Cuscuta form and function—evolutionary implications of its bizarre development

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Mahadevan S 1992. *Cuscuta* form and function—evolutionary implications of its bizarre development. *Palaeobotanist* **41** : 198-203.

During its evolution from an autotrophic ancestor, parasitic *Cuscuta* has lost roots, cotyledons, expanded green leaf, and cambium and has gained haustorium and heterotrophy. Though the expression of thousands of genes is expected to be permanently altered during this transformation, the extensive morphological alterations resulting from certain single gene mutations in plants suggest that evolutionary alterations in just a few higher order regulatory genes acting either early in embryogenesis or at 'developmental forks' may have sufficed to initiate the change. Possible turning points and candidate genes associated with loss of organs and functions are identified based on similar effects in other plants. The suspected homology between root and haustorium, suggested by ontogenetic and hormonal considerations, can now be directly tested by modern recombinant DNA methods.

Key-words—*Cuscuta*, Mutation, Haustorium, Evolution, Skotomorphogenesis.

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सारांश

कस्क्यूटा का स्वरूप एवं कार्य – इसके विलक्षण विकास का वैकासिक महत्व

एस० महादेवन

अपने स्वपोषी पूर्वज से विकास के समय परपोषी **कस्क्यूटा** में जड़ें, बीजपत्र, पत्तियाँ एवं एधा विलुप्त हो गये हैं तथा विषमपोषिता एवं चूषकांग विकसित हो गये हैं। हालाँकि इस स्थायी परिवर्तन में हजारों जीनों का योगदान रहा होगा परन्तु एक जीन उत्परिवर्तन से इतने आकारिकीय परिवर्तन या तो भ्रूण-उत्पत्ति के समय अथवा 'विकासीय दुशाख' के समय ही हो सकते हैं। अन्य पौधों में इसी प्रकार के परिवर्तनों के लिए उत्तरदायी जीनों का अभिनिर्धारण किया गया है जिनके कारण कि पौधों में अंग विलुप्त हो जाते हैं अथवा उनके कार्य में अत्याधिक परिवर्तन हो जाता है। जड़ एवं चूषकांग के मध्य समजातीयता अब आधुनिक पुनःसंयोजक डी-एन-ए विधियों द्वारा अन्वेषित की जा सकती है।

THE dodders, members of the monogeneric family Cuscutaceae, are perhaps the best known among parasitic plants, with over 150 species spread over five continents and parasitizing a range of host plants (Kuijt, 1969; Cronquist, 1968). During the course of evolution from its putative, autotrophic green ancestor, possibly a twining Convolvulaceous member, *Cuscuta* has lost roots, expanded leaves, cotyledons and cambium to become heterotrophic with the evolutionary gain of haustorium, the organ of nutrient absorption from its host. The vegetative plant body, reduced to a yellow stringy vine with no connection with the soil following seed germination (as the radicular end of the embryo does not develop), continues growth as an epiphyte, now coiling around a host that triggers the production of haustoria which literally sink into it to tap the phloem, only to grow out again as a free, circumnutating vine capable of a fresh conquest. A severed piece of this vine is literally infectious, capable of coiling around and parasitizing a new host on which it may happen to fall. With their unusual appearane and mysterious but treacherous way of life, the cuscutas have many endearing names—*amarbel, akashbel*, strangleweed, devil's gut, beggar weed to name a few (Mahadevan, 1983).

The bizarre development of *Cuscuta* raises several interesting ontogenetic and phylogenetic questions. How has evolution brought together so many apparently diverse 'developmental lesions' to yield a product so exquisitely adapted to its parasitic

Essays in Evolutionary Plant Biology
Editors : B. S. Venkatachala, David L. Dilcher & Hari K. Maheshwari
Publisher : Birbal Sahni Institute of Palaeobotany, Lucknow

mode of life? Has this assembly been piecemeal, as so many separate microevolutionary steps or had 'hopeful monster' type of macromutations helped bridge the evolutionary gap? Has there been an 'evolutionary facilitation' (Wills, 1989), a sort of predisposition in the ancestral genome that allowed its reorganization in a way that led to the rapid emergence of the parasitic phenotype? What genes have been shuffled, silenced, lost or gained during the process? This essay is an attempt to analyze some of these questions.

TAXONOMIC AFFINITY AND ANTIQUITY OF *CUSCUTA*

Only similarity of floral structure and a shared twining habit links the dodders to Convolvulaceae at present. There are hardly any vegetative characters in the former for comparison to extant plants (Kuijt, 1969). The basic chromosome number (x) is 10-11 in Convolvulaceae and 7 in Cuscutaceae, with diploid number of individual species ranging from 20 to 50 in the former and between 14 and 42 in the latter (Darlington & Janaki Ammal, 1945). It is not known how different their geonomic sizes are, nor have their genomes been compared in any way.

A solitary fossil pollen record suggests a Lower Eocene origin for Convolvulaceae about 55 Ma, a period when several angiospermic families first made their appearance (Muller, 1981). The antiquity of dodder, if derived from this family, should therefore be < 55 million years. Molecular 'dating' may give a more precise time of divergence.

HOW MANY GENES QUALIFY AN ORGAN—A NUMBERS GAME

Our present appreciation of the magnitude and diversity of processed gene transcripts associated with an organ stems exclusively from polysomal (or m) RNA excess/single copy DNA hybridization studies (Kamalay & Goldberg, 1980; Willing & Mascarenhas, 1984). Each organ-leaf, stem, root, anther, ovule or pollen grain-contains about 6,000-8,000 transcripts not processed in any other organ unless it shares homology with it, as it between leaf and petal (Kamalay & Goldberg, 1980).

While gene transcripts (and therefore genes) qualifying an organ run into thousands, genes expressed in an organism as a whole is an order greater in magnitude. About 60,000 diverse structural genes get expressed during the dominant phase of the life cycle of a complete plant having all organs such as tobacco. But even this complexity is but a fraction (11%) of all single copy DNA present in this plant (Kamalay & Goldberg, 1980).

If one extrapolates these figures to *Cuscuta* with the evolutionary loss of so many organs and functions, it is reasonable to conclude that thousands of genes once expressed in its autotrophic ancestor now remain silent forever in this parasite. How did this come about?

HAUSTORIUM—MODIFIED ROOT OR ORGAN *SUI GENERIS*

The evolutionary gain of an organ, the haustorium in *Cuscuta*, poses the question in reverse. How many genes were rendered 'expressible' with the advent of this organ? As is for any other organ one expects this to run into the thousands. What, if any, was the role of these thousands of genes in the ancestor of *Cuscuta*? The question is a tricky one. For while it is easy to visualize loss of expression of genes—after all thousands of 'leaf' genes remain silent in roots though root cells contain these genes—it is much more difficult to explain 'gain' of expression, specially for thousands of genes, unless homology to previously existing organ is invoked. If the haustorium is a modified root as many believe (Kuijt, 1969), most, if not all, of the expressed genes possibly formed the set that was expressed in the ancestor's root. Support for such a view comes from the shared transcripts of leaves and petals observed in tobacco as mentioned above.

The question of ancestry of the putative set of 'haustorium-specific' genes becomes more intangible if one considers the haustorium as an organ *sui generis*, that is an organ of its own kind with no homology, as some others believe (Kuijt, 1969). What if anything were these thousands of genes doing in the ancestor and how were they orchestrated together in the haustorium? The problem becomes more acute when it is realized that less than 55 million years were available for this to have happened.

The 'numbers game' of organ-specific genes tends to push one into the 'haustorium is a modified root' camp—for the problem now appears easier to comprehend. Besides, it provides a framework for experimental verification; one can compare 'haustoria and roots for shared gene transcripts not expressed elsewhere.

HOW MANY GENES CONTROL A MORPHOLOGICAL CHARACTER—THE GENETIC EVIDENCE

If thousands of genes are specifically expressed

during the functioning of an organ, how many genes are involved in the manifestation of the organ itself? Paradoxically, the answer appears to be—very few, sometimes even one!

Since the time of Mendel, the profound effect of single genes on morphological characters in plants has been repeatedly documented. The literature is replete with examples of how one, two or a few genes govern either the presence or absence, or otherwise influence the shape or architecture of every concievable plant part such as leaf, tendril, stem, root, inflorescence, floral parts, fruit and seed (Gottlieb, 1984; Hilu, 1983). Single gene mutations can bring about profound changes during embryogenesis or floral evocation altering the very character of development (Jurgens *et al.*, 1991; Coen & Meyerowitz, 1991).

Apparently plants tolerate to a very great extent mutation in genes which bring about great morphological change. This tolerance is primarily due to the 'open, less interactive and plastic pattern of morphogenesis in plants' (Hilu, 1983). As a consequence single-gene mutations are believed to have had a powerful influence in the rapid evolution of flowering plants (Hilu, 1983).

HIGHER ORDER REGULATORY GENES, POTENTIAL ALTERING MUTATIONS AND EVOLUTION

If mutations in one, two or a few genes cause so profound an effect in a system involving thousands of genes, it can only mean that these genes have a central regulatory role. Such genes, essentially at the head of developmental hierarchies, may act early in embryogenesis when pattern is being determined (Meinke, 1991; Mayer *et al.*, 1991), or at developmental forks' switching further development into any one of alternate pathways (Deng *et al.*, 1991; Bejarano & Lichtenstein, 1991). Some act homeotically, others heterochronically (Carpenter & Coen, 1990).

It has been argued that regulatory change is the crucial ingredient for evolution (Gould, 1977). Regulatory changes are, however, locked up in the genome of the organism. One would have to recognize and search for such higher order regulatory genes with their potential to suppress or activate the development of entire organs, should one wish to understand how organs were lost or gained during evolution.

Unlike most mutations that act in a small way, the mutations stated above, though simply inherited, have large effects—they are indeed 'potential altering mutations' (Wills, 1989). While such mutations by themselves do not lead to evolution—there are no instant 'hopeful monsters' *a la* Goldschmidt (1940)—they certainly can lead to rapid change after being filtered through natural selection. Once the basic features of flowering plants were genetically established through evolution, further modifications were quickly possible by such potential altering mutations with 'their capacity to deflect the pathway of primordial differentiation' (Hilu, 1983). Natural selection thereafter guided subsequent evolution under the influence of other associated genes.

CUSCUTA EVOLUTION—EVOLUTIONARY FACILITATION, TURNING POINTS AND CANDIDATE GENES

In his perceptive book, Wills (1989) has persuasively argued that 'evolution is getting easier with time by means of a process that we might call evolutionary facilitation' when 'genes of many organisms have become altered, grouped and rearranged into patterns that actually facilitate further evolution.' Going along with this argument and given that *Cuscuta* evolved from a twining, autotrophic, possibly Convolvulaceous ancestor, can we identify candidate genes whose altered activity were turning points in this transformation? Such an exercise has two parts to it: (i) when and where do these candidate genes express themselves leading to the changed (*Cuscuta*) phenotype, and (ii) the likely identity of these genes inferred from mutated genes in other plants causing a similar phenotype change. The candidate genes are likely to include mutated forms of higher order regulatory genes outlined earlier. With the techniques now available for manipulating genes, identifying them in any one plant paves the way to fish them out in any other plant including *Cuscuta*.

Absence of root and cotyledons

Embryogenesis in *Cuscuta* is abnormal, a feature common to most holoparasitic plants (Kuijt, 1969)—and a forerunner to their aberrant lifestyle. The globular embryo does not develop into the heart-shaped stage; consequently no cotyledons are formed. At the radicular end neither a root meristem nor a root cap is formed; so no true root develops upon germination (Johri & Tiagi, 1952; Kuijt, 1969). Attempts to induce growth and differentiation of the radicular end by *in vitro* culture of embryos or its parts either failed or produced callus (Truscott, 1966; Maheshwari & Baldev, 1961). These observations suggest a genetic lesion at the globular

stage suppressing both normal root and cotyledon development in *Cuscuta*.

Single gene mutations resulting in rootless phenotypes have been reported in several plant species (Schiefelbein & Benfey, 1991; Sheridan, 1988; Meinke, 1991). Likewise single gene mutations, the *lanceolate* in tomato (Caruso & Cutter, 1970) and *gurke* in *Arabidopsis* (Mayer *et al.*, 1991), eliminate both cotyledons and shoot apical meristem but not the root meristem. In *Arabidopsis*, a recessive apical-basal pattern deletion mutant *gnom* deletes root meristem and strongly reduces or eliminates cotyledons (Mayer *et al.*, 1991; Jurgens *et al.*, 1991). Though some of its extreme alleles totally eliminate axial development, *gnom* appears to be a promising candidate gene for investigation in *Cuscuta* once it is identified and cloned from *Arabidopsis*.

Shoot development—is it skotomorphogenesis in light?

Morphologically *Cuscuta* resembles a plant under perpetual etiolation—a syndrome comprising exaggerated internodal elongation, arrested leaf expansion, absence of greening, poor vascularization and suppressed secondary growth. Besides exhibiting these features to varying extents, certain light associated phenomena are either sluggish or totally absent in *Cuscuta*. For instance 'hook opening', normally a highly light-sensitive dark to light transition phenomenon, occured only after prolonged exposure to red, far red or blue light in *C. gronovii* seedlings (Kujawski & Truscott, 1974). And photosynthesis may be either absent as in *C. europaea* or highly repressed as in *C. reflexa* (Machado & Zetsche, 1990). Developing in light, *Cuscuta* appears more a product of skotomorphogenesis than photomorphogenesis.

Twiners as a class exhibit some of these features during primary growth. Their vine-like appearance is a result of extensive internodal elongation preceding leaf expansion, suggesting a heterochronic lag in the expression of certain photomorphogenetic genes that suppress internodal growth and promote leaf expansion. If this is so, a permanent repression of these genes should yield a *Cuscuta*-like morphology.

Mutant studies in *Arabidopsis* have uncovered the presence of two classes of light-associated de-etiolation genes whose recessive mutant forms *hy* and *blu* exhibit just such an effect (Bejarano & Lichtenstein, 1992; Chory *et al.*, 1989a; Liscum & Hangarter, 1991). Both classes of mutants failed to show light-induced suppression of hypocotyl elongation, the *hy* mutants in the red/far red phytochrome-associated region, the *blu* mutants in the blue region and the *hy/blu* double mutant in all wavelengths of visible light. Though terms such as hypocotyl or epicotyl are meaningless with reference to *Cuscuta* which has no cotyledons, the morphogenetic effects of these mutant genes are truly impressive to consider as candidate genes in *Cuscuta* evolution, especially since their pleiotropic effects include increased apical-dominance, reduced greening and reduced leaf size.

In addition to these genes associated with light-induced development, two other classes of genes in *Arabidopsis* promote etiolation in the dark by repressing the de-etiolation developmental programme. Their recessive mutant forms, *det* (Chory *et al.*, 1989b) and *cop* (Deng *et al.*, 1991), result in de-etiolation even in the dark. Obviously the wild type alleles of these genes allow etiolation by disallowing de-etiolation. Could constitutive over expression of such genes reinforce the bizarre 'etiolation' syndrome in *Cuscuta*?

Shoot development—a role for abscisic and gibberellic acids?

Reported effects of abscisic acid (ABA) on plants (Letham *et al.*, 1978; Zeevaart & Creelman, 1988) include induction of scale leaves, poor vascular and stomatal differentiation, inhibition of cambium formation, reduced lignification and degreening-features associated with *Cuscuta* development. In *Cuscuta reflexa*, in the absence of cambium there is no secondary growth, nor a true secondary xylem formed (Rajagopal *et al.*, 1990). Interestingly substantial amounts of ABA and a compound crossreactive with ABA antibody occur in *Cuscuta* (Ihl *et al.*, 1987; Kimura *et al.*, 1982; Vasanthi, unpublished observations). Is its bizarre development associated with an aberrant ABA metabolism?

One distinctive ABA effect not observed in *Cuscuta* is its inhibition of shoot elongation growth. Exogenous ABA had little inhibitory effect on stem elongation growth either *in vivo* or *in vitro* in the presence of auxin (Rajput, 1987; our unpublished observations). The behaviour resembles the reduced inhibition of growth by ABA in certain ABA-insensitive mutants of *Arabidopsis* (Klee & Estelle, 1991). Is *Cuscuta* similarly ABA insensitive?

Besides insensitivity to ABA, *Cuscuta* exhibits sensitivity to gibberellic acid (GA) not unlike that observed in *slender* mutants of pea and barley, a class of GA-responsive mutants with a phenotype characterized by thin, elongated internode (Scott,

1990). Shoot apical segments of *Cuscuta* in culture respond to GA with dramatic elongation of internodes. In the absence of GA or of the apical bud, a lateral bud grows out in a truly slender fashion (Maheshwari *et al.*, 1980; Maheshwari & Sreekrishna, 1982). Does *Cuscuta* harbor constitutively a genetic sensitivity to GA as in these *slender* mutants?

Haustorium—is it a modified root?

While there appears to be little doubt in the evolutionary origin of haustorium from root in other parasitic plants, its origin appears to be debatable in *Cuscuta* (and in *Cassytha*) (Kuijt, 1969). The *Cuscuta* haustorium, if a modified root, arose not from the radicular pole of the ancestral embryo but rather from adventitious roots of a twining ancestral vine. Unfortunately no extant species of Convolvulaceae is known to produce such roots (Kuijt, 1969).

The *Cuscuta* haustorium consists of two parts—an outer 'prehaustorium' of differentiated epidermal and outer cortical cells, and an inner 'true haustorium' that grows through the prehaustorium into the host to become the organ of absorption (Kuijt, 1969). It is the true haustorium then that has homology to root owing to its endogenous origin and absorptive function.

A doubt was cast on the 'root' nature of *Cuscuta* haustorium when its formation was shown to be induced by cytokinin and the process inhibited by auxin—the reverse of the now classical auxin promotion and cytokinin inhibition of root formation (Paliyath *et al.*, 1978). However this objection may not be tenable for two reasons. Auxin inhibits only early events of the induction process and not later ones (Ramasubramanian *et al.*, 1988) when the 'true haustorium' is expected to be formed. Cytokinin treatment, by inhibiting both auxin transport and conjugation (Paliyath *et al.*, 1989) may indeed be raising the endogenous level of auxin in tissue—a possibility that can be experimentally verified.

Once formed, the root apex becomes a site for the production of cytokinins and ABA (Davies & Zhang, 1991). Besides free cytokinins and ABA, *Cuscuta* haustorial coils contain substantial amounts of a cytokinin conjugate tentatively identified as isopentenyladenine-9-glucoside (Ramasubramanian, 1987) and the unidentified ABA derivative referred to earlier. Are these indications of the 'root' nature of the haustorium?

As suggested earlier, a strategy to establish homology between root and *Cuscuta* haustorium would be to identify organ-specific transcripts shared by these organs. This may be accomplished in two ways : search for 'root-specific' transcripts identified from other species in a *Cuscuta* haustorium c-DNA library, and conversely, search for 'haustorium-specific' transcript initially identified in *Cuscuta*, that may be present in the root-c-DNA libraries of other plants.

Differential screening of c-DNA libraries have led to gene clones specifically or preferentially expressed in roots or expressed at specific stages of lateral root development (Schiefelbein & Benfey, 1991; Conkling *et al.*, 1990; Keller & Lamb, 1989). 'Root-specific' expression of some of these genes has been established using the GUS reporter system (Keller & Lamb, 1989; Conkling *et al.*, 1990). For the present these are candidate gene probes available to start answering the question whether the evolutionary precursor of *Cuscuta* haustorium was indeed a root.

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