



REVIEW

The Evolution of Plant Body Plans—A Biomechanical Perspective

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Defining ‘plants’ inclusively as ‘photosynthetic eukaryotes’, four basic body plans are identifiable among plant lineages (unicellular, siphonous, colonial and multicellular). All of these body plans occur in most plant lineages, but only the multicellular body plan was carried onto land by the embryophytes. Extensive morphological and anatomical homoplasy is evident among species with different body plans. This is ascribed to the facts that the acquisition of nutrients and radiant energy is affected by plant body size, shape and geometry, and that, with the exception of the unicellular body plan, each of the other body plans involves an ‘open and indeterminate’ ontogeny capable of modifying body size, shape and geometry regardless of how organized growth is achieved. In terms of unicellular species, the available data indicate that size-dependent variations in surface area, metabolic constituents (e.g. photosynthetic pigments), and reproductive rates limit maximum body size in nutrient poor habitats or those that change rapidly or unpredictably. This maximum size can be exceeded in more stable niches by either the cooperation of conspecific cells sharing a common extracellular matrix (i.e. the ‘colonial’ body plan) or by repeated mitotic cellular division associated with sustained cytoplasmic (symplastic) continuity (i.e. multicellularity). The siphonous plant body plan may have been evolutionarily derived from a unicellular or multicellular ancestral life form. Each of the plant body plans is reviewed in terms of its biomechanical advantages and disadvantages. Variants of the multicellular body plan, especially those of the Chlorophyta, Charophyta, and Embryophyta, are given special emphasis.

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Key words: Algae, biomechanics, body plans, body size, embryophytes, evolution, multicellularity, plants.

... all organic beings have been formed on two great laws—Unity of Type and the Conditions of Existence. By unity of type is meant that fundamental agreement in structure, which we see in organic beings of the same class, and which is quite independent of their habits of life. The expression of conditions of existence ... is fully embraced by the principle of natural selection [which] acts by either now adapting the varying parts of each being to its organic conditions of life; or by having adapted them in long-past periods of time.

—Charles Darwin

INTRODUCTION

Much has been written about the initial appearance and subsequent evolution of metazoan body plans, particularly in terms of the great Cambrian ‘explosion’ and the attending evolutionary debut of multicellular animal body plans during a comparatively brief period of time (see Gould, 1989; Valentine, Jablonski and Erwin, 1991; Lipps and Signor, 1992; Valentine, 1995; Raff, 1996; Miller, 1997; Martindale and Henry, 1998; Knoll and Carroll, 1999). In contrast, the evolution of body plans among plants, here defined as photosynthetic eukaryotes, has received comparatively much less attention and has been discussed largely in the context of the radiation of the early vascular land plants and their terrestrial non-vascular predecessors during early Paleozoic times (Banks, 1975; Chaloner and Sheerin, 1979; Graham, 1993; Taylor and Taylor, 1993;

Stewart and Rothwell, 1993; Niklas, 1997). This focus has significantly advanced our understanding of the evolution of the embryophytes, but it has largely ignored a complex antecedent history during which different body plans evolved within and among the genetically distinct but morphologically homoplastic aquatic plant lineages, collectively called the ‘algae’ (Bold and Wynne, 1978; Graham and Wilcox, 2000). This history involved evolutionary modifications in a variety of body features that undoubtedly prefigured to some degree the highly stereotyped embryophyte body plan (see Graham, 1993). For this reason, no synoptic discussion of plant body plan evolution is possible without reference to those still represented among the modern-day algal lineages that share the same grade level of cytological and physiological organization.

Unlike those of the metazoans, the body plans of plants are difficult to categorize or define. Setting aside the similarities among unicellular (uni-nucleate) or colonial plant species, which are arguably trivial owing to their typically simple geometries and shapes, extensive morphological and anatomical convergence is evident among metaphytes, so much so that it is often impossible to distinguish between species drawn from diverse lineages on the basis of their general appearance, size, or internal structure (Bold, 1967; Bierhorst, 1971; Bold and Wynne, 1978; Gifford and Foster, 1989; Niklas, 1997; Graham and Wilcox, 2000). The perspective taken here is that plant *Baupläne* are far more profitably discussed in terms of how organized growth is achieved and how different tissue fabrics are used to

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construct the plant body. Importantly, most of these body plans have an ‘open and indeterminate’ ontogeny—one involving multiple growing points and persistent cellular divisions throughout the lifetime of the individual such that adult size, geometry and shape are not necessarily developmentally prefigured in the juvenile condition (Esau, 1965). Arguably, this ontogeny permits morphological and anatomical convergence as well as divergence among phyletically otherwise divergent plant lineages because it holds the potential to bypass many of the developmental constraints imposed on metazoans that often have a ‘closed and determinate’ ontogeny.

Developmental ‘constraints’ are important to body plan evolution (Waddington, 1957; Gould, 1977; Wimsatt and Schank, 1988; see, however, Raff, 1996). For plants, one of the most obvious of these is the phyletic legacy of a cell wall, which evolved independently many times among the various plant lineages and whose mode of deposition and material properties profoundly influence how cell size and shape are free to change (Green, 1960; Mark, 1967; Preston, 1974; Cooke and Lu, 1992; Niklas, 1992). Perhaps more subtle are the various developmental constraints that influence the relationship between the body surface areas, volumes, and cytoplasmic machinery of cells. Nowhere are these more clearly expressed than among plant species sharing the unicellular plant body plan, which is typically determinate in growth in size, geometry and shape (Bold and Wynne, 1978). The data reviewed here show that physiological and reproductive rates fail to increase in pace with interspecific increases in body (cell) size. This feature of the unicellular plant body plan may be legitimately considered a ‘developmental constraint’ operating at the level of size-dependent variations in the intracellular concentrations of important cellular components (e.g. photosynthetic pigments). Indeed, allometric (size-dependent) variations suggest that an ‘upper size limit’ exists for the unicellular plant body. If so, then natural selection probably favoured multiple independent origins of other body plans that permitted an increase in overall size by the addition of cells, each capable of optimal growth or reproductive rate.

If it is true that developmental constraints play an important role in plant evolution, then it is equally true that biomechanical relationships have influenced the evolution of body plans at the cell, tissue, organ, and organismic levels of organization (Wainwright *et al.*, 1976; Speck and Vogellehner, 1988; Cooke and Lu, 1992; Niklas, 1992, 1994, 1997). Biomechanical limitations obviously exist for all types of organisms, since no life form can violate physical laws or processes. For plants, which all perform essentially the same biological tasks to assure growth and reproduction (light harvesting, nutrient acquisition and storage, etc.; see Nobel, 1983), these limitations are readily apparent in terms of quantifiable design considerations that emerge when two or more tasks are performed simultaneously. These biomechanical ‘constraints’ undoubtedly evoke morphological or anatomical reconciliations that scale with respect to body size, geometry and shape rather than with how a particular body plan achieves its organized growth. As a consequence, body plan diversification within, and convergence among, different lineages become likely,

provided that development permits plants to assume a body size, geometry and shape convivial to survival in a particular niche.

In the sections that follow, I briefly review the ‘body plan’ concept in the context of the historical debate between ‘the unity of type’ and the ‘conditions of existence’. This is followed by a brief discussion of the key features that distinguish the comparatively few basic plant body plans, which are defined on the basis of how organized growth is achieved and how, if present, different tissue fabrics are used to construct the plant body. The remainder of the paper is devoted to a discussion of each body plan in terms of its biomechanical advantages and ‘constraints’. Limited space allows for neither a detailed nor comprehensive treatment of each of these subjects, which can be only broadly outlined here.

Finally, in terms of phyletic affiliations, with the exception of our current understanding of the systematic relationships among the charophycean algae and their relationship to the embryophytes (see Mattox and Stewart, 1984; Graham, 1993; Graham and Wilcox, 2000), the phycological taxonomy adopted throughout this paper is that of Bold and Wynne (1978). This reference is based largely on morphological rather than molecular information. Arguably, therefore, it offers a conservative view of body plan differences within each of the algal lineages (see Table 1), and thus tends to bias against some of the following.

‘UNITY OF TYPE’ VS. ‘CONDITIONS OF EXISTENCE’

The concept of the ‘body plan’, layout, or *Bauplan* can be traced to the work of Georges Cuvier, Richard Owen, and other nineteenth-century comparative morphologists who showed that organisms can be classified according to their shared structural and anatomical traits, many or some of which have no obvious connection to the ecological lifestyles of the organisms sharing them (Mayr, 1982; see also Woodger, 1945; Brusca and Brusca, 1990). For example, trilobites and butterflies possess a bilaterally symmetrical, segmented body plan in which the first few anterior segments are fused to form a head. These and other shared traits permit trilobites and butterflies to be grouped together along with other arthropods by virtue of a ‘unity of type’ that nevertheless achieves so great a diversity in its ‘conditions of existence’ (e.g. aquatic, terrestrial, and aerial species) that many of the features characterizing arthropods can be identified in terms of their location and contribution to the body layout without compelling one to ascribe an adaptive role to each.

Although Cuvier, Owen, and others maintained that the ‘conditions of existence’ were subordinate to the ‘unity of type’, Charles Darwin observed that many traits are a consequence of descent from a last common ancestor that are themselves the products of earlier, presumably adaptive evolution. Darwin maintained that currently adaptive traits can and do co-exist with highly conserved traits having no apparent adaptive purpose. He nonetheless maintained that the ‘conditions of existence’ take priority over the ‘unity of type’. Darwin, like many others, was impressed by the

TABLE 1. Distribution of body plans among the land plants (*Embryophyta*) and extant algal lineages (with the exception *Charophyta*, the systematics used here and throughout the text are based on *Bold and Wynne, 1978*)

	Siphonous	Unicellular	Colonial ¹	Filam.	Multicellular Pseudo.	Parench.
Embryophyta	—	—	—	+ ²	—	+ ³
Charophyta ⁴	—	+	+	+	+	+
Chlorophyta	+	+	+	+	+	+
Chrysophyta	+	+ ⁵	+	+	+	+
Rhodophyta	—	+	+	+ ⁶	+ ⁶	+ ⁶
Phaeophyta	—	— ⁷	+	+	+	+
Pyrrhophyta	—	+	+	—	—	—
Euglenophyta	—	+	+	—	—	—
Cryptophyta ⁸	—	+	+	—	—	—

Filam., filamentous (unbranched or branched); Pseudo., pseudoparenchymatous tissue construction; Parench., parenchymatous tissue construction.

¹Aggregates of cells lacking cellular interconnections; excludes 'volvocine algae' that have cellular interconnections early in development or that maintain them when mature (e.g. *Pandorina* and *Volvox*, respectively).

²Generally expressed in the gametophyte generation.

³Expressed in the gametophyte and sporophyte generations of all species.

⁴*Sensu* Mattox and Stewart (1984); includes Charales, Coleochaetales and Zygnematales.

⁵Includes amoeboid (rhizopodial) types, and the Bacillariophyta.

⁶In the form of secondary pit-connection formation.

⁷Presumably either lost over the course of evolution or represented by a heterokont currently assigned to another phylum.

⁸Molecular evidence indicates this is likely a polyphyletic group.

remarkable 'match' between body traits and the ecological conditions in which each particular organism lives and reproduces. Clearly, his theory of natural selection argued in favour of the adaptive role of the majority rather than the minority of body traits.

It is undeniable that some shared ancestral traits have been conserved long after their initial adaptive significance has vanished. The coelom, which evolved more than once, may have been an adaptation for burrowing by soft-bodied animals, but its current function in the vertebrate body plan is radically different from that of any of its presumed antecedent functions. Indeed, assertions that otherwise diverse organisms share a common ancestry are based typically on the presence of ancestral traits. The real issue is not whether some body plan traits are conserved but why some traits are lost, whereas others are not. Flightless birds have reduced flight muscles and wings. Yet, all birds develop feathers and a beak. Parasitic angiosperms have reduced leaves, stems, or roots, or lack some of these organs entirely, but they all retain the capacity to produce flowers and vascular tissues.

The typical explanation for the conservation of ancestral body plan traits is the presence of pivotal developmental processes whose mutation would be difficult or impossible—processes so basic to how an organism achieves its organized growth that any significant deviation would result in death or severe impairment. It is evident that 'developmental constraints' exist and play an important role in the conservation of some traits. The so-called spiral determinate cleavage of many planktotrophic spiralian species so rigidly casts the fate of each embryonic cell early in the four- and eight-cell stage of embryo development that it is difficult (although not impossible) to imagine that mutations causing this embryology to deviate from the

norm would be anything but lethal. Among the diploblastic eumetazoa, the outer body wall, sensory and nervous tissues, and associated structures are derived from ectodermal cell lineages, whereas the archenteron and the organs that develop along with it are derived from endodermal cell lineages. Likewise, among all triploblastic animals, a third germ layer, the mesoderm, develops from either ectodermal or endodermal cell precursors to give rise to muscles, muscular organs, gonadal tissues and other internal organs. Thus, developmental constraints are commonly evoked to explain why some animals, like molluscs, annelids, and arthropods, retain the same general body plan (characterized by the formation of a mouth from the blastopore and a coelom from splits in the mesoderm). Although 'direct development' frequently occurs in a variety of animal lineages (see Raff, 1996), the traditional view of animal body plan evolution maintains that nearly all are achieved as a result of well defined embryologies that give rise to a highly conserved set of body plans (the 'unity of type'). Indeed, animal body plans are generally so conservative that many zoologists believe that all modern-day animal phyla trace their ancestry back to a last common (protist) ancestor (see Wainright *et al.*, 1993; Valentine, 1995; Valentine and Hamilton, 1997).

PLANT BODY PLANS

The evolution of plant body plans is far more complex than that of animals because the organisms called plants are polyphyletic (Schlegel, 1994; Graham and Wilcox, 2000). Rather than constituting a single clade that can be traced back to a single last common ancestor, plants (i.e. eukaryotic photoautotrophs) have multiple evolutionary origins presumably as a consequence of primary endosymbiotic

events, giving rise to lineages like the Chlorophyta, or as a result of secondary endosymbiotic events, giving rise to others like the euglenids and chromists (Cavalier-Smith, 1992; McFadden and Gilson, 1995; Wastl *et al.*, 1999). This early phase in plant evolution, which involved extensive lateral gene transfer among pro- and eukaryotic unicellular organisms, was followed by one characterized by increased genetic isolation and divergence. By late Mesoproterozoic or early Neoproterozoic time, the major radiation events distinguishing modern-day eukaryote lineages had already taken place (Knoll, 1995; Porter and Knoll, 2000).

Plants can be thus classified and sorted into different lineages based on molecular, cellular, or ultrastructural features. These and other criteria support the generally held view that each algal lineage traces its ancestry back to a unicellular ancestral organism, that colonial and multicellular life forms have evolved independently many times, that the land plants (embryophytes) and the charophycean algae share a last common ancestor, and that the embryophytes are a monophyletic group. However, it is strikingly evident that the general appearance, size, or growth form of plants cannot be used to distinguish the various lineages. Setting aside the obvious if somewhat trivial phenotypic similarities among the comparatively simple unicellular or colonial species found in each of the major algal lineages, it is commonplace to find plants with filamentous, membranous, foliar, tubular, kelp-like, and coralline life forms in each of the red, green, and brown algal clades (Fig. 1). Some acellular (siphonous) species, like those of *Caulerpa*, can attain body lengths in excess of 20 m and a general morphology strikingly reminiscent of the rhizomatous growth habit of the vascular land plant without benefit of multicellularity (Fig. 2). General appearance and size also belie very different tissue constructions and developmental capacities. The non-vascular blade-stipe-holdfast architecture of some marine brown algae is constructed with an intercalary meristem (e.g. *Agarum* and *Macrocystis*) and yet is remarkably similar to the leaf-stem-root configuration of the vascular land plants. By the same token, the arborescent growth habit of many present-day and extinct vascular plants which is achieved by virtue of secondary tissues produced by the vascular and cork cambia (e.g. *Lepidodendron*, *Calamites* and *Pinus*) is mimicked by monocot and fern species lacking cambia (e.g. *Cocos nucifera* and *Cyathea medullaris*).

Mindful of the extensive morphological and anatomical homoplasy among the various plant lineages, plant body plans are far more easily distinguished on the basis of how they achieve their organized growth and, if present, their basic tissue constructions. This approach identifies only four basic body plans—the unicellular, colonial, siphonous and multicellular body plan. These can be distinguished on the basis of a few basic developmental processes or events (Fig. 3): (1) the presence or absence of vegetative cytokinesis determines whether the plant body is based on a uni- or multi-nucleate cellular plan (e.g. *Chlamydomonas* or *Bryopsis*); (2) the separation of cell division products or their aggregation by means of a common extracellular matrix, pit connections, shared loricas, stalks, etc. determines whether the body plan is unicellular or colonial (e.g. *Calcidiscus* or

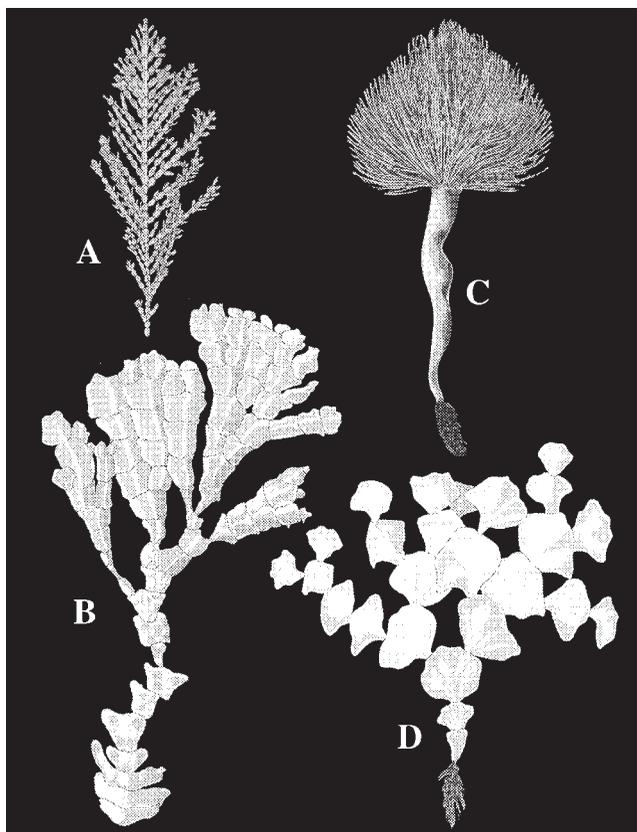


FIG. 1. Convergent evolution among coralline red (A, B) and green algae (C, D). A, *Corallina mediterranea*. B, *Bossiella* sp. C, *Penicillus capitatus*. D, *Halimeda opuntia*.

Phaeocystis); (3) indeterminate growth of the multinucleate cell results in the siphonous body plan (e.g. *Bryopsis* and *Caulerpa*); and (4) symplastic continuity among cells during and after cell division by means of 'cytoplasmic bridges', plasmodesmata, etc. establishes the multicellular body plan (e.g. *Volvox* and *Polytrichum*).

The multicellular body plan has three basic variants that can be described morphologically, albeit not mechanistically, in terms of the number of planes of cell division (Fig. 3): when restricted to one plane or orientation, unbranched filaments can be formed (e.g. *Spirogyra*); when confined to two orientations, cell division can give rise to branched filamentous, monostromatic, or pseudo-parenchymatous tissue constructions (e.g. *Stigeoclonium*, *Volvox* and *Ralfsia*, respectively); and, when cell division occurs in all three planes, a multicellular body layout is possible, which can simultaneously manifest a filamentous and parenchymatous construction (e.g. *Fritschiella*). Since each of these three multicellular variants can involve diffuse, trichothallic, intercalary, or apical cell divisions, or some combination of all four, a large number of multicellular body plan variants can be codified (i.e. 3 cell division planes \times 5 meristematic locations = 15 variants *de minimis*), although the usefulness of doing so is questionable. Although a number of growing point (meristematic) characteristics collectively influence whether a variety of

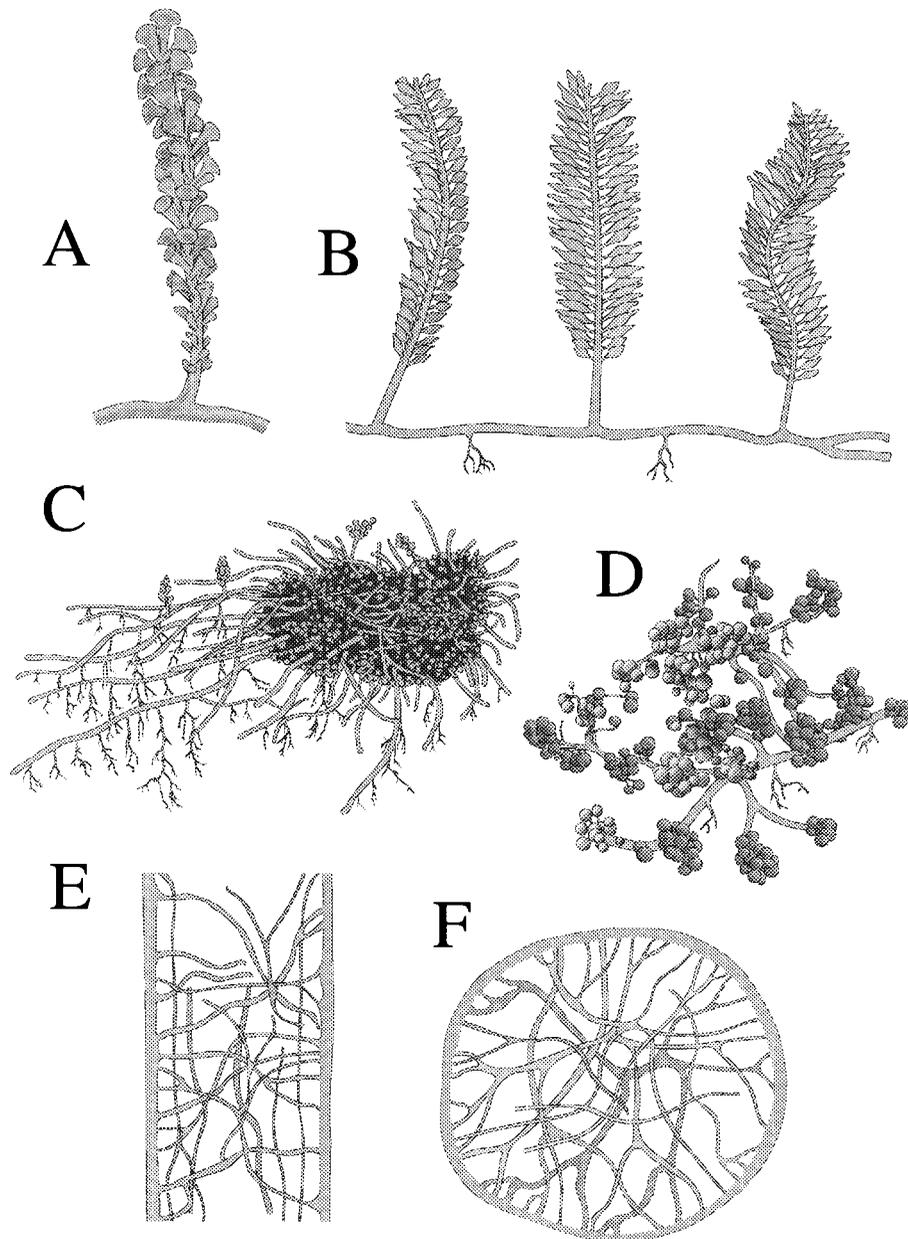


FIG. 2. Representative morphologies of the siphonous green alga *Caulerpa* (A–D) and infrastructure of trabeculae in the symplast (E, F). A, *C. chemnitzia*. B, *C. floridana*. C, *C. racemosa* var. *clavifera*. D, *C. racemosa*. E and F, Longitudinal and transverse views of trabeculae in ‘assimilator’ (vertical portions of plant body) and ‘rhizome’, respectively.

morphological and anatomical features are achieved in a particular body part or plan (e.g. the duration of activity and the number of cells involved at each location, as well as the extent to which cells, tissues or organs differentiate or differ in symmetry, number, etc.; see Fig. 4), none of these features is considered here to be especially relevant to the fundamental distinctions that can be drawn among the four basic plant body plans.

This body plan classification scheme draws sharp attention to the extent to which body plans have diversified within or converged among the various plant lineages and how they have become confined in number in evolutionarily more derived groups, such as the Charophyta and Embryo-

phyta (Table 1). For example, all four *Baupläne* occur in the Chlorophyta and Chrysophyta, two of the most species-rich plant phyla. The unicellular body plan, which is presumably the ancestral condition in each algal lineage, is absent only in the Phaeophyta, whereas the colonial body plan is not represented among embryophyte species. The multicellular body plan occurs in all but three algal lineages each of which presumably evolved as a consequence of secondary endosymbiotic events. Unlike the Charophyta, which have unicellular and colonial representative species (e.g. *Stichococcus* and *Chlorokybus*, respectively), all embryophytes are multicellular and have the capacity to fabricate parenchymatous tissue by means of apical, intercalary, or

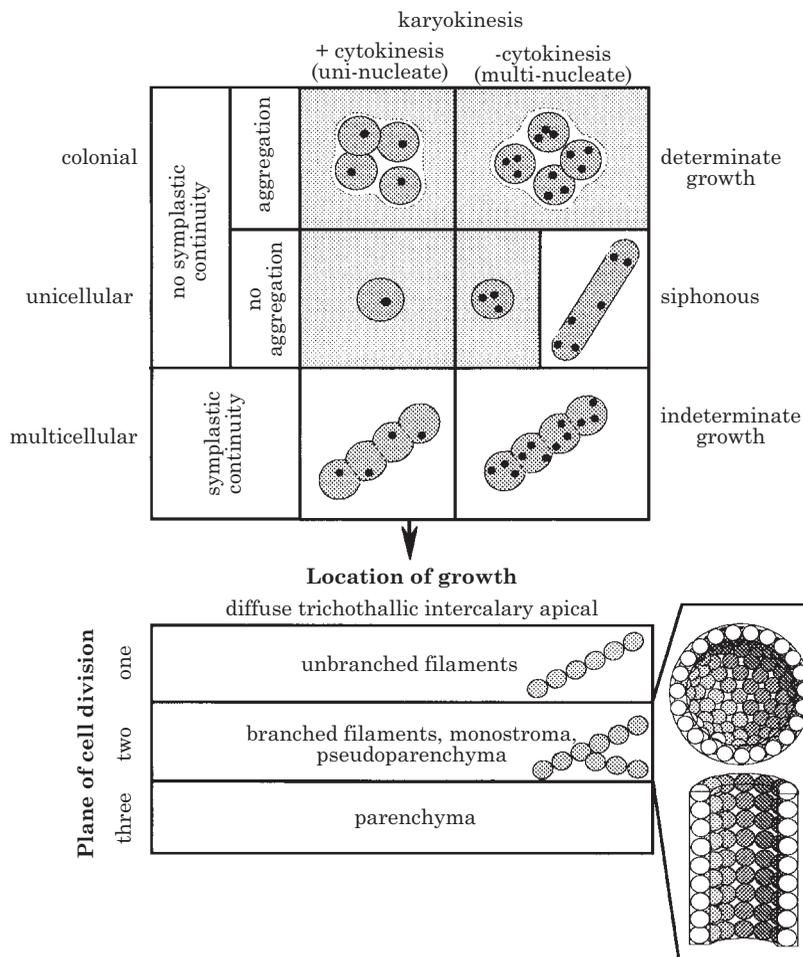


FIG. 3. Basic plant body plans (unicellular, colonial, siphonous and multicellular), their defining features, and methods of achieving organized growth. The unicellular body plan is generally considered the most ancient among all plant body plans and is characterized by the separation of cell division products after cytokinesis; uni- or multi-nucleate variants occur depending on whether cytokinesis keeps pace with karyokinesis (e.g. the uni-nucleate chlorophyte *Chlamydomonas* and the multi-nucleate chrysophyte *Botrydiopsis*, respectively). The colonial body plan is a collection of uni- or multi-nucleate cells aggregated together but lacking symplastic continuity among cells (e.g. the chrysophyte *Synura* and the chlorophyte *Hydrodictyon*, respectively). The unicellular and colonial body plans are determinate in cell size (shown in shaded area), although the overall size of a colony may increase by the addition of cells. The siphonous and multicellular body plans are indeterminate in their growth in size (unshaded area). The siphonous body plan consists of a single multi-nucleate cell (e.g. *Caulerpa*). The multicellular body plan consists of uni- or multi-nucleate cells that maintain symplastic continuity after cytokinesis (e.g. the unbranched filamentous chlorophytes *Ulothrix* and *Urospora*, respectively). The multicellular body plan can achieve organized growth by means of diffuse, trichothallic, intercalary, or apical cell divisions involving one, two, or three orthogonal planes of cell division. Cell division restricted to one plane produces unbranched filaments; cell division confined to two planes constructs branched filaments, monostroma (sheets of cells or hollow structures one-cell thick), or pseudoparenchyma; cell division in three orthogonal planes can be used to construct parenchymatous tissues.

diffuse meristematic activity. Among the land plants, the filamentous variant of the multicellular body plan may be expressed transiently in the sporophyte generation (e.g. the filamentous embryo stage of seed plants), among free-living gametophytes (e.g. the mosses *Buxbaumia* and *Polytrichum*), or not at all (e.g. the liverworts *Scapania nemerosa* and *Conocephalum*). Likewise, the siphonous body plan is expressed briefly among embryophytes (e.g. the 'free-cellular' condition of endosperm).

In this sense, the embryophyte body plan, especially that of the sporophyte generation, evinces the greatest 'unity of type' among all the plant lineages. This may reflect a 'founder effect' when the last common ancestor of modern-day embryophytes successfully invaded the terrestrial land-

scape presumably during Ordovician times. If so, then the land plants and the eumetazoa afford the best candidates with which to study the broad effects of developmental constraints on body plan evolution. Alternatively, the embryophyte body plan may confer the highest relative fitness in terrestrial habitats, and thus may be the result of extreme directional (canalizing) selection. It is noteworthy that the capacity to form parenchyma by means of a variety of meristematic configurations and locations permits the construction of all multicellular tissue fabrics in the same organism, ranging from unbranched and branched filaments to parenchymatous tissues (e.g. moss gametophyte protonema and phyllids, respectively). Thus, the 'conservative' nature of the embryophyte body plan may be more

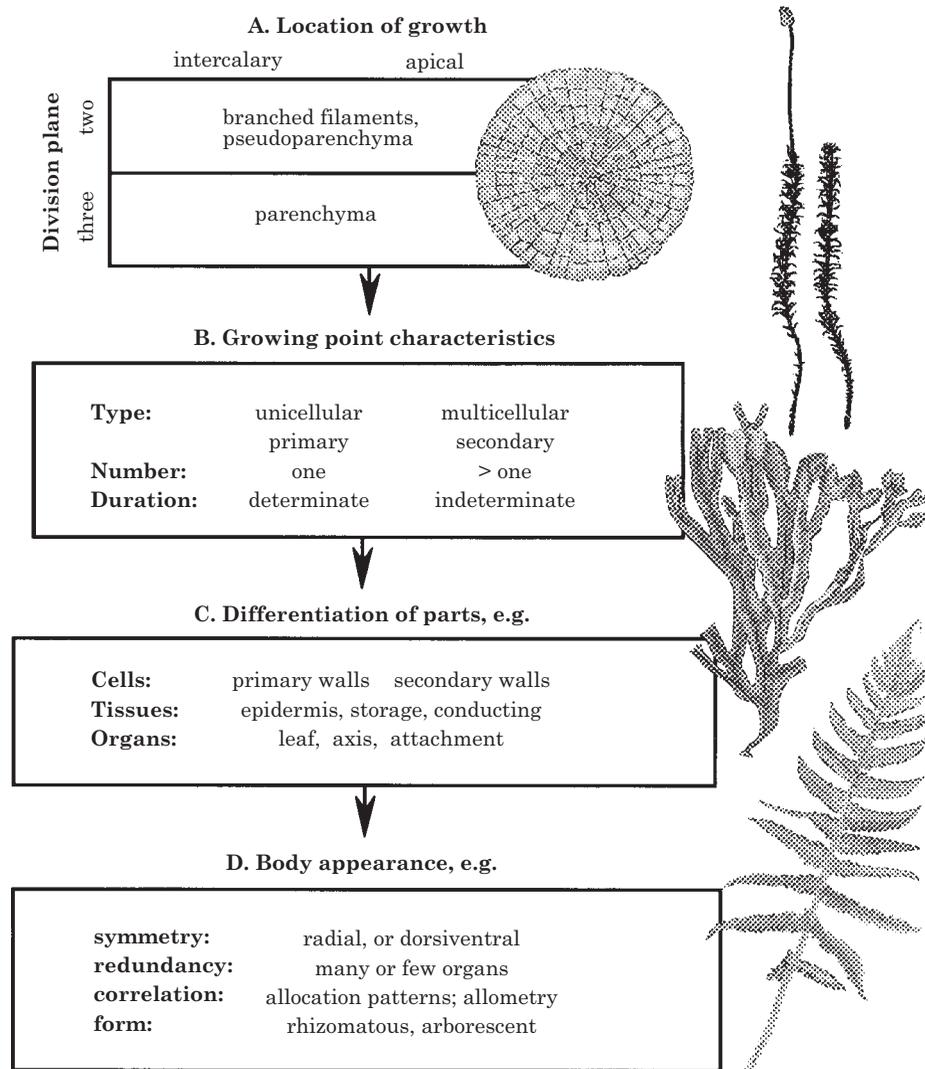


FIG. 4. Examples of the multicellular body plan constructed from intercalary or apical meristematic activity involving two or three orthogonal planes of cell division (A) and some developmental features influencing the general appearance of the plant body (B–D). A, Two or three orthogonal planes of cell division in intercalary or apical meristematic regions can be used to construct branched filaments (or pseudoparenchymatous tissues) and parenchymatous tissue, respectively. Some taxa are represented by species composed of branched filaments (organized into pseudoparenchymatous tissues) or parenchyma (e.g. the chlorophyte *Coleochaete*); some taxa have both intercalary and apical meristems (e.g. the sporophyte of the moss *Polytrichum*). B, Growing point characteristics influence cellular configuration of meristems (meristems composed of one or many cells), whether new meristems develop later in ontogeny (primary vs. secondary meristems), and the number of meristems and their duration of growth. Some taxa have a single apical meristem composed of a single apical cell whose duration of growth is determinate (e.g. *Polytrichum* sporophyte). Other taxa have multiple apical meristems composed of many cells whose duration of activity is indeterminate (e.g. the phaeophyte *Fucus*). C and D, Patterns of cell, tissue, or organ differentiation and a variety of allometric phenomena influence in part the general appearance and internal structure of the multicellular plant body.

apparent than real. It undeniably imposes no barrier to the successful exploitation of terrestrial habitats, as is evident by the great morphological and anatomical diversity of modern embryophytes whose species number exceeds that of all algal lineages combined.

In general, the body plan classification scheme presented here does not drive a deep conceptual wedge among the various life-forms or 'generations' that participate in the sexual life cycle of individual species. For example, although most ectocarpalian algae have an isomorphic alternation of generations, divergent gametophyte and sporophyte morphologies are reported for some species

(e.g. *Ectocarpus*, *Feldmannia*, and *Giffordia* species). Yet, both generations in the life cycle of all ectocarpalian species share a filamentous body plan. Likewise, despite the dramatic morphological disparities seen among the haploid and diploid generations in the triphasic life cycle of florideophycean algae (i.e. the diploid carposporophyte and tetrasporophyte, and the haploid gametophyte), all of these life forms share a branched filamentous body plan, just as the haploid gametophytes and diploid sporophytes of embryophytes share a multicellular body plan. There are nonetheless some exceptions to the uniformity in the body plans of the different life forms in the life cycles of some

species. Kelps have filamentous gametophytes and parenchymatous sporophytes, whereas some unicellular haptophytes have a branched, filamentous *Apistonema*-stage in their life cycle (e.g. *Pleurochrysis*).

In general, however, the body plans seen in the same plant life cycle are similar, paralleling what is typically seen among the animals. Thus, insect juveniles often depart morphologically and anatomically from their corresponding adult forms, especially among holometabolic species, which undergo a profound metamorphic molt associated with quiescent pupation. However, like plants with life cycles involving two generations differing in size, external appearance, tissue construction, etc. all morphs in the insect life cycle share the same general body plan (characterized by bilateral symmetry, paired segmental coelomic body compartments, a contractile heart, and a nervous system with a double nerve trunk and segmental ganglia).

'CONDITIONS OF EXISTENCE' AND PLANT ONTOGENY

It is apparent that the disparity among *Baupläne* does not increase dramatically as comparisons are drawn among higher taxonomic ranks, since all four plant body plans have evolved independently in many plant lineages (Table 1). This suggests that plant evolution is more responsive to the 'conditions of existence' than confined by the 'unity of type', and, in turn, that 'developmental constraints', which undoubtedly exist for all organisms, may be less prevalent in plant than in animal development.

This supposition is consistent with how the majority of plants grow and develop. With the exception of unicellular uni-nucleate species, few plants are determinate in growth in size (e.g. *Volvox* and *Arabidopsis*) and this ontogeny appears to be a highly derived condition for the multicellular body plan. In contrast, most multicellular plants achieve their organized growth by means of diffuse, trichothallic, intercalary or apical cellular divisions at growing points that can remain active throughout the lifetime of the individual. This 'open and indeterminate' ontogeny affords an individual the opportunity to adaptively adjust its size, shape, or internal structure to its local environmental conditions and to changes in these conditions as the individual continues to grow during its lifetime. It also provides each species with a heritable degree of phenotypic 'plasticity' that allows conspecifics to assume different morphologies or anatomies depending on local environmental conditions.

The capacity to developmentally modify shape and internal structure by virtue of 'open and indeterminate' growth is evident even among acellular species. *Caulerpa* species growing in wave-swept, high-energy environments have a 'dwarfed' morphology and produce an internal system of cell wall extensions forming a mechanically resilient and strong beam-like infrastructure that is far more extensively developed than that found in conspecifics with more 'luxuriant' morphologies growing in less mechanically energetic habitats. In this sense, the morphology and anatomy of plants, regardless of whether they are acellular or multicellular, are not prefigured as uniformly or precisely

as they are for animals, the majority of which are characterized by the 'closed and determinate' ontogeny.

The importance of the 'open and indeterminate' ontogeny of most plants takes on added significance when we consider how these organisms manufacture their living substance and how this mode of life is largely dependent on form and appearance rather than on how the plant body achieves its organized growth. Unlike animals, which capture their prey or graze on plants in a variety of different ways, all photosynthetic eukaryotes, regardless of their phyletic affiliation or particular ecology, require essentially the same resources for growth and reproduction (i.e. light, water, atmospheric gases, minerals, and space). The acquisition of these resources is not intrinsically dependent on the behaviour or characteristics of other life forms, and, perhaps for this reason, plant life is more dependent on and attuned to abiotic than biotic factors. Importantly, the ability to acquire the resources essential for growth depends on the external surface area of the plant body, some of which is internalized to reduce tissue dehydration (e.g. aerenchyma). Water, minerals and atmospheric gases are absorbed from the external environment through cell walls directly exposed to these substances. Irradiant energy is also intercepted and thus primarily absorbed by the body surface where chloroplasts are generally positioned. The body surface is also used to discharge a variety of metabolic products, particularly in the aquatic environment. The magnitude of body surface area thus provides a reasonable morphometric measure of the capacity to absorb and exchange energy and mass with the external environment.

Likewise, body volume provides a very indirect measure of metabolic capacity, nutrient demand, and the capacity (or need) to translocate materials. Here, 'volume' refers to the amount of the living substance in the plant body (i.e. the symplast). Clearly, there is certainly metabolism outside the protoplast membrane (e.g. enzymatic restructuring of the cell wall) as well as within vacuoles (Raven, 1997). However, the metabolic events in these compartments may be viewed as qualitatively different from those that occur within the symplast. A meaningful calculation of 'volume', therefore, includes neither the cell wall infrastructure and fluid-filled spaces (i.e. vacuoles and the apoplast) nor metabolically 'inert' internal or external materials (e.g. crystals and mucilage).

If body surface area to volume ratios are adopted as crude surrogate measures of the plant body 'acquisition and demand ratio', then simple analytical geometry shows that a unicellular, filamentous, colonial, or any other plant body plan can achieve different or identical ratios of surface area to volume, because these ratios are not intrinsically dependent on body layout, mode of organized growth or tissue construction. The critical features influencing surface area to volume ratios are body size, geometry and shape. This may account for body plan divergence in each algal lineage, since very different plant *Baupläne* can achieve the same size, shape or geometry, and thus the same or very similar surface area to volume ratios. If true, then body plan divergence within some lineages may reflect 'diffuse evolution' and not the intense operation of natural selection

per se. Mutations altering how organized growth is achieved may go largely unseen by the environment provided they are not developmentally deleterious and do not lower the capacity to adjust shape or geometry during ontogeny and development to maintain or increase body surface to volume ratios as overall size increases. Likewise, the dependence of bodily functions on the surface to volume ratio, which is itself dependent on body size, shape and geometry, helps to explain why species possessing very different body plans often converge on similar morphologies or anatomies. In these instances, the operation of natural selection rather than ‘diffuse evolution’ is the most likely explanation.

THE UNICELLULAR BODY PLAN

Small body size confers numerous metabolic advantages, as is evident from a biomechanical examination of the unicellular *Bauplan*, which is the most ancient among all plant body plans. For example, all unicellular plants obtain carbon dioxide, oxygen, and other non-electrolytic substances dissolved in water from the external environment often by means of passive diffusion. Under these circumstances, Fick’s law shows that the time t required for the concentration of a non-electrolyte j , initially absent from a cell, to reach one-half the concentration of the external concentration of j is given by the formula

$$t = \frac{V}{P_j S} \ln \left[\frac{(c_o - c_i)_{t=0}}{(c_o - c_i)_{t=0.5}} \right]$$

where V is cell volume, S is cell surface area, c_o is the external concentration of j , c_i is the internal concentration of j , P_j is the permeability coefficient of j , $(c_o - c_i)_{t=0}$ is the initial difference in the external and internal concentrations of j at time zero, and $(c_o - c_i)_{t=0.5}$ is the difference in the external and internal concentration of j when $c_i = c_o/2$. Since $\ln[(c_o - c_i)_{t=0}/(c_o - c_i)_{t=0.5}] = \ln[(c_o - 0)_{t=0}/(c_o - c_o/2)_{t=0.5}] = \ln 2 = 0.693$, it follows that $t = 0.693V/P_j S$ (see Nobel, 1983; Niklas, 1994). This formula shows that, for any series of unicellular organisms differing in size but sharing the same geometry and shape, the time required to concentrate nutrients within cells by means of passive diffusion increases dramatically with increasing cell size (Fig. 5). Similar results are obtained when the effects of boundary layers on the pool of substances around and absorbed actively by cells are considered (see Niklas, 1994). Natural selection, therefore, would favour photosynthetic organisms with small body (cell) sizes in the aquatic environment.

Light harvesting in water is also favoured by small body size, because equivalent amounts of pigments contained in discrete ‘packages’ or units (i.e. chloroplasts, cells, or colonies of cells) are less effective at harvesting light as the size of these units increases. For example, this ‘package effect’ is quantitatively expressed for spherical cells by the formula

$$I = I_o e^{-(k+nAa)d \operatorname{cosec} \beta}$$

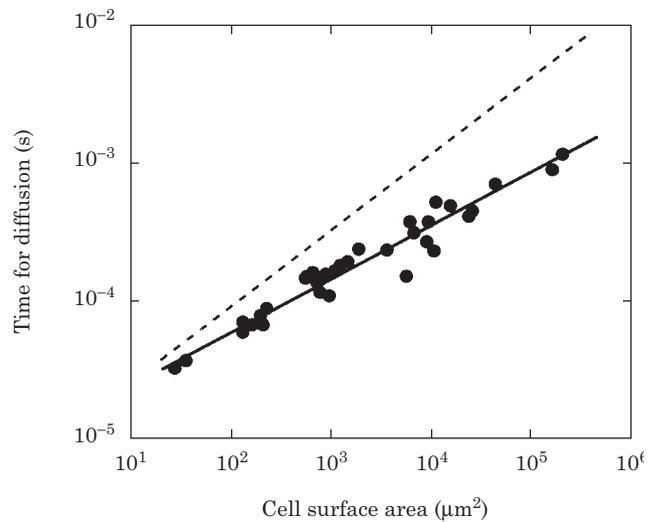


FIG. 5. Estimated time for the passive diffusion of a substance originally lacking in a cell to reach one-half the external concentration in the cytoplasm of a unicellular plant plotted against cell surface area. Dashed line denotes the time required for the substance’s passive diffusion assuming that cell surface area scales as the 2/3-power of cell volume; solid line is the ordinary least squares regression curve for the time of diffusion calculated on the basis of empirically measured cell volume. The lower slope of the regression curve indicates that surface area scales with respect to cell volume with a higher power than that of 2/3 (see Fig. 7).

where I is the downward flux of light energy per unit area on a horizontal plane at depth d , I_o is the flux of radiation on a horizontal plane just beneath the water surface, k is the total absorption coefficient of water (and any dissolved substances), n is the number of packages (cells) per cubic metre, A is the average projected cell area in the suspension, a is the average proportion of total irradiant energy incident on a cell, and β is the angle of incident light with respect to the horizontal plane (e.g. when the direction of light is normal to the horizontal, $\operatorname{cosec} \beta = 1.0$) (see Kirk, 1975). Assuming that cells have equivalent amounts of chlorophyll, this formula shows that the average light absorption in a suspension of unicellular plants sharing a spherical geometry dramatically decreases as cell (body) size increases (Fig. 6; see Niklas, 1994 for details of simulation).

Finally, small cell size is favourable in terms of reducing the rate at which a unicellular organism settles in a column of water—the terminal settling velocity v of aquatic unicellular organisms lacking flagella or cilia is approximated by Stokes’ law, which states that v increases in proportion to the square of the radius r of a sphere (i.e. $v \propto r^2$). Stokes’ law also indicates that v is proportional to the difference between the density of an organism and its surrounding fluid—a parameter that can be altered by many unicellular plants by regulating vacuolar and cytoplasmic contents.

Despite the phenotypic plasticity evident among conspecifics of uni-nucleate and unicellular plant species, the evolution of this body plan was undoubtedly influenced by its ‘closed and determinate’ ontogeny, which prefigures adult body (cell) size, shape and geometry. However, interspecific comparisons among unicellular species indicate that

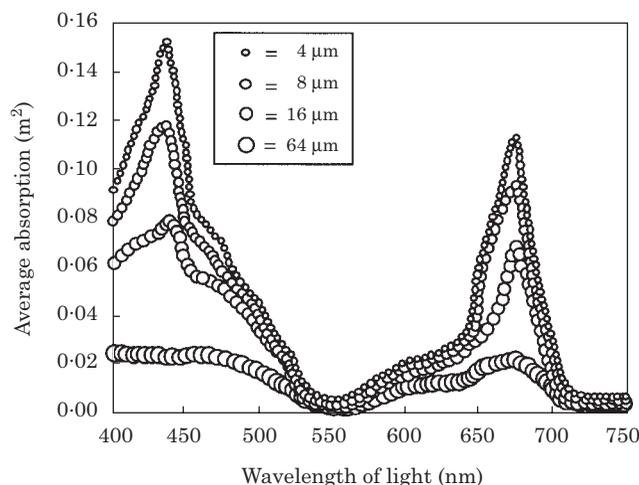


FIG. 6. Average absorption of light by a population of spherical cells differing in diameter (see insert) plotted as a function of the wavelength of light (within the absorption range of chlorophyll *a*). The average absorption of cells in the population decreases as a function of increasing cell diameter for all wavelengths, but is particularly diminished in the red and blue wavelengths critical for photosynthesis (Adopted from Niklas, 1994).

cell geometry and shape, or both, change as a function of an increase in body size. In fact, these changes allow unicellular organisms to 'push to the limit' of cell size. Specifically, when representative unicellular species from diverse algal lineages are examined, the relationship between body surface area and volume is anisometric such that an increase in surface area fails to keep pace with an increase in body volume (i.e. $S \propto V^{0.70}$) (Williams, 1964; Eppley and Sloan, 1965; Mullin, Sloan and Eppley, 1966; Niklas, 1994). However, the empirically observed size-dependent variation in body surface area and volume deviates significantly from the '2/3-power rule' (i.e. $S \propto V^{0.67}$) (Fig. 7A) which describes the relationship expected between S and V for any series of objects differing in size but sharing exactly the same geometry and shape (Fig. 7A). The violation of the 2/3-power rule clearly indicates that either body geometry or shape, or both change as size increases. Indeed, smaller unicellular species tend to have a spherical or spheroidal (oblate or prolate) geometry, whereas larger species tend to have a cylindrical geometry, and, within each class of cell geometry, larger species tend to be either more flat (spheroids) or more slender (cylinders) than their smaller counterparts. Therefore, the issue is not whether the geometry or shape of the unicellular body plan changes with increasing size, but whether the differences observed among species evidence an 'adaptive' trend.

In this regard, computer simulations indicate that interspecific differences in body geometry and shape achieve the theoretically greatest increase in cell surface area with respect to an increase in cell volume. Simulations identify a series of geometries and shapes, beginning with very small spheres and ending with large and very slender cylinders, that are virtually indistinguishable from those observed among algal species differing in cell size (Fig. 7B). These simulations provide evidence, albeit circumstantial that the size-dependent relationship between cell surface area and

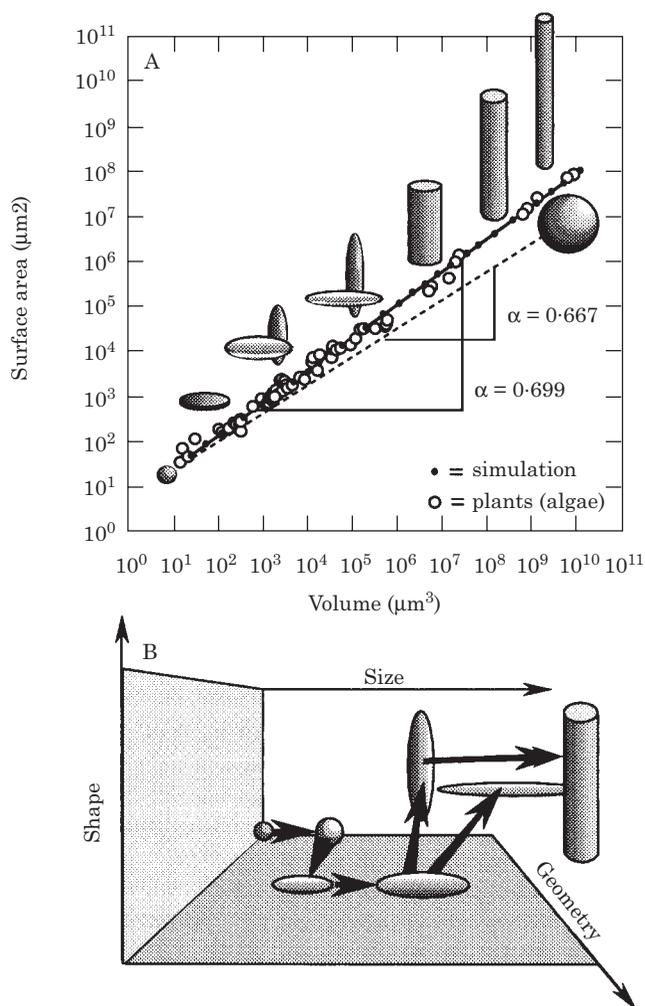


FIG. 7. Empirically determined relationship between cell surface area S and volume V measured for 57 species of unicellular algae (shown by solid regression curve with slope $\alpha = 0.699$) (A) compared to the relationship between S and V for a series of spheres differing in size (volume) (shown by dashed line with $\alpha = 0.667$) and a computer simulated series of different geometries and shapes differing in size that maximizes S with respect to V as size increases (B). The smallest algal species in the data set have spheroidal geometries; the largest species in the data set have cylindrical geometries. Within each class of geometry, shape changes (e.g. squat to slender cylinders). The computer-generated series of objects obtains the same slope for the relationship between S and V as observed for the 57 alga species ($\alpha = 0.699$). The series begins with small spheres and spheroids and ends with large slender cylinders similar in appearance to unicellular plants (Adopted from Niklas, 1994).

volume has played an important role in the evolution of the unicellular body plan.

An upper limit to unicellular *Bauplan* size may exist, but it is not a simple consequence of size-dependent variations in surface area. Size-dependent variations in the 'metabolic machinery' packaged in the unicellular body also exist. Comparisons among unicellular eukaryotic species show that an increase in body mass M (measured in picograms of carbon per cell to avoid any ambiguity resulting from the presence of vacuoles or intracellular crystals differing in size) fails to keep pace with increasing body volume

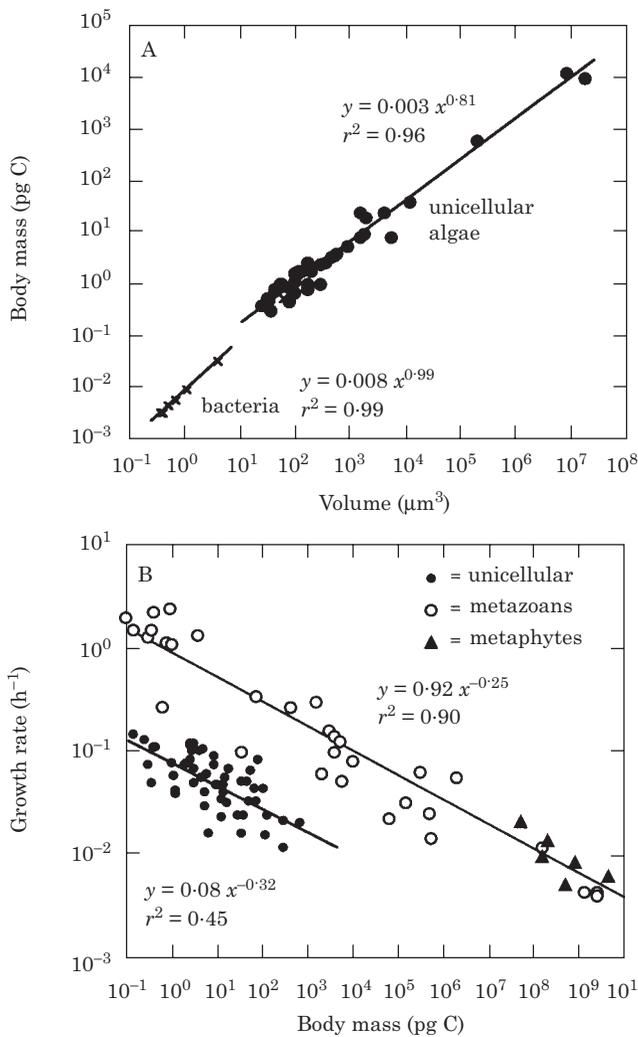


FIG. 8. Allometric relationships among the body mass (measured as picograms of carbon per cell), body volume and maximum reported growth rate for bacteria, unicellular plants (algae), animals and multicellular plants. A, Body mass plotted as a function of cell volume for bacteria and unicellular algal species. B, Maximum growth rate (picograms of carbon produced per cell body mass per hour) plotted against body mass for algae, metazoans and metaphytes (i.e. *Lemma* and *Azolla*). Solid lines denote reduced major axis regression curves for data (see regression formulae) (Data taken from Niklas, 1994).

(i.e. $M \propto V^{0.81}$) (Fig. 8A). Likewise, the growth rate G (measured as the maximum rate of cell division for cultures grown under optimal growth conditions) decreases with increasing body mass M (i.e. $G \propto M^{-0.32}$) in much the same way it decreases among metaphytes and metazoans (Fig. 8B) (see Fenchel, 1974; Banse, 1976; Peters, 1983; Reiss, 1989; Niklas, 1994). The available data indicate that the cellular concentrations of many important constituents decrease relative to an interspecific increase in body size. For example, the amount of chlorophyll *a* per cell C does not increase proportionally with respect to cell mass M (i.e. $C \propto M^{0.79}$) such that the concentration of chlorophyll per unit cell mass decreases (Fig. 9A). Likewise, phosphorus and nitrogen subsistence quotas fail to keep pace with increasing body volume (Fig. 9B). These and many other

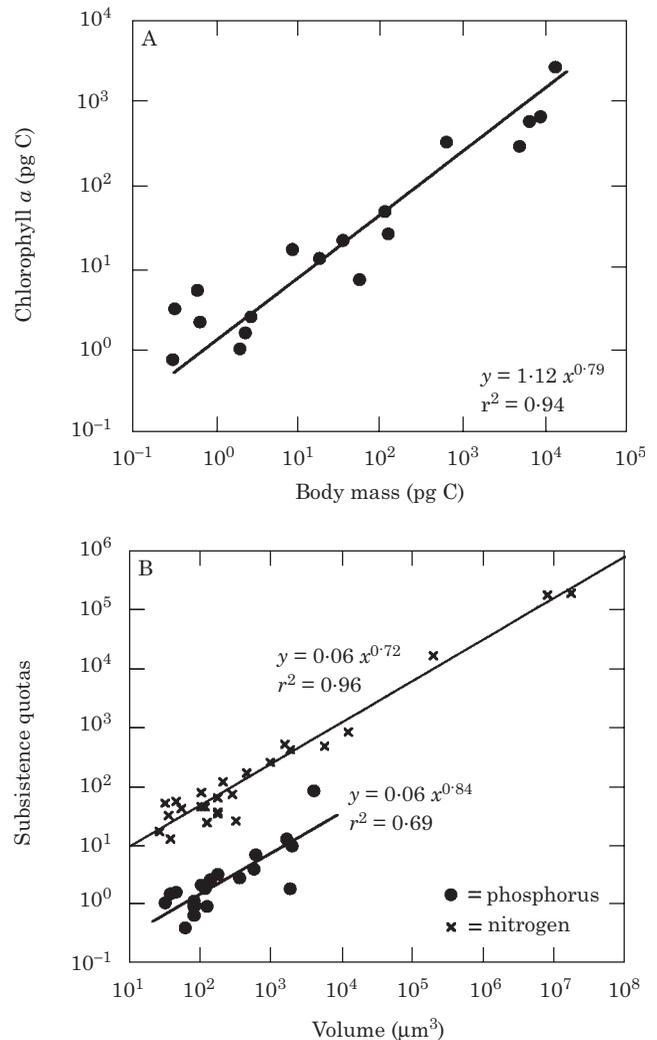


FIG. 9. Allometric relationships among chlorophyll *a* concentration, body mass (measured as picograms of carbon per cell), cell volume, and phosphorus and nitrogen subsistence quotas reported for unicellular plants (algae) drawn from diverse lineages. A, Chlorophyll *a* concentration plotted as a function of cell (body) mass. B, Subsistence quotas plotted as a function of cell (body) volume. Solid lines denote reduced major axis regression curves for data (see regression formulae) (Data taken from Niklas, 1994).

size-dependent relationships indicate that, even though larger cells contain higher concentrations of photosynthetic pigments and require larger amounts of metabolically important substances, the metabolic 'machinery' of the unicellular body plan becomes progressively 'diluted' as body size increases (measured either in terms of cell mass or volume). Together with the size-dependent decrease in cell surface area, this phenomenon may be directly or indirectly responsible for the decline in the growth rate as the unicellular body plan increases in size across species.

Regardless of their proximate cause(s), from an ecological perspective, size-dependent variations in metabolism and growth rates help to explain why the unicellular body plan is confined to a comparatively small size, and why the organisms possessing this body plan are generally confined

to low nutrient concentrations or habitats characterized by rapid environmental changes. Regardless of shape or geometry, a small body size confers a large surface area relative to body volume containing a proportionally more 'condensed' metabolic machine. Smaller organisms can thus obtain nutrients more rapidly, are better equipped to metabolize these nutrients, and can grow in size and reproduce faster than their larger unicellular counterparts. All of these features confer the ability to take advantage of brief or intermittent 'windows of environmental opportunity' to complete the life cycle. It is also reasonable to suppose that small unicellular organisms are capable of rapid physiological dormancy, and are thus able to adapt to and 'weather out' inclement but transient environmental conditions.

THE COLONIAL AND SIPHONOUS BODY PLANS

Some of the advantages conferred by a small body (cell) size are retained when individual cells become loosely aggregated together. Each cell is free to capitalize on its capacity for rapid growth and reproduction, and, provided that cells are spaced some distance apart in a pattern that reduces self-shading, the attenuation of light by neighbouring cells can be minimized. Indeed, there are some advantages to clumping cells. Metabolites can be exchanged among neighbours and used as lines of chemical communication to coordinate metabolic activities, patterns of vegetative cell division, or sexual reproduction. Local fluid flow patterns can be modified and used to remove substances or concentrate anti-microbial or toxic substances to deter pathogens or predators in the immediate vicinity. Clumped cells can also reduce the rate at which each loses water during dry periods.

Some of the advantages of clumping cells together can be illustrated by drawing on the very loose physical analogy between mass transport in a very low Reynolds number environment where viscous forces dominate and the electrostatic problem of a charged conductor in a charge-free homogeneous dielectric medium. For small unicellular organisms existing in an environment dominated by low fluid-flow speeds, nearly stagnant physiological conditions can prevail. In this environment, the ability of a cell to exchange mass with its surrounding fluid can be crudely gauged by the equivalent external conductance \mathfrak{J} for an object of similar size, shape and geometry (Niklas, 1994). In electrostatics, \mathfrak{J} equals the quotient of the capacitance and the permittivity of the medium, and, for a single sphere (cell) with radius r , $\mathfrak{J}_1 = 4\pi r \sim 12.6r$, whereas, for two touching spheres (cells) with equivalent radii r , $\mathfrak{J}_2 = 8\pi(\ln 2)r \sim 17.4r$. Since $[(\mathfrak{J}_2/\mathfrak{J}_1) - 1] \times 100\% = 38\%$, the analogy between mass exchange and conductance suggests that two adjoining cells may physiologically benefit from each other's presence in terms of respiration or photosynthesis. Naturally, this analogy erroneously suggests that mass exchange will increase as a function of cell radius, which is not likely to be the case for real cells depending on passive diffusion. Also, adjoining cells will compete for the same resources (but by doing so they are likely to accentuate gradients of

materials dissolved in their immediate fluid environment, thereby enhancing their collective access to nutrients).

Mass exchange and other density-dependent phenomena can be facilitated if neighbouring cells are bound together by a common extracellular matrix that is both permeable to and can retain water, metabolites, hormones, and other substances. Such a matrix can be also used to anchor non-motile cells to a substrate to prevent the collective from being washed away, elevate cells above a potentially stagnant boundary layer, or construct comparatively large non-cellular surfaces capable of physically modifying fluid flow patterns, thereby assisting in the circulation of inorganic nutrients around cell clusters. A matrix is similarly beneficial to cells with flagella or cilia whose collective activities are capable of stirring the boundary layer near the matrix surface and thus contribute to the metabolism as well as the locomotion of the whole (Knight-Jones, 1954; Blake and Sleight, 1974; Niklas, 1994). The specialization of some cells is likewise made possible. Some individuals can retain flagella or cilia and thus provide water circulation or locomotion, whereas others can devote their existence to reproduction (Kirk, 1998). Yet another potential advantage of operating as a loose confederacy is that the ecological 'presence' of the aggregate is retained even if some cells die or reproduce, whereas the unicellular (uni-nucleate) organism ceases to exist when it enters its sexual life cycle, since each 'adult' assumes the role of a 'gamete' (Fig. 10). It is not surprising, therefore, that colonial life forms have evolved independently many times among the different algal lineages (Table 1).

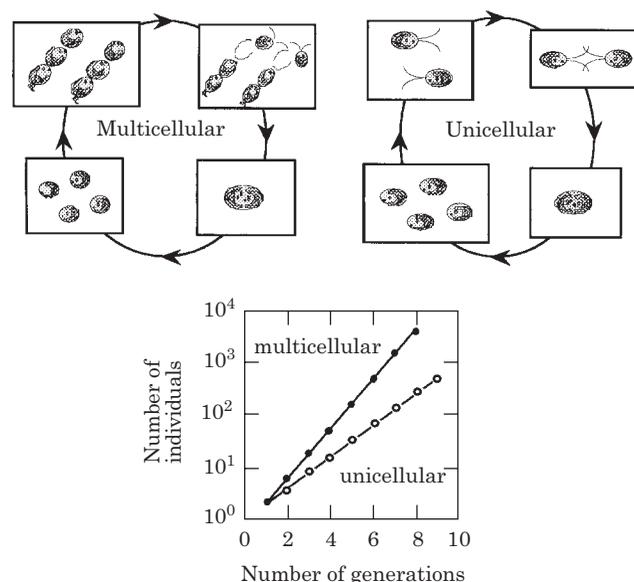


FIG. 10. Hypothetical increase in the number of sexually reproductive individuals in a population of a multicellular plant (life cycle shown in upper left) and a unicellular plant (life cycle shown in upper right) plotted as a function of number of generations (reproductive cycles). Each population starts with one individual; each individual produces one 'gamete' (the adult plant body in the unicellular organism). Each individual is assumed to survive across all generations (Adopted from Niklas, 1997).

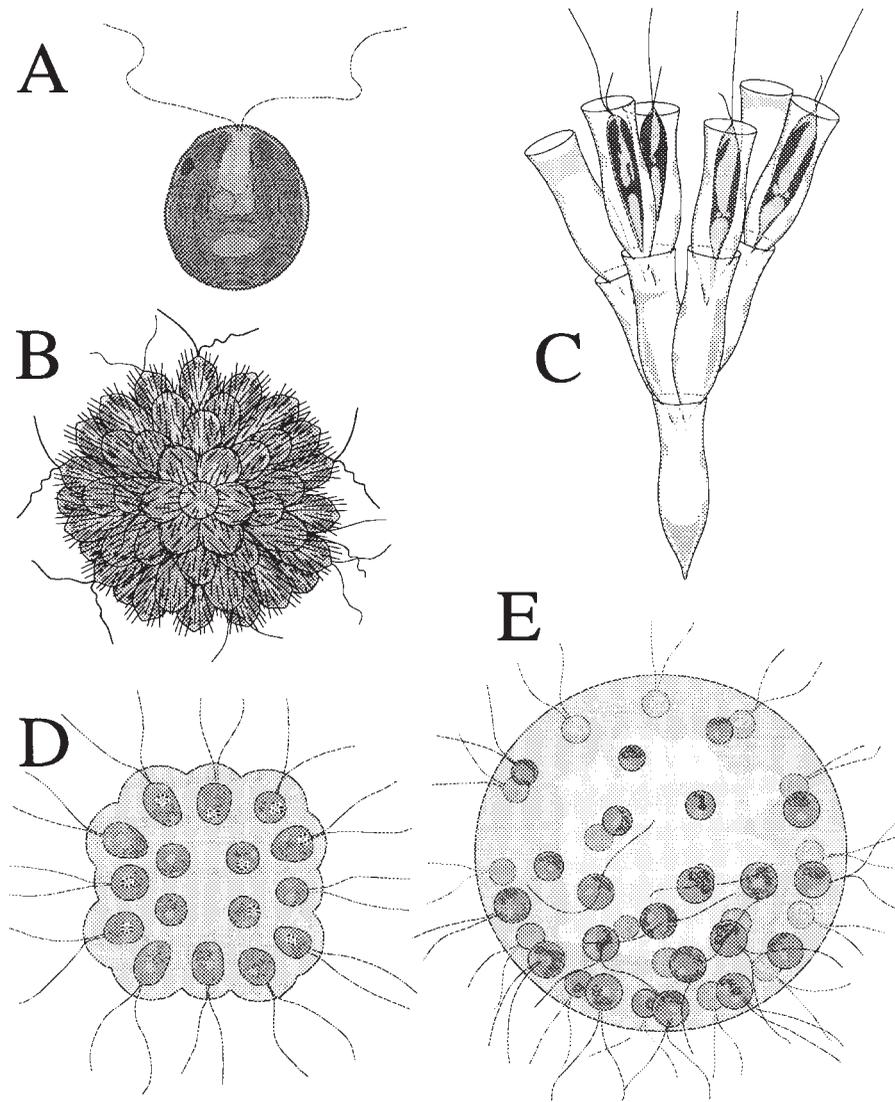


FIG. 11. Unicellular (uni-nucleate) (A) and colonial body plans (B–E). A, *Chlamydomonas* sp. (Chlorophyta). B, *Synura splendida* (Chrysophyta). C, *Dinobryon sertularia* (Chrysophyta). D, *Gonium sacculiferum* (Chlorophyta). E, *Pandorina morum* (Chlorophyta).

However, a sharp biological distinction must be drawn between the colonial body plan and the colonial growth form. The latter is sometimes adopted temporarily by a variety of unicellular and multicellular species in response to nutrient depletion, desiccation, low light intensity, or some other type of environmental stress. For example, *Chlamydomonas* (Fig. 11A) and many unicellular organisms in the Chlamydomonadaceae (Chlorophyta) can lose flagella, form ‘colonial’ aggregates on a substrate, and enter a period of metabolic or reproductive dormancy until environmental conditions return to normal (Bold and Wynne, 1978). The cells in the filamentous body plan of the chrysophycean alga *Phaeothamnion confervicola* can dissociate and form a mucilaginous ‘colony’ when physiologically stressed (Bold and Wynne, 1978). Conversely, it must be noted that some cellular prokaryotes and non-photosynthetic eukaryotes aggregate to form morphologically complex colonies when starved of nutrients or

otherwise stressed (e.g. *Chondromyces crocatus* and *Dictyostelium discoideum*, respectively), leading some to speculate on the transition from the unicellular to the multicellular body plan in distantly related groups of organisms (see Kaiser, 1993 and references therein). Regardless of the inferences that can be drawn from these organisms, many examples suffice to show that the ‘colonial’ (palmelloid) growth habit is adopted by species with a variety of different body plans in response to inclement environmental conditions. Conceptually and biologically this contrasts with the colonial body plan that is adopted as a consequence of normal growth and development (e.g. *Synura splendida* and *Dinobryon sertularia* in the Chrysophyta, and *Gonium sacculiferum* and *Pandorina morum* in the Chlorophyta) (Fig. 11B–E).

Yet, even among *bona fide* colonial species, a further distinction must be drawn between colonies with an ‘open and indeterminate’ ontogeny involving the mitotic division

of cells that remain physically attached but cytoplasmically disconnected from one another (e.g. *S. splendida*) vs. colonies with a 'closed and determinate' (coenobial) ontogeny that produces a multicellular body plan with a prefigured number of cells. In some cases, the multicellular body plan is retained in the adult condition (e.g. *Volvox*) (Starr, 1968), whereas in other cases the multicellular body plan is adopted early in development but is subsequently lost with the dissolution of cytoplasmic connections among adjoining cells before the adult condition is reached (e.g. *G. sacculiferum*) (Kirk, 1988, 1998). Thus, the colonial body plan may have evolved either from a unicellular organism that biologically benefited from the presence of conspecifics, or from an inherited developmental 'demolition' of a multicellular body plan. Attempts to use certain plant groups, such as the volvocine green algae, as exemplars of how multicellularity may have evolved from a presumed antecedent loose confederacy of cells are thus highly problematic (Buss, 1987), especially since, among the volvocine algae, the available information indicates that the colonial body plan is most probably the derived rather than the ancestral condition. Under any circumstances, based on molecular data, some of the 'genera' in the volvocine 'lineage' are undoubtedly polyphyletic (e.g. *Chlamydomonas*, *Eudorina* and *Volvox*), making it difficult or impossible to adduce a 'linear sequence' of evolutionary transformations (Adair *et al.*, 1987; Larson, Kirk and Kirk, 1992).

The evolutionary origins of the siphonous (unicellular multi-nucleate) body plan are equally unclear. Although rare (Table 1), the siphonous body plan has an 'open and indeterminate' ontogeny that arguably confers some advantages over the 'closed and determinate' ontogeny typical of the unicellular (uni-nucleate) body plan, since siphonous plants can (and typically do) conserve or elaborate their body surface area with respect to volume by adopting a cylindrical geometry as the iterative unit of their body construction. Simple analytical geometry shows that the cylinder is one of the few geometries that can indefinitely increase in volume (size) without decreasing its ratio of surface area to volume (i.e. since $S = 2\pi rl$ and $V = \pi r^2 l$, where r is radius and l is length, it follows that $S/V = 2/r$, indicating that the ratio of S to V is proportional to the radius of a cylindrical body plan and is independent of body length). The delicate, feather-like 'fronds' of many chlorophycean siphonous species, such as those of *Bryopsis* (which generally attain a length of 10 cm but which can reach 40 cm in length in the case of *B. maxima*) and *Caulerpa sertularioides* and *C. florida* (which exceed 15 cm in length), are all constructed out of very slender tubular elements that have very large surface areas with respect their volume. Likewise, the coenocytic vegetative axes of many xanthophycean species, such as *Vaucheria* and *Ophiocytium*, have a cylindrical geometry. Additionally, large body size in the siphonous body plan can be achieved by appressing the majority of organelles against the cell wall by a large vacuole. This cytological configuration minimizes the transport distance (and thus the transport time) for the passive diffusion of nutrients or wastes across the cell membrane and wall.

The comparative rarity of the siphonous body plan may be related to the fact that microbial or viral infections are difficult or impossible to localize and thus can become systemic in the absence of the compartmentalization of the protoplast by cell walls. Mechanical perforation of the single cell wall also can result in the evacuation of a substantial amount of protoplasm before the damaged wall can be repaired. These and other features may explain why this body plan is found among a comparatively small number of species. In terms of the origin of the siphonous body plan, either the unicellular or multicellular ancestral condition is theoretically possible. It must be noted, however, that all siphonous species are capable of partitioning their protoplasts by means of cell walls during the formation of reproductive structures (Bold and Wynne, 1978) and that some multicellular taxa are multinucleate (e.g. *Urospora* and *Cladophora*). These features suggest that some siphonous algae are evolutionarily derived from multicellular organisms by the modification of the relationship between cyto- and karyokinesis, whereas other siphonous algae evolved from unicellular multi-nucleate organisms that attained the capacity for indeterminate growth in cell size.

Unfortunately, our current understanding of the cellular mechanics and genetics responsible for disparity between karyo- and cytokinesis, and thus the distinction between the uni- and multi-nucleate cellular condition is incomplete. It has long been known that the volume of the nucleus with respect to that of the cytoplasm is fairly constant across unicellular and siphonous plants (Sharp, 1926; Sitte, 1992). 'Super-cell' organisms, like *Caulerpa*, *Valonia*, *Bryopsis* and *Vaucheria*, contain nuclei whose collective volume is proportional to the volume of the cytoplasm enveloped by their single cell wall. This phenomenology is consistent with the 'energid' concept of Sachs (1892), which postulates that each nucleus in a cell 'dominates' a certain volume of the cytoplasm. In the parlance of this theory, unicellular organisms are 'monoenergidic', whereas siphonous organisms are 'polyenergidic'. Yet, the mechanism(s) responsible for the disparity between cyto- and karyokinesis remain(s) poorly understood. Among bacteria, cytokinesis by cleavage is mediated by a set of proteins, principally FtsZ (Bramhill, 1997), which has sequence similarities to eukaryotic tubulins (Erickson, 1997). Although it has yet to be proven, cleavage among eukaryotic plants appears to be predicated on an actin-based phenomenon. Spatial apporportionment of the cytoplasm and control over cytokinesis in multicellular plants are dependent on nuclear-based radial systems of microtubules that define what have been called nuclear-cytoplasmic domains (see Brown and Lemmon, 1992). Genetic alterations of these systems arguably may account for evolutionary transitions between uni- and multi-nucleate unicellular organisms.

FILAMENTOUS MULTICELLULAR BODY PLAN VARIANTS

The evolution of the multicellular body plan was a major evolutionary achievement that required precise control over the plane of cell division and the establishment of

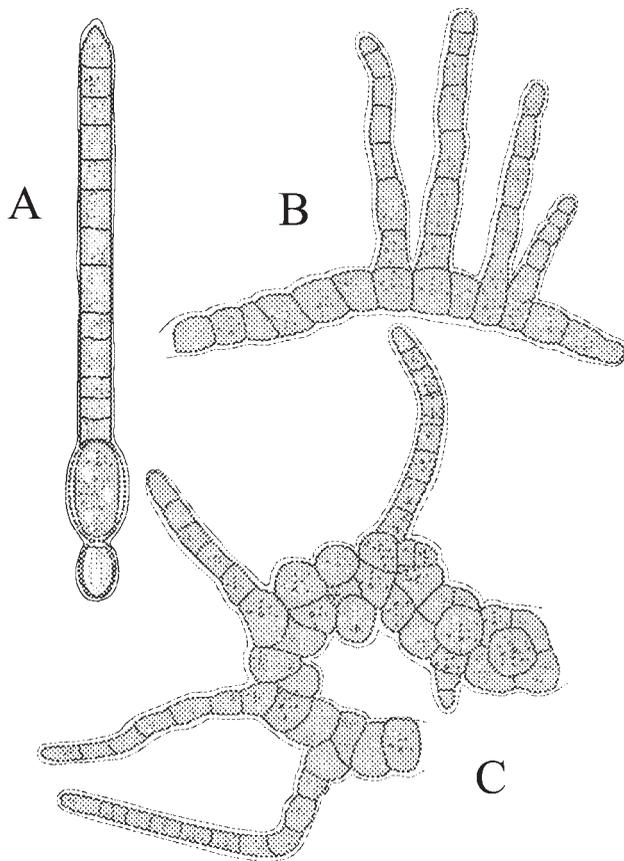


FIG. 12. General morphology of representative cyanobacteria with unbranched and branched filamentous (A and B) and parenchymatous-like (pluriserate) constructions in which symplastic continuity may be maintained among adjoining cells (C). A, *Cylindrospermum* sp. B, *Hapalosiphon* sp. C, *Fischerella* sp.

cytoplasmic (symplastic) continuity among adjoining cells. Interestingly, the capacity to regulate cell division planes, differentiate cell types, and fabricate unbranched filaments, branched filaments, and cellular configurations similar in general appearance to parenchyma (i.e. pluriserate filaments) is evident among the cyanobacteria (e.g. *Cylindrospermum*, *Hapalosiphon* and *Fischerella*, respectively; Fig. 12), many of which can also establish symplastic continuity among neighbouring cells in the form of delicate ('micro') plasmodesmata that cross the transverse walls of adjoining cells (Bold and Wynne, 1978; Westermann *et al.*, 1994). Whether these structures are primary or secondary, and whether they provide robust avenues for metabolic transport or communication as plasmodesmata do among eukaryotic photoautotrophs remain conjectural. However, it cannot escape attention that many chloroplast genes currently reside in the nuclear genomes of plants and that chloroplasts are presumed to have evolved from ancient forms of blue-green bacteria. It is conceivable, therefore, that some of the genetic material encoding for cyanophycean multicellularity may have been transmitted to 'host' cell genomes shortly after the primary endosymbiotic events occurring in the Precambrian. In this sense, some of the features of eukaryotic multicellularity may have been prefigured during the early evolution of many of the ancient algal

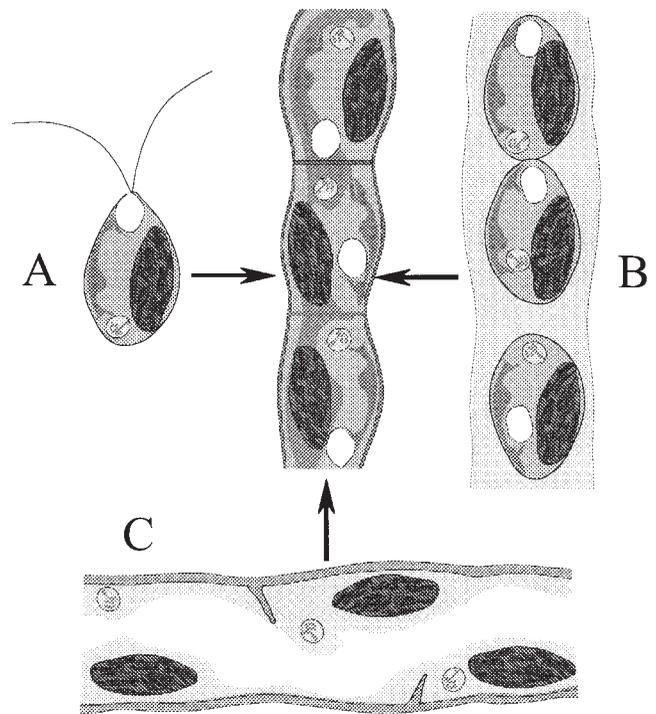


FIG. 13. Hypothetical derivation of a multicellular (simple filamentous) body plan (centre) from a unicellular (A), colonial (B), and siphonous (C) body plan. See text for further details.

lineages. Under any circumstances, the basic elements of the multicellular body plan evidently predate the eukaryotic condition.

Although the genetic mechanisms required for multicellularity are undoubtedly complex, on strictly morphological grounds, the multicellular body plan may have evolved directly from a unicellular, colonial, or siphonous *Bauplan* (Fig. 13). It is currently impossible to say which, if any of these was the antecedent condition for the most ancient multicellular organisms in any particular plant lineage. The view taken here, however, is that the unicellular body plan is the most plausible morphological antecedent condition to multicellularity in the majority of the algal lineages and that the unbranched filament is the most ancient variant of the multicellular body plan (see Fig. 13A). Cell division in one plane followed by cytokinesis and the retention of cytoplasmic 'bridges' or the formation of plasmodesmata between derivative cells immediately establish the unbranched filamentous multicellular body plan. Diffuse cellular division would increase body size and produce a cylindrical body geometry. As noted, this geometry is one of the few that can increase in size without reducing the ratio of body surface area to volume. Filaments of cells can increase in size by the addition of new cells anywhere along their length, and each individual cell can increase in length, thereby allowing the surface area to volume ratio of constituent cells as well as the entire plant body to either remain constant or increase depending on metabolic demands. The derivation of an unbranched filamentous multicellular body plan from a unicellular organism is consistent with the widely held view that the

latter is the most ancient body plan in each algal lineage. It is also consistent with the ontogeny of many filamentous species, which begin their vegetative existence as flagellated zoospores, lose their flagella, and subsequently undergo an indeterminate number of mitotic cellular divisions to form an unbranched filament (e.g. *Stichococcus chloranthus* and *Ulothrix zonata*).

The ability to form simple unbranched filaments requires a cell division mechanism sensitive to the orientation of cell growth with respect to adjoining cells such that the plane of cell division is consistently confined to the perpendicular direction with respect to the body axis. Subsequent evolutionary modifications were required to alter this mechanism such that two or more orthogonal planes of cell division become possible to form branched filaments and parenchymatous tissues (see Fig. 3). A variety of mechanisms responsible for the orientation of cell division has been proposed. The preprophase band is considered pivotal by some workers, especially in terms of the evolution of the embryophytes (see Brown and Lemmon, 1990), since the developmental switch from the tip growth in the filamentous (protonemal) stage of moss gametophyte growth to gametangiophore bud formation is correlated with the appearance of preprophase bands in the latter stage (Doonan, 1991). Nonetheless, preprophase bands are absent among many organisms that manifest precise control over their planes of cell division and thus produce filamentous or parenchymatous growth (e.g. *Coleochaete* and *Chara*). For this reason, other workers have emphasized the importance of mechanical stresses generated during cell division, draw attention to plastid orientation, or implicate the role of cytoskeletal elements of the phragmosome as factors influencing the site of future cell wall formation (e.g. Lintilhac, 1974; Brown and Lemmon, 1984; Green, 1987; Lloyd, 1991; Cooke and Lu, 1992; Oates and Cole, 1992).

Perhaps the most far-reaching mechanism for cell division orientation thus far is the ‘tensegrity’ concept of Pickett-Heaps *et al.* (1999; see also Ingber, 1993), which proposes that each cell is organized by an integrated cytoskeleton of tension elements (actin fibres) extended over a compression resistant domain composed of microtubules. If so, then mechanical as well as chemical cues are required for the orientation of the cell division plane. Although all of these explanations are plausible mechanistically, considerable variation in mitosis and cytokinesis occurs across plant lineages (see Pickett-Heaps, 1972) and most explanations cannot be applied universally across all of the pro- and eukaryotic lineages in which multicellularity is expressed, indicating that our understanding of the mechanism(s) responsible for the planes of cell division is incomplete.

From a functional perspective, even the most morphologically simple variants of the multicellular body plan (e.g. unbranched and branched filaments) confer similar advantages to that of the colonial body plan—body size can increase by the addition of cells that metabolically or reproductively benefit by virtue of their comparatively small size and large surface area to volume ratios, and the organism as a whole can devote some cells to sexual

reproduction without sacrificing its ecological persistence in a population (see Fig. 10). Unlike the colonial body plan, cells in a multicellular organism remain symplastically interconnected by means of cytoplasmic bridges, plasmodesmata, etc. that establish a large continuous internal plasmalemma system that can be used for chemical exchange and intercellular communication. The number and distribution of these cytoplasmic bridges between cells can also be developmentally adjusted to create preferred routes of intercellular transport for nutrients and growth hormones (Ding, Itaya and Woo, 1999). Cell-to-cell trafficking of macromolecules can be used to generate chemical gradients to regulate cell, tissue, and body plan polarity, help define where and how long meristematic activity occurs, and that can isolate reproductive cells by the dissolution of symplastic continuity (Kwiatkowska, 1988).

Patterns of cellular differentiation become possible as well, since plasmodesmata are known to preferentially traffic different hormones (Drake and Carr, 1978, 1979) and since each cell in the multicellular organism is no longer entirely responsible for its own metabolic requirements and survival (e.g. non-photosynthetic cells can be metabolically sustained by photosynthetic cells or tissues; some cells can be developmentally programmed to die after they deposit their cell walls whose lumens can be used to transport water and growth hormones). Since body shape and geometry can be specified by cell-to-cell coordinated efforts, multicellularity confers numerous advantages in terms of acquiring nutrients, intercepting sunlight, occupying space, and thus competing with other species for the same or similar resources.

The filamentous body plan confers a number of mechanical as well as physiological advantages, especially when anchored by a specialized basal cell to a substrate under water. For example, the net hydrodynamic force F_N exerted on any plant body is the vector resultant of two orthogonally opposed forces—the lift force F_L , which operates perpendicular to the direction of fluid flow, and the two horizontal force components, which are the pressure (drag) force F_D and the acceleration force F_A . When fluid-flow is accelerating, the two horizontal forces act in the same direction; when the fluid decelerates, these two forces act in opposing directions (Fig. 14). Mathematically, these three force components are given by the formulae

$$F_L = 0.5\rho u^2 S_{\text{plan}} C_L$$

$$F_D = 0.5\rho u^2 S_p C_D$$

$$F_A = \rho C_m Va,$$

where $0.5\rho u^2$ is the dynamic pressure, S_{plan} is the ‘planform area’ (the area of the plant body projected perpendicular to the direction of flow), C_L is the lift coefficient, S_p is the surface area of the plant body projected against the direction of fluid flow, C_D is the pressure (drag) coefficient, C_m is the inertia coefficient, V is plant body volume, and a is the fluid acceleration (Denny, 1988; Niklas, 1994). In an environment with rapid and steady fluid-flow, the planform area and the projected area of a flexible filamentous body

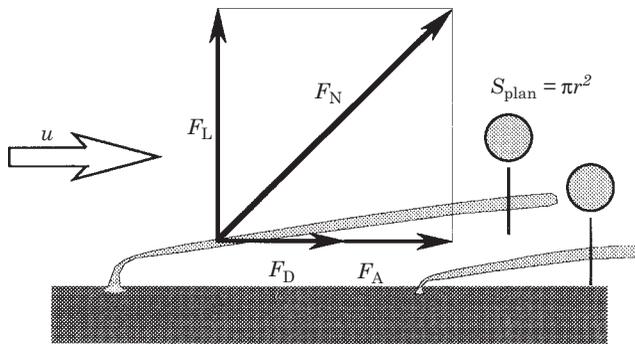


FIG. 14. Diagram of hydrodynamic force components exerted on a multicellular (simple filamentous) body plan attached to a substrate subjected to a fluid-flow with velocity u . The net hydrodynamic force F_N equals the vector sum of the vertical lift force F_L and two horizontal force components, the pressure (drag) force F_D and the acceleration force F_A . The planform surface area projected toward the direction of fluid-flow, which influences the magnitude of F_L and F_D (see text for formulae), is independent of body length and depends on cell radius r .

plant roughly equal the cross-sectional area of an average cell in the filament, and thus the lift and drag forces on a filament aligned in the direction of flow are largely insensitive to the number of cells along the length of the plant body (Fig. 14). By the same token, the drag and inertia coefficients for a cylinder are independent of the length of a cylindrical filament, whereas the inertia coefficient ranges from 1.62 to 2.0 for a cylinder with length to diameter ratios of 1.2 and infinity, respectively. Consequently, the principal variables influencing the net hydrodynamic force on an unbranched filamentous body plan are fluid-flow speed u and acceleration a , which cannot be controlled by the plant, and body volume V , which is determined by an organism's ontogeny and life-expectancy. Although an indefinite increase in body volume can engender large acceleration forces, provided the organism gets big enough to experience turbulent flow regimes, the filamentous body plan, whether branched or unbranched, can metabolically benefit, in terms of mass exchange, from forced convection. Indeed, for some filamentous algae (e.g. *Cladophora*), the frequency of branching increases (to a limit) in proportion to water speed, presumably because high flow regimes favour more rapid mass exchange between the plant body and its surrounding water and thus higher respiration and photosynthetic rates (see Parodi and Cáceres, 1991).

It is worth noting that cell division in two orthogonal directions is required to construct branched filaments. This also affords the opportunity to construct monostromatic thalli that have large surface areas with respect to their volumes, since cells are exposed on both sides to water and dissolved atmospheric gases and nutrients. Provided cell walls are flexible, cylindrical and plate-like plant bodies anchored to a substrate are capable of streamlining and reducing drag in rapid fluid-flow environments by deflecting and/or folding upon themselves downstream. Extensible hollow tubes can also sustain very large recoverable elastic longitudinal deformations by circumferential contraction.

Multicellular plants composed of a pseudoparenchymatous tissue can be viewed as having a modified filamentous body layout when diffuse, trichothallic, or apical cell divisions are not developmentally coordinated to produce a species specific body shape or geometry. Variants of this kind are especially well represented by species currently assigned to the Leathesiaceae in the Phaeophyta (e.g. *Leathesia difformis*). In contrast, a *bona fide* pseudoparenchymatous body plan is achieved when branched or unbranched filaments are formed and regulated by specific meristematic regions whose activities are coordinated to produce species specific adult morphologies and anatomies, as is seen in many plant lineages such as the Rhodophyta. In either case, a pseudoparenchymatous tissue fabric can be used to construct comparatively large and potentially morphologically complex organisms containing a large non-symplastic volume fraction that is 'internal' with respect to the outer surface of cells but that is topologically external with respect to the organism and the fluid surrounding it. This extracellular but 'inner body compartment' can be used to concentrate metabolites, retain water, or serve as an extracellular system for the transport of substances from one part of the organism to another (see Raven, 1997; Kirk, 1998). Developmental control of the orientation of filamentous and pseudoparenchymatous tissues by specialized meristematic regions can also provide for a mechanically anisotropic plant body, one that can deform or resist externally applied mechanical forces differently depending on the direction these forces are applied with respect to the three principal body axes. Tissue mechanical anisotropy may be especially important to organisms living in high-energy, wave-swept habitats.

THE PARENCHYMATOUS PLANT BODY

Arguably, the most evolutionarily derived variants of the multicellular plant body plan are constructed out of parenchymatous tissues produced by spatially discrete meristematic regions rather than diffuse cell division. The capacity to establish or sever protoplasmic interconnections among all the surfaces of adjoining cells affords the opportunity to develop complex lines of lateral and longitudinal chemical communication in the plant body by means of cytoplasmic 'domains', the construction of specialized tissues and tissue systems, and the coordination of the physiological efforts of vegetative and reproductive organs. In essence, the multicellular parenchymatous plant body is composed of a single functional symplast incompletely partitioned by an infrastructure of cell walls, very like the siphonous plant body plan but with all the mechanical and physiological benefits conferred by a cellular condition.

These features of the parenchymatous body plan must be conceptually linked to the spatial and temporal coordination of cellular division and the evolution of meristematic regions. Without exception, all contemporary parenchymatous species possess well defined meristems that are either intercalary or apical in location. Unfortunately, the fossil record does not provide sufficient information about how this body plan configuration evolved in each of the plant lineages in which it occurs. It is nonetheless tempting to

derive the parenchymatous plant body and its specialized meristematic regions from either a filamentous or pseudoparenchymatous precursor in which meristematic activity was confined to developmentally specified locations, presumably as a consequence of chemical and physical controlling mechanisms relying on plasmodesmata trafficking.

Some evidence supports this point of view. Among the charophycean algae, which probably share the same last common ancestor with the embryophytes, meristematic growth is typically confined to the apices of filaments, whereas, among parenchymatous charophycean species, meristematic growth is confined to the margins of thalli. The juxtaposition of these contemporary species may shed light on how the parenchymatous body plan with apical meristems evolved in these algae and was carried forth into the land plants (see [Graham, 1993](#)). Specifically, the discoid thallus of some *Coleochaete* species is composed of laterally adjoining filaments that grow in length at their tips by means of transverse (circumferential) cell divisions and that branch (radially) at their tips to create a pseudoparenchymatous tissue system as evidenced by the appearance of Y-shaped cells (e.g. *C. nitellarum*) ([Fig. 15A, B](#)). Other species in this genus construct discoid purportedly parenchymatous thalli by means of a marginal apical meristem that produces coherent cell lineages derived by circumferential and bisecting (radial) divisions (e.g. *C. orbicularis*) ([Fig. 15D](#)). Species in which Y-shaped and radially bisected cells are located at the perimeter of thalli may represent the intermediate condition between a filamentous and parenchymatous organism (e.g. *C. soluta*) ([Fig. 15C](#)).

Likewise, recent studies of cytokinesis in *Chara* species indicate that this filamentous organism establishes plasmodesmata among all nodal cells that thus assume the role of discrete lateral meristematic regions ([Franceschi, Ding and Lucas, 1994](#); [Cook, Graham and Lavin, 1998](#)), suggesting how the parenchymatous plant body evolved from an ancestral branched (pseudoparenchymatous) filamentous one. By the same token, the transition from a marginal meristem composed of many initials to an apical meristem composed of one or a few initials can be represented by the juxtaposition of some parenchymatous phaeophycean genera, among which some have a marginal zone of many apical meristematic cells (e.g. *Padina*) similar to that of parenchymatous *Coleochaete* species and others have a meristem composed of a single apical cell (e.g. *Dictyota*) similar to that of *Chara* and many non-vascular land plants ([Fig. 15E–I](#)).

Scenarios such as these, however, are highly speculative since the sequence of *Coleochaete* species purported to show the evolution of parenchymatous tissue from branched filaments ([Fig. 15B, C](#)) can be read in the opposite direction; the charophycean and phaeophycean algae do not share the same last common ancestor; and many parenchymatous phaeophycean algae possess intercalary rather than apical meristems (e.g. *Laminaria* and *Macrocystis*). Alternative and equally plausible evolutionary scenarios also exist. It is possible to derive a parenchymatous plant body with apical meristems from a filamentous body layout similar to that of *Chara*. In the absence of additional data, therefore, the origins of parenchymatous

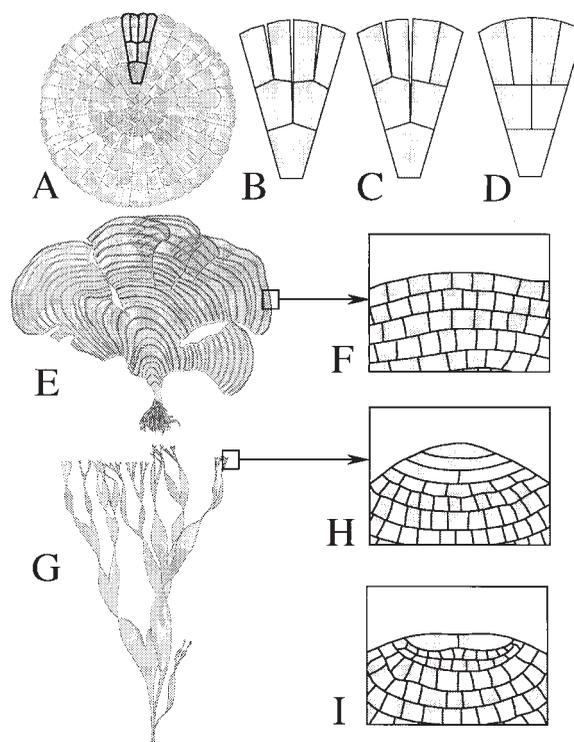


FIG. 15. Scenarios for the evolution of a parenchymatous tissue fabric constructed by means of a marginal (peripheral) zone of meristematic cells (A–D) and the evolution of an apical meristem consisting of one cell (capable of dichotomization) from a marginal (peripheral) zone of meristematic cells (E–I). Among species of the charophycean alga *Coleochaete*, a discoid thallus (A) can be constructed out of branched abutting filaments (pseudoparenchymatous tissue) characterized by Y-shaped cell walls (sector of cells diagrammed in B corresponding to cells outlined in A). An intermediate condition between branched filaments and parenchymatous clusters of cells is reported for some species (sector of cells with Y-shaped and bisecting cell walls shown in C). Species with purportedly parenchymatous thalli have radial and circumferential cell divisions that form bisecting cell walls (D). The transition from a parenchymatous organism, like the brown alga *Padina* (E) whose marginal apical meristem consists of many cells (F) to a parenchymatous organism, like that of the brown alga *Dictyota* (G), may have been accomplished by reducing the number of meristematic cells at different points in the plant body to individual apical cells (H), each capable of bisecting to produce ‘branches’ (I).

plants with well defined meristems, apical or otherwise, remain conjectural.

Regardless of its evolutionary origins, a parenchymatous plant body with meristematic activity confined largely to one or more apical cells or cell clusters is advantageous in a number of respects. Body size can be increased indefinitely by the exogenous addition of new body parts at growing tips without interrupting the bulk flow or the active transport of metabolites by specialized tissues that develop and mature in older portions of the plant. Reiteration of the body layout is made possible by repeated bifurcation of growing points to produce a ramified (branched) morphology. Multiple apical meristems provide a margin of safety for the continued existence of the organism, since the life of the individual is not cut short by the decapitation or death of one or more of its distal parts. Some meristems can be

devoted to the formation of specialized vegetative or reproductive organs that are determinate in size, shape and geometry (e.g. leaf-like functional analogues and sporangia, respectively), whereas other meristems can continue to grow indefinitely. Many of these features are difficult or impossible to achieve with intercalary meristematic growing regions, although it cannot escape attention that some of the largest marine plant species have a parenchymatous body plan that employs intercalary meristems to achieve its organized growth, presumably as a failsafe against the high probability of distal mechanical failure by shearing water currents (e.g. *Macrocystis*).

EMBRYOPHYTE BODY PLAN VARIANTS

Embryophytes and charophycean algae share a common ancestor that probably had (1) cell walls containing cellulose microfibrils that afforded mechanical support when placed in tension but that deformed easily under compression, (2) a parenchymatous body plan lacking a waxy cuticle with a high surface area with respect to body volume, (3) a life cycle involving only one multicellular life form that functioned as the gametophyte (i.e. a haplobiontic haploid life cycle), and (4) motile sperm requiring liquid water to fertilize eggs (Graham, 1993; Niklas, 1997). Each of these traits is poorly suited for survival on land where access to water may be limited. For example, like those of many algae, charophycean cells and tissues mechanically function as hydrostats—fluid-filled devices whose stiffness is proportional to their inner positive (turgor) pressure (Fig. 16). When fully turgid, the living protoplast in each cell is compressed against its wall where the resulting circumferential tension is mechanically sustained by cellulose microfibrils (Niklas, 1989). For its density, cellulose is the strongest known biopolymer measured in tension. However, like all long-chained biopolymers, it provides little mechanical support when compressed along the backbone of its molecular structure, and so, when cell turgor pressure is lost, algal protoplasts deflate, their cellulosic cell walls lose their rigidity, and cells or tissues collapse under their own weight when exposed to air.

In water, hydrostatic devices are mechanically reliable, and, since they are nearly neutrally buoyant, they exert little or no weight on adjoining cells. On land, however, hydrostatic tissues are approximately 1000 times more dense than air and thus generate compressive forces within themselves. This mechanical force can be resisted by turgid cells and tissues, since it is transmitted to cell walls in the form of tensile forces that are mechanically sustained by cellulose microfibrils. However, when protoplasts are deprived of water, compressive bending stresses develop in cell walls that are better equipped to cope with tensile stresses (Niklas, 1989). One solution is to produce tissues composed of small cells with thick walls, since the hydrostatic stresses in a cell wall σ generated by any internal hydrostatic pressure P are directly proportional to cell radius r and inversely proportional to cell wall thickness t (e.g. for an isodiametric cell, $\sigma = rP/2t$; see Niklas, 1992).

Another solution is to insert a chemical 'bulking agent' in the cell wall matrix that can buttress cellulose microfibrils

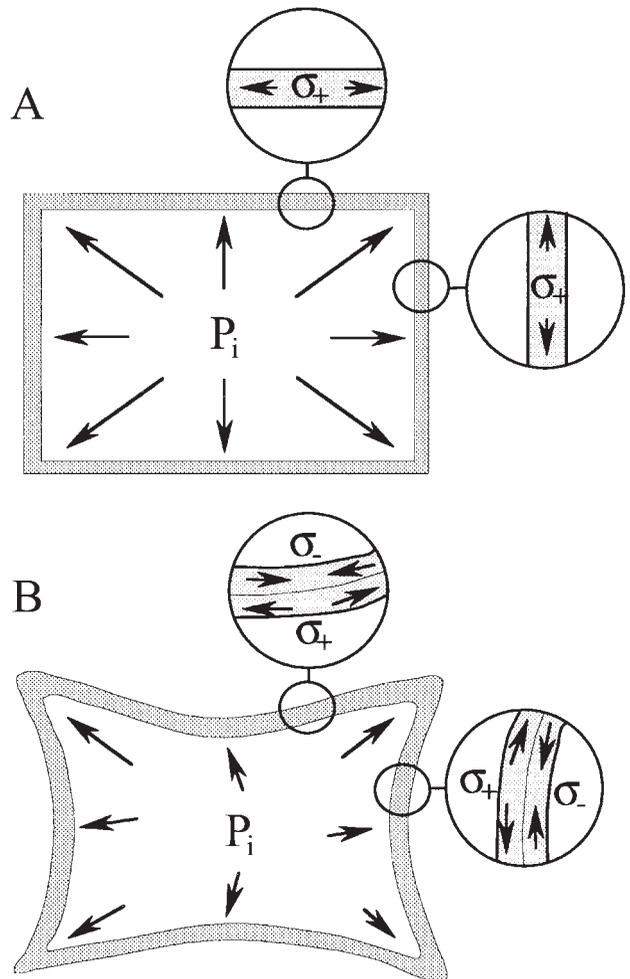


FIG. 16. Mechanical behaviour of a thin walled cell in a hydrostatic tissue. A, The protoplast of the cell is appressed to its cell wall (shaded area) by an internal positive (turgor) pressure P_i placing the cell wall in uniform tensile stress σ_+ . Any externally applied tensile or compressive force magnifies tensile stresses in wall (not shown). B, A reduction in turgor pressure reducing the volume of the protoplast and thus the force it exerts on the cell wall which deforms and is subjected to tensile and compressive bending stresses (σ_+ and σ_- , respectively) (Adopted from Niklas, 1992).

against lateral flexure. Lignin provides this service, and, since dehydrated cellulose is stiffer than wet cellulose, lignin has the additional advantage of being a hydrophobic material. Likewise, lignin can provide some protection against high intensity ultraviolet light and microbial degradation of cell walls. Resistant polyphenolic compounds occur in *Coleochaete* and various bryophyte species (Delwiche, Graham and Thomson, 1989), and lignins have been reported for hornwort species (Takeda, Hasegawa and Shinozaki, 1990). However, larger phenolic polymers that can be unambiguously assigned to lignin have not been demonstrated for any species other than tracheophytes [see, however, Gunnison and Alexander (1975) who report 'lignin' in the walls of *Staurostrum*]. However, extensive biochemical surveys of the algae have not been conducted, and so the distribution of biosynthetic pathways underlying the formation of lignin is uncertain.

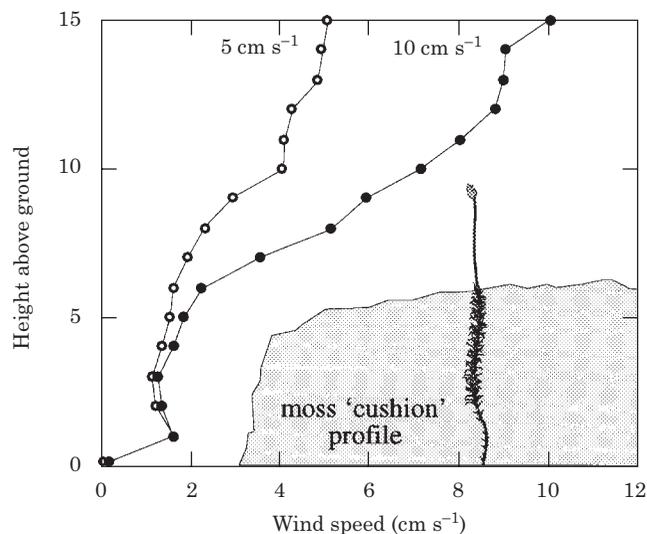


FIG. 17. Wind speeds at different locations with respect to height above ground within a moss gametophyte 'cushion' measured in a wind tunnel at two different ambient wind speeds (5 and 10 cm s^{-1}). Shaded region indicates vertical shape of cushion; archegoniophore with sporophyte denotes location of anemometer used to measure wind speeds in cushion. Sporangium is elevated above the region of attenuated wind speeds created by cushion. Gametophyte located in region of comparatively low wind speeds and thus within a boundary layer.

The amplification of body surface area with respect to volume is beneficial in terms of mass and energy exchange and can proceed indefinitely in an aquatic environment where desiccation is unlikely. On land, however, water must be conserved within the plant body as well as absorbed from a substrate. In the absence of a cuticle perforated with pores or stomata, or some physiological means to tolerate dry conditions or suspend metabolic activity, a morphological dilemma ensues for a land plant—large surface areas are required to absorb water and minerals from substrates, but large surface areas can lose water rapidly. Under these circumstances, growth and survival on land is largely confined to dependably moist microhabitats.

Hugging a moist substrate and growing within its boundary layer by means of a dorsiventral thallus, or generating a boundary layer around an elevated plant body by appressing vertical but short wick-like body parts closely together are reasonable morphological solutions for water conservation on land (Fig. 17). These body plan symmetries are reminiscent of the multicellular gametophyte generation of charophycean algae, such as *Coleochaete* and *Chara*, and resurface on land over and over again in the form of the thalloid or 'leafy' morphologies assumed by the gametophyte generation of bryophytes (see Bold, 1967). When combined with short stature, these layouts can retain a thin layer of water over their surfaces and are thus well suited for the survival and transit of flagellated sperm cells.

Additionally, all modern-day land plant groups, including the bryophytes, appear to possess the capacity to produce extracellular lipids and cutin, and thus all have the ability to form an extracellular 'cuticle' that impedes water loss from the plant body surface to some degree. In

contrast, cuticles like those chemically identified for the land plants have not been demonstrated for any extant aquatic species, although epidermal cutin- and waxy-like chemical moieties are known to occur on the submerged leaf surfaces of some marine and freshwater macrophytes (Holloway, 1982) and on the thalli of some *Coleochaete* species (Cook and Graham, 1998; Graham and Wilcox, 2000). Since the land plant cuticle is more resistant to the passive diffusion of water than to either carbon dioxide, oxygen or other substances (e.g. the permeability coefficients of the *Citrus* cuticle for H_2O , CO_2 and O_2 are in the order of 10^{-9} , 10^{-8} and 10^{-7} m s^{-1} , respectively; see Lenzian, 1984), a cuticle-like precursor is not antithetic to an aquatic existence, especially since a polyesterified surficial layer has the capacity to retard microbes, absorb ultraviolet light, and, when confined to the surfaces of an aquatic plant body that are predictably exposed to the air, can impede water loss. It is not unreasonable to assume, therefore, that cuticle-like materials may have been produced by the last common ancestors of the embryophytes and the charophycean algae.

A land plant cuticle *sensu stricto* must be perforated to permit efficient gas exchange between the plant body and air. Among modern-day embryophytes, perforations take the form of epidermal pores or stomata that open into topologically external but spatially internalized surfaces forming chambers or labyrinthine spaces within the plant body. Although not widely appreciated, this configuration fosters very different gradients of water vapour and carbon dioxide at the plant/air interface. Since the air within a hypodermal chamber is saturated with water vapour and is lost from a small pore into a potentially moist boundary layer, a shallow water vapour diffusion gradient can be created. In contrast, since carbon dioxide is absorbed by moist cell surfaces everywhere along the surface of the chamber, a steep gradient of carbon dioxide can be established at the pore opening. In this way, the rate at which water vapour is lost to the air can be reduced relative to the rate at which carbon dioxide is gained by photosynthetic tissues (Cooke and Rand, 1980; Rand and Cooke, 1980). Clearly, the evolution of guard cells that can regulate pore diameter and thus control the rate of water vapour loss was a significant event in the history of plant life. But, even in their absence, the physics of passive and active diffusion indicates that the 'internal' surface areas of terrestrial plants are highly adaptive.

If it is reasonable to assume that the gametophyte generation of the first land plants retained some of the phyletic legacy of its ancestral charophycean-like alga, it is not unreasonable to suppose that the land plant sporophyte generation represents a life cycle innovation that evolved primarily or exclusively on land. All extant multicellular members of the Charophyta have a haplobiontic haploid life cycle in which only the gametophyte expresses multicellularity. This is a poor 'design', since a unicellular diploid phase is poorly equipped to disperse meiospores into the air. Thus, the issue of how the embryophyte sporophyte generation evolved is an important one.

Traditionally, the origin of the embryophyte sporophyte is described in terms of 'delayed zygotic meiosis', that is, the

intercalation of a multicellular diploid generation as the result of one or more mitotic cell divisions of the zygote. However, the phrase ‘delayed zygotic meiosis’, conveys little with regard to the mechanisms responsible for the evolution of the sporophyte generation of embryophytes, which could have made its evolutionary debut in a haplobiontic haploid life cycle as a result of either the inhibition of zygotic meiosis or the stimulation of zygotic mitosis. Likewise, delayed zygotic meiosis implies neither the existence of a multicellular sporophyte nor an archegonium, both of which are hallmarks of the embryophytes.

In terms of mechanisms, it must be borne in mind that a large number of genetic and physiological factors influence the onset and successful completion of meiosis and mitosis. These factors establish extremely complex and extensive networks that control the cell cycle. For example, in many eukaryotes, *cdc2/cylin B* mitosis-inducing kinase is activated when the tyrosine-14 or -15 residue in its ATP-binding region is dephosphorylated by *cdc25* phosphatase-10-15. In these organisms, *cdc2/cylin B* kinase is inhibited when the tyrosine residues are phosphorylated by Wee 1 tyrosine kinase-4-9, which, in turn, is inhibited by Nim-1 kinase (i.e. Nim1 promotes the onset of mitosis by inhibiting Wee 1; see Wu and Russell, 1993). Genetic modification of these or other kinases can alter when and where mitosis occurs. Studies also show that dividing cells can be induced to undergo mitotic cell division during, as well as after, their first meiotic cell division by either changes in the physical environment (e.g. high temperature) or genetic mutation, indicating that the ‘commitment to meiosis’ does not involve an irreversible inhibition of mitosis as previously thought (see Honigberg and Esposito, 1994). Thus, the modification of any one of a number of physical or genetic factors attending the evolution of the archegonium may have been responsible for the evolutionary origin of the embryophyte sporophyte by ‘delayed zygotic meiosis’.

As noted, ‘delayed zygotic meiosis’ *per se* does not imply the existence of an archegonium or a multicellular sporophyte. Theoretically, zygotic mitosis may result in a population of cytoplasmically disconnected diploid cells in which each cell may function as a zygote. This caveat is important in light of the fossil record, which indicates that considerable life cycle ‘experimentation’ may have occurred during the early Paleozoic when the embryophytes were becoming firmly established on land. Some of this experimentation is illustrated by the charophycean-like alga *Parka decipiens*, which ranged from the Upper Silurian to the Lower Devonian. The discoid thalli of this enigmatic alga were large (0.5 to 7.5 cm in diameter), pseudoparenchymatous, monostromatic, and attached to their substrate by a centrally located ventral holdfast-like structure (Fig. 18A, B). Scanning electron microscopy and mathematical simulations indicate that *Parka* grew by means of both anticlinal and periclinal cell divisions along the margins of its outwardly radiating branched filaments in a manner very similar to that of some modern-day species of *Coleochaete* (Niklas, 1976). Little is known about the life cycle of *Parka* other than that multicellular structures on the dorsal surface of thalli contained numerous small cells

(25–45 μm in diameter) (Niklas, 1976). These cells had sporopollenin-rich walls but lacked haplotypic markings (Fig. 18C). Nonetheless, their cell walls are reported to be similar to those of the spores of some modern-day bryophytes (Hemsley, 1990).

If an analogy is drawn between *Parka* and *Coleochaete*, as suggested by the similarities in their general morphology and mode of growth, then it is not unreasonable to suppose that *Parka* had an haplobiontic haploid life cycle. If so, then *Parka*’s multicellular structures may have developed around fertilized egg cells that divided meiotically to produce haploid cells much like *Coleochaete*. However, the presence of a large number of spore-like cells in *Parka*’s reproductive structures suggests a number of scenarios. For example, *Parka*’s zygotes may have divided meiotically first, then divided mitotically to produce a large population of cells that later developed sporopollenin containing walls (Fig. 18D). Under these circumstances, the gametophyte generation of *Parka* would have begun its existence as a dormant spore-like entity, albeit lacking haplotypic markings rather than as a zoospore as in the case of modern-day *Coleochaete*. Alternatively, the zygotes of *Parka* may have divided mitotically to produce a coterie of diploid cells that developed thick walls (also lacking haplotypic markings). These cells may have remained dormant for a time, only to divide meiotically to produce zoospores after being released from the gametophyte. In either case, the benefits of potentially rare egg fertilization events would have been amplified. Both of these scenarios are admittedly highly speculative, but the latter is advanced here simply to show that ‘delayed zygotic meiosis’ does not logically require a multicellular sporophyte.

Regardless of its evolutionary origins, the land plant sporophyte typically takes the form of an unbranched or branched cylinder in contrast to the diversity in body shape observed for the gametophyte generation of charophycean algae and embryophytes, which can be either axial (cylindrical) or thalloid (dorsiventral) in symmetry. Arguably, the ‘unity of type’ characterizing the land plant sporophyte reflects the unity of the ‘condition of existence’ and the reproductive role played by this ‘intercalated’ generation (i.e. to produce, elevate, and disperse spores into the air above the substrate), whereas the diversity in charophycean or embryophyte gametophyte symmetry may reflect greater latitude in aquatic or semi-aquatic habitats in terms of the successful fertilization of eggs by motile sperm and the survival of zygotes. In this sense, the land plant sporophyte generation may be viewed as an adaptation to the aerial environment, whereas its corresponding gametophyte generation retains the ‘aquatic’ legacy of its algal ancestors.

Under any circumstances, the cylindrical geometry achieved by the apical and intercalary meristematic growth of the land plant sporophyte confers numerous physiological, mechanical, and reproductive advantages. As noted, a cylinder can continue to elongate without sustaining a reduction in surface area with respect to volume. Likewise, a vertical cylinder incurs little or no bending moment and is one of the few geometries that can grow in length without sustaining a significant reduction in its ability to harvest

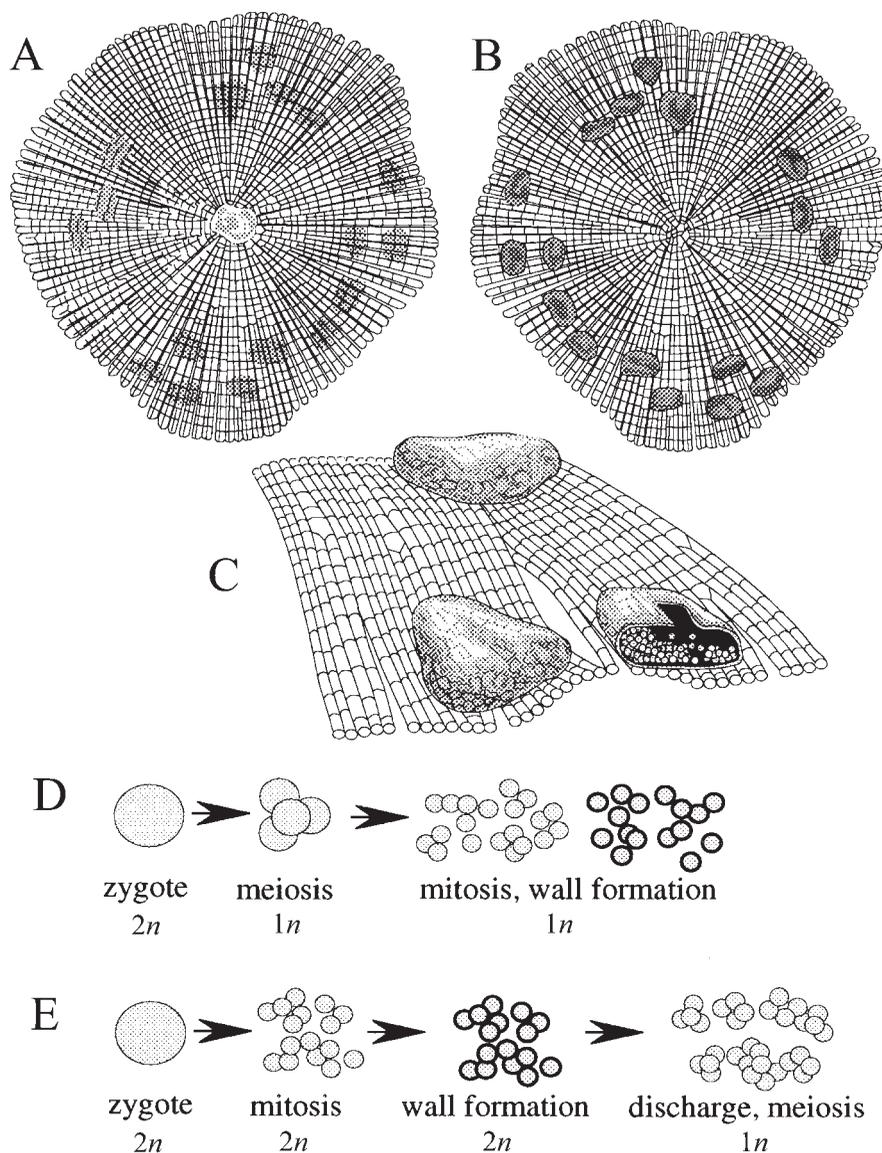


FIG. 18. Morphology (A–C) and hypothetical reproductive biology (D and E) of the charophycean-like fossil alga *Parka decipiens*. A and B, Ventral and dorsal views of a *Parka* thallus. A, Ventral view of discoid pseudoparenchymatous thallus with a holdfast. B, Dorsal view of thallus showing reproductive structures containing cells with thick walls containing sporopollenin and lacking haplotypic markings. C, Dorsal view of a portion of thallus showing three reproductive structures one of which is cut open to show thick-walled cells. D and E, Two scenarios for the formation of cells with thick walls (indicated by bold outlines) lacking haplotypic markings. D, Within reproductive structures, zygotes divide meiotically and then mitotically to produce a number of haploid cells that subsequently form cell walls. E, Within reproductive structures, zygotes divide mitotically to produce a population of diploid cells with cell walls; diploid cells subsequently divide meiotically after their release from reproductive structures. In this scenario, ‘delayed zygotic meiosis’ does not establish a multicellular sporophyte generation. See text for further details (Fig. A–C adopted from Niklas, 1976).

light (Niklas and Kerchner, 1984). And, because the axial and torsional second moments of area of a circular cross section are equivalent regardless of how the cross section is bisected (Wainwright *et al.*, 1976; Niklas, 1992), a terete cylinder is especially well suited to resist externally applied bending or twisting forces. Finally, in moderate to high winds, a cylinder generates a thicker boundary layer and a concomitant reduction in the rate of water loss than either a sphere or flat plate (‘leaf-like’ shape) of comparable diameter or length (Nobel, 1983; Niklas, 1994). Since a cylindrical morphology is simultaneously physiologically

and mechanically adroit and can elongate and elevate sporangia above ground where spores can be released into the wind for long-distance dispersal, it is not surprising that this geometry serves as the basic building block for the most ancient land plant sporophytes.

By the same token, the methods by which land plant sporophytes organize their growth confer obvious benefits. An intercalary meristem can contribute to growth in body length (and thus elevate the plant apex further above ground) even after its apical meristem begins to differentiate into a sporangium (Fig. 19A). Among modern-day

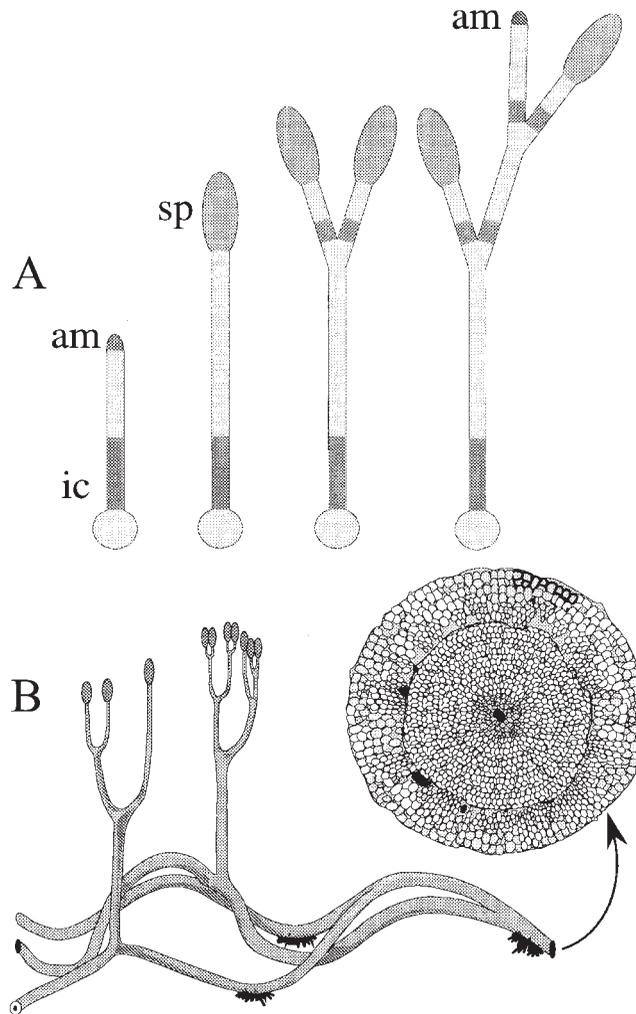


FIG. 19. Hypothetical transformation of a monosporangiate sporophyte with a 'closed and determinate' ontogeny into a branched polysporangiate sporophyte with an 'open and indeterminate' ontogeny (A) similar to an early vascular land plant (B). A, A series starting with a uniaxial sporophyte elongating by means of intercalary (ic) and apical meristems. Intercalary meristem elevates sporangium after apical meristem differentiates into a sporangium (sp). Bisporangiate sporophyte results from bifurcation of apical meristem before sporangium formation and continues to grow in length by means of intercalary meristems. Polysporangiate plant with indeterminate growth in body size resulting from apical meristematic growth. B, Reconstruction of branched sporophyte of *Aglaophyton (Rhynia) major* bearing terminal sporangia on aerial axes with centrally located strands of conducting tissues (after Edwards, 1986).

bryophytes, this mode of growth is generally associated with a 'closed and determinate' ontogeny that results in a morphologically simple and short-lived sporophyte with a final 'adult' size and limited reproductive output. Among the most ancient vascular land plants, larger sporophytes with greater reproductive potential were achieved by the bifurcation of apical meristems to produce a population of apical growing points some of which could reiterate the bifurcation process, whereas others differentiated into sporangia. This 'open and indeterminate' ontogeny, which was passed on to each of the major tracheophyte lineages, can indefinitely magnify the benefits of potentially rare fertilization events among terrestrial plants whose sperm require water for survival (Fig. 19A). Manifold meristems also open the door for the specialization of body parts for mechanical support, photosynthesis and anchorage (the stem, leaf and root embryophyte organization).

An indefinite increase in the land plant body plan, however, requires tissues specialized for the bulk transport of nutrients, since aerial portions became progressively distanced from the substrate that supplies water and other nutrients. Tissues specialized for mechanical support are also required to cope with the bending moments generated in the plant body by gravity and wind pressure. The vascular tissues of tracheophytes are clear adaptations for rapid nutrient transport. They also provide avenues for hormonal transport, which can be used to control vegetative and reproductive growth patterns. Among the most ancient vascular land plants, vascular tissues were centrally located in cylindrical axes where they were least likely to experience high tensile, compression or torsional shear stresses, but where they were least effective in stiffening or strengthening organs (Fig. 19B). For these plants, the epidermis probably served as a high strength 'skin' that

rigidified the plant body when it was placed in tension by the hydrostatically inflatable inner core of thin walled parenchymatous tissue it enveloped (see Niklas and Paolillo, 1997).

Since the stiffness of any hydrostatic device is a function of its water content, and at best is low in comparison to its weight per unit volume, land plants relying on hydrostatic mechanical support are typically confined to hydric habitats and have a comparatively short stature. In contrast, tissues with lignified and thick cell walls are mechanically less dependent on water content and are far stiffer and stronger. When placed at or near the perimeter of the cross section of a vertical or cantilevered stem, such a tissue can resist elastic deformation and provide protection against herbivory or microbial attack. In this location, however, lignified and thick walled tissues also attenuate the intensity of sunlight, especially in the blue and red wavelengths used by photosynthetic tissues. Indeed, in the absence of secondary growth, the ideal location for structural and photosynthetic tissues is much the same, which may, in part, explain why the functional analogues to the foliar leaf and the mechanically supportive stem evolved early in land plant history (Chaloner and Sheerin, 1979; Taylor and Taylor, 1993).

HOMEOTIC GENES AND CLOSING REMARKS

Currently, we know comparatively little about the evolution of the various plant body plans. The early history of the various algal lineages remains obscure, in part because well preserved fossils of the vegetative structure of these organisms are infrequently found, and because the assignment of these fossils to specific lineages becomes highly problematic in light of the extensive morphological and anatomical convergent evolution evident among modern-day species. Algal Lägerstätten are known, but these are too stratigraphically scattered to build a sufficiently detailed picture of algal evolution to adduce plant body plan transformations even in comparatively well known lineages (see Knoll, 1995 and references therein). Likewise, cladistic phylogenetic hypotheses for algae are still in their formative stages of development and those that are currently available are often based wholly or partly on molecular or cytological features whose preservation in the fossil record is unlikely and which by themselves shed little light on morphological evolution (Martin, Somerville and Loiseaux, 1992; Schlegel, 1994; Graham and Wilcox, 2000). Detailed developmental studies for many important taxa are currently lacking yet badly needed, especially since this avenue of research holds particular promise in shedding light on the mechanisms responsible for body plan transformations among modern-day algal species. With all the emphasis placed on embryophyte growth and development, we are still remarkably ignorant about the developmental details of many important non-vascular and relictual vascular taxa, which arguably are more reflective of the early stages in the evolution of the land plant body plans than those of the more derived seed plants. For all these reasons, any treatment of the various plant bodies and their evolution

is unavoidably and undeniably highly speculative and idiosyncratic. Yet, this topic is pivotal to our understanding of the history of life, since all but a very few ecosystems are dependent on photoautotrophs as primary producers and since much of animal evolution cannot be understood without at least passing reference to plant biology.

Clearly, the role of homeotic genes in the evolution of body plans needs to be explored. These genes encode for transcription factors similar to bacterial repressor proteins and thus appear to be taxonomically ubiquitous and very ancient (Sommer *et al.*, 1990; Davies and Schwarz-Sommer, 1994; Gerhart and Kirschner, 1997; Knoll and Carroll, 1999). In arthropods, vertebrates and flowering plants, these transcription factors can serve as molecular markers for the position of cells along an organ or body axis (Carroll, 1995; Akam, 1998*a,b*), and, in both plants and animals, the activation of individual homeotic genes at different positions in meristematic or embryonic regions is associated with patterns of differentiation that are maintained throughout ontogeny. Since the differential expression of homeotic genes is correlated with the adoption of different developmental fates in different regions of the plant or animal body axis by cells that appear otherwise equivalent and since mutations at these loci shunt the development of meristematic or embryonic cell clusters from normal to typically dysfunctional developmental fates, homeotic genes shared by otherwise diverse organisms may shed light on why some body plans are highly conservative and why others are not.

It is now clear that the family of homeotic genes diversified early in the radiation of the metazoa and possibly metaphytes. Within some lineages, these genes can be used to establish phylogenetic relationships among different groups. Thus, patterns of expression of homeotic genes can provide markers to relate body plan variants, as is the case for the head segmentation patterns of chelicerate and mandibulate arthropods. Comparisons of gene expression between more distantly related taxa are far more difficult to interpret, however, since we currently neither understand how homeotic gene regulation influences the pathways available for cell and tissue differentiation nor how changes in the roles of these genes occurred even among closely related groups (see Wray and Abouheif, 1998).

Homeotic genes will undoubtedly continue to figure prominently in speculation about the evolution of animal and plant body plans. However, homology at the molecular level of DNA base-pair sequences does not imply that the developmental or structural features they influence are homologous. Genes for transcription factors are undoubtedly very ancient, as attested to by the fact that homeotic gene analogues occur in bacteria, and these factors have undoubtedly been shuttled within eukaryotic genomes for hundreds of millions of years. Importantly, no gene acts in isolation. Each is part of a variety of complex genetic and developmental cascades such that the product a gene encodes may perform very differently depending on the molecular, physiological, or developmental context. Indeed, organisms differ largely because of combinatorial variations of genes rather than as a result of an unlimited capacity to

endlessly add new ones to those that came before (e.g. Theissen, Kim and Saedler, 1996). Homeotic genes are undoubtedly important to our understanding of the evolution of plant and animal body plans, but their ability to potentially define or transform body plans is expressed within a complex genetic and epigenetic milieu of which we are currently incompletely aware.

What is clear is that different body plans in very different plant lineages are capable of extensive morphological and anatomical homoplasy and that this convergence on similar structural solutions using different ways of achieving organized growth reflects the nearly identical functional requirements for plant growth and survival regardless of phyletic legacy. In turn, these structural solutions are explicable, or at least quantifiable in terms of the relationship between the surface area of the plant body through which plants acquire nutrients and energy, and the living body volume (= symplast), which dictates metabolic demand and the capacity for nutrient utilization. The open and indeterminate ontogeny, which characterizes all but the unicellular (uni-nucleate) plant body plan, permits the amplification of body surface area with respect to volume as overall size increases. The capacity to exchange mass and energy between the plant body and its external environment is thus largely unconfined developmentally such that very different body plans can converge on the same or very similar morphologies and anatomies.

The advent of multicellularity characterized by cytoplasmic (symplastic) continuity permitted the establishment of different physiological domains within the plant body that could serve as a basis for cell, tissue and organ differentiation. Although perhaps not overly emphasized in this review, some of the features characterizing the multicellular plant body, such as cellular differentiation, plasmodesmata-like structures, control mechanisms for the orientation of cell cleavage, and cellular differentiation, are evident among extant and presumably very ancient cyanobacteria, indicating that the rudiments of multicellularity existed well before the advent of the eukaryotic condition (see Maddock, 1994; Gober and Marques, 1995). This draws attention to the tantalizing possibility that multicellularity among the various plant lineages evolved in part as the result of lateral gene transfer occurring during or shortly after primary endosymbiotic events in the very distant past. The curious absence of multicellularity in plant lineages believed to have evolved as a result of secondary endosymbiotic events presumably involving unicellular eukaryotes (e.g. euglenoids and cryptomonads) is consistent with this conjecture. The view taken here is that the genetic and epigenetic phenomena influencing cell cleavage, differentiation and morphogenesis are buried deep in evolutionary time and that the expression of these phenomena among contemporary prokaryotes will provide fertile grounds for future research in the evolution of plant body plans.

Finally, little has been said here regarding the charophyte-embryophyte 'connection', in large part because the evolutionary relationships between these two plant lineages are extensively and well reviewed elsewhere (see Graham, 1993), although in a taxonomic format that rarely addresses

the adaptive relationship between form and function (see Kenrick and Crane, 1997). Among the various plant lineages, the embryophytes, particularly the sporophyte generation of tracheophytes, are the most conservative in terms of their body plan, being largely confined to the parenchymatous multicellular variant predicated on a cylindrical morphology fabricated by means of intercalary and apical meristematic regions. In contrast, the charophytes manifest a variety of body plans that achieve their organized growth differently, perhaps reflecting the many 'degrees of freedom' permitted in an aquatic habitat in contrast to the adaptive versatility of the parenchymatous tissue fabric of embryophytes, which clearly permitted the full exploitation of the terrestrial landscape. The evolutionary derivation of the embryophyte body plan from one (or more) of the multicellular variants seen among extant charophyte algae remains conjectural, but it cannot escape attention that the latter includes filamentous and parenchymatous tissue fabrics constructed from diffuse, intercalary, or apical meristematic regions, nor that axial (cylindrical) and dorsiventral body symmetries mimicking those of bryophyte gametophytes are represented among modern-day charophyte species. This suggests that the ancestral algal plexus from which extant charophytes and embryophytes evolved and subsequently diverged from contained a developmentally rich repertoire. If so, then a strictly 'linear' scenario for the transformation of a charophyte-like body plan to the embryophyte body plan, while parsimonious, may be misleading.

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