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APPROACH TO THE CURRENT STATE OF KNOWLEDGE ON DODDERS (*CUSCUTA L. CONVOLVULACEAE*) FROM A TAXONOMIC, MORPHOLOGICAL AND PHYSIOLOGICAL POINT OF VIEW

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Abstract

This paper aims at representing a synthesis of studies, researches and experiments of bibliographic and original scientific papers that provide information on the level of current knowledge regarding cuscuta; as well as a starting point for further research. The genus Cuscuta L. (dodder) is one of the most significant groups of holoparasite-anthophytes, mostly economically, because infestation with some of its species can lead to significant production losses in a wide variety of crops, both quantitatively and qualitatively. The dodder has long been considered a curiosity by botanists and evolutionary biologists because it has particularly interesting and even enigmatic features when examined with great care and interest. Cuscuta offers many curiosities and features that explain the plant's adaptation to parasitism: an enormous fertility of up to 10,000 seeds per plant; a long subsistence in the search for host plants; a long-lasting and staggered germinative faculty, due to the phenomenon of skin inhibition; a lack of cotyledon (though still considered to belong to the Dicotiledonatae class); the presence of chlorophyll in all organs of the plant, with the exception of the root (and nonetheless the inability to photosynthesize, unless under conditions of a carbon dioxide-enriched atmosphere); lack of a meristem and root sculpture, which results in a solely ascending migration of assimilates; the resistance of living haustoria in the host plant while the parasite's stem is dead, thus enabling the parasitic plant to regenerate and become perennial; the ability to transmit diseases such as viruses and mycoplasmas; etc. The purpose of this paper is to highlight the current state of knowledge on cuscuta species, in terms of taxonomy, ecology, agriculture, economy and management, by applying concepts that prove significant to biodiversity conservation and the agronomic value of landscape.

Key words: *Cuscuta L., holoparasite, taxonomy, morphology, physiology*

INTRODUCTION

The topic of the paper subscribes to a field that seeks to develop agricultural scientific knowledge; a field of vital importance for the future, especially regarding the increase of agricultural production. The paper aims to highlight the current state of research on dodder species from a taxonomic, ecological, agricultural, economic and applied management point of view, as well as to underline important notions concerning biodiversity conservation, the agronomic value and the aesthetics of the landscape. The paper has, by its specificity, several major objectives and components: documentation, information, analysis, scientific research, evaluation, as well as implementation of the integrated management system of the protection of prato-ecosystems, given that in Romania cuscuta has been spreading substantially, thus influencing the quality, quantity and production price, as a consequence of poor agricultural practices.

MATERIALS AND METHODS

The methods used to reach the goals were various, depending on the proposed activities. The analysis of the infected fodder crops and the damage caused by cuscuta was carried out by means of some expeditions in the area that is under scrutiny, carried out during the time frame May-October, for the detection and collection of the dodder. Biological material was used to determine the different stages of development, from the first stages to the fructification phase. In order to determine the host and the sowing species, a recent bibliography with current scientific nomenclature was used; and confirmation regarding the correctness of the determinations was made with the help of the Romanian researcher Mihai Costea, Associate Professor and Curator of Herbarium at the Wilfrid Laurier University Department of Biology in Waterloo, Ontario, Canada; a researcher mainly specialized on taxonomy. The identified species were then introduced into the WLU (Wilfrid Laurier University, Waterloo, Ontario, Canada), and the specimens are designated M. Tanase s.n. ("sin numero") and stored as vouchers in the herbarium of the University.

To analyze the plant materials, the flowers were rehydrated and then dissected, and the images can be visualized in the "Digital Atlas of Cuscuta" (http://www.wlu.ca/page.php?grp_id=2147&p=9022). [21].

RESULTS AND DISCUSSIONS

Bibliographic information on dodders around the world is abundant and varied: In 1937 Dean [25] reported a total of 464 publications, and from the 1950s to the ‘70s dodders were the subject of over 1,000 publications [33]. This demonstrates that parasite anthophytes have increased the curiosity of researchers, thus becoming the subject of numerous studies. In our country I. Prodan and Tr. Săvulescu were the first ones to establish the existence of the main species of cuscuta; whereas [9], [10], managed to identify the species existing at that time on the territory of Romania; and E. Rădulescu and V. Bulinaru , followed by Hălălău, Paun and Şarpe (1980) synthesized morphological and systematic knowledge on cuscuta, as well as its prevention and control in cultures [92].

Over time, research has diversified and numerous studies have verified the physiological mechanisms and tropisms of autotrophic plants in terms of whether they are sewn on dodders or not; what is their mineral composition, the (high) content in potassium and phosphorus and (low) content in calcium: [82], [2], [73]; [83]. It is now well known that dodders, considered holoparasitic plants completely devoid of chlorophyll, do in fact have small amounts of chlorophyll and are thus capable of photosynthesis [29]; [60]; [61]; [109]; [4], [5]; [51];, [62]. Moreover, there is a transfer of trophic substances from the host to the parasite [69]; [70]; [59]; [81]; [51]; [101]; [102].

The absorption mechanisms at the level of the haustorial apparatus are highlighted by the use of the electronic microscope [26], [27], [6]; [100]; [102]; [103]; [104] and by means of radioactive tracers [32]; [33] for determined the nature of photosynthetic products, the parasitic synthesis power; identified the substances that the parasite takes from the host plant and what substances are transferred to the parasitic plant.

These parasites were used to create biological bridges between botanically very different hosts; as well as to study the transmission of viruses and mycoplasmas [30]. Newer studies on the morphological diversity of species, a morphometric analysis of floral characters and a molecular study using plastids and nuclear DNA sequences are supported by recent researchers of cuscuta, who have made biogeographic reconstructions of the genre and its phylogeny [18]; [17]; [106].

Taxonomy. The history of these interesting parasitic plants can be traced back to antiquity [64]; [54]. Costea and Tardif [19] examined the etymology and the first names of cuscuta, as well as aspects unexplored in the early history of the concept of parasitism. The etymology of the name has been declared to be either of Greek origin [23] Arabic, or as unifying different languages and cultures such as Aramaic, Hebrew, Arabic, Persian, and Greek [20].

Although it is devoid of cotyledon, botanists nowadays consider it a dicotyledon: according to some, it represents the only genus of the Cuscutaceae family [39]; according to others – based on modern phylogenetic studies, a genus of the Convolvulaceae family [65]; [66]; [89].

Although they are very difficult to identify, given that the main variables used to

identifying species usually rely on microscopic differences of the plant's flowers, [90]; [3]; [21] revealed the real thing, as compared to mere lines and drawings, as Yuncker did in his iconography [107]; the former thus using a depth-creating methodology, with new morphological details, three-dimensional pieces, textures, thickness, visible on microscope photographs.
The taxonomy provided by Yuncker proved to be extremely ironclad, but eight decades after the monograph of Truman G. Yuncker (1932) the cuscuta species is yet again under scrutiny [107]; [90]; [20]; [17]; [91]. The phylogeny, character evolution and biogeography of dodder (Cuscuta, Convolvulaceae) can be deduced from plastid encoding and nuclear sequences (García et al., 2014). Cuscuta includes, according to the newest research, over 200 species (Table 1) around the world (Mihai Costea), grouped into four subgenera: Monogynella, Cuscuta, Pachystigma and Grammica, with a broad geographical distribution [15].

Table 1. Number of identified Cuscuta species*

Choisy (1841)	39 spp.
Engelmann (1859)	77 spp.
Yuncker (1932)	165 pp.
The new species identified and published after 1932 (to be added to the initial 165 above)	
Truman G. Yuncker (1934-1965)	18 spp.
Armando Hunzinker (1944-1947)	10 spp.
Naomi Feinbrun (1965, 1970)	2 spp.
Miquel A. García (1999-2001)	3 spp.
Mihai Costea (2010)	10 spp.
Total	**> 200 species**

Source: *Mihai Costea, Atlas Digital [21]

Cuscuta's morphology and biology. The root, with a normal geotropism, has a limited elongation of up to 1-3 centimeters, but a considerable increase in thickness; it also has neither meristem or scrub [37]; [95], it is not characterized by any mitotic division or cell elongation [86], and it seems that the only role of this organ is to supply the plant with water [13]; [86]. The root has an ephemeral existence of only 20-25 days, degenerating rapidly, approximately 7 days after germination; the process of necrosis thus being much faster than that of apical growth. Therefore, in the absence of a host plant, the dodder plant dies after about a month of life.
The stem is the most developed organ, being able to reach up to a few meters in length. It is called filament and it is characterized by a very rapid growth process. Also, it is filiform, almost cylindrical, always twisted around the host plant, with the number and speed of lateral branches (shoots) varying a lot from one species to the other. The stem acts as a reserve of substances (water, phosphates, starch) that the parasite accumulates at high temperatures, forming a reserve for future fruit development, even after the necrosis of the host plant [87]; [88]; [102].
The dodder is devoid of green leaves, their role being taken by foliar nematodes in the form of scales, which are found by the branching nodes. The lack of real leaves and their replacement by rudimentary ones is evidence of a degeneration due to parasitism. The scales are small in size (a few millimeters), sessile and often partly co-grown with the lateral branches that are born next to them.
After settling itself as a parasite, simultaneously to its growth and branching, the dodder performs volubility movements not only when it turns around the host plant but also when it moves from one plant to another [9]. During this movement no haustoria are formed. It is only when the plant slows down its growth rhythm and moves from broad and lax movements to making tight spirals around the organ around which it is rotating, that the haustoria are formed. Haustoria have between 10 and 30 sucking extensions, as small protuberances that have an area similar to an adhesion disk on the contact surface of the plant [79].
In order to perforate tissues, haustoria make use of mechanical and chemical means: lithic enzymes (cytoses, amyloses) and hormones (cytokinin) [48]. Haustoria are genuine absorption organs, capable of extracting 100% of the soluble organic compounds from broad beans (Vicia faba) [98]. The incompatibility of anthophytes with101any host plants is not well known at the molecular level [76]; [91], but it has been observed that extracts from resistant plants cause an inhibition of dodder

enzymes – enzymes that destroy the cell wall. It has been shown that dodders have a selective system that allows them to dissolve the walls of the host cells without destroying their own walls. However, this system does not function when cuscuta grows on itself; case in which it only uses mechanical pressure [99].

Opinions on whether haustoria are in fact modified roots differ among scientists: some say they are roots [54] because they have meristems [32] and they can survive the winter in host plants, thus becoming perennial [97]. Others consider that the haustoria are not roots because they do not appear at the base of the seeds as roots [24], [1]); and the cytochinins that inhibit root formation stimulate the formation of haustoria [67]; [75]; [57]; [58].

The first flowers appear about 4-6 weeks after germination, in a number of 5-20 flowers, presented as inflorescences of the types racem or cyme, and adapted for both cross-pollination – given that they attract a large number of pollinating insects [107]; [63] and for self-pollination, when the flowers are formed on covered filaments, which cannot be visited by insects. Flowers (Fig.1) are hermaphrodite, generally pentamere, 1.5-5 mm long, of either shorter or longer peduncles. The calyx is gamopetalous, tubular, membranous or fleshy, with obtuse or acute lobes, erectile or slightly reflective, often glued to the corolla, with wide edges. The corolla is gamopetaly, tubular, having triangular lobes at its tip, ovate or lanceolate, erectile, with either obtuse or acute tips. At the base of the corolla tube there are scales, stiffenings of the stamens, as membrane scales, than can be whole or divided, with finely denticulate edges or fringes. Cuscuta is the only genus in the Convolvulaceae family and the Solanales order, in which these structures have reached a high degree of elaboration and diversification [78]. The stamens are of equal numbers to the corolla lobes, being co-grown with the corolla tube. The ovary is bilocular, consisting of 2-4 ovules; whereas the two styles can be free-standing or united; the stigmas can be capitate, ovoid or prolonged.

The fruit is a conical, globular or flattened capsule, irregularly dehiscent or indehiscent, with 2-4 small seeds [19]; [74].

Fig. 1. Dodder's flowers (original)

Seeds are small, 0.4-4 mm in diameter and 1-2.2 mm in length, depending on the species, ovoid, globular or elongated, yellowish-brown, rusty, grayish or greenish, glabrous, with a reticular surface. Depending on the size of the seeds, dodder species are often grouped into two categories: large dodders, whose diameter is greater than 1.3 mm, and small ones with a diameter equal to or less than 1.3 mm. While these terms are sometimes used, they do not enable an identification of species [79]. The seed color ranges from gray to brown, depending on the thickness of the cuticle, the surface is cross-linked due to the peeling of the outer membrane of the cuticle [79]. The seed embryo can be twisted, spiral shaped or double-spiral shaped and the seed is devoid of cotyledons, which is a defining characteristic of the cuscuta genus. This can be explained by the fact that the main concern of the plant is to look for a host, and not to photosynthesize [22]. The morphological variations of the seeds of the different cuscuta species deserve to be taken into account, not only because they provide a better understanding of the development of secondary cell wall sculpture (which range from striate to micro-crosslinked or fine-folded), but also because they provide a taxon identification key based on seed characters [52].

Pre-parasitic life. Germination occurs in April-May, influenced by latency [63] and when optimum conditions of heat and humidity are achieved in the soil (15-20^{0}C for small seed dodders ex. *C. trifolii*, *C. epithymum* and 20-30^{0}C for those with large seeds such as *C. campestris*) and is also possible from May to October only for those seeds in the superficial soil layer, that are not deeper than 10 cm in the soil [79]. The tegumentary repose, which characterizes dodder seeds, is determined by the water impermeability of the seminal skin [94]. In nature, the discontinuation of the tegumentary repose is not well-known, it is known however that it can be interrupted by the passage of seeds through the animal and poultry tube, these being vectors in spreading the parasite, either directly or via manure. Also, winter frosts, various bacteria or fungi can interrupt the tegumentary repose of dodder seeds, which are known to remain in the soil, retaining their germination capacity for up to 10 years [79] or even longer, between 10 and 40 years for seeds preserved under low humidity conditions [36].

An interesting aspect of germination ecology is the presence of the water-resistant seminal tegument, that is, physical hibernation [38], which can be interrupted by mechanical scarification [44], [45]. This determines the germination of seeds of many cuscuta species, including C. epithymum [35], [93], but not in a high percentage (maximum 23%) [93], Gaertner's explanation being that they also have a physiological hibernation [38]. Other authors support the idea that hibernation is only physical, not physiological, and give examples of parasitic species in which germination is controlled by temperature changes, not by other factors (chemical indices of the host plant): C. Campestris [6] și C. australis (Jayasuriya et al., 2008). In our experiments, we tested seed germination under laboratory conditions, seeds in which the tegument repose was discontinued by sinking them into concentrated sulfuric acid (96%; d=1.83) for different amounts of time [92]. The seeds germinated after about 7 days; the best germination being registered with the seeds kept in sulfuric acid for 15, 20 and 25 minutes. A time frame of less than 15 minutes proved insufficient to destroy the impermeability of the skin; and those seeds left in acid for more than 25 minutes did not germinate because of the destruction of the viable elements of the embryo [92].

Establishing parasitic contact and parasitic development. Circumnutation enables the contact between the stem of the parasite and the host plant, the dodder wrapping itself spirally around the host between 4-8 times, a process followed by the thickening of the contact surface (also called irritable region) and the emission of haustoria, which then sink into the tissues of the plant. After about a week, time frame that is necessary to the establishment of vascular connections between the parasite and the host, the growth of the parasite is accelerated, and the terminal shoots then form visible knots and interlocks, after which the stem resumes its circumnutating movements to spiral around another host. From now on, the invasion of the parasite on the host is carried out rapidly, each cuscuta species can parasitize a large number of plant species, especially the dicotyledonous species [25]. Simultaneously with the formation of the first haustoria, the root as well as the base of the stem become necrotic and die. This moment defines the start of parasitism, since from now on the dodder nourishes solely via its host plant. The duration the parasite needs to go through all the phases that have been mentioned, namely from the beginning of seed germination to the final set-up, is 20-30 days. If the filament cannot encounter any favorable host, it continues to live an independent life from its seed reserves, but for no longer than a month.

Ontogeny and the nature of vasculary interconnection between parasite and host. The physical conjunction between parasite and host plant is called „haustorium"; and is produced by a xylem-xylem attachment [14]. When it comes to parasitic angiosperms, the water and nutrition transfer from hosts to parasites is facilitated by a high degree of osmolarity [42] and a low water potential (due to the high perspiration rate [54]; [34]; [71], by means of keeping stomata open in order to encourage perspiration and thus facilitate the extraction of nutrients from the host [14].

A haustorium contains a large amount of suckers (10-30), which present themselves as protuberances in the contact location between a haustorium and the tissue of the host plant. Every single of these protuberances starts looking like a concave disk that adheres through its margins to the host's epidermis (adhesion disk) [108], from which the haustoria emerge. The junction between a haustorium cell and the ligneous vessels is mainly realized by a simple contact, meaning that the extremities of haustorium cells penetrate the interior of xylem [108], but when the same cells come into contact with the phloem of the host plant, its extremities start a digitiform ramification, surrounding the vessel without penetrating its interior [84]; [85]; [26], [27], [53]).

The perennity of *Cuscuta*. Cuscuta species habitating in temperate climate zones are usually regarded as annual plants, of which the entire population dies at the end of the vehetative period [96]; [19], but there are assumtions that haustoria survive thrughout the unfavorable season in the tissues of the perennial host plants, thus surviving the winter and showing a perennial character [63]. Even more, it was proven that those individuals belonging to the species of *C. Epithymum*, deriving from winter-surviving haustoria, are capable to grow and infect host plants at the beginning of season, several weeks before those individuals deriving from germinated seeds [98]; and the vegetative part of the plant is twice as well developed and forms more abundant flowers throughout the same vegetative period [49], [50]; [63].

Cuscuta photosyntesis. Like all evolved plants, Cuscuta has four organs: roots, stems, leaves and flowers, although the root and leaves are very diminished. Since under normal environmental conditions, cuscutas are not capable of photosynthesis by themselves, they need to parasitize other plants in order to finalize their life cycle, so cuscuta can be defined as an obligate holoparasitic plant living on the stem of the host plant. It was believed that as a totally parasitic plant, the cuscuta would be incapable of photosynthesis and entirely lacking chlorophyll, and that the absent photosynthesis is a consequence of its parasitic nature [74]. However, there is proof that other than the root of the plant, all organs are slightly chlorophyllide and "equipped" with stomata [64]; [107]; [7]. The presence of the chlorophylles **a** and **b** in many cuscuta species is a fact [60]; [61]; [55]; [56], whereas the value of the ratio chlorophylle **a**/chlorophylle **b** is between 2.2 and 3.5; value that is analoguous to that of autothrophic plants [41]; [80]; [12]; [6]. Moreover, [33] prooved that in a CO2-enriched atmosphere, the photosynthetic intensity of cuscuta is very enlarged, despite its small concentration of chlorophylle, thus being able to ensure at least a part of those substances that are necessary to its growth [11]; [8].

Fer [33] showed that when it comes to dodders, the migration of assimilates is exclusively carried out acropetally; an observation that is also supported by Haupt and Newmann [40]; and the absence of a descendent migration seems to be determined by the absence of a radicular meristem [64]; [37]; [95]; [68]. Based on the exclusively acropet migration of assmilates, numerous studies in which cuscutas have been used as virus vectors, support the existing analogy between the direction of virus transmission and the migration direction of assimilates [16]; [43]; [47]; [72]. The absence of a descendent migration also explains the ephemeral life of the root, which exhausts its reserves and dies unless it gets assimilates.

The nature of substances collected by cuscuta from its host plants represents a controversial issue: Poma and Ciferri [69], as well as [105] emphasize that the greatest part of the metabolites collected by the parasite is formed by carbohydrates. Kerstetter and Hull [51] signal that the marked carbohydrates constitute the majority (70%) of soluble assimilates; Suthoff (quoted by Jacob [33] mentions that the parasitic collections mainly transport sucrose, whereas [33] proves that 95-96% of collected substances are represented by carbohydrates, the most representative one among them being sucrose, followed by glucose and fructose. Additionally, the transportation of a significant quantity of marked assimilates from host plant to cuscuta is also underlined in various studies [51], [46], [100], [104], whereas according to the results of [81], the parasitic collection mainly consists of nitrogenous substances.

CONCLUSIONS

The genus Cuscuta L. (dodder) is a significant groups of holoparasite-anthophytes, long time considered a curiosity by botanists, with many curiosities and features: an enormous fertility, a long subsistence in the search for host plants; a long-lasting and staggered germinative faculty, a lack of cotyledon, the presence of chlorophyll in all organs of the plant, with the exception of the root, he inability to photosynthesize, unless under conditions of a carbon dioxide-enriched atmosphere; lack of a meristem and root sculpture, which results in a solely ascending migration of assimilates; the resistance of living haustoria in the host plant while the parasite's stem is dead, thus enabling the parasitic plant to regenerate and become perennial; the ability to transmit diseases such as viruses and mycoplasmas etc.

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