



Organogenesis of Dodders, Parasitism, Infestation and Development Phases

Innocent Osoro Ngare^{1*}, James Kibii Koske¹ and George Njagi Gathuku²

¹*School of Environmental Studies, Kenyatta University, PO Box 43844-00100, Nairobi, Kenya.*

²*School of Hospitality & Tourism, Strathmore University, PO Box 59857 – 00200, Nairobi, Kenya.*

Authors' contributions

This work was carried out in collaboration among all authors. Author ION designed the study, performed the experimental analysis and wrote the first draft of the manuscript. Author JKK managed the analyses of the study. Author GNG managed the literature searches. All authors read and approved the final manuscript.

Article Information

DOI: 10.9734/AJGR/2021/v4i130122

Editor(s):

(1) Dr. Armando García Chiang, Universidad Autónoma Metropolitana, México.

Reviewers:

(1) Mona M. Amin Abdel-Fatah, National Research Centre (NRC), Egypt.

(2) Tuğba Düzenli, Karadeniz Technical University, Turkey.

Complete Peer review History: <http://www.sdiarticle4.com/review-history/63333>

Original Research Article

Received 04 October 2020

Accepted 10 December 2020

Published 06 January 2021

ABSTRACT

Parasitic plants proliferation globally is daunting and a threat to our ecosystems. In this study we explore holoparasites with limitation to dodders (*Cuscuta spp.* & *Cassytha filiformis*). An experiment was performed to ascertain anatomical and morphological characteristics of dodder capsule and its stem. We present dodder infestation stages, development phases and close observable internal and external microscopic features. A distinct haustorium trait of dodders is shown by micrographs. The study finds that dodder seeds possess high ecological dispersal character with vast adaptability through morphological analysis. This ramifies their ecological phenotypic plasticity. Externally, dodder stems attack the host phloem through haustoria that suck nutrients from the sap weakening it.

Keywords: Organogenesis; dodder; cuscuta; cassytha; haustoria; dispersal.

*Corresponding author: E-mail: ngare.innocent@gmail.com;

1. INTRODUCTION

Dodders (*Cuscuta spp.* & *Cassytha filiformis*) are among the flowering autotrophic plants that constitute in predominant field weeds that are either parasitic and semi-parasitic flowering plants. Worldwide, parasitic plants represent approximately 4200 species classified in 274 genera that make 1% of flowering plants. From the 274 genera, roughly 11% of species make parasites to cultivated plants (hosts). A study by Nickrent [1] indicates that leading economic implication or damage is to the host plant accelerated by species from four genera, namely: *Cassytha*, *Cuscuta*, *Striga*, *Orananche*, and *Arceuthobium*. Different studies [2-4] have indicated that dodder is the most important and challenging parasitic group of weed of over 70 varieties and 200 species.

Holoparasite *dodder* stems are threadlike and coil around the host [5]. These plant parasites are leafless, or in some cases, their leaves are hardly visible with its nature of small scales. When *Cuscuta* seeds are fully mature, they fall off and hip on the ground in accumulation. At the ground, their germination will depend if there is a suitable host within the vicinity [6,7]. If none, the seeds are rendered dormant until suitable germinating conditions for them to germinate [8]. Dodder entirely attaches its stem to the host for nutrients access and water supply. This assists the parasitic weed to mature. When it reaches the appropriate maturation phase, it forms inflorescences accompanied by abounding actinomorphic and hermaphrodite flowers. These flowers are tiny, hermaphroditic, reddish and whitish or yellow.

According to Runyon et al. [9,10], for dodder seedlings to attach or identify the host plant, they use plant volatiles that act as chemo-attractants that serve as a guide for the growth of the seedling. This haustoria characteristic is important to them to survive. It escalates their survival chances to establish a connection with the host plant successfully. Additionally, scholars [11,12], *Cuscuta* stem is impacted by the light that actively facilitates its seeds to germinate. They argue that its seedlings grow towards the light, thus assisting them in finding the appropriate host.

Immediately dodder seed germinates and identifies the host; it undergoes three distinctive phases -the adhesive phase, the intrusive phase, and the conductive phase. During the adhesive

phase, a holdfast (specialized adhesive organ) develops at the *Cuscuta* stem that is in contact with the host plant [13]. Formation of the holdfast results from elongation of cortical layers of dodders and in the epidermal cells. This is characterized by the existence of secretory cells that churn or secrete adhesive compounds. At the intrusive phase, *Cuscuta* develops hook-like structures through haustorium. The haustorium behavior immediately gets into the host's vascular tissues; the haustoria cells differentiate, forming conductive cells that transform into the conductive phase. In the conductive phase as the final third phase, *Cuscuta* starts to exchange information molecules with the host where nutrients and water absorption is done through sucking [14].

This study presents the primary and secondary review findings by identifying dodder development phases from the onset. The anatomical and morphological capsule/berry (dodder seed) are shown to include dodder haustorium development stages.

2. METHODOLOGY

Mature *dodder* seed capsules were collected from Mombasa County on latitude & longitude (4° 2' 12.7608" S and 39° 40' 10.4556" E) at infested areas and taken to Kenyatta University on location coordinates (1°10'50.0"S, 36°55'41.0"E) laboratory for anatomical observation. Seed berries were packed in plastic sample collecting bottles, and experiments were done within 12 hours to avoid analyte loss. Mombasa County is a low altitude (50 m/160 ft elevation) setting with higher temperatures, unlike Nairobi of higher altitude (1,795 m/5,889 ft elevation) and low temperatures.

3. RESULTS AND DISCUSSION

3.1 Anatomy of Dodder Capsule

A cross-sectional cut of two of the collected samples (a, b) of succulent and dry dodder capsules was done respectively at Kenyatta University laboratory to observe the seed anatomical nature (Fig. 1). From the observation, dodder is a dicotyledonous plant parasite. The seed had duo cotyledons that primarily serve as the source of nutrient supply to the embryo's early development. The sticky, whitish sap of the capsule dries, turning brownish immediately the seed matures transforming as a berry skin that covers the Testa. The cotyledon turns from white

to glittering yellow color. Additionally, as the seed capsule dries, the size of cotyledons shrinks. Another noticeable feature at the cut dodder berry was its single seed trait per seed berry covered with mesocarp that dries as it matures and shrinks.

Dodder seed observable features that enhance its dispersal pathway towards its phenotypic plasticity were:

- a) *The sticky seed juice* – some animals are attracted to the juicy mature seeds, which they end up transporting to other areas as a stool. The fallen matures seed float on water, thus transported to other far distant regions surface runoff. This was observed too by Kidunda et al. [15] on assessing the existence and spread of dodders (*C. filiformis*) on Cashew Trees in Tanzania. Their findings conclude that dodder dispersal mechanisms were; wind, birds, water, machines, equipment, and animals that work at already dodder infested areas.
- b) *Hard, dry berries* – the dried hard berries develop into a hard seed coat that can withstand harsh environmental conditions

until they find a potential host that triggers their development life cycle.

- c) *Color change to brown* – this acts as camouflage while in or on the soil. The ability to identify the seeds is very limiting only with the use of specialized equipment like magnifying glasses.
- d) *Seed reserved endosperm* – the longevity of the seed reproductive life depends on its internal nutritional reserves. Dodders have endosperms that can remain actively dormant until favorable conditions for the seed to germinate are felt. This is triggered by the micropyle when a suitable environmental condition emerges. A similar claim is proposed by Ghantous and Sandler [16-18] in their study on dodder seed dormancy. They argue that seed scarification of capsuled dodder berries is a must for them to germinate. This is normally done to weaken hard coats of dodder seeds either mechanically (scratching or soaking in water), thermally (exposed to heat like fire or burning), and chemically (corroding and dissolving components of the seed coat)

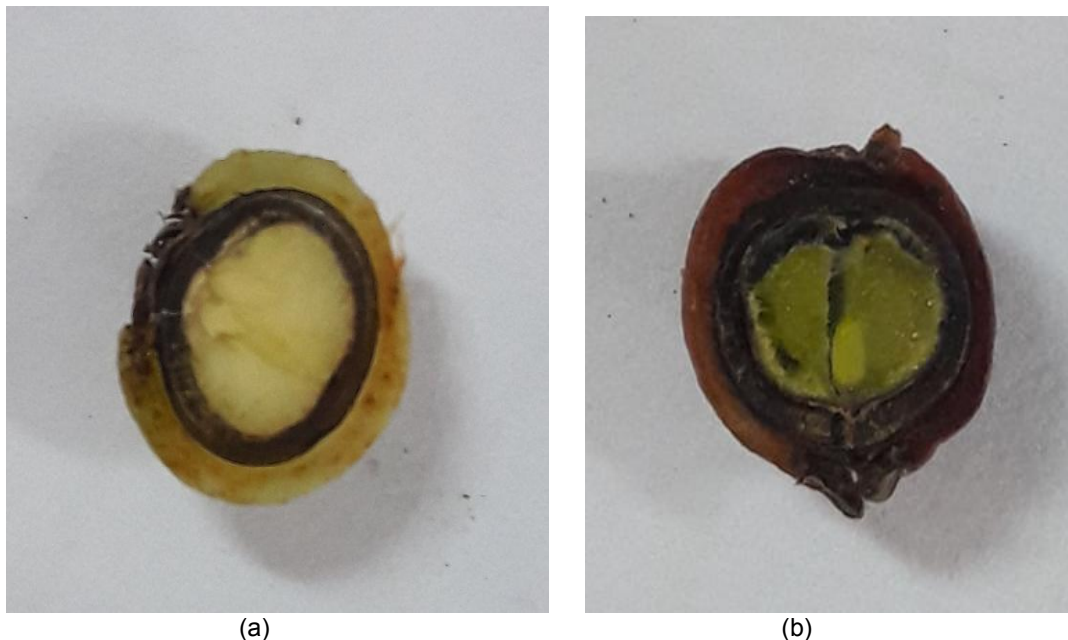


Fig. 1. Anatomy of dodder capsule

Fig. 1(a). shows succulent dodder capsule with the outer ring representing the Mesocarp, the Testa comes as the immediate dark brown ring and the interior is dominated by the whitish Endosperm. Fig. 1(b). is and dry dodder capsule with a berry skin at the outer layer, the Micropyle that opens for germination and the inner Radicle hosted by the cotyledons

3.2 Dodder Development Phases & Infestation Stages

Fig. 2 shows field dodder (*Cuscuta Competris*) attack on ornamental plant - *Arabidopsis thaliana*. (A) Presence of *Cuscuta campestris* (Cc) on the host's site - *Arabidopsis thaliana* (At) on its outer part. Dodder twines along the stem of *Arabidopsis thaliana*. Within a Scale bar of 1 cm as shown at (B–e). Additionally, transverse sections across all the phases of dodder parasitism processes. All scale bars of =200 μm.

Adhesive phase (B). The holdfast (ha) forms on the host surface, attaching to *C. competris*. Immediately prehaustorium starts at the inner cortex of the stem. The file cells (fc) and digital cells (dc) start to differentiate by elongation inside the endophyte primordium (ep).

Intrusive phase (C). The host's cortex stem is intruded by haustoria (ha); in some cases, it reaches the pitch (pi)

Conductive phase (D). This is shown within a red magnified square (e) where the vascular conductive elements (px, parasite xylem) develop in the haustorium. The red line shows the parasite xylem, where orange dots show haustorium. H, host; hp, host phloem; H, host; P, parasite; px, parasite xylem.

Other studies [20-22] show dodders start foraging on compatible ornamental host plant (*Pelargonium zonale*) in stages (Fig. 3). A & B show the onset of dodder infection to the host. C&F shows the beginning of dodder parasitism at the first stage termed as swelling; at this stage, the parasite stem increases in width towards the host. The second stage is penetration (D & G) when the parasite stem attacks the host surface through haustorium. During the penetration stage, the parasite invades the host's tissue. The mature stage (E & H) where dodder established itself through stable connection enhance by vascular systems between the host and the parasite. At this stage, more shoots are

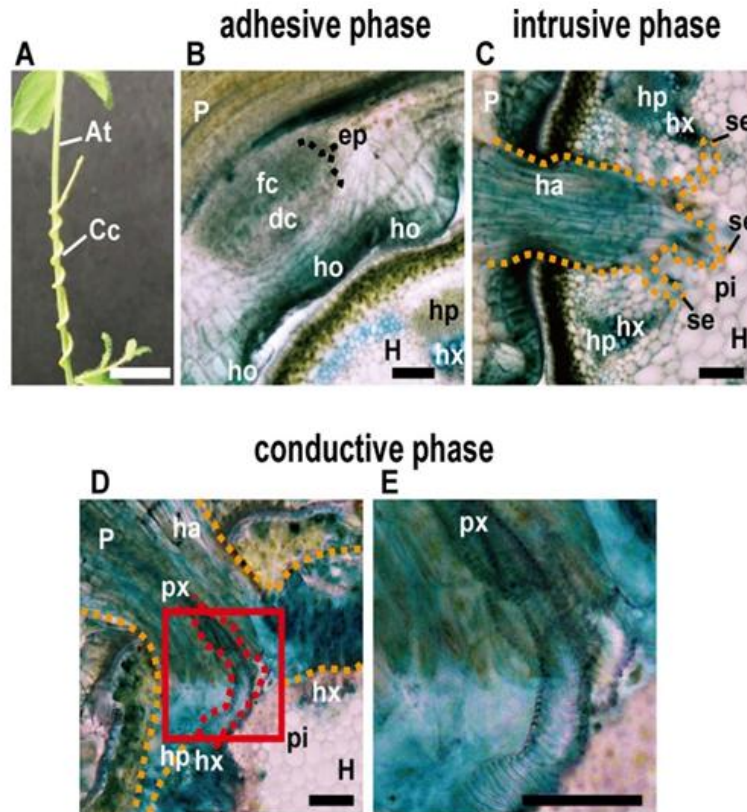


Fig. 2. Dodder-host interactions phases and haustorium development (Aoki and Shimizu, [19])

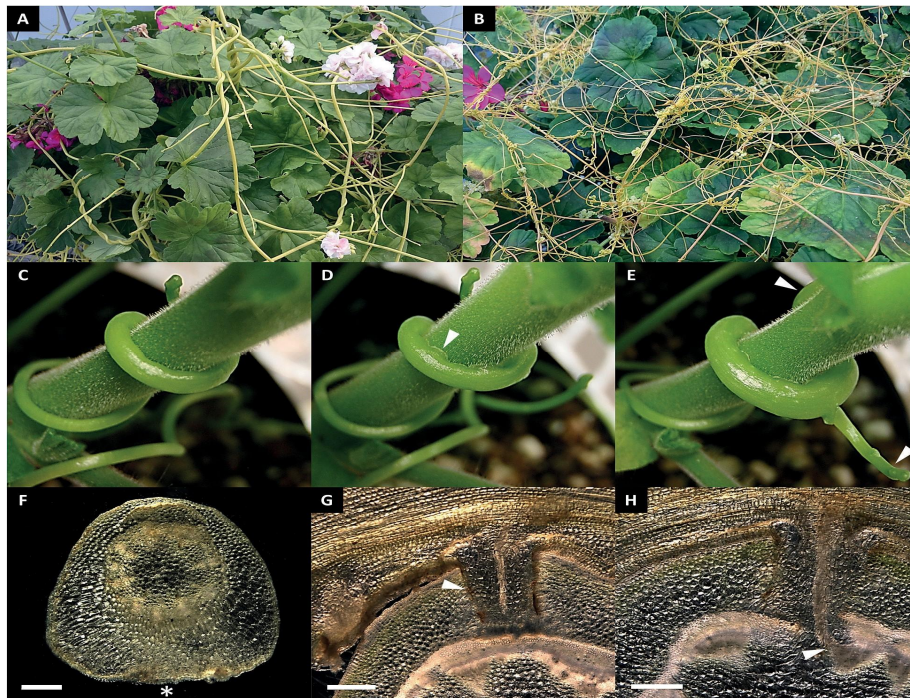


Fig. 3. Dodder infestation stages

formed (apical shoot) and other additional side shoots (the arrowheads in E). The presented cross-sections shown are in respect of (the parasite shoot axis at F and host shot axis in G and H)—the scale bars = 500 μ m.

4. CONCLUSION

Dodders are opportunistic foraging plant parasite weeds that are obligate. Their specialized haustoria trait propel their development that is notable in different phases and stages. Dodder seed capsules possess ecological phenotypic plasticity that is significant to their survival, through seed dormancy and dispersal abilities. Their stems are well adapted to spin around host with specialized hooks that suck sap to serve their nutritional demands from the host. These adaptations and biological character of dodder weed make it notorious and highly invasive.

ACKNOWLEDGEMENT

We acknowledge the support accorded by Kenyatta University's Environmental Science research team.

COMPETING INTERESTS

Authors declared no competing interests exist.

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