

# ON THE EVOLUTION OF COMPLEX LIFE CYCLES IN PLANTS: A REVIEW AND AN ECOLOGICAL PERSPECTIVE<sup>1</sup>

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## ABSTRACT

Complex life cycles and alternation of generations are characteristic of many plants, a diploid sporophyte typically alternating with a haploid gametophyte. The prominence of each generation varies greatly among taxa. Purely phylogenetic or morphogenetic explanations of these differences are unsatisfying, as are those based solely on population fitness. Existing adaptational explanations seek selective advantages in diploidy and in sexual reproduction, but these explanations leave much to be explained—i.e., the existence of asexuality and of haploid organisms. Much of the existing variation in life cycles can be explained by selection on reproductive rates to meet the ecological problems of dispersal, colonization, niche preemption and exploitation, and mate competition. Placement of complex life cycles of plants in an ecological framework will, I hope, encourage specific studies exploring possible adaptive aspects and limitations on the evolution of life cycles in plants with different life histories.

A prominent feature of most textbook introductions to various major groups of plants is the description of reputedly typical life cycles of selected forms. Attention is focused on the alternation of haploid and diploid phases (or generations) of the cycle, the relative “dominance” of one phase or another, the timing of meiosis and fertilization, the occurrence of asexual reproduction, and which phase is the dispersal or resting stage. Most of the available published literature on plant life cycles is directed toward elucidating developmental, morphological or physiological and, finally, phylogenetic patterns. A rather small number of papers (see below) addresses the possible selective advantages or disadvantages of reproducing sexually or asexually, of being haploid or diploid, or of having more than one morphological generation. Here, I use the word *generation* to refer to both the alternating diploid and haploid entities and to any intervening, asexually produced, progenies. So far as I can determine, virtually nothing has been written on the ecology (aside from genetics) of complex life cycles in plants. Several botanical reviewers have claimed that all of the ideas summarized here regarding the ecology and evolution of plant life cycles are “old hat.” They should be, perhaps, but no one has shown me evidence that they are. This review is presented in hopes of stimulating discussion and research that include an ecological perspective.

I begin by summarizing some apparently classic life cycles of selected plants (broadly defined to include fungi, but excluding prokaryotes). There follows a review of available hypotheses attempting to explain the evolution of such cycles in plants and a critique of these hypotheses. Finally, I review some of the liter-

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ature on complex life cycles in animals in hopes of unearthing some possible approaches useful in interpreting plant life cycles and close by posing some ecological suggestions about plant life cycles that, I think, provide a useful beginning in understanding the evolution of these cycles.

#### LIFE CYCLE PATTERNS IN PLANTS

Plant life cycles are many and varied and there are numerous and diverse ways of classifying them (e.g., Chapman & Chapman, 1961; Lindenmayer, 1964; Scott & Ingold, 1955). Although in most major taxa some species have become entirely asexual, it is generally considered that all plants exhibit a fundamental alternation of generations. The basic pattern is a  $2N$  sporophyte (producing spores) alternating with a  $1N$  gametophyte (producing gametes).

Relative dominance of one generation over another can be considered in terms of conspicuousness of "body size" and/or in terms of duration. Because an inconspicuous dormant zygote may persist longer than its ecologically active parent(s), I prefer to use body size as an index of dominance. However, if asexually produced progeny are viewed as part of an extended "evolutionary individual" (Janzen, 1977, 1979a), body size and duration may converge in meaning. [Janzen was challenged by Addicott (1979) specifically for aphids (which are obviously not plants, but the idea is relevant!), in which parthenogenesis does not necessitate invariant offspring identical to the parent. While the point is made that genetic identity of asexual parents and offspring cannot be assumed, this does not alter the general idea that asexually produced young are more similar than those produced sexually and the clone is still the unit of selection (Janzen, 1979b).] Some multicellular organisms have potential for large increases in body size (and may also expand by asexual means); other multicellular organisms and unicellular ones may "substitute" asexual multiplication for an increase in body size and prolong the duration of one or both generations by this means.

I am concerned in this paper mainly with plants in which both sporophyte and gametophyte are active, functioning (i.e., not resting or dormant) organisms at appropriate times of the life cycle. Therefore, algae (such as *Fucus* and most diatoms) that exist primarily as diploids, with meiosis during gametogenesis (as is the case in most animals, except certain Foraminifera that alternate haploid/diploid generations (Grell, 1967; Ghiselin, 1974), are of interest mostly as contrasts. Slime molds, as well as some yeasts and other fungi (Raper, 1966b), exist mainly as diploids. Meiosis produces  $1N$  spores that germinate into swimming cells; these fuse to form a zygote that eventually grows (sometimes several together) into a new organism. The seed plants are diploid-dominant also; the  $1N$  gametophytes are tiny and wholly dependent on the sporophyte. In an ecological sense, although not morphologically or genetically, the seed plants may be considered to lack alternation of generations.

On the other hand, certain plants exist primarily as haploids, with meiosis upon germination of the  $2N$  zygote. Many freshwater green algae, typified by *Chlamydomonas*, have a  $2N$  zygote, often dormant, that meiotically forms vegetative  $1N$  cells, which divide mitotically to form either gametes or more vegetative cells. Among the fungi, most phycomycetes are basically haploid (Burnett, 1976). Two hyphae fuse to form a  $2N$  zygospore, which is a multinucleate resistant



phase. This undergoes meiosis to form spores that grow into the macroscopically visible mold.

Between these two extremes are many plants that function actively in two (usually) phases. The gametophyte is more conspicuous in some, the sporophyte in others, and in a few the generations are similar in conspicuousness.

Most bryophytes are conspicuous as persistent, 1N gametophytes. These form gametes by mitosis, the sperm swims to the egg, which lies in a protective jacket of cells, and the resultant zygote grows into a 2N sporophyte, still attached to the (female) parent gametophyte. The sporophyte, generally less conspicuous than the gametophyte, appears seasonally and produces 1N spores meiotically; these disperse and grow into new gametophytes. The gametophyte is considered to be the independent generation and is longer lived. Vegetative propagation, especially by gametophytes, is apparently common.

The 2N sporophyte of the lower vascular plants is more apparent than the tiny, often subterranean, gametophytes. The sporophyte meiotically produces spores that grow into gametophytes that produce gametes by mitosis. Although in some fern populations (Farrar, 1967) no sporophyte is known to exist, the fern sporophyte typically develops on a small 1N gametophyte, which may eventually disappear. Spores have half the chromosome complement of the sporophyte, but high levels of polyploidy permit, in some species, recombination between duplicated, unlinked loci, which produces varied gametes on a gametophyte from a single spore (Chapman et al., 1979; Lloyd, 1974b).

A third pattern of alternation, occurring in several green, brown, and red algae, involves free-living, multicellular haploid and diploid phases. The phases may be similar in external morphology (isomorphic, as in *Ulva*) or dissimilar (heteromorphic, as in "*Derbesia*" and others) (Bold & Wynne, 1978; Fritsch, 1942; Wynne, 1969; Kung-Chu, 1959; Dube, 1967). Each phase may reproduce asexually, forming more individuals of the same phase. The isomorphic forms may grow side by side on the same rocks, thus apparently occupying the same spatial environment; this seems to be the case for *Ulva*. *Ectocarpus* (a brown alga) is intriguing in that it is reportedly isomorphic in warm seas but appears to have a reduced haploid phase in cold waters (Bell & Woodcock, 1968). *Prasiola stipitata* forms spores in the upper intertidal zone and gametes in the lower zone; curiously, the spores are diploid and the lower portion of the "gametophyte" is also while its upper portion is haploid (Friedmann, 1959).

Red algae have varied and complex life histories that are not well understood (P. S. Dixon, 1973). Some consist of three generations: a haploid phase and two diploid phases, one of which is small and attached to the haploid, followed by a free-living 2N phase that is isomorphic or heteromorphic with the haploid, depending on the species. In others the haploid phase grows on the free diploid, and in still others the free-living diploid seems to be lost altogether, meiotic products from the attached diploids growing directly into a new haploid. Many more variants are likely to occur (e.g., West & Norris, 1966).

The aquatic mold *Allomyces*, unusual among the phycomycetes (Darlington, 1958), has isomorphic generations, the haploid phase or gametophyte producing male and female gametes by mitosis on the same filament. These merge to form a 2N phase that can resist desiccation and may produce more 2N individuals by mitosis or 1N individuals by meiosis.



Ascomycetes and basidiomycetes are unusual; they can exist in two different conditions not defined by chromosome number. The  $2N$  zygote is borne on its parent and is highly ephemeral, immediately forming  $1N$  spores by meiosis. The spores disperse and eventually grow into a new  $1N$  generation of hyphae. These fungi resemble most phycomycetes in that the diploid phase is much reduced. However, two hyphae (of different mating strains) can join together to form binucleate cells; this dikaryotic condition may persist for some time. Nuclear status is technically haploid although the organism possesses a double complement of chromosomes. Thus these fungi exist primarily in a  $1N$  or in a  $1N + 1N$  phase.

In summary: some plants produce gametes meiotically; the  $1N$  generation is invariably much less conspicuous than the  $2N$  generation. Other plants produce gametes mitotically. In some of these the  $2N$  generation is inconspicuous. But in others the diploid generation has a period of growth and becomes "apparent" (sensu Feeny, 1976). The apparency of two generations presumably has an adaptive basis, but just how a functional alternation of generations could be adaptive seems to be largely unexplored. Existing adaptational hypotheses applied to plant life cycles address primarily the evolution of diploidy and the evolution of sex. Furthermore, several nonadaptational hypotheses can be found, although Allsop (1966) suggested that "in general terms, the entire life cycle may represent an evolutionary adaptation . . .," and Bonner (1965) noted that both phases of the life cycle are undoubtedly adaptive.

#### EXISTING HYPOTHESES SPECIFIC TO PLANT LIFE CYCLES

##### (A) PHYLOGENETIC AND MORPHOGENETIC EXPLANATIONS

A general trend in the plant kingdom from dominance of the gametophyte to dominance of the sporophyte is often noted (e.g., Chamberlain, 1935; Fuller, 1955; Bonner, 1965). Even taking into account the branching, nonlinear pathways of plant phylogeny, such trends can only be descriptive. The phylogenetic ideas regarding alternation of generations reviewed by Wahl (1965) and Roe (1975) are largely of historic interest. In any case, explanations for the phylogenetic preeminence of, for instance, the angiosperms, are legion (Mulcahy, 1979; Cavalier-Smith, 1978).

Morphogenetic "explanations" invoke genetic and developmental events as causes of morphological conditions (e.g., Bell, 1979). It is sometimes suggested that the function of sexuality in algae is the formation of resistant stages. Although sex may indeed precede the resistant phase and in some species the two events may have *become* tightly linked, it is absurd to suppose that sexuality evolved so that resistant phases could be formed. Asexual modes of reproduction could equally lead to a resistant, dormant stage and do in some organisms (Blackman, 1974; Drebes, 1977). Haploid and diploid conditions are associated with gametophyte and sporophyte conditions, respectively, and this relationship is sometimes taken to be causal (i.e., ploidy controls phenotype), rather than descriptive and associative, according to Bold & Wynne (1978). Nevertheless, haploid sporophytes are known in some algae (*Ulva*, *Cladophora*, Laminariales) and both haploid and diploid gametophytes occur in *Ectocarpus*. Furthermore, bryophyte



and fern gametophytes and sporophytes can apparently exist in either ploidy level (Watson, 1971; Bold, 1967; Bell & Woodcock, 1968) and bryophyte sporophytes can be induced by wounding the gametophyte (Crum, 1973). However, the reproductive potential of such individuals is not indicated (but see Hoxmark, 1975, on *Ulva*); if they cannot reproduce at a rate competitive with their normal conferees, they must be regarded as ecological "sports." However true such mechanistic links might be, they ultimately cannot provide an evolutionary, adaptational, explanation for life-cycle variations.

#### (B) EXPLANATIONS DEPENDENT ON POPULATION FITNESS

"The evolutionary significance of diploidy to higher organisms resides, therefore, in the greater flexibility which it confers on their populations" (Stebbins, 1960: 213; and see Bonner, 1965). Of necessity, the "selective advantage of evolutionary flexibility" in haploid organisms must then be less (Stebbins, 1960). In this sense, evolutionary flexibility is a population characteristic, not an individual one, and thus an indirect consequence of normal Darwinian selection. Such flexibility may indeed exist, however, but may be best interpreted as a population consequence of individual selection as discussed in (C) below.

Similarly, the flushing of the deleterious genes from a population is a consequence of the expression of a haploid generation. From the point of view of an individual, the loss of some proportion of its genes may seem unnecessarily detrimental, since many of them are deleterious only in the haploid state; if zygote formation followed meiosis with little delay, those "deleterious" genes might even have beneficial effects in the diploid. Furthermore, only genes that are "turned on" in a haploid phase could be affected (Bonner, 1965).

A model for the evolution of sexual reproduction as a repair mechanism (Walker, 1978) possesses some attractive features. However, it depends explicitly on population, not individual, fitness (Williams & Walker, 1978) and is not considered further here (but see Dougherty, 1955; Bernstein et al., 1981).

#### (C) ADAPTATIONAL EXPLANATIONS

(1) *Diploidy as an adaptation.*—Generally, diploidy is thought to buffer an individual, in some circumstances at least, from the effects of deleterious mutants and to offer the possibility of heterosis (e.g., Crow & Kimura, 1965; Stebbins, 1960; Raper, 1966a; Raper & Flexer, 1970; refs. in Levin & Funderburg, 1979; Rehfeldt & Lester, 1969). Sexual reproduction by diploids also releases genetic variation immediately; this is not true for haploids, which typically must first make a diploid entity as a means of releasing variation (Ghiselin, 1974). Adams & Hansche (1974) consider that these may be secondary effects that arose through time rather than initial advantages of diploidy. In addition, alternative alleles may switch on or off to deal with a fluctuating environment. Diploidy should therefore prevail in particularly variable, unpredictable, or difficult circumstances. These possibilities often seem to provide a standard "explanation" for the evolution of diploid dominance. They necessitate the assumption that all other patterns must occur in relatively benign environments in which the putatively delicate haploid is not at risk. Lewis & Wolpert (1979) suggest that diploids have spare copies of



all genes, which can be modified for new functions and thus easily expand the genome at a much faster rate than haploids, where an original gene must be duplicated before it can be modified. Diploids can therefore more easily evolve the complex gene control mechanisms that characterize complex multicellular organisms. (Lewis and Wolpert further explain sex as an adaptation that preserves diploidy.) Although diploidy may be a preadaptation that permits (through buffering, etc.) the evolution of complex developmental sequences and complicated organisms, this obviously cannot explain the origin of diploidy (Stebbins, 1960; Cavalier-Smith, 1978).

Cavalier-Smith (1978) made the fascinating suggestion that diploidy in eukaryote life cycles may have evolved when rapid growth is less important or larger cell size and lower growth rates are actually advantageous (see Willson & Burley, in press). The volume of  $2N$  nuclei and cells is commonly twice that of haploids and rates of cell division and development are strongly inversely correlated with DNA content (though other factors can be involved also, Bennett, 1974; Price & Bachmann, 1976; Price et al., 1973). Bennett (1971, 1972, 1974) argued explicitly that short generation times require low nuclear DNA content and that high DNA content necessitates a longer generation time. This idea is likely to be involved with haploid/diploid life cycles (Cavalier-Smith, 1978). Furthermore,  $1N$  cells have higher surface/volume ratios, and enzymes active at the cell surfaces may also contribute to faster haploid growth (Weiss et al., 1975; Adams & Hansche, 1974). Such differences in growth and development are only sometimes apparent when conspecific cells of different ploidy ( $\geq 2N$ ) are compared (e.g., D'Amato, 1977; Willson & Burley, in press). However, because there is often variation among conspecific individuals in the amount of DNA, we should not yet reject the notion that alternating generations differing in ploidy may have different growth potential. Evans's (1968) interpretation of Durrant's (1962) experiment on the induction by fertilizer treatments of heritable changes in *Linum* is tantalizing: plants with intermediate amounts of nuclear DNA have very plastic growth responses; when grown in conditions inducing large size, the offspring have increased DNA content. Jones (1975) cited evidence from a grass (*Lolium*) that the frequency of accessory or B chromosomes increased significantly with increasing plant density and competition. Intraspecific, clinal variation in DNA content may occur also in *Picea sitchensis* (Burley, 1965; Mitsche, 1971; Moir & Fox, 1977; Mergen & Thielges, 1967; Sparrow et al., 1972; but see Dhillon et al., 1978) and some other conifers (Mergen & Thielges, 1967; Mitsche, 1968). Geographic variation in frequencies of B chromosomes is not uncommon (e.g., Sparrow et al., 1952; Bosemark et al., 1956a, 1956b; Fröst, 1957; Müntzing, 1957; Teoh & Jones, 1978). It would be interesting to learn if this kind of variability occurs in species with alternating generations.

Although B chromosomes apparently carry no major genes themselves, they can affect gene activity and rates of crossing-over on regular chromosomes (Rees, 1972; Jones, 1975, 1976). Altogether, as little as 10% of the eukaryotic genome may exist as unique-sequence DNA that codes for RNA and functional polypeptides (Jones, 1976); much DNA exists as repetitive sequences (more than  $10^6$  repeated sequences in some cases (Lewin, 1974) and up to 95% of total nuclear DNA content (Flavell et al., 1974) in B chromosomes or other conditions, some



of which are genetically inactive and even non-Mendelian. The preferential transmission of B chromosomes to functional gamete nuclei in both male and female of several angiosperms (Stebbins, 1971) deserves special attention. Although Stebbins (1966) interpreted certain changes in DNA content in terms of possible genetic consequences (e.g., sequential gene action on long chromosomes, reduction of chromosome number to reduce genetic variability, and stabilizing new genotypes in polyploids), it seems reasonable to consider nongenetic consequences of DNA content as well (see also Hinegardner, 1976; Bennett, 1971, 1972).

(2) *Sex as an adaptation to environmental uncertainty*.—Having a sexual generation may be adaptive to changing conditions (Ghiselin, 1974; Williams, 1975; Emlen, 1973). These authors argue that sex is adaptive when production of a varied progeny enhances reproductive success of the parent. Thus, sexual reproduction should occur where or when the environment is unpredictable. Because sex involves recombination, it often results in a more varied array of offspring, which increases the likelihood that some will be able to successfully cope with environmental changes. Without disputing the possible advantages of sex, which have often been debated, I would like to provisionally accept the notion that sex is adaptive in physically and especially biologically varying environments (Williams, 1975; Levin, 1975; Ghiselin, 1974; Treisman, 1976; Glesener & Tilman, 1978; Warner, 1978; Calow, 1978b; Hamilton, 1980; and others).

The timing of sex is also commonly interpreted in terms of environmental change, imminent or just past. Considering spores to represent sex and recombination, Bonner (1958) says that "the spores, when they emerge, have previously undergone recombination (or do so upon germination)." Bonner, Williams, and Ghiselin all provide examples of asexual generations repeating through benign seasons and a sexual generation intervening when the environment is soon to change or has just done so.

#### CRITIQUE OF EXISTING ADAPTATIONAL HYPOTHESES

First, the supposed delicacy of 1N entities (relative to those of 2N) is somewhat debatable. In bryophytes and green algae the haploid gametophyte is the persistent form; in some algae, 1N and 2N generations have similar gross morphology and may live side by side. Furthermore, haploid cells in vitro are sometimes less sensitive to stresses (putative mutagens, fungicides) than expected (Metzger-Freed, 1974; Henriques et al., 1977; Upshall et al., 1977). And a growing literature on diploidization and gene silencing in polyploids (e.g., Ferris & Whitt, 1977a, 1977b; Garcia-Olmeda et al., 1978) and differential chromosome elimination (Collins et al., 1978) suggests that buffering functions may not necessarily be central. Conversely, the arbitrary suppression of one X chromosome, possibly as a means of dosage compensation (Lyon, 1974; Monk & Kathuria, 1977; Lucchesi, 1978; Epstein et al., 1978), in female mammals suggests that partial haploidy may not be deleterious. Certain parasitic protozoans reduce their chromosome number by means of zygotic meiosis and restore the 2N quantity of DNA just in time for mitotic gametogenesis (Canning & Morgan, 1975). And haploid males occur regularly in certain groups of rotifers, arachnids, and insects (White,



1973). In fact, the tendency of many organisms, both plant and animal, to protect the (2N) zygote in some way could be interpreted to signal its great vulnerability to assorted environmental hazards (just as resistance of the spore is often interpreted). Even in diploid organisms there is variation in amounts of DNA present (Price, 1976; Cavalier-Smith, 1978), even among conspecific individuals (Jones, 1975).

Second, there is increasing evidence (from insects, Rasch et al., 1977; bryophytes, Longton, 1976; ferns, Klekowski & Baker, 1966; *Ulva*, Hoxmark & Nordby, 1974) that DNA synthesis in originally haploid individuals restores the 2N quantity of DNA (but, of course, not heterozygosity and perhaps not reproductive performance; Hoxmark, 1975).

Third, fitness of isogenic haploid and diploid forms of *Saccharomyces* grown in competition with each other were similar when dosages of enzymes active in the cell interior differed with ploidy. But 1N cells out-competed 2N cells when dosages of surface-active enzymes differed. These experiments suggest no advantage to diploidy per se under these experimental conditions (Adams & Hansche, 1974; Weiss et al., 1975). Cavalier-Smith (1978) argues that haploidy may indeed be favored where rapid growth and development are advantageous. Taken together, such evidence suggests that the perils of haploidy may be minor or, at least, could be avoided in many ways. (It may still be true, of course, that a switch from diploidy to haploidy could be difficult once diploidy is entrenched in a group, because many biological features may then come to depend on the diploid conditions and would be disrupted.)

The timing of reproduction must depend on divers factors differing among populations. The production of variability actually occurs twice in a life cycle characterized by alternation of generations, once when meiosis occurs and again when gametes join to form a zygote (see below). For a sexual generation, mate-finding may be a critical problem to overcome, and physiological changes and special mating structures may entail costs in energy or nutrients (Daly, 1978; Calow, 1978b; Muenchow, 1978; Solbrig, 1979). Biological factors including population density and sex ratio are also potentially relevant. A constellation of factors related to the probability of juvenile survival and/or to costs and risks encountered by reproducing adults must be considered with respect to the timing of any phase of reproduction: the availability of suitable (biotic or abiotic) dispersal agents and of "safe sites" (Harper, 1977) for establishment, the risks of "predation" (or herbivory) on young plants of the next generation, the intensity of competition from ecologically similar species (e.g., Schaffer, 1977), the time required and the resources available for maturation (Boyce, 1979), and so on. Predation risks may be particularly relevant to uni- (or few-) cellular phases subject to capture by size-selective predators. Fungal infection of sori may select against a prolonged season of spore production in *Chondrus crispus* (Prince & Kingsbury, 1973). Therefore, aside from a broad correlation of sex with certain kinds of environmental uncertainty, I conclude that existing explanations for the timing of alternation of generations are probably inadequate.

Furthermore, while existing hypotheses aim at explaining the existence of a sexual or diploid portion of the life cycle, they do not suggest why a free-living haploid phase is sometimes retained. Nor have I found many suggestions in the



botanical literature that help explain the relative body sizes of gametophyte and sporophyte or which phase is the dispersing phase, the resistant phase, or the growing multiplicative stages. To begin answering such questions, I present a selective survey of literature, largely zoological, that bears on the ecology and evolution of complex life cycles. From this I hope to glean suggestions that foster the understanding of complex life cycles in plants.

### COMPLEX LIFE CYCLES IN ANIMALS

Animal life cycles can be broadly classified into two categories. Simple life cycles are characterized by direct development from young to adult. Simple cycles are found among most vertebrates (except many amphibians and some fishes), anthozoan coelenterates, some free-living flatworms and some annelids, hemimetabolous insects, and a few other invertebrates scattered in many taxa. This is not to say that the niches of young and old individuals might not differ greatly, but the transition is relatively gradual. By analogy, seed plants could be viewed as possessing a simple life cycle, since the gametophytic phase has no life of its own. In contrast, complex life cycles exhibit two (or more) distinct phases with very different ecologies and very different morphologies and behavior. There are two kinds: (1) Every surviving individual passes through each phase. Reproduction usually is performed by one phase of the cycle. Typical examples are the anuran tadpole that metamorphoses into a frog or toad and caterpillars that are transformed into butterflies. Complex life cycles of this sort are characteristic of most major animal phyla except chordates, in which only protochordates, some fishes, and amphibians conform to this pattern. (2) Other animals with complex life cycles, such as aphids, rotifers, and cladocerans, and many parasites, are more similar to the "lower" plants: several asexual generations may be followed by one in which sexual reproduction occurs. Each physiologically defined individual usually exists in only one phase, although sometimes females may switch from asexual to sexual reproduction and back. In any event, reproduction occurs in both phases rather than in one.

Istock's (1967) seminal paper focused on the ecology of complex life cycles, particularly of the first sort, noting that distinct phases of the life cycle are largely independent of each other in terms of morphological and behavioral adaptations but are ecologically dependent in that each furnishes individuals to the other part of the cycle. He argued that changes in adaptation of the different phases of the life cycle are not likely to proceed at equal rates and, as a consequence, one phase will sooner or later be unable to supply the other phase with enough individuals, and the population will gradually spiral to extinction. In short, complex life cycles would seem to be evolutionarily unstable. Istock's dilemma lies in the conflict between ecological rationalization and the palpable fact that complex life cycles are extremely common. Considering just the insects, as many as 85% of the species may have complex life cycles (E. McLeod, pers. comm.), indicating that extensive adaptive radiation may accompany life-cycle complexity—which hardly suggests the brink of extinction.

Slade & Wassersug (1975) later showed that instability is not a necessary feature of complex life cycles. Gill's (1978) study of the red-spotted newt (*No-*



*tophthalmus viridescens*) indicates that adult reproductive failure is common and a small number of adults can produce enough young to maintain many local populations. This suggests that the ecological dependence of population levels at different phases of the life cycle may be loose and that a good deal of variation in recruitment rates can be tolerated. Furthermore, larval and adult phases can not be evolutionarily independent—the life history pattern is a unit (Strathmann, 1974). Ewing (1977) describes a genetic model for the stable maintenance of cyclic haploid and diploid phases.

Indeed, Slade and Wassersug argue that complex life cycles are adaptive, noting (as had Istock) that seasonal (or other frequent) changes in the environment provide temporary changes in resource abundance upon which creatures may capitalize. Fluctuating environments and/or a colonizing or opportunistic life history (e.g., Lewontin, 1965; Hutchinson, 1951) may select for high reproductive capacity of individual parents and possibly also a life-cycle stage with the capacity to exploit ephemeral resources as a means of increasing parental reproductive output. Furthermore, Slade and Wassersug suggest that a second (or third) life-cycle stage may open new means of dispersal—as a means of reaching new sites of ephemerally available resources. Bryant (1969) also argued for the adaptiveness of complex life cycles in insects, especially in spatially heterogeneous environments.

Some evidence is available to support the idea that complex life cycles are adaptive. I divide a series of examples into two “models” for descriptive purposes and convenience (see also Wilbur, 1980).

#### THE DISPERSAL MODEL

In effect, adult salamanders are viewed as a dispersal phase of the life cycle, metamorphosis from larva to adult often occurring in larvae that are less successful than other individuals in exploiting the aquatic larval habitat (Wilbur & Collins, 1973) or that happen to live in ephemeral ponds (Rose & Armentrout, 1976). Larval phases seem to be prolonged in areas where the terrestrial environment is unsuitable for adults and when the aquatic environment is free from major predators (Sprules, 1974; Bruce, 1979). Sexual maturity may be reached by individuals with larval morphology. This condition is not necessarily associated with an early achievement of reproductive status and, in fact, may be associated with delayed reproduction (Gould, 1977). Delay can have far-reaching consequences because the age of first reproduction may be a critical factor in determining the rate at which a genotype contributes genes to future generations (Cole, 1954; Lewontin, 1965). Goin et al. (1968) note that salamanders inhabiting permanent waters generally have higher DNA content (and slower growth) than those adapted to exploit temporary pools, a suggestion in line with that of Cavalier-Smith (1978).

The red-spotted newt is unusual in having a tripartite life cycle: the aquatic larva transforms into a terrestrial “eft,” which eventually returns to water as an adult. Efts are lacking in populations occupying ponds that are suitable year-round. Efts grow and mature more slowly than fully aquatic individuals (Healy, 1973), so the advantage of having an eft stage must outweigh this potential dis-



advantage. Healy (1975) suggests it may reduce the chance of capture by certain pond predators. Perhaps even more importantly, the eft may be a specific adaptation for the colonization of ponds, particularly beaver ponds, that are geologically temporary—lasting for less time than it takes for a population of newts to saturate it (Gill, 1978).

Some salamanders have lost the free-living larval stage and may fall under the next model. Others have lost the adult, dispersing phase, and the "larva" becomes reproductive. I do not know of any salamanders in which the larval stage is the main disperser, but larvae are often the principal dispersal phase of many aquatic invertebrates, such as tunicates (Ghiselin, 1974), and a number of animal parasites, such as trematodes. Holometabolous insects clearly fit the dispersal model as well, adults commonly being the dispersal phase.

#### THE RESOURCE-EXPLOITATION MODEL

In contrast to salamanders, reproduction by larval anurans is unknown, and only the tadpole stage is ever deleted from the life cycle. Anuran larvae are highly specialized for feeding and rapid growth, and tadpoles are often found in ephemeral ponds very rich in nutrients (Wassersug, 1974, 1975). The larval stage may be lost by species for which no suitable larval environments are available or if the risks of predation outweigh the advantages of rapid growth (Wilbur, 1980). Similarly, planktonic larval stages of invertebrates are often suppressed if potential larval habitats fluctuate wildly (Calow, 1978a). In this model, one phase of the life cycle is viewed as a means of capitalizing opportunistically on rich resources. It may also have been a means of reducing competition between juveniles and adults. In some cases, such as sessile marine invertebrates, asexual multiplication coloniality may be associated with preemption of space (Jackson, 1977).

In some respects rotifers are similar to anurans but with the addition of asexual multiplication of individuals. Most rotifers reproduce rapidly and asexually through the summer (Birky & Gilbert, 1971) when resources are high and, eventually, a sexual generation (King & Snell, 1977) produces overwintering eggs. Rapid asexual reproduction is considered to be an adaptation of opportunistic species that annually recolonize the ponds and lakes in which they live (Birky & Gilbert, 1971). It is likely that different asexual clones have differing capacities for converting food into offspring, thus exhibiting different rates of increase—with the result that the potential for producing sexual young at the end of the season must differ greatly among genetic lineages (see e.g., Snell, 1979, for rotifers; Shick et al., 1979, for sea anemones; Turkington et al., 1979, and Turkington & Harper, 1979, for seed plants).

A complex life cycle of an aphid is described in some detail in the next three paragraphs, because more ecologically relevant details seem to be available. This case seems to combine elements of both dispersal and resource exploitation (see also Bryant, 1969, on holometabolous insects).

*Myzus persicae*, an aphid, reproduces parthenogenetically through the summer, first on *Prunus* spp. hosts, later and for a longer time on a wide diversity of herbaceous host plants (Newton et al., 1953; van Emden et al., 1969). Reproduction is asexual, although some recombination occurs and offspring are variable



(Addicott, 1979), though perhaps less so than if they were produced sexually. At the end of summer when populations are presumably high, a sexual phase occurs and overwintering, sexually produced, eggs are deposited on *Prunus* hosts. The sexual phase is unusual in that females produce males and winged females. These females return to *Prunus* hosts and asexually produce several wingless daughters that mate with the males. Winged aphids produce fewer and smaller young than wingless morphs (A. F. G. Dixon, 1973) and mature earlier (Davies & Landis, 1951). The sexual grandmothers thus obtain multiple granddaughters, centrally located on the winter host (Gould, 1977).

Changes in the host plant may be advantageous in summer because the nutrient content of *Prunus* leaves drops dramatically (A. F. G. Dixon, 1973) and average aphid fecundity, which is very sensitive to soluble nitrogen availability (van Emden et al., 1969), drops to about  $1/22$  of what it was (Davies & Landis, 1951; van Emden et al., 1969). This suggests that, like tadpoles, the asexual summer aphids on herbaceous host may be a way of exploiting an ephemeral flush of resources. Aphid mortality is high when dispersing to new hosts, but the ephemerality of resources on any one host necessitates dispersal (Kennedy & Stroyan, 1959). A return to *Prunus* in the fall may be less related to the senescence of herbage (since aphids seem to like senescing tissue) than to an early and reliable availability of *Prunus* leafbuds in the spring (B. McPherson, pers. comm.), despite the possibly higher predation there (van Emden et al., 1969; A. F. G. Dixon, 1973). Some populations, in regions with no unfavorable season or no *Prunus*, have entirely asexual reproduction (Broadbent & Heathcote, 1955; Blackman, 1974). Overwintering eggs do not ultimately require sexuality for their production inasmuch as two families closely related to aphids produce resistant eggs asexually (Blackman, 1974). The timing of the sexual phase of the cycle may be related both to high population density at the end of a season of intensive multiplication of individuals and to environmental uncertainty.

Reproduction by parthenogenetic aphids is rapid, not as a result of individual fecundity but of phenomenally rapid maturation (Kennedy & Stroyan, 1959; Gould, 1977). The generations are "telescoped," and each grandmother may contain within her body the embryos for the next two generations of aphid. Gould considers the acceleration of maturation and the rapid turnover of generations to be adaptive in reaching and exploiting ephemeral, patchy resources—it is a way of generating large numbers of dispersing young (e.g., Lewontin, 1965; Cole, 1954) to colonize and exploit new patches (see also Ehrendorfer, 1965). Further advantages of asexual reproduction, commonly discussed for plants, may lie in the possibility of establishment of a single propagule (Ehrendorfer, 1965; Allard, 1965; Baker, 1965, 1967; Lloyd, 1974a, 1974b; Holbrook-Walker & Lloyd, 1973; Singh & Roy, 1977) after dispersal has been accomplished—thus enhancing the likelihood of success in dispersal.

This selective survey of complex life cycles and reproductive life histories of animals suggests several ecological principles of possible relevance to plant life cycles. (1) In some instances, all parthenogenetically produced daughters of a single female can be viewed as extensions of that female, in terms of exploiting the environment. (2) Asexual reproduction (in various forms) and high rates of



reproduction may be adaptations for colonization and for outcompeting other colonists for available resources. At least one phase of a complex life cycle may be viewed as a means of exploiting ephemeral resources. (3) A dispersal phase is associated with fluctuating environments as a means of escaping to a more reliable patch or as a colonization strategy, enhancing the survival of the offspring. Whether dispersal or exploitation is more important will depend on the population in question. Clearly, several of these principles could apply to any one kind of organism.

These ecological ideas, taken largely from studies of animal life cycles, and others discussed below, are surely germane to plants. In the next section some of these applications are developed.

### TOWARD AN ECOLOGY OF PLANT LIFE CYCLES

For ease of presentation I have segregated this discussion under headings but do not mean to imply that these pieces are unrelated. Nevertheless, it is possible to argue that various life-history features have *gradually* become associated; that is, they are not intrinsically linked (Drew, 1955).

### SEXUAL AND ASEXUAL GENERATIONS

The environmental uncertainty hypothesis seems to be the best available hypothesis for the presence of a sexual generation. What then remains is to explain the persistence of an asexual phase in complex life cycles and the timing of each phase. A series of asexual generations probably can be viewed best as a process of self-multiplication. The successful asexual parent, which is well adapted to its circumstances, produces equally well-adapted young rather than variants, some of which would be adaptively inferior in an unvarying environment. To the extent that some form of recombination may be possible in the asexual phase (as in endomeiosis or automixis in certain insects, White, 1973), or if mutations occur, the progeny may not be completely invariant. (Recombinations among genes of a single individual may be considered sexual processes, but I prefer, in the present context, to label as sexual those reproductive processes that can involve two individuals.)

Asexual reproduction (here used to exclude vegetative propagation by rhizomes, stolons, etc.) can often occur more rapidly and less expensively than sexual (Calow et al., 1979; Congdon et al., 1978; Walker, 1979; Whittier, 1970), although this may not always be true (Lamb & Willey, 1979). Coulter (1914), Scott & Ingold (1955), and Ghiselin (1974) hint that the life cycle might be timed around the period favorable for "vegetative" growth. It is likely, even, that the timing of sex is governed more by the advantages of asexual reproduction during seasons favorable for multiplication than by proximity of sexual reproduction to environmental uncertainty—in short, the advantages of asexual reproduction in suitable seasons could delay sexual reproduction until the end of that period.

The costs of mating will also influence the timing of sex. There is evidence for certain algal species that *increased* light or nutrients may induce sexuality directly or indirectly, which hints at resource limitation of sexual activity for



those species (Coleman, 1962; Sager & Granick, 1954). Added carbon sources facilitate production of apogamous sporophytes (not from a fertilized egg) in *Pteridium* ferns (Whittier, 1964; Bell, 1979); could similar effects be found for sexually produced sporophytes? Most experiments in induction of sexual activity in plants have been concerned with proximate triggers rather than nutritive condition of the plants that might determine receptivity to those stimuli. We need to know why particular stimuli (such as N depletion) are appropriate signals to certain species and how the receptivity varies with condition of the organism.

Asexual reproduction is probably adaptive in colonizing and in exploiting ephemeral, patchy resources. Burnett (1976: 550) briefly mentions this possibility of fungi, as does Robinson (1967: 29) for parasitic basidiomycetes. The life histories of many freshwater green algae would seem to conform to this pattern.

#### HAPLOID AND DIPLOID GENERATIONS

By analogy with animals possessing complex life cycles, it seems likely that gametophytes and sporophytes (as well as asexual and sexual generations) tend to occupy different environments. White (1973: 751) says that alternation of generations *presupposes* two alternative ecological niches. How the niches for plants might differ seems less evident than for animals, in which habitats and/or resources are distinct, but that obviously does not mean that niche differences do not exist. Spatial differentiation of gametophytes and sporophytes is not evident in *Ulva*, bryophytes, or some ferns, but some seasonal or physiological segregation would be possible, as may be true for *Ectocarpus* (Chapman & Chapman, 1973), *Cladophora* (Fritsch, 1935), *Batrachospermum/Audoninella*, and others (Bold & Wynne, 1978: 486). Lubchenco & Cubit (1980) relate heteromorphic phases to herbivory pressures, upright stages accomplishing high rates of growth and reproduction in the absence of predation and crustose stages surviving periods of heavy grazing. However, such morphological differences are not always associated with differences in ploidy and can sometimes be induced by the physical environment (e.g., *Saccorhiza polyscides*, Norton, 1969).

The red alga *Chondrus crispus* is relatively well studied; it apparently exhibits extraordinary variability in seasonal patterns of reproduction by each isomorphic generation, both regionally and between habitats (Prince & Kingsbury, 1973; Mathieson & Burns, 1975; Chen & McLachlan, 1972; Taylor & Chen, 1973; Mathieson & Prince, 1973; Hehre & Mathieson, 1970). Such variability could provide an excellent system for exploring possible adaptive values of seasonal patterns. Unlike the kelps and *Postelsia*, which depend on seasonally opened patches for settlement (see below), *Chondrus* spores settle in quiet microsites protected by other plants (Prince & Kingsbury, 1973) and maturation may be slow (Chen & McLachlan, 1972; Mathieson & Burns, 1975).

Strong seasonal patterns of reproduction (e.g., Longton & Greene, 1969; Tallis, 1959) and marked seasonal differences in sporophyte production (e.g., Greene, 1960; Jones, 1947; Arnell, 1905) are known among many groups of closely related mosses, for example, although the ecological basis for such patterns seems to be unstudied. Ecological comparisons of such species might well elucidate the adaptive basis of seasonal differences in reproductive schedules and the timing of each generation.



If niche differences between gametophyte and sporophyte indeed exist, we can begin to search for possible advantages accruing from the exploitation of different environments. The "models" derived from animals suggest that two likely factors are resource exploitation and dispersal. However, the question still remains as to why it is often entities of different ploidy levels that serve different functions and why, instead, plants with complex life cycles have not evolved, for instance, a  $2N$  "larva" to exploit certain conditions. In fact, it seems that a few algae do exhibit heteromorphic juvenile forms that transform, without a reproductive event, into the adult of that generation (Fritsch, 1942; Allsop, 1966). But the existence of such forms only changes the question to why are they not more common. In short, the possible existence of niche differences does not explain why those niches are often exploited by a haploid and a diploid generation. (In some cases of heteromorphic life cycles, ploidy levels are not regularly associated with a particular morph; Lubchenco & Cubit, 1980.)

Haploids can commonly grow and multiply (asexually) faster than diploids (Cavalier-Smith, 1978; Adams & Hansche, 1974; Weiss et al., 1975), owing to their smaller volume and relatively greater surface area. Therefore they may be suitable entities whenever rapid multiplication is advantageous. If food or space resources are limiting, selection may favor rapid multiplication as a means of preempting the resource and outcompeting lineages that multiply more slowly (see also Cohen, 1977). Such a tactic can be advantageous only up to the point where sibling competition outweighs nonsibling competition. Two factors may alleviate sibling competition: (1) Siblings disperse before sibling competition becomes too intense. (2) Siblings can sequester resources and keep them from other sibling groups. Then if sibling competition becomes intense, death of some siblings might release enough resources that the success of remaining siblings is compensatingly enhanced. Rapid multiplication may also be advantageous if the season suitable for multiplication is short but selection favors production of large progenies. Many offspring improve the success of dispersal (see below). Finally, if there is competition for the privilege of participating in fertilization, there is selection for being well represented in the gamete pool at the time that fertilization occurs. If haploids can replicate faster than diploids (either for intrinsic reasons such as cell size or because the environment they exploit permits them to do so), then a haploid generation may be an evolutionary means of generating numerous gametes to increase the probability that the diploid of one generation will be the parent of many diploids in the next generation. In this case loss of genes that are deleterious in the haploid state may be more than compensated, particularly if release from sibling competition among the haploids allows the remainder to multiply still more.

Diploidy is generally considered to have evolved after haploidy, and therefore it might be thought that the only thing to be explained is diploidy itself. As we have seen, there exist several suggestions about the origin and maintenance of diploidy; the other side of the question is, why retain the haploid? Furthermore, even if haploidy were the primitive condition, it does not follow that extant organisms were originally haploid and secondarily evolved a diploid generation. Diploidy is well established in most major algal groups and goes hand-in-hand with the condition of eukaryosis (Raper & Flexer, 1970). What needs to be ex-



plained *here* is not so much the existence of the diploid, but rather the balance between haploid and diploid phases. Differences in potential growth rates of the two phases seem a likely basis for differential niche exploitation. To the extent that cells modify their DNA content and nuclear size (Jones, 1975; Cavalier-Smith, 1978), such differences may be either decreased or increased.

The peculiar institutions of prolonged dikaryosis or heterokaryosis found among the fungi attracts special consideration (e.g., Raper, 1966b). In a number of species the dikaryon or heterokaryon grows vegetatively, independent of the haploid phase. In many smuts and some yeasts, the dikaryon is not only well developed and long lasting, it has quite different nutritional requirements and/or host specificity than the haploid phase (Raper, 1966b). Thus niche differences are clear. However, the functional significance (in terms of evolutionary adaptation) of dikaryosis compared to true diploidy seems unclear, and Raper (1971) calls them "functional substitutes." Furthermore, many asexual fungi recombine somatically in the dikaryotic phase, forming haploid recombinant products similar to those of sexual reproduction (Raper, 1966b). However, although the genes of dikaryons may usually be expressed as if they were truly diploid and the genes of one nucleus may often compensate for a deficiency in the other (e.g., Medina, 1977), such complementation is not always observed (e.g., Fincham et al., 1979; Lewis & Vakeria, 1977; Medina, 1977; Senathirajah & Lewis, 1975; Roberts, 1964; Pontecorvo, 1963). Darlington (1958) suggests that dikaryosis reduces the costs of reproduction by permitting one fully developed mycelium to fertilize another; the invading nucleus divides upon entry and its descendants move along the receiving mycelium, so that the whole mycelium becomes dikaryotic from a single fertilization event. Furthermore, the genetic character of the dikaryotic mycelium, at least in Ascomycetes, can adjust directly to environmental changes (often created by its own activities; Burnett, 1976) by differentially changing the relative numbers of each type of nucleus (Darlington, 1958). Selection may favor small size of nuclei (and thus 1N) to facilitate division and movement along the hypha (Cavalier-Smith, 1978).

In addition, there is some evidence from several basidiomycetes that dikaryons can grow faster (in the lab) than their uninucleate forms (e.g., Croft & Simchen, 1965; Simchen & Jinks, 1964). A rapidly expanding, dikaryotic mycelium might be advantageous in reaching and preempting such substrates as lignin (B. Benner, pers. comm.). Many basidiomycetes, including these, feed on lignin (Webster, 1970), which persists in the forest soil for a long time and is relatively common (Robinson, 1967). The sugar and cellulose substrates commonly used by other fungi are more ephemeral than lignin, and these fungi have contrasting adaptations that emphasize rapid dispersal and waiting for the resource to become available (Robinson, 1967). However, how general is the occurrence of faster growth rates, and whether (and how) the dikaryotic condition *itself* is the factor responsible, seem to be unknown.

An intriguing but unexplored possibility is that of conflict between the nuclei of heterokaryons. G. C. Williams reminds me that the interests of the nuclei from two different sources may differ, and it is conceivable that one nucleus competes with the other for resources. A winning nucleus could replicate faster and come to dominate the hypha and perhaps future reproduction in that heterokaryote.



Mechanisms such as synchrony of nuclear division would keep such "cheating" from occurring; but the control of synchrony and its adaptive function need to be elucidated. The persistence of dikaryotic states in the face of such potentially destabilizing tendencies deserves attention.

#### DISPERSAL

Either the haploid or the diploid phase, or both, may disperse. The 1N stage disperses in many lower plants, although it is the 2N phase in *Fucus* and both in some green algae. The diploid phase is dispersed in seed plants and in animals. (For purposes of this essay, I am excluding pollen dispersal for seed plants because that is not directly involved with establishment of a new individual.) I suspect that dispersal occurs whenever in the cycle it is possible and expedient. Expediency is controlled by a variety of factors, including the availability of proper currents or other vectors that aid dispersal and the presence of suitable safe sites for colonization (Armstrong, 1976). Typically, the dispersal state occupies more continuous habitat than the establisher, whose habitat is often patchy.

A good example may be provided by the kelps (S. E. Franson, pers. comm.), which release their spores in winter, when storms create new openings for establishment in the rocky subtidal zone (Dayton, 1975). The tiny gametophytes can settle in these sites, claiming them for the far larger sporophytes that grow, initially, on the parent and later take its place. The annual brown alga *Postelsia palmaeformis* also depends on continual re-creation of new habitat openings for survival (Paine, 1979). The first sporophytes germinate in February and March, when colonization sites are most available, and grow rapidly, partly as an escape from grazing by chitons (Paine, 1979). Spores are produced through the summer and usually settle near the parent. Short-distance dispersal coupled with an unusual ability of this alga to clear substrate and make it available for its later siblings is apparently a means for this alga to preempt space and thus to maintain the colony through time (Dayton, 1973).

Dispersal is typically a high-risk tactic for colonization—a shotgun search for safe sites (see Hamilton & May, 1977; Strathmann, 1974); because mortality of dispersing propagules is likely to be high, large numbers of such units are commonly produced (e.g., Kennedy, 1975; Ehrendorfer, 1965). The greater the advantage of large numbers, the smaller each propagule may be (to some limit) (see e.g., Smith & Fretwell, 1974). This means that dispersal should usually be preceded by a multiplicative phase, particularly one of high fecundity. In some cases, as in many animal parasites, fecundity is enhanced by asexual reproduction of "larvae," as an adaptation to the uncertainties of dispersal (Kennedy, 1975). Larval reproduction exploits resources not directly available to the parent and thus effectively increases the parental fecundity. The life histories and dispersal ecologies of many green algae and mosses with unusual distributions of habitats may exhibit especially strong selection for high fecundity [e.g., algae saprophytic on nitrogenous wastes or oozing tree sap, or those colonizing the backs of turtles (Prescott, 1968) or sloths, and mosses that specialize to areas burned by hot, slow fires (Southron, 1976) or to the dung of herbivores or carnivores (Crum, 1973)].



However, if these species use sit-and-wait tactics, with long dormancies of the dispersing propagules, the effects on fecundity should be smaller. The astronomical differences in spore production of different mosses—differing by as much as  $8 \times 10^7$  (Crum, 1973)—are surely related to the probability of juvenile survival and availability of safe sites. Dispersing propagules tend to be small, although spore size in closely related ferns is related to ploidy levels (Walker, 1979), and apogamous fern spores tend to be fewer and larger than those of allied sexual species (Bell, 1979).

#### RELATIVE DOMINANCE OF THE GENERATIONS

For purposes of discussion, I deal first with multicellular plants that have the evolutionary potential for significant increases in body size of the physiologically defined individual. Typically we find a contrast in body size of the larger parent and the smaller, dispersing offspring. Dispersal units tend to be small, not only because offspring are usually initially smaller than their parent, but for several ecological reasons.

First, to the extent that the success of dispersal is enhanced by production of numerous propagules, the parental resources available for reproduction should be divided as finely as possible, consistent with other constraints on propagule size. Second, they may be carried about more easily by currents or other vectors. Third, perhaps they may have more potentially suitable safe sites in which to land and become established.

Fecundity is often broadly correlated with body size, larger bodies producing more young than smaller ones of the same species; this is true for many invertebrates, fishes, amphibians, reptiles, and even mammals, as well as many seed plants (e.g., Werner, 1975; Leverich & Levin, 1979; Harper & White, 1974). Not only can large bodies often capture more nutrients, perhaps having a competitive edge over other plants (Grime, 1977), they can also structurally carry more offspring (e.g., Calow, 1978b). *Fucus vesiculosus*, for example, has a minimum size for reproduction; if that minimum is not reached in time for the sexual season, sexual reproduction is delayed until the following season. Large plants can bear over 3200 receptacles for egg development. Juvenile mortality is very high, due to washing away and mollusc grazing; adults may live as much as 4–5 years in sheltered locations (Knight & Parke, 1950). Selection for production of numerous offspring is presumably strong, the reproductive season is long, and body size clearly affects “litter” size.

In addition, the very small gametophyte of some leptosporangiate ferns may have eliminated production of multiple zygotes and multiple sporophytes (Buchholz, 1922), potentially reducing both total output and the means available to a female of choosing among potential fathers for her offspring.

So we might predict that large body size (“dominance”) may be characteristic of the life-cycle generation subject to the greater intensity of selection for high fecundity (and capturing resources). This could be the generation that precedes the dispersal phase and/or the one whose offspring begin exploitation and preemption of an ephemeral environmental patch. At the same time, there is likely to be a cost associated with growth (e.g., in terms of increased risk of mortality; Sarukhán, 1977), which is one source of limitation on the achievement of large body



size. Other limits on achieving a large body size exist (Littler & Littler, 1980) and include grazing pressure (Lubchenco & Cubit, 1980).

Other reproductive functions may also affect body size. The height of the sporophyte in mosses and the lower vascular plants often increases greatly at maturity (Crum, 1973) and may increase dispersal potential of the airborne spores (Coulter, 1914). On the other hand, gametophytes may be most successful if small, thereby increasing access to water for gamete movement (Coulter, 1914). Given that the sporophyte is borne by the gametophyte, rather than vice versa, perhaps for the above reasons, in mosses another factor may be involved. The moss sporophyte is supported and often nourished by the gametophyte (Thomas et al., 1978; Bell & Woodcock, 1968; Crum, 1973; but compare Bold, 1940). Physiological dependence of sporophyte on gametophyte suggests that bryophytes may often have difficulty in getting enough "food." Even though many sporophytes are independent in terms of carbon supply (Bold, 1940), much nutrition is apparently garnered by gametophyte leaves (Watson, 1971; Tamm, 1964; Clymo, 1963) and gametophyte growth is seemingly correlated with moisture availability (Pitkin, 1975; Tallis, 1959). A conspicuous gametophyte is probably a means of feeding a growing sporophyte; a striking reduction of gametophyte size in mosses, such as *Ephemerum* (Crum, 1973), and some ferns (Lloyd, 1974a) may indicate that nutrient capture is less critical than claiming a site for settlement. Finally, the risk of damage by herbivores may vary with size, and change in size is one evolutionary means of reducing such risks.

For unicellular plants (and others with strict size limitations on physiological individuals), the fecundity and nutrient capture arguments may be germane from the viewpoint of evolutionary individuals. Even though body size of physiological individuals remains small, high fecundity and resource acquisition may be achieved through asexual multiplication (especially of haploids?). A limit may be placed on the extent of such multiplication if local sibling competition reduces the reproductive ability of each individual.

Body size and fecundity also have potential effects on the generation of variable offspring through sexual reproduction. If meiosis follows fertilization without intervening cell division, as happens in many algae (Round, 1973; Fritsch, 1945), only two possible recombinations can be realized (Svedelius, 1929). The more cells are dividing meiotically (up to a point), the closer the theoretical maximum number of variants can be approached (see also Ghiselin, 1974: 72; Burnett, 1976: 550). This argument was also presented for red algae by Searles (1980). Thus, physiological individuals producing large litters and evolutionary individuals that achieve the same fecundity in different ways both generate variable progenies. For species with both sporophyte and gametophyte generations, variability is produced at two points in the cycle (neglecting somatic mutations and recombinations), when meiosis produces segregant combinations and when those join in new combinations to form a zygote (Ghiselin, 1974).

### CONCLUSION

The interpretation of plant life cycles as ecological "strategies" remains unsatisfactorily general and incomplete for many reasons. I have suggested that complex life cycles may be adaptive in dispersal and colonization, in competitive



interactions and resource preemption, in competition for mating privileges, and in increasing fecundity to increase the likelihood of success in the first three endeavors. By calling attention to some likely kinds of interpretations, I hope to encourage both tests of these ideas and the generation of new and more specific ecological hypotheses relevant to complex life cycles in plants. The incredible array of life cycle variants seems bound to be linked to an equally fascinating variety of ecological conditions—an array perhaps unmatched in animals.

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