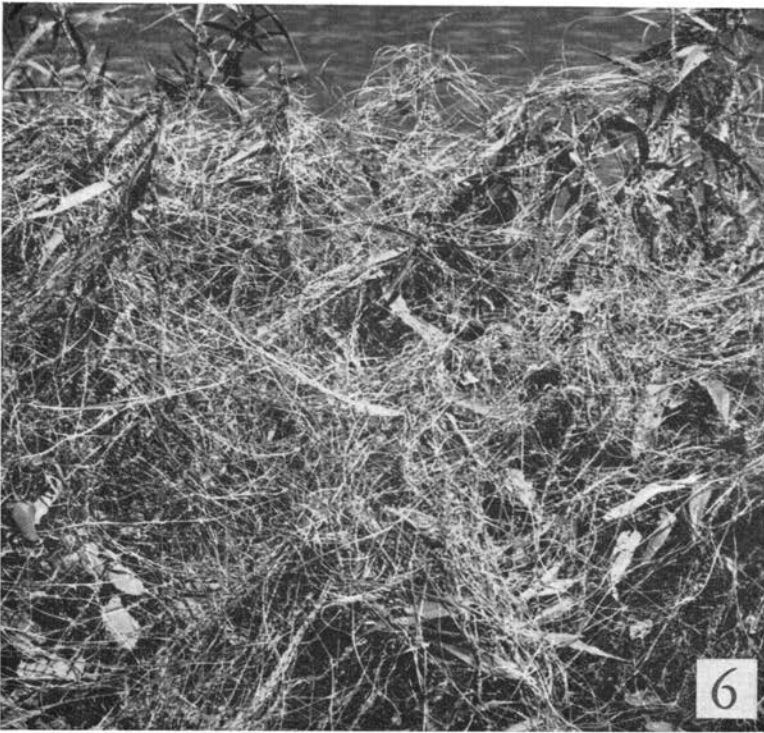


PLATE II

Fig. 6. *Cuscuta polygonorum* infesting willow plants along the Iowa River near Iowa City, Iowa. Typical of much material outdoors used for overwintering experiments by the writer.

or early summer were marked by wiring on numbered metal tags in order that the same ones could be located again the following year. Beginning in the early spring, a year after tagging, observations were made every third day of each marked gall to determine the date new stems of the dodder appeared. Similarly, the ground in the vicinity of the tagged galls was carefully examined every third day for germinating dodder seeds and such observations continued until they were found. Twenty willow galls were tagged each year this study was conducted. Results of these observations on willow galls are tabulated below (Table 1).

In each instance, the dodder lived overwinter as haustorial tissues buried within the galls and emerged the following spring as one or more new stems of the parasite, appearing 11 to 16 days before germinating dodder seeds were found on the ground in the same area.

Table 1

Dodder overwintering within *Cuscuta*-induced galls on willow.

Date new stems appeared from galls	Date germinating seeds found on ground	No. days until germinating seeds found	No. galls overwintering dodder
May 2, 1932	May 16, 1932	14	10
May 10, 1933	May 21, 1933	11	10
May 6, 1935	May 22, 1935	16	9
April 28, 1937	May 10, 1937	12	8
April 22, 1938	May 5, 1938	13	12

(No galls were tagged in 1934 or 1936.)

Frequently, examples of what appeared to be new dodder stems developed from haustorial tissues overwintering within evident year-old galls on willow were found during the many observations necessary for this study. Only those galls which had been previously tagged and their history known are included in the above tabulation. No similar studies of tagged galls have been possible since 1938. However, from incidental field observations at irregular intervals since then, an estimated 75 additional examples of dodder overwintering in willow galls have been seen by the writer.

SUMMARY AND DISCUSSION

Previous writers have reported clover dodder (usually *C. epithymum*) as probably more characteristically perennial in its habit than annual, commonly overwintering as a mass of short stems attached to protected parts of perennial hosts. *Cuscuta reflexa* in India has been found to survive the dry season (perennate) as haustorial fragments within woody host stems and an instance of perennation from a few *Cuscuta*-induced galls was recorded for the same species. Similarly, one unidentified species of *Cuscuta* in Mexico has been described as overwintering in a semi-dormant condition on woody hosts. *Cuscuta americana*, parasitizing trees of Tahiti lime in Florida, readily developed aerial shoots from haustorial fragments within galls induced by this dodder.

In the present note, 3 species of *Cuscuta* (*C. Gronovii*, *C. glomerata* and *C. polygonorum*) are described as forming new stems from haustorial tissues within 47 *Cuscuta*-induced galls developed on 3 species of herbaceous host plants. Additional experiments are reported, covering a discontinuous period of 5 years, which demonstrate the frequent overwintering (a more precise term than perennation?) of *C. polygonorum* as haustorial tissues within 49 similar galls formed outdoors on 2 species of willow host plants.

From the results of these experiments by the writer it would appear that proliferation of fresh dodder shoots from growing points developed by living haustorial tissues within *Cuscuta*-induced galls is of rather common occurrence. With both woody and herbaceous hosts this habit may aid in propagating the dodder during the summer months, while with woody hosts overwintering of the dodder may be expected to occur. It might also be expected that *Cuscuta* would overwinter as haustorial tissues within those portions of infested willow or similar stems not producing galls.

More examples of successful overwintering of dodder from willow galls might have been recorded if all tagged galls could have remained undisturbed. Some were lost by persons clearing away areas of the river banks for boat landings, buildings and fishing spots; some lost due to erosion by high water and a number destroyed by curious small boys who removed the metal tags, damaged the host plants and despoiled much of the immediate area.

The fact that haustorial tissues of dodder may continue to live within *Cuscuta*-induced galls naturally invites comparison with the vegetative body of members of the Rafflesiaceae. In *Rafflesia*, for example, the vegetative body of the parasite is reduced to a web of irregularly branching filaments growing throughout the parenchymatous cortical tissues of a host root and completely enclosed within its bark. Buds and flowers breaking through the bark of a root are the only external evidences of this parasite. The vegetative body of *Rafflesia* thus resembles a fungus mycelium in organization and represents the ultimate reduction of vegetative tissues of a parasitic seed plant. The living masses of haustorial tissues within a gall also appear to approach this permanent condition of *Rafflesia* and may indicate an evolutionary trend toward still further reduction of the vegetative body of *Cuscuta*. This trend seems further evidenced by the manner of perennation described for *C. reflexa* in which this dodder appears to approach still closer to this habit of members of the Rafflesiaceae, especially those in the genera *Pilostyles* and *Apodanthes* parasitic on vines and stems.

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