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ARE VASCULAR PLANTS “INSIDE-OUT” LICHENS?

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INTRODUCTION

This essay considers the possibility that vascular plants originated from an algal–fungal mutualism. Among land plants, the vascular forms are in many ways extraordinary; they seem to be far more than simple evolutionary “extensions” of green algae. They are comparatively too complex, and they diversified too quickly. More important, they contain numerous overtly funguslike cells. It is primarily this observation that leads me to speculate that these elaborate organisms are the genetic legacy of both algal and fungal ancestors.

We can reasonably assume that the fungi have an ancient history of intimate association with the algae (Ahmadjian 1987) and were probably involved in the original transition to land. First Jeffrey (1962) and then Pirozynski and Malloch (1975) hypothesized that all terrestrial plants arose from an ancient symbiosis between a semiaquatic ancestral green alga and an aquatic fungus, an oomycete. The essence of this important proposal, elaborated by Pirozynski and Malloch, is that land plants are “reverse-phase” lichens in which the alga evolved into the dominant component and the fungus became a mineral-scavenging endophyte, much as we see today in extant mycorrhizal associations. Indeed, this alga-dominant prototype is reflected in many marine associations called “mycophycobioses” (Ahmadjian and Paracer 1986).

The merger I will propose came much later but prior to the evolution of vascular tissue, perhaps in a close ancestor of the Rhyniophyta, but probably in a more *Coleochaete*-like organism (Bold et al. 1987). It began with fungal parasitism, may have evolved into a mutualism, and culminated in the acquisition of the fungal genome by the plant host. My story is in accord with mounting evidence that parasites can rapidly become required cellular components (Jeon 1987) and have provided the genetic substrate for evolutionary innovations in many types of host populations (Price et al. 1986). In this essay, I will argue that vascular plants

may in fact be lichenlike chimeras that have genetically internalized their fungal partners.

W. F. Lamboy (1984) has developed a somewhat similar albeit less encompassing view. Lamboy suggests that some of the evolution that has taken place in the angiosperms (and other plant groups) is attributable to horizontal gene transfer (hgt) from parasitic or symbiotic fungi to their flowering-plant hosts. He describes three conditions necessary for fungus-to-angiosperm hgt and suggests that all can be satisfied by normal fungus–angiosperm interactions: (1) the fungus must be in intimate contact with the host’s reproductive cells or the meristematic cells that give rise to these structures; (2) physical barriers to DNA transfer must be overcome; and (3) the transferred DNA must be incorporated into the genome of the host’s reproductive cells. As one example of the kind of trait that could have resulted from hgt, Lamboy suggests that corn evolved from teosinte by hgt from the fungus *Ustilago maydis*, which could have provided the genes responsible for sex change and dwarfing of the teosinte tassel. Although hgt is a reasonable mechanism for the acquisition of fungal genes, this process is too “piecemeal” to give vascular plants the kinds of genetic endowment that I visualize.

NUCLEAR TRANSFER, FUSION, AND CELLULAR TRANSFORMATION

I am particularly enthusiastic about the concept of nuclear transfer from parasite to host, followed by cellular transformation (Goff and Coleman 1984, 1985, 1987). The parasitic red algae are funguslike, obligate biotrophic parasites composed of branching filaments of cells that penetrate between the cells of their related red alga hosts. During the normal course of infection, nuclei are delivered via secondary pit connections; they are cut off into specialized conjuctor cells each of which fuses with an adjacent host cell, thereby transferring nuclei and other cytoplasmic organelles into the host-cell cytoplasm (Fig. 1A). One outcome of this unique regulatory mechanism is especially pertinent to my thesis that some vascular plant cells behave like endophytic fungi. Certain parasitic red algae have little or no somatic tissue development of their own. Following nuclear transfer, the host cell is effectively trans-

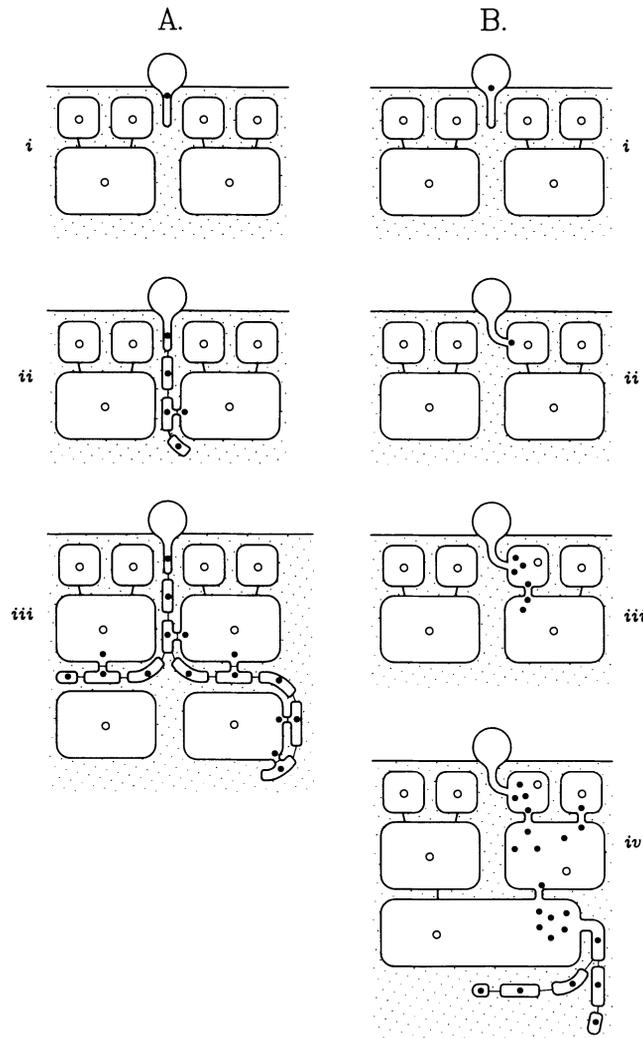


FIG. 1. A comparison of nuclear colonization (A) and nuclear transformation (B) of host cells by parasitic red algae. The black nuclei are parasitic nuclei. In model (A) the parasitic genome is spread by parasite cells, which grow intrusively throughout the host and transfer nuclei to adjacent cells. In model (B) the parasite nuclei rapidly divide and eventually outnumber the resident host nuclei. The transformed host-cell lineage then produces cellular filaments that grow intercellularly and fuse with other host cells, thereby spreading the parasite genome throughout localized regions of the host. The process of conjuncture cell formation is not shown here. From Goff and Coleman (1987:420: Fig. 12). Reproduced by permission.

formed into a heterokaryotic funguslike cell that continues to disperse nuclei within the host (Fig. 1B). In the authors' words, "From localized regions of these heterokaryotic cells, parasite nuclei (and occasionally some host nuclei) are cut off into 'bud' cells. These cells elongate and divide apically to form filaments of colorless cells that branch and grow intrusively through adjacent host tissues." The Goff and Coleman model of parasite nuclear transformation of a host cell robustly explains the kind of cellular transformation that I have envisioned for the haustorial cells of parasitic vascular plants (Atsatt 1973, 1983, 1986).

This very significant finding in the parasitic red algae need only be slightly modified to apply to vascular plants, whose cells are totipotent with respect to development and, for the most part, not multinucleate. Fusion of the fungal and host nuclei would have to occur, resulting in a chimeric nucleus whose two genomes might remain physically separate (as in allopolyploids) but be integratively controlled. Here I lean heavily on the concept of promiscuous DNA and the idea that the nucleus has evolved ways of selectively accumulating and rearranging incoming DNA in novel combinations with pre-existing genes and controlling

sequences (Timmis and Scott 1984). Goff and Coleman (1985) review the short literature on the fusion of genetically distinct nuclei. See Orton (1984) for a relevant discussion of genetic variation in somatic tissue.

The minimal requirement for achievement of this fusion is obviously nuclear transfer into a host protoplast, which then recovers and reproduces. Several mechanisms can be envisioned. For example, *Plasmodiophora brassicae*, an obligate fungal parasite of higher plants, "fires" a hole through the host wall with a bullet-shaped "stachel" and then injects a naked protoplast into the host cytoplasm (Beckett et al. 1974). The fungal plasma membrane, or even a thin wall, might be ruptured in a variety of ways, e.g., by host-cell enzymes, by hormonal changes resulting from host wounding (Stutz et al. 1985), by internal parasites such as dsRNA (Elliston 1985) or mycoparasites (Vakili 1985), by the extracellular hydrolases of a coparasitizing fungal species, or certainly by the stylets of sucking insects. In the case of a coevolved fungal endophyte, a heterokaryotic cell might result from slight alterations in the normal process of cell colonization. The haustorial cells of VA mycorrhizal fungi lose their chitinous structure and become extremely thin during the biotrophic phase of development. When these intracellular haustoria senesce, the fungal cytoplasm undergoes autolysis, and the hyphae collapse. During this process of parasite breakdown, the integrity of the host membrane is maintained, and the cytology of the host cell then returns to the pre-infection state (Gianinazzi-Pearson 1986). Alternatively, we cannot rule out the possibility that the fungal protoplast simply fused with the host protoplast and transferred most or all of its contents (see later discussion).

FUNGUSLIKE CELLS AND OTHER MAVERICK TYPES

In what ways would this hybrid nucleus manifest itself? One general expectation might be a plastid-containing cell with fungal characteristics such as intrusive intercellular growth and either intercellular or intracellular haustorial feeding, a combination clearly expressed by the parasitic vascular plants. For example, following intrusive intercellular growth, the haustorial cells of *Cuscuta* (Cuscutaceae) penetrate the walls of living cells (Dörr 1968), whereas those of *Comandra* (Santalaceae) usually enter host vessels by forcing their way through a pit area and then expanding inside (Toth and Kuijt 1976). In a very real sense these parasitic vascular plants are functionally biotrophic fungi. Many have reduced photosynthetic capacity and others are wholly heterotrophic, but none has yet lost its plastids. They parasitize their "own kind" as do the parasitic red algae and many fungi called mycoparasites.

The overall biology of haustorial mycoparasites is

strikingly similar to that of many parasitic plants. If, in the following description from Ahmadjian and Paracer (1986), one switches key words such as spore/seed, cell/tissue, sporangia/fruit, etc., there is little to distinguish the two types of parasites: "Spores of the mycosymbiont germinate in response to substances that diffuse from a host mycelium. The germ tube grows toward the host hyphae, and upon contact, the tip of the germ tube swells to form an appressorium, which is a flat, hyphal cell. Fine hyphal branches from the appressorium penetrate the host cell and then enlarge to form inflated haustoria. An internal mycelium develops from the haustoria, and on maturity hyphae emerge from the host and form sporangia." In parasitic plants the internal "mycelium" that develops from the haustorium is called the "endophyte." This organ is sometimes filamentous, can be rampantly systemic, and in some groups only emerges from the host to flower and fruit. Nearly 20 yr ago it was Job Kuijt's (1969) description of these cells that initially sparked my curiosity about their genetic origins (Atsatt 1973). He wrote: "The nature of the endophyte of Rafflesiaceae, constituting the entire vegetative body, defies description. The uniseriate filaments which form the youngest portion leave scarcely a tissue or an organ of the host unexplored. The endophyte has frequently been compared to a fungus mycelium, ramifying and anastomosing throughout the host." Some of the dwarf mistletoes are equally impressive; these intercellular funguslike organisms also emerge from the host at multiple "eruptions" and reproduce on short vegetative stalks.

Pollen tubes are also manifestly funguslike and often parasitic. In *Pinus*, cycads, and *Ginkgo* the pollen tube is branched and haustorial (absorptive). Growth of the pollen tube through the megasporangium is slow and involves enzymatic activity. In many angiosperms the pollen tube is quite ephemeral and may not require much nutrition, but in other cases the pollen tube grows slowly or over a great distance, and here parasitism may be significant (Bold et al. 1987). Callose formation, which normally occurs in response to parasite infection, also occurs in the wall surrounding the developing microspore and again later in the intine wall surrounding germinating tube cells growing in vitro (Foster and Gifford 1974). Perhaps this callose formation can be viewed as a reaction to parasitic genetic elements that may be carried by the generative cell or other components of this elongating haustorial tube. The resistance of a genetically incompatible style to "infection" by pollen also has many of the earmarks of host-non-host interactions between plant cultivars and races of fungal pathogens (for example, see Wood 1986).

In the angiosperms, a brief heterokaryotic state typically forms part of the reproductive cycle, when two sperm nuclei enter an embryo sac that may contain

numerous free nuclei. One of the sperm nuclei unites with the egg nucleus, while the other fuses with one, two, or several (as many as 14) "polar" nuclei to form a polyploid endosperm nucleus, from which the endosperm tissue originates. Interestingly, another haustorial cell develops soon after this nuclear fusion. To quote Foster and Gifford (1974), "a truly bizarre characteristic of endosperm that has been observed in a number of angiosperms is the formation of more-or-less prominent endosperm haustoria. These remarkable outgrowths may arise at either or both ends of the developing endosperm and in some plants aggressively invade adjacent parts of the ovule such as the chalaza, the integuments, or even the funiculus."

Vascular plants contain many other maverick cell types that markedly differ in form, size, content, and wall structure from other cells in the same tissue (Esau 1977). Usually called idioblasts, these remarkable examples of cell specialization include a bewildering array of cell types: (1) "excretory" idioblasts such as oil cells, mucilage cells, tannin cells, lithocysts, myrosin cells, and latex cells; (2) tracheoid idioblasts, which resemble tracheids but differ in their form, size, and position; and (3) sclerenchymatous idioblasts, commonly designated as sclereids. Unicellular trichomes are epidermal idioblasts, and from an ontogenetic point of view the guard cells of stomata may be regarded as paired idioblasts (Foster 1956).

A few of these maverick cells behave remarkably like endophytic fungi. For example, nonarticulated laticifers are elongate, multinucleate cellular tubes that grow throughout the plant body in many members of the Euphorbiaceae, Asclepiadaceae, and other dicotyledonous families. As Mahlberg and Sabharwal (1968) have demonstrated, "they appear at the time of initiation of the cotyledons, and, during subsequent development of the embryo, the growing extensions of these cells penetrate along the hypocotyl toward the root meristem and into the enlarging cotyledons. The growing tips of the cell ramify in different directions permeating various tissues of the shoot and root axes." Sclerids are another intrusively growing cell and are among the most bizarre and polymorphic of all types of idioblasts (Foster 1956). They range in form from polyhedral to profusely branched or filiform cell types. The initial cell of a branched sclerid may not differ in appearance from neighboring parenchyma cells, but later, instead of enlarging uniformly as a parenchyma cell, it develops processes that elongate into branches (refer again to Fig. 1B). The branches not only invade the intercellular spaces but also force their way between the walls of other cells (Esau 1977).

UNEQUAL DISTRIBUTION OF FUNGAL GENES

A major common denominator in the origin of these specialized cell types seems to be polarized or unequal

cell division, wherein the smaller of the two daughter cells is densely cytoplasmic, possesses an enlarged nucleus, and develops into the specialized cell, whereas the larger of the two daughter cells becomes the more generalized cell type of a particular tissue (Foster 1956, Esau 1977). The phenomenon of asymmetric cell division provides a reasonable fit to the theoretical expectations logically derived from the Goff and Coleman transformation model (Fig. 1B). In the parasitic red alga system, the original parasitic cell is largely reconstituted from a localized region of the larger heterokaryotic host cell when predominantly parasitic nuclei are cut off into smaller "bud" cells. In my chimeric nucleus analog of this model, cellular differentiation might also proceed by unequal distribution of fungal genes or gene products into specialized primordial initials.

Asymmetric cell division is particularly pronounced in the outer protective layer of vascular plants. In grass epidermis, for example, unequal divisions result in the formation of short and long cells, and only the short cells produce the specialized cells or cell complexes such as trichomes, guard cells, and cork-silica cell pairs (Esau 1977). Unequal divisions also occur when root-hair-forming cells originate. In *Hydrocharis*, the small root-hair-forming cells differ from their long sister cells in having larger nuclei and nucleoli, simpler plastids, more intense enzyme activity, and larger amounts of nucleohistone, total protein, RNA, and nuclear DNA (Cutter and Feldman 1970a, b). Branched tracheidlike sclerids also originate from polarized or unequal cell divisions in the aerial roots of *Monstera deliciosa*. The smaller of the two daughter cells has a large nucleus, is densely cytoplasmic, and eventually develops into a ramified "trichosclerid." Enlarged nuclei similarly characterize the haustorial cells produced by parasitic dicots. Asymmetrical cell divisions also produce tannin-containing secretory cells in *Ricinus* (Foster 1956). A similar unequal genomic distribution may be expressed in phloem sieve elements, where the "companion" cell remains nucleated and physiologically active while the larger cell loses its nucleus and becomes specialized for conduction.

FENESTRATED PIPELINES

Any discussion of the evolutionary origins of the "Tracheophyta" must certainly include the vascular system. This efficient plumbing system is largely responsible for the evolution of the massive, physiologically independent sporophyte that has come to dominate most terrestrial ecosystems. Typical tracheids are characterized by their elongated form and by the elimination of their protoplasmic contents at functional maturity, two morphological features that enhance the longitudinal movement of water. From primitive tracheids, two lines of specialized cells apparently di-

verged, one toward the vessels, the other toward fibers. Fibers are long, slender cells (up to 55 cm!) that show a combination of coordinated and intrusive growth, but up to 75% of their length may be attained by intrusive growth carried out at both apices (Esau 1977). Like their tubular latex-carrying cousins, fibers may also become multinucleate during elongation.

In my view, both the water and food conduits of vascular plants represent highly modified fungus-type cells that ramify and anastomose throughout the plant body. Why, then, didn't these pipelines evolve as single tubes, stretching from top to bottom? One important reason why tracheids might have suppressed their potential for intrusive growth is the fact that excessively elongating cells must retain their living protoplasts, and it is the very early loss of these cell contents that makes tracheary cells (and vessels) such efficient conductors (Bailey 1953). This explanation does not apply to the phloem, however, which retains a modified protoplast. The red algal model upon which I have already relied so heavily suggests another more fundamental explanation for why vascular tissue is constructed from many individual cells connected by wall pores called "pits." The explanation will require a brief detour into first principles.

THE PIT CONNECTION: A CYTOPLASM-CONNECTING PARASITIC ELEMENT

Goff and Coleman (1985) suggest that the origin of parasitism by red algae may rest squarely on the phenomenon of secondary pit connection formation, that is, on the ability of nonsister vegetative cells to form cytoplasmic connections. But how did this rudimentary parasitic trait evolve? I suspect that it is induced by a viruslike genetic element and represents a mechanism whereby the parasitic element disperses itself from cell to cell. There is a reasonable body of evidence that viruses move from cell to cell through plasmodesmata (intercellular cytoplasmic connections) and that they directly or indirectly modify these cytoplasmic strands (Robards 1975). More to the point, the two plant groups with highly specialized pit connections, the parasitic red algae and vascular plants, both contain a similar viruslike element. It has been observed in nonparasitic vascular plants (Anton-Lamprecht 1965, Ie 1972, Sigeo 1974), in parasitic angiosperms (Dörr and Kollmann 1974; P. R. Atsatt, *personal observation*), and in the parasitic red algae (Kugrens and West 1973, Goff 1976). Goff (1976) notes that these elements are a universal inclusion in cells of the parasite *Harveyella mirabilis* but are found only in host cells connected to the parasite by secondary pit connections. These spherical particles range in diameter from ≈ 50 to 100 nm, are enveloped by a unit membrane, usually have dense centers, and some have a tail-like protuberance. They are exceedingly similar to

the enveloped spherical viruses carried by the mycoplasma *Acholeoplasma laidlawii* (Cole 1979).

Could this theoretical cytoplasm-connecting genetic element have hopped its way up the phylogenetic tree? The Ascomycetes, which include most of the lichen-forming fungi and the fungal endophytes of vascular plants, are a logical donor candidate for the hypothesized fungal genome of vascular plants. Some believe that the red algae gave rise to the Ascomycetes, whereas Kohlmeyer (1973, 1975), Demoulin (1974), and Hawksworth (1982) suggest that they evolved specifically from the parasitic forms of red algae. Alternatively, these two groups of parasites may have shared a common ancestor (Goff and Coleman 1985). However convoluted, the pathway certainly seems to have existed. This parasitic genetic element can be envisioned as the prime mover in a series of escalating parasitic events that first yielded both a parasitic algal and a fungal lineage, either sequentially or in parallel. The fungal lineage then formed a new alliance with prevascular plants and later re-emerged in the form of parasitic angiosperms.

Given the scenario that vascular plants acquired a fungal nucleus plus a cytoplasm-connecting genetic element, we might expect to find very prominent expression of the "pit connection syndrome" in vascular plants, and indeed, it is strongly manifested in those cells that I have suggested are especially funguslike. Intercellular cytoplasmic connections (plasmodesmata) are very common in plants, occurring in the bryophytes and algae as well as in vascular plants. They are extremely variable structures, and many appear to develop from ER strands that traverse the cell plate of dividing cells. My concern is only with those forms that occur between *nondividing* walls (nonsister cells). These cytoplasmic strands appear to develop secondarily, by penetrating an existing wall. They may or may not be associated with wall pits and somehow develop in a coordinated fashion and meet (fuse) in the midregion of the wall (Robards 1975).

In the parasitic red algae, intercellular cytoplasmic fusions are accomplished by a small "conjuncter" cell that is cut off from a larger sister cell by asymmetric cell division and then enlarges so as to come into contact with an adjacent cell. Wall dissolution occurs at the point of contact, and the membranes of the two protoplasts fuse. By this process a pit connection is formed that links the two cells (Goff and Coleman 1985).

The development of phloem plasmodesmata is strikingly similar (Esau 1948, Esau et al. 1962). In the angiosperms, sieve-tube elements and companion cells originate from the same mother cell and remain physiologically interconnected by multibranching plasmodesmata. Where the endwalls of two nonsister sieve-tube elements meet, multiple pits (sieve plates) are

formed by hydrolysis of the wall, and cytoplasmic fusion ensues. Thus, sieve cells and conjuctor cells appear to use the same mechanism to make cytoplasmic connections with nonsister cells. Correlated with the development of these phloem-connecting strands is the appearance of callose. Again, as in pollen tubes, the "host cell" may be reacting to the biochemical activity of a viruslike parasitic element. It is interesting to note that this completed chain of modified phloem protoplasts transports scores of parasites, among which viruses and mycoplasmas are best known.

Xylem cells are also riddled with paired pit connections, but here the protoplast is prematurely digested. The secretion of extracellular and intracellular hydrolases is an important common denominator in fungi and higher plants (Matile 1974). Precise control of intracellular digestion was certainly a prerequisite for the evolution of major pipelines such as sieve tubes, tracheids, and laticifers. These conduits, and some intrusively growing fibers and sclerids as well, undergo complicated processes of internal autophagy. I find it curious that this spatially clumped set of hyphalike cells is also richly endowed with specialized digestive properties.

CONCLUSIONS

In summary, I have proposed that the nucleus of vascular plants is a dual entity in which a fungal genome makes varying contributions to the differentiation of highly specialized cells. The plant body can be visualized as a mosaic of generalized alga-type (photosynthetic) cells interspersed with highly specialized fungus-type cells, plus many intermediate forms. Cells with genetically unique fungal contributions have become specialized for transport, support, and protection (biotic and abiotic). The pollen tube seems to be a close analog of the nucleus-dispersing parasitic red alga cell, which in seed plants invades conspecific individuals and transports nuclei to specialized reproductive cells.

My conceptual models have grown from and been supported by three fundamental characteristics of the parasitic red algae: (1) their ability to form intercellular cytoplasmic fusions, (2) the transfer of parasitic nuclei into host cells via these connections, and (3) the genetic transformation of host cells into funguslike chimeras that disperse the parasite nuclei. I concur with Goff and Coleman's (1985) conclusion that intercellular cytoplasmic fusions represent the genesis of parasitism in the red algae. I have suggested that this trait arose from an earlier viral colonization, as a mechanism of intercellular dispersal. These inherited cytoplasmic intrusions opened the door for the parasitism of related species via nuclear transfer and genetic transformation of host cells (Goff and Coleman 1987). Subsequently, a fungal descendant carrying this cytoplasm-connecting element joined with an ancestor of the vascular

plants. This nuclear union produced an immense library of genetic sequences, and the ensuing phenotypic experiments now dominate terrestrial ecosystems. These experiments included several independent origins of parasitic flowering plants, a natural "recapitulation" engendered by ancient parasitic genes.

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