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Title: Evolutionary and Ecological Interactions Affecting Seaweeds

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The term "interaction" in evolutionary biology and ecology describes the relationships among variables in two classes of causal models. In the first, "interaction" refers to the influence of a single putatively causal variable on a variable of interest. In the second class of models, the term applies when a third variable mediates the relationship between two variables in the first class of models. The development of multi-factor causal models in evolutionary biology and ecology represents a stage in the construction of theory that usually follows from complexities discovered in single-factor analyses. In this thesis, I present three cases that illustrate how results of simple single-factor models in the population genetics and community ecology of seaweeds may be affected by incorporation of a second causal factor.

In Chapter II, we consider how the effect of natural selection on genetic variability in seaweeds and other plants may be mediated by life history variation. Many seaweeds have haplodiplontic life histories in which haploid and diploid stages alternate. Our theoretical analysis and review of the electrophoretic literature show

that the level of genetic polymorphism in haplodiplonts is not necessarily reduced relative to that in diploids. In Chapter III, I take an experimental approach to understanding how herbivory may mediate the effect of desiccation on the upper intertidal limit of a red alga, *Iridaea cornucopiae*. *Iridaea* appears to be grazer-limited in dry, but grazer-dependent in moist environments, suggesting that a third factor may mediate the interaction of desiccation and herbivory. Finally, in Chapter IV, we consider research strategies for studying how the outcome of competitive interactions is affected by seaweed traits. Some of the problems that arise in applying simple models of competition to plants suggest the need for theory that explicitly incorporates plant traits in two- (or more) factor models of interspecific competition. In particular, we note that unique traits of seaweeds require development of new approaches to understanding competition.

Single-factor causal models represent an indispensable stage in the development of evolutionary and ecological theory. Properly conceived theoretical and empirical studies focus attention on the assumptions under which such models will hold and suggest lines of inquiry that ultimately lead to the integration of additional causal factors in conceptual models of natural processes. Identifying the circumstances under which simple models will suffice remains one of the most important challenges of evolutionary and ecological scholarship.

Evolutionary and Ecological Interactions Affecting Seaweeds

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Typed by Annette M. Olson

In memory of Marilyn Potts Guin

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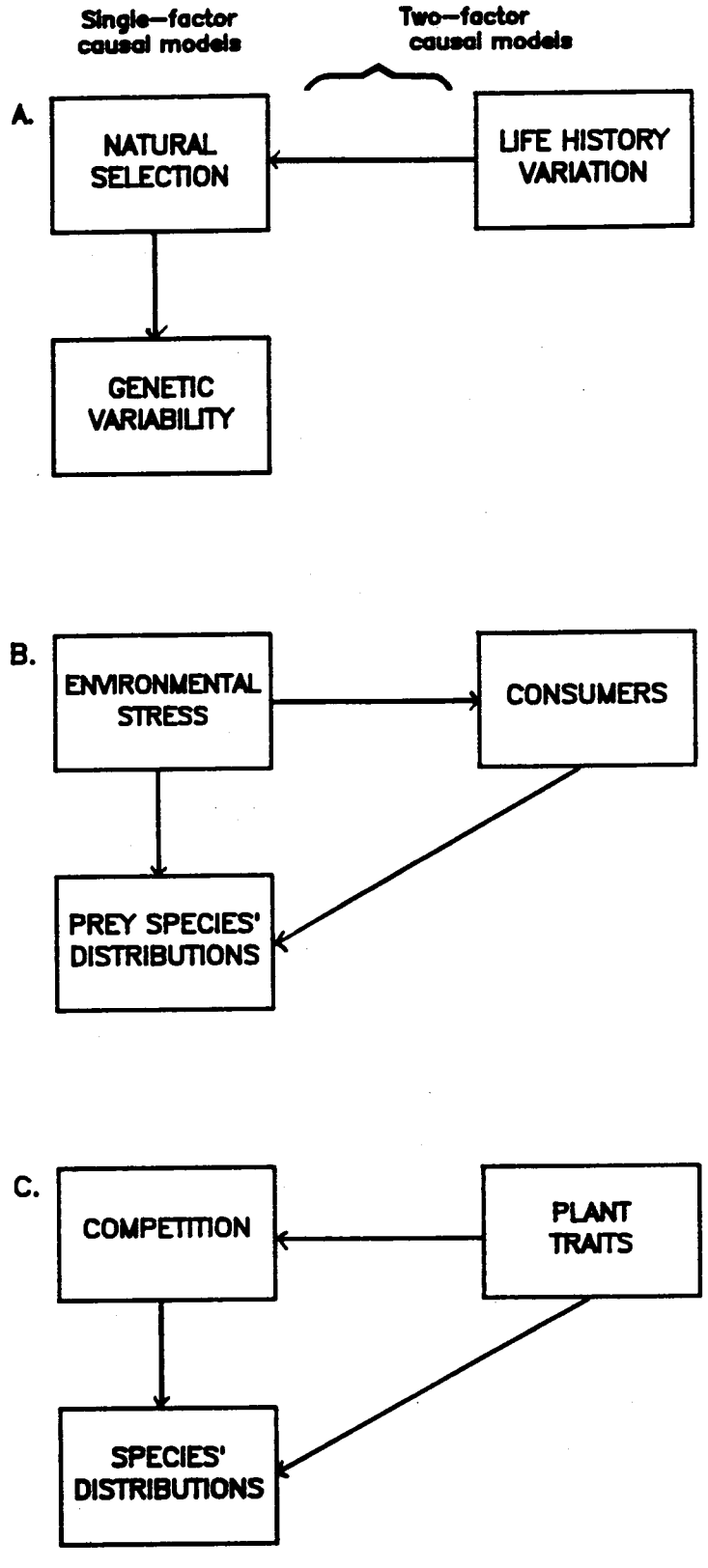
Chapter I

INTRODUCTION

The term "interaction" in evolutionary biology and ecology refers to the relationships among variables in causal models. There are two main ways in which the term is used. The first use is the common-sense definition of "interaction" as the influence of one evolutionary or ecological factor on a second object, process, or class of objects or processes. It is relevant to a class of models (Fig. I.1) that relate the quantity or rate of a dependent variable to a single putative independent variable (although the influence may be reciprocal). The shape of the function describing that relationship may be linear or non-linear. Non-linear relationships may display thresholds, attenuation, and unimodal or cyclical effects. The presence of a non-linear relationship between variables in a single-factor model suggests that constituent or extrinsic variables may mediate the interaction between the two variables in the first class of models. This is the second definition of "interaction"--the dependence of a relationship between two variables on the level of a third variable (Fig. I.1). In two-factor analyses of variance, the presence of this type of relationship is reflected in a significant two-way interaction term. The development of two- (and more) factor causal models in evolutionary biology and ecology represents a stage

Figure. I.1. Single- and two-factor causal models for evolutionary and ecological interactions affecting seaweeds.

Figure I.1.


Single–factor causal models
Two–factor causal models
A.
NATURAL SELECTION
LIFE HISTORY VARIATION
GENETIC VARIABILITY
B.
ENVIRONMENTAL STRESS
CONSUMERS
PREY SPECIES' DISTRIBUTIONS
C.
COMPETITION
PLANT TRAITS
SPECIES' DISTRIBUTIONS

in the construction of theory that usually follows from complexities discovered in single-factor analyses.

In this thesis, I present three cases that illustrate how results of simple single-factor models in the population genetics and community ecology of seaweeds may be affected by incorporation of a second causal factor. In Chapter II (Olson and Murphy, *in revision*) we consider how life history variation in many seaweeds may mediate the effect of natural selection on genetic variability--the interaction (in the first sense) between the fitness of genotypes and allele frequencies. The classical haploid and diploid models predict the effect of natural selection on allele frequencies (Fig. I.1A), with emphasis on the rather restrictive conditions for retention of genetic variability under natural selection. Numerous two-factor models have considered the ways that intrinsic (stage of the life history, gender) or extrinsic (temporal or spatial environmental heterogeneity) factors mediate the effect of natural selection on genetic variability, by permitting balancing selection to expand the conditions for maintenance of genetic variability.

Many seaweeds and most other plants have haplodiplontic life histories in which haploid and diploid stages alternate. In verbal models it has been predicted that selection in haplophase should result in levels of genetic polymorphism intermediate between those in organisms with strictly haploid or diploid life cycles. However, mathematical models predict that, under certain conditions, genetic polymorphism could be maintained in haploidplonts under conditions that would preclude polymorphism in diploids.

We use a comparative approach to explore the theoretical and

empirical evidence concerning the consequences of variation in life history--from haploid, to haplodiplontic, to diploid--for the maintenance of genetic polymorphism. In a new analysis of the haplodiplontic model, we show that the probability of polymorphism in haplodiplontic populations is not necessarily lower than that in diploid populations. We also review electrophoretic evidence that suggests that levels of enzyme polymorphism in natural populations of haplodiplonts are comparable to those in predominantly diploid plant and animal taxa. By using a comparative approach to evaluate the relationship of life history variation to the maintenance of polymorphism, we call into question the basic assumptions of previous verbal arguments regarding the evolution of life histories in plants.

In Chapter III, I take an experimental approach to understanding how herbivory may mediate the effect of desiccation in regulating the upper intertidal limit of a red alga. Early models of intertidal zonation suggest that a single-factor model--the effect of desiccation on plant distribution--is sufficient to explain the upper limits of species (Fig. I.1B). However, a class of two-factor models, environmental stress models, suggests that the effect of stress may be mediated by the effects of consumers (Fig. I.1B). In particular, the consequences of the interaction for the distribution of prey species is predicted to depend on the relative susceptibility to stress of consumers and prey. If consumers are more affected than prey, the consumer stress model predicts that prey species will find refuge from consumers in stressful environments. On the other hand, if prey are relatively more susceptible to stress, the prey stress model predicts that consumers may eliminate prey from stressful habitats. In

numerous terrestrial systems, desiccation stress is correlated with susceptibility to herbivory (consistent with the prey stess model). Consequently, I tested a two-factor model for the interaction of desiccation and herbivory.

I manipulated both desiccation (rock-surface moisture) and herbivory (limpet abundance) in a factorial experiment designed to evaluate their separate and joint effects on the upper intertidal limit of a perennial red alga, *Iridaea cornucopiae*. I found that in the presence of limpets, desiccation inhibited upward vegetative growth. A significant desiccation-by-grazer interaction affected both reproduction near, and recruitment above, the initial upper limit of *Iridaea*. In dry plots, grazers inhibited recruitment; in moist plots, grazers enhanced vegetative growth. Thus, *Iridaea* appears to be grazer-limited in dry environments, but grazer-dependent in moist environments, results that are not consistent with either the consumer or the prey stress models. These results suggest that a two-factor model is not sufficient to explain the interaction of desiccation and grazing.

It is likely that a third factor, the abundance or productivity of microalgae, may mediate the effects on recruitment. Limpets may remove competing microalgae from moist plots, enhancing establishment of *Iridaea*. In dry plots, where microalgal production is likely to be lower, limpets may switch to *Iridaea*.

Finally, in Chapter IV (Olson and Lubchenco 1990), we consider research strategies for investigating the effect of plant traits on the outcome of competitive interactions in seaweed communities. Simple models of competition (Fig. I.1C) assume a constant,

homogeneous environment and invariant plant traits. Some of the problems that arise in applying such simple models to plants suggest the need for theory that explicitly incorporates plant traits in two- (or more) factor models of interspecific competition (Fig. I.1C). For example, competitive interactions among seaweeds depend upon the position, biomass, architecture and potential for vegetative expansion or plasticity of response of competitors. Interactions with consumers may also affect competitive outcomes. Recent theoretical developments incorporate some of these factors in more complex models; we identify other priorities. In particular, we note that unique traits of seaweeds--such as isomorphic life histories, somatic polyploidy, and thallus fusion--require development of new approaches to understanding competition.

In addition, we note that historically, empirical studies of seaweeds have followed separate but parallel lines of inquiry in the lab and field. Lab studies have focused on variation in plant traits assumed to be associated with competitive performance; field studies have tended to focus on competitive outcomes, with less attention to the plant traits that influence competition. Consequently, the causal relationships between plant traits and competitive outcomes (Fig. I.1C) remain a crucial gap in understanding competition among seaweeds. To bridge this gap, we identify two research priorities: (1) establish rigorously the competitive consequences of variation in traits (among and within species) observed in laboratory studies, and (2) evaluate experimentally the hypothesized mechanisms of competition (in the context of other ecological interactions) proposed as a result of field studies. Single-factor causal models represent an

indispensable stage in the development of evolutionary and ecological theory. Properly conceived theoretical and empirical studies focus attention on the assumptions under which such models will hold and suggest lines of inquiry that ultimately lead to the integration of additional causal factors in conceptual models of natural processes. Identifying the circumstances under which simple models will suffice remains one of the most important challenges of evolutionary and ecological scholarship.

Chapter II

NATURAL SELECTION AND GENETIC POLYMORPHISM IN HAPLODIPLONTIC ORGANISMS

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ABSTRACT

In the haplodiplontic life history of most plants, both haploid (gametophytic) and diploid (sporophytic) stages are multicellular. Natural selection in haplophase is often assumed to reduce genetic variability in populations of haplodiplonts. In a new analysis of the haplodiplontic model (HDM)--a one-locus, two-allele deterministic model with selection in both phases--we show that the probability of polymorphism in haplodiplontic populations is not necessarily lower than that in diploid populations.

The sign of correlations in fitness of alleles between the two life-history phases determines whether genetic variability will tend to be lost or retained. We introduce two new terms, *reinforcing* and

opposing selection, to describe those cases where correlations in fitness between the two phases are positive or negative, respectively. Reinforcing selection reduces the probability of polymorphism in the HDM; under opposing selection of intermediate intensity, stable polymorphism is more likely than in the diploid model. Furthermore, electrophoretic evidence suggests that levels of enzyme polymorphism in natural populations of haplodiplonts are comparable to those in predominantly diploid plant and animal taxa. Observed levels of polymorphism do not appear to be correlated with the size, complexity, or duration of haplophase in the life history of haplodiplonts. These results call into question the basic assumptions of theories that link the population-genetic consequences of the haplodiplontic life history with explanations for the evolution of the life history itself.

INTRODUCTION

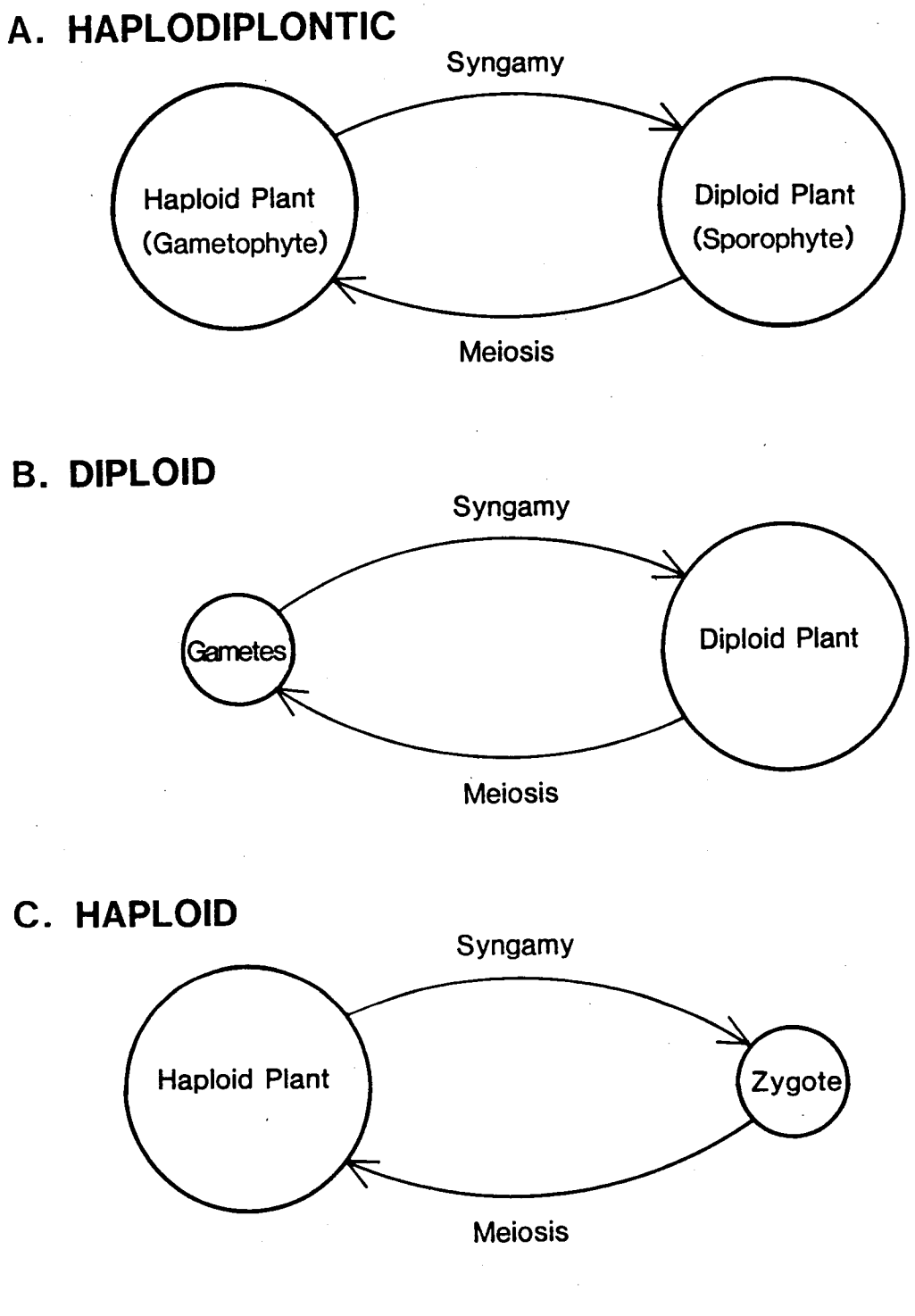
The maintenance of genetic polymorphism is a central issue in evolutionary population biology both because it reflects evolutionary processes within populations, and because it potentially has important evolutionary consequences. The ability of natural selection to maintain genetic variation within populations is powerfully affected by the life histories of organisms. In the vast majority of plants the life history is haplodiplontic (fig. II.1A), i.e., both diploid (sporophytic) and haploid (gametophytic) stages are multicellular and sometimes physiologically independent (Bold et al. 1987). Because each stage is developmentally complex and often long-lived, the potential exists for natural selection to alter allele frequencies in both stages. In this paper, we explore theoretical and empirical evidence concerning the consequences of life history variation for the maintenance of genetic polymorphism in haplodiplontic populations.

The haplodiplontic life history is one of three life history patterns that differ in the ploidy level of the dominant phase (fig. II.1). Each of these life histories presents different constraints on the maintenance of genetic polymorphism by natural selection. For example, in diploid populations (fig. II.1B), simple, deterministic, single-locus models (e.g., Wright 1969) predict that heterozygote superiority is both necessary and sufficient for the maintenance of stable genetic polymorphism. In haploid populations (fig. II.1C), on the other hand, natural selection alone is insufficient to maintain stable polymorphism (e.g., Haldane and Jayakar 1963), because the heterozygote does not exist in haploid organisms. In diploid

Figure II.1. Idealized life histories (after Searles 1980). A. Haplo-diplontic, with sporic meiosis and mitotic gametogenesis (e.g., most plants and algae). B. Diploid, with gametic meiosis (e.g., fucoid algae, most metazoa). C. Haploid, with zygotic meiosis (e.g., many flagellates). Departures from idealized life cycles include asexual reproduction in either the haploid or diploid stage and plasticity in the degree of coordination among nuclear (haploid *versus* diploid), reproductive (gametophytic *versus* sporophytic), and morphological phases (Clayton 1988, Maggs 1988).

NOTE.--Among haplodiplontic life histories, haploid and diploid stages may be isomorphic (i.e., morphologically similar) or they may be heteromorphic (i.e., dissimilar), with either stage more prominent. Haplophase is dominant among bryophytes (mosses and liverworts, Divisions Bryophyta and Hepatophyta, respectively), where the diploid sporophyte is smaller and more short-lived than the haploid gametophyte. Multicellular algae (chiefly in the Divisions Chlorophyta, Phaeophyta, and Rhodophyta) display the full range of life histories including haploid, haplodiplontic, and diploid. Among higher plants, the diploid sporophyte dominates the life history: In pteridophytes (ferns, clubmosses, and horsetails; Divisions Pteridophyta, Microphyllophyta, and Arthrophyta, respectively), the independent haploid gametophyte is reduced in size and usually dies following development in situ of the large, often long-lived sporophyte. Among gymnosperms (largely conifers, Division Coniferophyta) and angiosperms (flowering plants, Division Anthophyta), the female gametophyte is enclosed in, and dependent upon, sporophytic tissue; the male gametophyte is contained in the pollen grains. The female gametophytes of gymnosperms are both larger ($\sim 10^4$ cells) and more differentiated than those of angiosperms, which are reduced to fewer than 10 cells. (See Bold 1970 and Bold et al. 1987 for recent classifications of the plant kingdom and descriptions of life cycles.)

Figure II.1


A. HAPLODIPLONTIC
Syngamy
Haploid Plant
(Gametophyte)
Diploid Plant
(Sporophyte)
Meiosis
B. DIPLOID
Syngamy
Gametes
Diploid Plant
Meiosis
C. HAPLOID
Syngamy
Haploid Plant
Zygote
Meiosis

populations, the fitness of heterozygotes relative to that of the homozygotes both regulates the rate at which deleterious alleles are eliminated and determines whether natural selection can maintain stable polymorphism. Populations of haploid organisms lack this mechanism for retaining genetic variability.

Some authors have inferred from this difference between haploid and diploid populations that the potential for natural selection to maintain genetic polymorphism should be intermediate in populations of haplodiplonts (e.g., Stebbins 1950, 1960; Bonner 1965; reviews in Willson 1981; Szweykowski 1984; Wyatt 1985; Wyatt et al. 1989b; Ennos 1990). In particular, it is commonly thought that genes should be exposed to intense purifying selection in the gametophytic stage of the haplodiplontic life history, due to the absence of heterozygotes in haplophase (e.g., Yamazaki 1981, 1984; Pfahler 1983; Weeden 1986). Selection in haplophase is thus considered to be inherently "strong," quickly eliminating inferior variants and reducing the probability of stable genetic polymorphism in haplodiplontic relative to diploid populations. Populations with a prominent haploid stage are therefore expected to harbor less genetic variation affecting fitness than are populations of predominantly diploid organisms.

In this paper we examine the validity of such expectations in order to better understand the conditions governing evolution in haplodiplontic populations. Existing theoretical studies of natural selection in populations of haplodiplonts predict that conditions governing polymorphism in the haplodiplontic model (HDM) may be either more restrictive or more lenient than in the classical diploid model (DM) (Scudo 1967; Wright 1969; Hartl 1975; Ewing 1977; Gregorius

1982). Specifically, these authors note that certain fitness combinations in the HDM preclude stable polymorphism despite heterozygote superiority in diplophase, while others permit polymorphism in the absence of heterozygote superiority. However, the net effect of natural selection in haplophase on the maintenance of polymorphism was not analyzed in any of these studies. We address two related questions (1) "What are the fitness combinations under which natural selection tends to eliminate or retain genetic variation in populations of haplodiplonts?" and (2) "How does the presence of haplophase in the life cycle affect the maintenance of genetic polymorphism?" To address the first question, we review the results of the HDM, demonstrating how selection in each phase constrains or potentiates the effects of selection in the alternate phase and clarifying the conditions under which polymorphism is disrupted or enhanced by selection in haplophase.

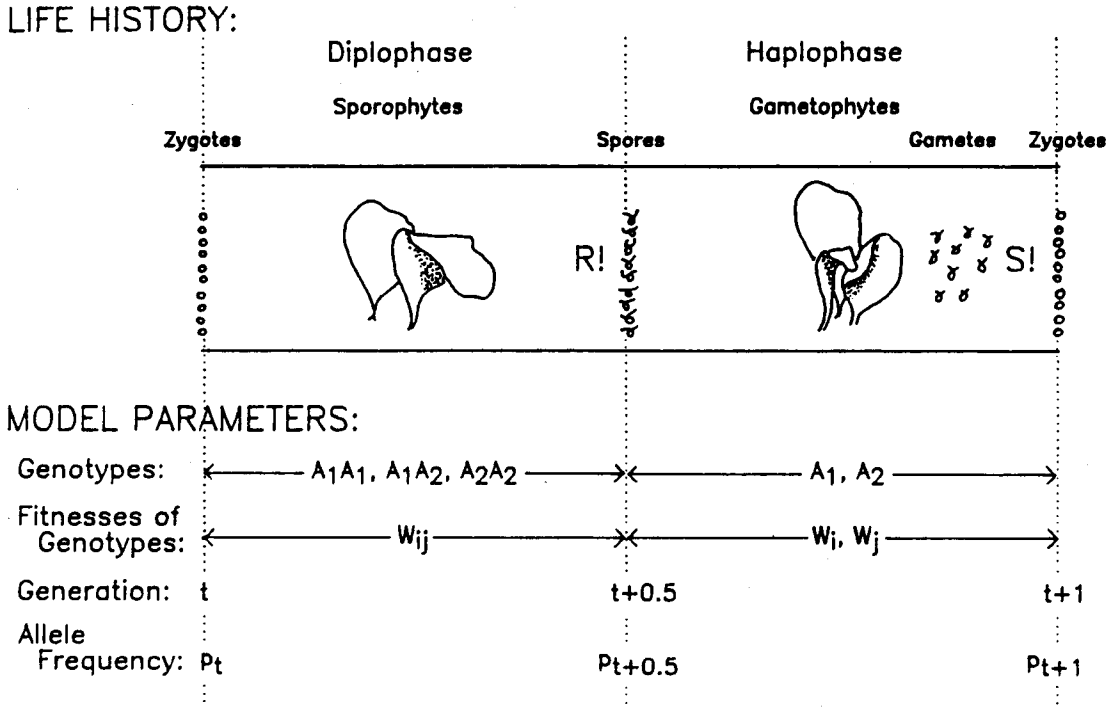
To address the second question, we compare predicted and observed levels of polymorphism in populations that differ in the presence, or the prominence, of haplophase in the life history. We present a new analysis of the HDM that gives the first quantitative comparison of the probability of polymorphism in the HDM (where haplophase is present) and in the DM (where it is absent). We also compare the frequency of polymorphism among haplodiplontic populations that differ in the relative prominence of haplophase. To the extent that selection in haplophase tends to eliminate genetic variation, levels of polymorphism within natural populations of haplodiplonts should be inversely correlated with the relative prominence of the gametophytic and sporophytic stages. Few empirical studies exist on

genetic variation in species with a prominent or independent haploid stage; none compare polymorphism among taxa that differ in the relative duration or development of the two phases. Ours is the first comprehensive survey of the literature on electrophoretic variation among several plant divisions that represent a continuum of life-history variation from gametophyte- to sporophyte-dominance.

We conclude our discussion by considering the relevance of our results and approach to arguments concerning both the population-genetic consequences, and the evolutionary causes, of life-history variation in plants. Selection in haplophase potentially has important evolutionary implications in haplodiplontic populations. However, at least two contrasting accounts of its significance have been proposed. Some authors have suggested that retention of a discrete haplophase in the life history is favored because it serves a "cleansing" function, rapidly eliminating deleterious mutations (e.g., Mulcahy and Mulcahy 1987; Klekowski 1988). In contrast, others have predicted that a diplophase-dominant life history should evolve in the absence of constraints, in part, because selection in haplophase can eliminate potentially adaptive genetic variation from populations (e.g., Stebbins 1950, 1960; Bonner 1965). Each of these arguments is dependent on the expectation that levels of polymorphism in haplodiplonts are reduced relative to those in diploids. Our results indicate that this expectation is not necessarily warranted.

Figure II.2. Features of a generalized haplodiplontic life history and parameters of the haplodiplontic model (HDM). R! denotes meiosis; S!, syngamy. (Modified from Roughgarden 1979, figure 3.1.)

Figure II.2


LIFE HISTORY:
Diplophase
Haplophase
Sporophytes
Gametophytes
Zygotes
Spores
Gametes
Zygotes
R!
S!
MODEL PARAMETERS:
Genotypes:
A1A1, A1A2, A2A2
A1, A2
Fitnesses of Genotypes:
Wij
Wi, Wj
Generation:
t
t+0.5
t+1
Allele Frequency:
Pt
Pt+0.5
Pt+1

THE MODEL

The haplodiplontic model predicts changes due to natural selection in the frequencies of two alleles at one locus. We assume an infinite population with no gene flow or mutation, with fitnesses constant and equal between the sexes, and with discrete generations. Extensions of the model include the cases of stochastically or cyclically varying fitnesses (Hartl 1975 and Ewing 1977, respectively) and of fitness differences between the sexes (Gregorius 1982).

Figure II.2 relates parameters of the model to the haplodiplontic life cycle. The period from the zygotes of the parental generation to the zygotes of their offspring (from time t to time t+1) is defined as a single "generation." (Although some authors refer to the haploid and diploid stages as alternate "generations" of the plant life cycle, we reserve the term for the zygote-to-zygote period. We use "stage" or "phase" to refer to the haploid or diploid portions of the life cycle.) The generation time is divided into the diploid and haploid phases--from t to t+0.5 and from t+0.5 to t+1, respectively. Frequencies (p and q) of alleles (A_1 and A_2) are censused in the zygotes (at times t+n). This formulation is essentially the same as that of Hartl (1975) and Ewing (1977); other formulations census gametes (Scudo 1967) or meiospores (Wright 1969; Gregorius 1982). The action of natural selection is modeled as the relative fitness (w) of diploid (w_{ij}) and haploid (w_i, w_j) genotypes.

The frequency of alleles in the current cohort of zygotes (p_{t+1}) is a function of that in the parental cohort (p_t) and the fitnesses of diploid and haploid genotypes:

$$p_{t+1} = f(p) = p_t w_1 [p_t w_{11} + (1-p_t) w_{12}] \; / \; D, \qquad (1)$$

where $D = p_t w_1 [p_t w_{11} + (1-p_t) w_{12}] + (1-p_t) w_2 [p_t w_{12} + (1-p_t) w_{22}]$. For a particularly succinct derivation of this recursion equation, see Hartl (1975).

Under a given selection regime (i.e., combination of w's), allele frequencies will change until they reach equilibrium, after which, by definition, they remain constant [i.e., f(p) = p at equilibrium]. Two types of equilibria--boundary and internal equilibria--are defined in the HDM. A boundary equilibrium exists when A_1 is either eliminated (p = 0) or fixed (p = 1). An internal equilibrium (and, thus, polymorphism) exists only if $f(p) = \hat{p}$ and $0 < \hat{p} < 1$ (i.e., if both alleles are present at equilibrium). Because equilibrium exists when allele frequency is constant, we solve f(p) = p for p (Appendix A), verify that the boundaries p = 0 and p = 1 are equilibria, and show that an internal equilibrium must satisfy

$$\hat{p} = \frac{w_2 w_{22} - w_1 w_{12}}{w_2 w_{22} - w_1 w_{12} + w_1 w_{11} - w_2 w_{12}}. \qquad (2)$$

Thus, the equilibrium frequency is determined by the relative fitnesses of the genotypes (the w's) and, in some cases, by the initial allele frequency, p_0. The qualitative selection regimes (i.e., relationships among the w's) governing the existence and stability of equilibria in the HDM can be inferred from the shape of the function y = f(p), i.e., of equation (1) (see Appendix B). These results are summarized in table II.1 and presented graphically in figure II.3.

Table II.1. Conditions governing the existence and stability of boundary and internal equilibria in the haplodiplontic model.

Case	$f'(0)$[1]	$f'(1)$[1]	Selection in haplophase relative to selection in diplophase		Stability of equilibria[2] $p = 0$[3]	$p = 1$[4]	$\hat{p}$[5]
0	=1	=1	$\frac{w_2}{w_1} = \frac{w_{12}}{w_{22}}$	$\frac{w_2}{w_1} = \frac{w_{11}}{w_{12}}$	N	N	N
1[+]	≥1	≤1	$\frac{w_2}{w_1} \leq \frac{w_{12}}{w_{22}}$	$\frac{w_2}{w_1} \leq \frac{w_{11}}{w_{12}}$	U	S	---
2[+]	≤1	≥1	$\frac{w_2}{w_1} \geq \frac{w_{12}}{w_{22}}$	$\frac{w_2}{w_1} \geq \frac{w_{11}}{w_{12}}$	S	U	---
3	<1	<1	$\frac{w_2}{w_1} > \frac{w_{12}}{w_{22}}$	$\frac{w_2}{w_1} < \frac{w_{11}}{w_{12}}$	S	S	U
4	>1	>1	$\frac{w_2}{w_1} < \frac{w_{12}}{w_{22}}$	$\frac{w_2}{w_1} > \frac{w_{11}}{w_{12}}$	U	U	S

[1] See Appendix B for definitions of $f'(0)$ and $f'(1)$.

[2] N = neutrally stable, U = unstable, S = stable, --- = equilibrium does not exist.

[3] A_2 fixed.

[4] A_1 fixed.

[5] Polymorphism.

[+] $f'(0)$ and $f'(1)$ cannot simultaneously equal 1, or Case 0 would hold.

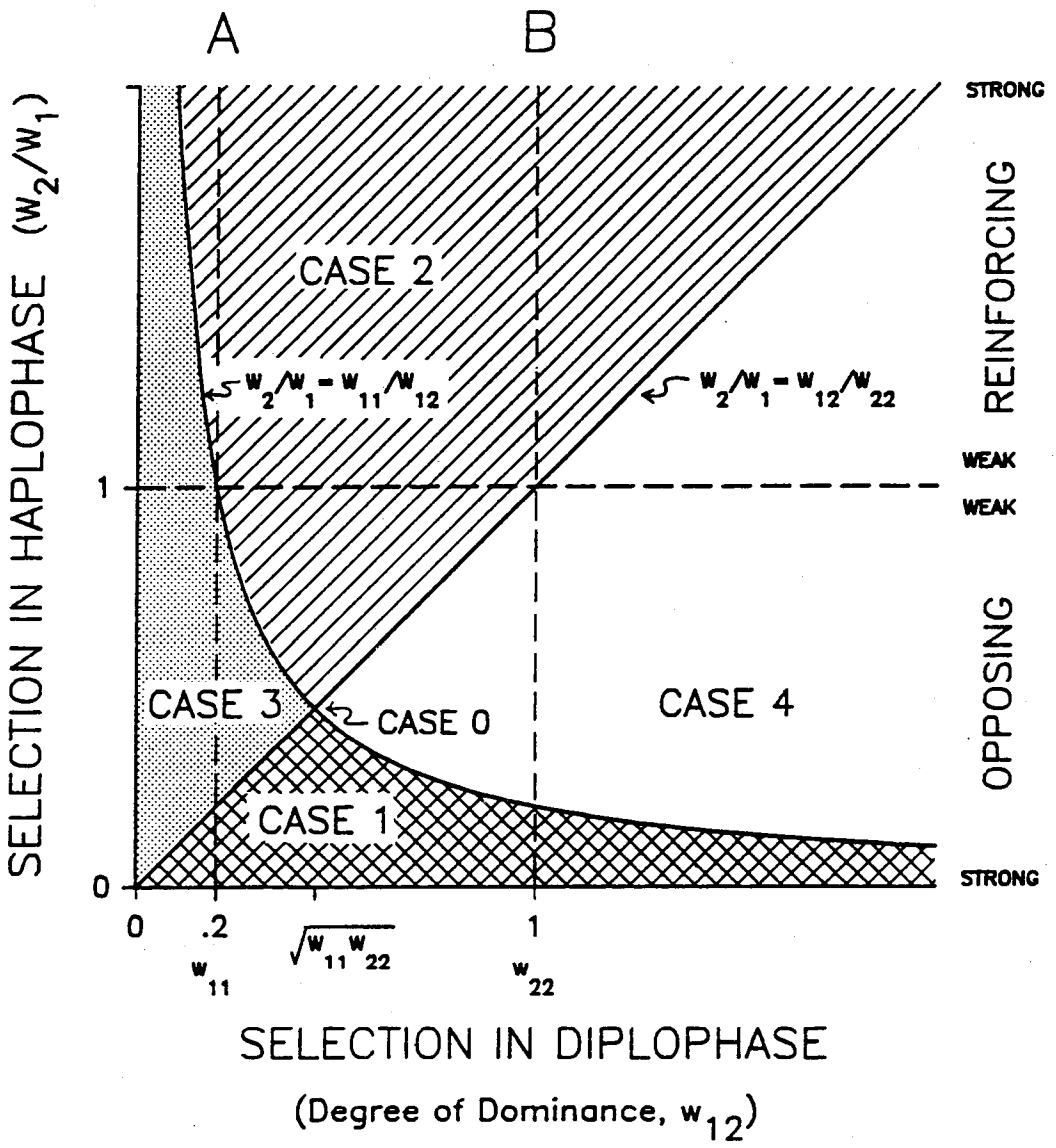
The strength and direction of selection in haplophase relative to the selection regime in diplophase determines the qualitative results of the HDM. The critical relationships between selection in haplophase and that in diplophase, $w_2/w_1 = w_{12}/w_{22}$ and $w_2/w_1 = w_{11}/w_{12}$, are graphed in figure II.3. (We arbitrarily assume A_2A_2 to be the superior homozygous genotype, by setting $1 = w_{22} > w_{11} = 0.2$.) A neutrally stable, Hardy-Weinberg-like equilibrium (Case 0, table II.1) exists at the intersection of the two curves ($w_{12}/w_{22} = w_2/w_1 = w_{11}/w_{12}$, fig. II.3). Otherwise, dynamically stable boundary or internal equilibria exist: A_1 will be fixed (Case 1, table II.1) if w_2/w_1 is equal to or less than both w_{12}/w_{22} and w_{11}/w_{12} (fig. II.3, cross-hatched region). Conversely, A_1 will be eliminated and A_2 fixed (Case 2, table II.1) if w_2/w_1 is equal to or greater than both w_{12}/w_{22} and w_{11}/w_{12} (fig. II.3, hatched region). An internal equilibrium (i.e., polymorphism) is ensured if w_2/w_1 lies between the curves, $w_2/w_1 = w_{12}/w_{22}$ and $w_2/w_1 = w_{11}/w_{12}$ (fig. II.3): The equilibrium is unstable (Case 3, table II.1) if $w_{12}/w_{22} < w_2/w_1 < w_{11}/w_{12}$ (fig. II.3, stippled region). A stable polymorphism (Case 4, table II.1) will persist if and only if $w_{12}/w_{22} > w_2/w_1 > w_{11}/w_{12}$ (fig. II.3, unshaded region). (Note that a necessary, but not sufficient, condition for a stable polymorphism is that $w_{12}/w_{22} > w_{11}/w_{12}$ or, equivalently, $w_{12} > \sqrt{w_{11}w_{22}} = 0.45$, in this example.) Thus, unless an allele is lethal in haplophase (see Scudo 1967, p. 695), the sign and magnitude of selection in haplophase relative to the selection regime in diplophase determines whether fixation or polymorphism will result.

Figure II.3. Parameter space of the haplodiplontic model in two dimensions. Selection regime in diplophase: Fitnesses of the homozygotes are fixed (w_{11} = 0.2, w_{22} = 1). Fitness of the heterozygote, w_{12}, relative to that of the homozygotes (i.e., the degree of dominance) varies from inferior (to the left of line A); to intermediate (incomplete dominance, between lines A and B); to superior (to the right of line B).

Selection regime in haplophase: The ratio w_2/w_1 represents relative fitnesses of the haploid genotypes. The DM holds when selection is absent in haplophase (i.e., $w_2 = w_1$, or $w_2/w_1 = 1$; points along the horizontal dashed line).

The critical relationships between the selection regimes in haplophase and diplophase (table 1, Appendix B), are graphed as $w_2/w_1 = w_{12}/w_{22}$ and $w_2/w_1 = w_{11}/w_{12}$, defining regions of the parameter space corresponding to Cases 1-4 in table 1. Note that all points on the curves $w_2/w_1 = w_{12}/w_{22}$ and $w_2/w_1 = w_{11}/w_{12}$ are associated with regions of stable boundary equilibrium (table 1), except $w_{12}/w_{22} = w_{11}/w_{12}$, where a neutrally stable equilibrium (Case 0) results.

Figure II.3


A
B
STRONG
REINFORCING
WEAK
WEAK
OPPOSING
STRONG
CASE 2
$w_2/w_1 = w_{11}/w_{12}$
$w_2/w_1 = w_{12}/w_{22}$
CASE 3
CASE 0
CASE 4
CASE 1
1
0
0
.2
1
w_{11}
$\sqrt{w_{11}w_{22}}$
w_{22}
SELECTION IN HAPLOPHASE (w_2/w_1)
SELECTION IN DIPLOPHASE
(Degree of Dominance, w_{12})

PREDICTIONS OF THE MODEL

In this section we examine the equilibrium conditions in detail, exploring the predictions of the haplodiplontic model relative to those of the classical diploid model. First we note that the DM is a special case of the HDM (also see Ewing 1977). The DM assumes the absence of selection in haplophase (i.e., $w_2/w_1 = 1$, fig. II.3, all points on the horizontal dashed line). A neutrally stable (Hardy-Weinberg) equilibrium exists if selection is also absent in diplophase (i.e., $w_2/w_1 = w_{12}/w_{22} = w_{11}/w_{12} = 1$). Further, with partial or complete dominance ($w_{11} \leq w_{12} \leq w_{22}$, $w_{11} \neq w_{22}$), the allele that is favored when homozygous in diplophase (henceforth A_2) will be fixed. Finally, internal equilibria exist when the heterozygote is inferior [$\hat{p}$ unstable for $0 \leq w_{12} < \min(w_{11}, w_{22})$] or superior [$\hat{p}$ stable for $w_{12} > \max(w_{11}, w_{22})$] to the two homozygotes. Thus, when $w_1 = w_2$, the conditions permitting stable polymorphism in the DM [i.e., $w_{12} > \max(w_{11}, w_{22})$] are satisfied by conditions for polymorphism in the HDM (i.e., $w_{12}/w_{22} > w_2/w_1 > w_{11}/w_{12}$; table II.1).

With selection in haplophase, however, the HDM differs from the DM in the conditions for the existence and stability of internal equilibria and in the rate of approach to stable equilibria. First, a neutrally stable equilibrium exists if and only if $w_{12} = \sqrt{w_{11}w_{22}} = w_2/w_1$ (or $w_2/w_1 = w_{12}/w_{22} = w_{11}/w_{12} \neq 1$) (fig. II.3; Scudo 1976). Second, the degree of dominance in diplophase constrains the effect of haplophase selection--increasing dominance enhances the likelihood of stable polymorphism (Hartl 1975). Third, selection in haplophase may either reinforce or oppose selection in diplophase.

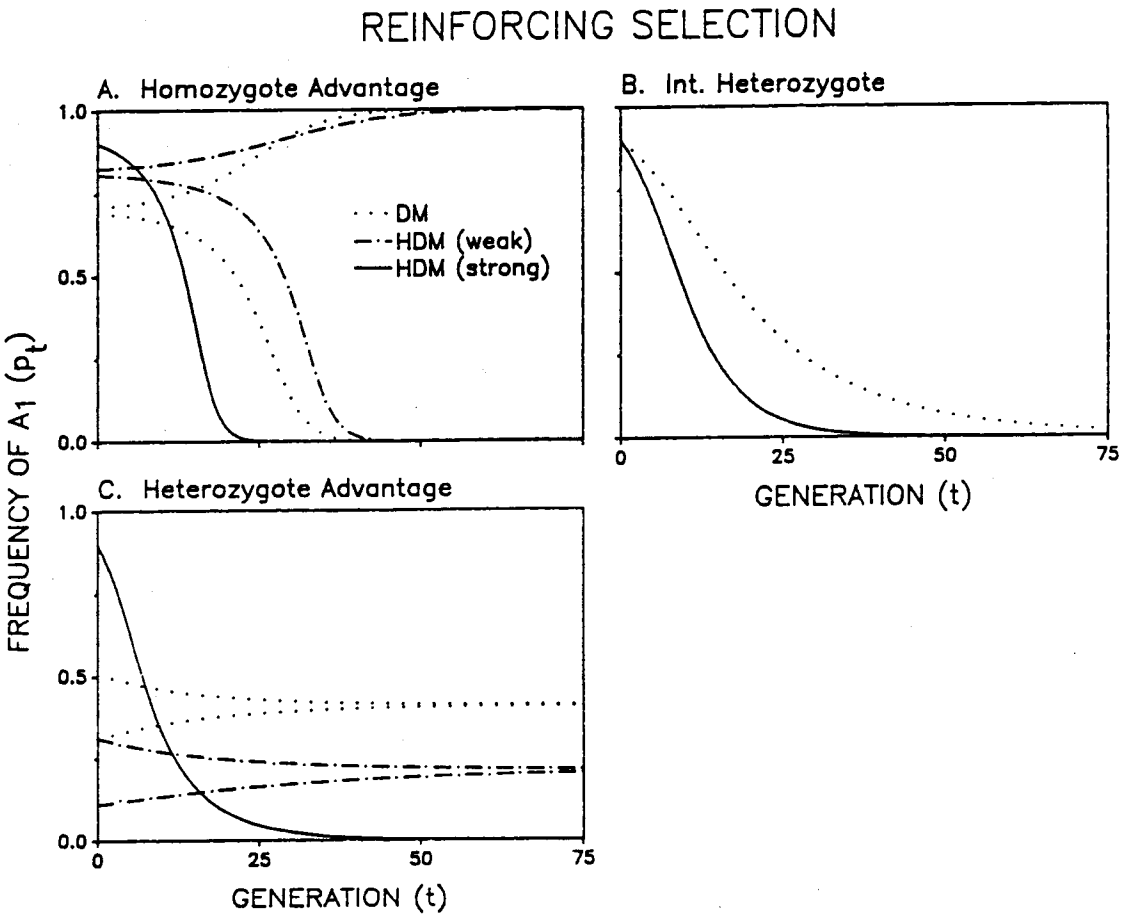
Here we introduce two new terms to differentiate these contrasting patterns of selection. Specifically, haplophase selection is considered *reinforcing* if an allele that is advantageous when homozygous in diplophase (henceforth, A_2) is also advantageous in haplophase (i.e., if $w_{11} < w_{22}$ and $w_1 < w_2$, fig. II.3, upper half). *Opposing* selection occurs, however, if an allele is advantageous in diplophase and disadvantageous in haplophase (i.e., if $w_{11} < w_{22}$ and $w_1 > w_2$, fig. II.3, lower half). Opposing selection between the phases of haplodiplonts is one type of balancing selection considered by Haldane and Jayakar (1963). Next we show that the results under reinforcing or opposing selection depend on the degree of dominance expressed and the magnitude of selection in diplophase.

Reinforcing Selection

Reinforcing selection in the HDM ($w_2/w_1 > 1$, fig. II.3, area above the horizontal dashed line) accelerates fixation of the favored allele and restricts the conditions under which polymorphism will be maintained. With homozygote advantage (selection against the heterozygote) in diplophase [$w_{12} < \min(w_{11}, w_{22})$, fig. II.3, area to the left of vertical line A], an unstable internal equilibrium will exist as long as haplophase selection is weak relative to the selection differential between the heterozygote and the disadvantageous homozygote in diplophase ($w_2/w_1 < w_{11}/w_{12}$, fig. II.3, stippled region; or $w_1 > w_{12}/w_{11}$, fig. II.4A). Either A_1 or A_2 may be fixed, depending on the initial allele frequency, p_0. The equilibrium, $\hat{p}$, is shifted toward $p = 1$ and the approach to $p = 1$ is

Figure II.4. Results of simulations in which the strength of reinforcing selection in haplophase was varied, while the selection regime in diplophase was held constant. Because we arbitrarily assume $w_{22} > w_{11}$, then $1 = w_2 > w_1$ implies reinforcing selection under the HDM. (Note that $w_2 = w_1$ implies the DM.) A. Homozygote advantage in diplophase: $w_{12} < \min(w_{11}, w_{22} = 1)$. Reinforcing selection (HDM): weak, $w_1 > w_{12}/w_{11}$; strong, $w_1 \leq w_{12}/w_{11}$. B. Intermediate heterozygote (partial or complete dominance) in diplophase: $w_{11} \leq w_{12} \leq w_{22} = 1$. Reinforcing selection (HDM): strong, any $w_1 < w_2 = 1$. C. Heterozygote advantage in diplophase: $1 = w_{12} > \max(w_{11}, w_{22})$. Reinforcing selection (HDM): weak, $w_1 > w_{22}$; strong, $w_1 \leq w_{22}$.

Figure II.4


REINFORCING SELECTION
A. Homozygote Advantage
B. Int. Heterozygote
C. Heterozygote Advantage
DM
HDM (weak)
HDM (strong)
FREQUENCY OF A_1 (p_t)
1.0
0.5
0.0
0
25
50
75
GENERATION (t)

slowed, while the approach to p = 0 is accelerated (fig. II.4A). Strong selection in haplophase ($w_2/w_1 \geq w_{11}/w_{12}$, fig. II.3, hatched region; or $w_1 \leq w_{12}/w_{11}$, fig. II.4A), however, precludes an internal equilibrium. Thus, A_1 is eliminated and A_2 is fixed (fig. II.4A).

With reinforcing selection in haplophase and partial or complete dominance (intermediate heterozygote) in diplophase ($w_{11} \leq w_{12} \leq w_{22}$, $w_{11} \neq w_{22}$, fig. II.3, area between vertical lines A and B), A_1 will be eliminated (fig. II.3, hatched region). Thus, the stable boundary equilibrium (p = 0) under reinforcing selection is identical to that in the DM (Hartl 1975). However, the rate at which the inferior allele is eliminated increases with any amount of reinforcing selection (fig. II.4B).

Finally, with heterozygote advantage (selection against homozygotes) in diplophase [$w_{12} > \max(w_{11}, w_{22})$, fig. II.3, area to the right of vertical line B], a stable internal equilibrium will persist in the HDM, as long as reinforcing selection in haplophase is weak relative to selection on the alternate allele in diplophase ($w_2/w_1 < w_{12}/w_{22}$, fig. II.3, unshaded region; or $w_1 > w_{22}$, fig. II.4C). Weak reinforcing selection shifts the polymorphism frequency toward the boundary (p = 0) and slows the rate of approach to equilibrium (fig. II.4C). However, when reinforcing selection is strong ($w_2/w_1 \geq w_{12}/w_{22}$, fig. II.3, hatched region; or $w_1 \leq w_{22}$, fig. II.4C), it disrupts the equilibrium produced by the diplophase selection regime (Wright 1969; Ewing 1977) and results in fixation of the allele favored in haplophase (fig. II.4C). Thus, under reinforcing selection, the conditions favoring polymorphism are restricted in the HDM, relative to those in the DM. In general, polymorphism

persists only when selection in haplophase is weak relative to the selection regime in diplophase.

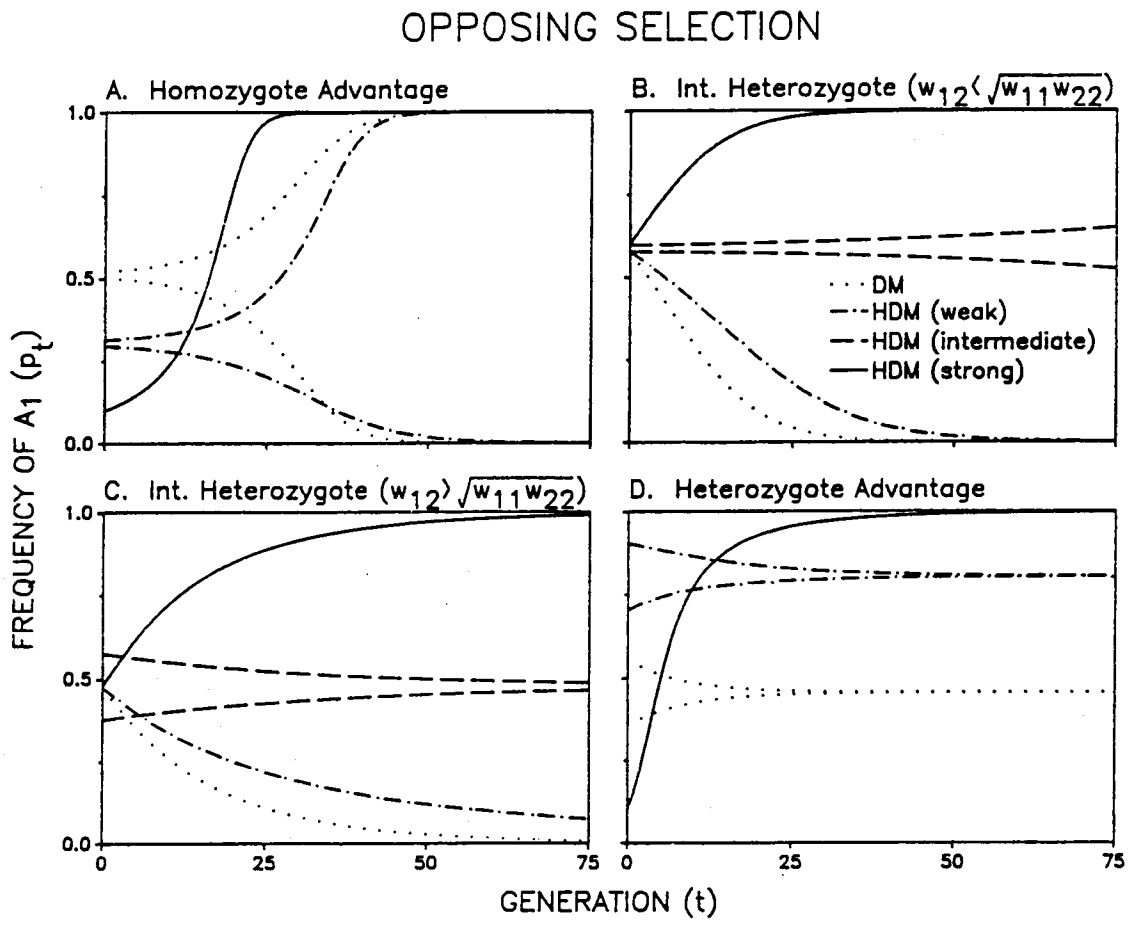
Opposing Selection

In contrast, the conditions for stable polymorphism may be either restricted or expanded under opposing selection in haplophase ($w_2/w_1 < 1$, fig. II.3, area below the horizontal dashed line). First, the selection regime in diplophase sets the necessary conditions for polymorphism (i.e., $w_{12}/w_{22} > w_{11}/w_{12}$, or $w_{12} > \sqrt{w_{11}w_{22}}$). This set of necessary (but not sufficient) conditions for polymorphism is less stringent than that in the DM, because $\sqrt{w_{11}w_{22}}$ is always less than or equal to $\max(w_{11}, w_{22})$. Second, the relative strength of opposing selection determines whether an internal equilibrium exists and, if not, which allele is fixed. When homozygotes are favored in diplophase [$w_{12} < \min(w_{11}, w_{22})$, fig. II.3, area to the left of vertical line A], an unstable internal equilibrium exists, as long as opposing selection is weak ($w_2/w_1 > w_{12}/w_{22}$, fig. II.3, stippled region; or $w_2 > w_{12}$, fig. II.5A). The equilibrium frequency is shifted toward $p = 0$ and the rate of approach is slowed, while the approach to $p = 1$ is accelerated (fig. II.5A). Strong opposing selection ($w_2/w_1 \leq w_{12}/w_{22}$, fig. II.3, cross-hatched region; or $w_2 \leq w_{12}$, fig. II.5A) precludes internal equilibrium (Scudo 1967), resulting in fixation of A_1, the allele favored in haplophase (fig. II.5A).

The results are more complex, however, under opposing selection in haplophase with partial or complete dominance (intermediate

Figure II.5. Results of simulations in which the strength of opposing selection in haplophase was varied, while the selection regime in diplophase was held constant. Because we arbitrarily assume $w_{22} > w_{11}$, then $w_2 < w_1 = 1$ implies opposing selection under the HDM. A. Homozygote advantage in diplophase: $w_{12} < \min(w_{11}, w_{22} = 1)$. Opposing selection (HDM): weak, $w_2 > w_{12}$; strong, $w_2 \leq w_{12}$. B. Intermediate heterozygote (superior allele in diplophase partially or completely recessive): $w_{11} \leq w_{12} \leq \sqrt{w_{11}w_{22}}$. Opposing selection (HDM): weak, $w_2 \geq w_{11}/w_{12}$; intermediate, $w_{12} < w_2 < w_{11}/w_{12}$; strong, $w_2 \leq w_{12}$. C. Intermediate heterozygote (superior allele in diplophase partially or completely dominant): $\sqrt{w_{11}w_{22}} < w_{12} \leq w_{22} = 1$. Opposing selection (HDM): weak, $w_2 \geq w_{12}$; intermediate, $w_{11}/w_{12} < w_2 < w_{12}$; strong, $w_2 \leq w_{11}/w_{12}$. D. Heterozygote advantage in diplophase: $1 = w_{12} > \max(w_{11}, w_{22})$. Opposing selection (HDM): weak, $w_2 > w_{11}$; strong, $w_2 \leq w_{11}/w_{12}$.

Figure II.5


OPPOSING SELECTION
A. Homozygote Advantage
B. Int. Heterozygote ($w_{12} < \sqrt{w_{11}w_{22}}$)
C. Int. Heterozygote ($w_{12} > \sqrt{w_{11}w_{22}}$)
D. Heterozygote Advantage
DM
HDM (weak)
HDM (intermediate)
HDM (strong)
FREQUENCY OF A_1 (p_t)
GENERATION (t)
1.0
0.5
0.0
0
25
50
75

heterozygote) in diplophase ($w_{11} \leq w_{12} \leq w_{22}$, $w_{11} \neq w_{22}$, fig. II.3, area between vertical lines A and B). Weak opposing selection [$w_2/w_1 \geq \max(w_{12}/w_{22}, w_{11}/w_{12})$, fig. II.3, hatched region; or $w_2 \geq \max(w_{12}, w_{11}/w_{12})$ figs. II.5B and C] slows the rate of fixation of A_2, the allele favored in diplophase (figs. II.5B and C) (Scudo 1967). Strong opposing selection [$w_2/w_1 \leq \min(w_{12}/w_{22}, w_{11}/w_{12})$, fig. II.3, cross-hatched region; or $w_2 \leq \min(w_{12}, w_{11}/w_{12})$, fig. II.5B and C] reverses the effect of diplophase selection and fixes A_1, an allele that is deleterious in diplophase, but advantageous in haplophase (figs. II.5B and C) (Scudo 1967). Intermediate values of opposing selection, however, permit an internal equilibrium: If the superior allele in diplophase is partially or completely recessive (i.e., $w_{12} < \sqrt{w_{11}w_{22}}$), then $w_{12}/w_{22} < w_2/w_1 < w_{11}/w_{12}$ results in unstable equilibrium (figs. II.3, stippled region, and II.5B). However, if the superior allele in diplophase is partially or completely dominant (i.e., $w_{12} > \sqrt{w_{11}w_{22}}$), then $w_{12}/w_{22} > w_2/w_1 > w_{11}/w_{12}$ results in a stable equilibrium (figs. II.3, unshaded region, and II.5C). Thus, under opposing selection in the HDM, stable polymorphism may be maintained in the absence of heterozygote advantage in diplophase (Wright 1969; Ewing 1977).

Finally, with heterozygote advantage in diplophase [$w_{12} > \max(w_{11}, w_{22})$, fig. II.3, area to the right of vertical line B], and with weak opposing selection ($w_2/w_1 > w_{11}/w_{12}$, fig. II.3, unshaded region; or $w_2 > w_{11}$, fig. II.5D), polymorphism persists, but the equilibrium frequency is shifted toward the boundary ($p = 1$) and the rate of approach to equilibrium is slowed (fig. II.5D). Strong opposing selection $w_2/w_1 \leq w_{11}/w_{12}$, fig. II.3, cross-hatched region;

or $w_2 \leq w_{11}$, fig. II.5D), however, precludes a stable polymorphism--the allele that is deleterious in diplophase (A_1) is fixed (fig. II.5D) (Scudo 1967).

In summary, reinforcing selection should tend to reduce genetic variation by speeding the rate of elimination of deleterious alleles and by disrupting polymorphism that could otherwise be maintained by the selection regime in diplophase. The consequences of opposing selection, however, are more complex. On the one hand, strong opposing selection disrupts polymorphism that would persist under selection in diplophase and results in fixation of alleles that are deleterious or even lethal in the homozygous state in diplophase. On the other hand, opposing selection potentially enhances genetic variation by slowing the loss of alleles that are deleterious in diplophase and by maintaining stable polymorphism that would not otherwise persist under selection in diplophase.

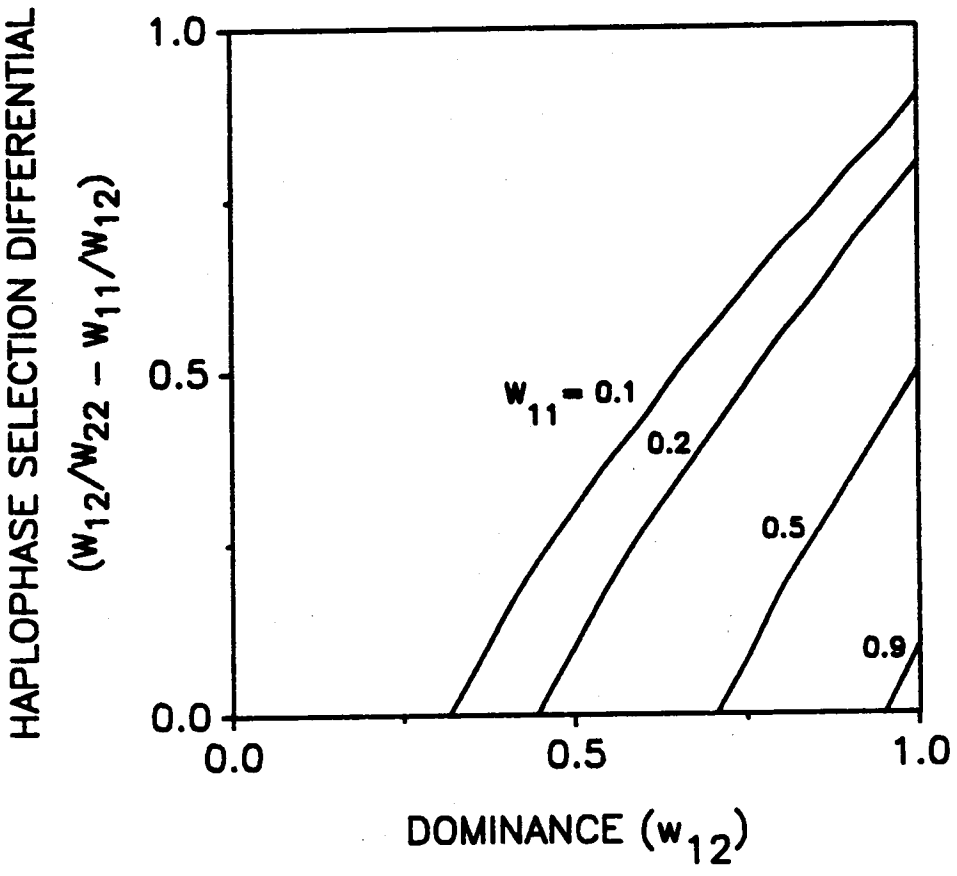
THE PROBABILITY OF POLYMORPHISM

What is the net effect of haplophase selection on the probability of polymorphism in the HDM? The results outlined above indicate that under reinforcing selection and with heterozygote advantage under opposing selection, conditions permitting polymorphism are more stringent in the HDM than in the DM. However, under opposing selection, conditions permitting polymorphism in the HDM are expanded if the fitness of the heterozygote is greater than the geometric mean of the fitnesses of the homozygotes (given partial or complete dominance of the advantageous allele). The range of values over which haplophase selection will increase the likelihood of polymorphism is defined by $w_{12}/w_{22} - w_{11}/w_{12}$ (i.e., by the vertical distance between $w_2/w_1 = w_{12}/w_{22}$ and $w_2/w_1 = w_{11}/w_{12}$ in fig. II.3). This distance is correlated with the degree of dominance (Hartl 1975; Ewing 1977), as illustrated in figures II.4 and II.6: As dominance in diplophase (w_{12}) increases, the range of values over which haplophase selection will permit stable polymorphism increases monotonically for a given fitness differential between homozygotes ($w_{22} - w_{11}$) (fig. II.6). Hence, the degree of dominance in diplophase defines the range of haplophase selection in the HDM that would permit "new" stable polymorphism otherwise precluded in the DM.

The potential for gain in polymorphism under opposing selection depends not only upon the degree of dominance, but upon the relative fitness of the two homozygotes. In figure II.3 the fitness (w_{11}) of the inferior homozygote (A_1A_1) is set at 0.2. Relative to the alternate homozygote, selection against the A_1A_1 genotype is strong in

Figure II.6. Effects of selection in diplophase (dominance and fitness of the inferior homozygote) on the range of haplophase selection differentials that permit "new" polymorphism under opposing selection in the HDM. Note that with heterozygote advantage in diplophase, there is no potential for gain in stable polymorphism in the HDM, under either reinforcing or opposing selection. Sufficiently strong haplophase selection disrupts the stable polymorphism that would otherwise exist under the DM.

Figure II.6


HAPLOPHASE SELECTION DIFFERENTIAL
$(w_{12}/w_{22} - w_{11}/w_{12})$
1.0
0.5
0.0
0.0
0.5
1.0
w_{11} = 0.1
0.2
0.5
0.9
DOMINANCE (w_{12})

this example. If dominance is also high (i.e., w_{12} close to w_{22}), then the range of allowable values in haplophase supporting "new" polymorphism approaches $1 - w_{11}/w_{12} = 0.9$ (fig. II.6). That is, even quite strong opposing selection will result in a gain in polymorphism. However, if the fitness differential between the two homozygotes is small (e.g., $w_{11} = 0.9$, $w_{22} = 1$, fig. II.6), then the maximum range of haplophase fitness resulting in a gain in polymorphism would be small.

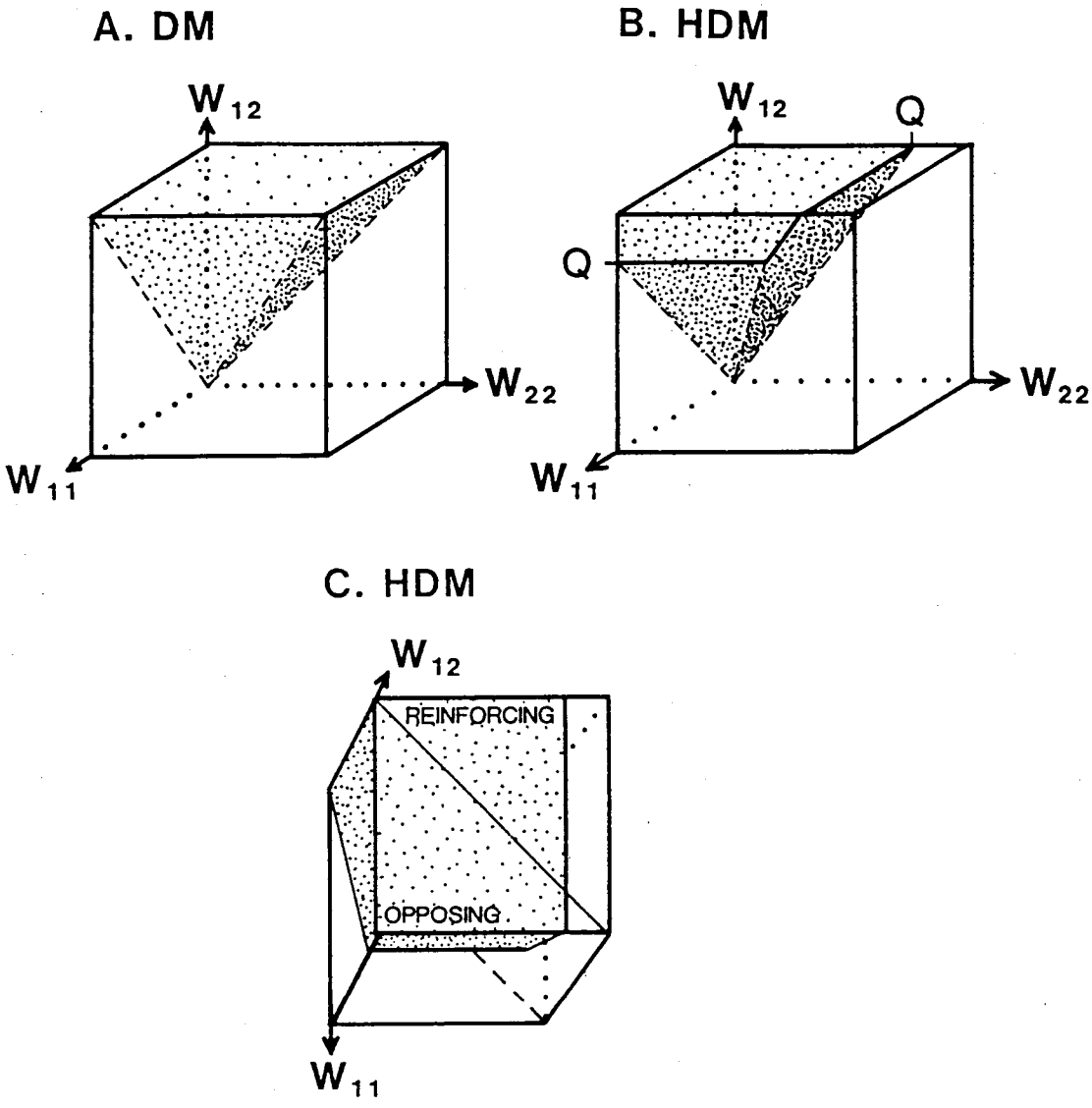
An Analytical Approach

The net gain or loss of polymorphism under the HDM relative to the DM is difficult to evaluate using qualitative, case-by-case analyses (e.g., figs. II.3-II.6). A more general analysis is possible if the entire parameter space of the models (i.e., all possible combinations of w_{ij}, w_i, w_j) is abstracted. For example, two-dimensional formulations of the parameter space of the HDM facilitate comparison of the results of the HDM and the DM (e.g., fig. II.3; Scudo 1967, figs. 1 and 2; Wright 1969, fig. 3.8; Ewing 1977, fig. 1). However, these analyses do not permit a quantitative assessment of the probability of polymorphism under the two models. By representing the parameter space in three, rather than two, dimensions we derive the first general, quantitative assessment of the net effect of selection in haplophase on the maintenance of polymorphism. (For more complex models, it may be necessary to use numerical techniques to explore the relative sizes of various regions of the parameter space, e.g., Feldman and Liberman 1984.)

The conditions permitting stable polymorphism in the DM are

Figure II.7. Parameter space of the HDM in three dimensions (the unit cube). The shaded regions indicate the conditions permitting stable polymorphism: A. In the DM; B. and C. In the HDM. The figure in panel C is rotated to show a top view of the cube in panel B under reinforcing and opposing selection in the HDM. (See Appendix C for proofs.)

Figure II.7


A. DM
W12
W22
W11
B. HDM
W12
Q
Q
W22
W11
C. HDM
W12
REINFORCING
OPPOSING
W11

represented by the shaded volume (V_D) of figure II.7A--the space in which $w_{12} > \max(w_{11}, w_{22})$. One can easily confirm that the volume of this space is one-third of the unit cube (i.e., $V_D = 1/3$). In the HDM (fig. II.7B), the shape of the shaded volume changes as a function of the strength of haplophase selection ($s_H = 1 - Q$, where $Q = w_1/w_2$, $w_1 \leq w_2$, and $0 \leq Q \leq 1$). (See Appendix C for definition of terms and proof.) With haplophase selection, the volume of the space in which polymorphism is possible is given by

$$V_H = \frac{Q}{2} - \frac{Q^3}{6}. \tag{3}$$

For all defined values of $Q < 1$, the volume V_H is smaller than the equivalent volume for the diploid model, V_D (fig. II.8A). Consequently, for the entire parameter space, additional selection in haplophase creates more stringent conditions for stable polymorphism than selection in diplophase alone. The net effect of haplophase selection is to reduce the probability that polymorphism will occur.

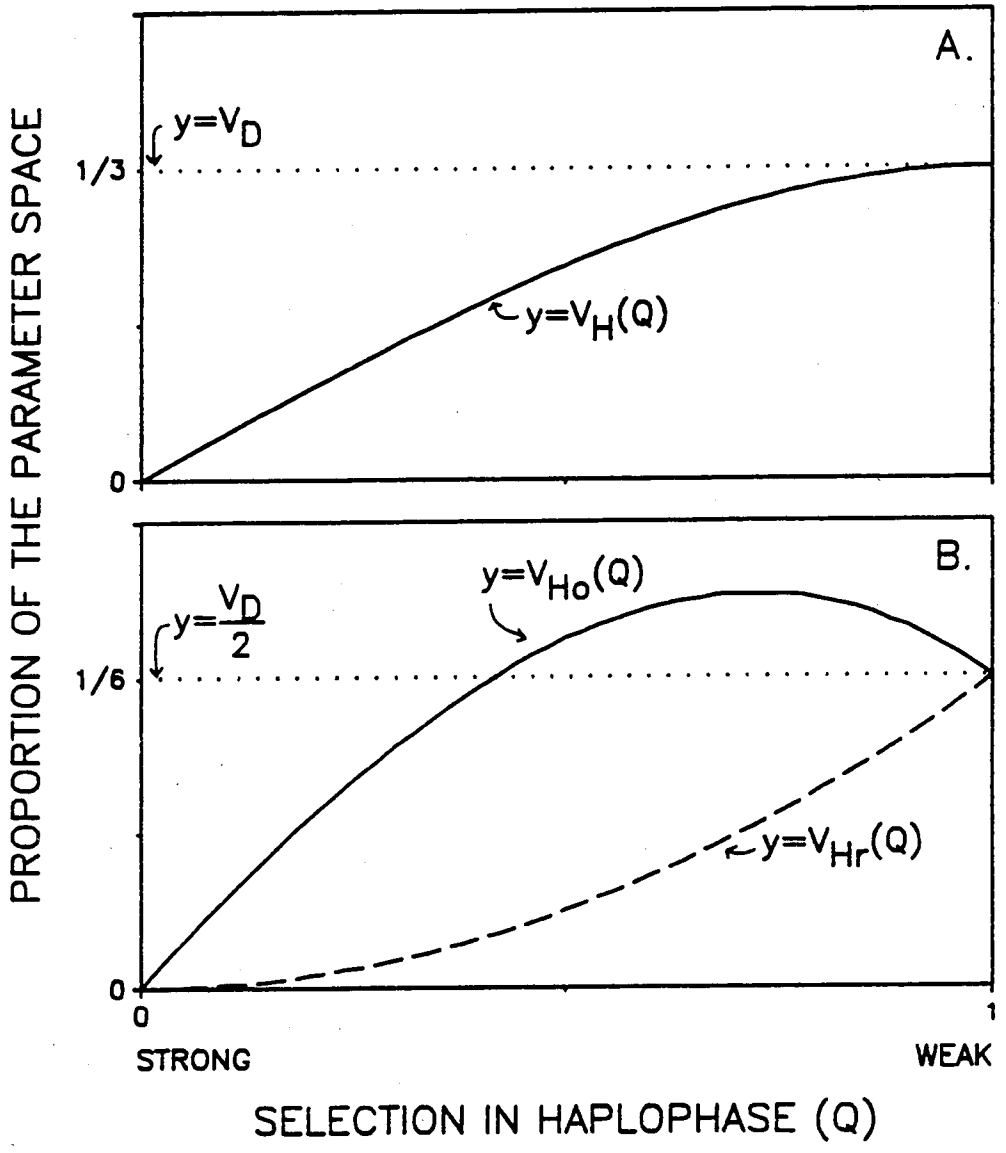
However, reinforcing and opposing selection may also be considered separately. The diagonal plane in figure II.7C divides the unit cube into regions of reinforcing and opposing selection. Under reinforcing selection, the volume of the space permitting polymorphism is

$$V_{Hr} = \frac{Q^2}{6}. \tag{4}$$

(See Appendix C for proof.) For any defined value of $Q < 1$, V_{Hr} is smaller than half the volume for the DM ($V_D/2 = 1/6$, fig. II.8B).

Figure II.8. Volume of the parameter space supporting polymorphism as a function of selection in haplophase (Q). A. Polymorphism in the DM (V_D) and in the HDM [$V_H(Q)$] (see eq. 3 in text). B. Polymorphism under reinforcing [$V_{Hr}(Q)$] (eq. 4) and opposing [$V_{Ho}(Q)$] (eq. 5) selection, compared to the DM ($V_D/2$).

Figure II.8


A.
y=V_D
1/3
y=V_H(Q)
0
B.
y=V_Ho(Q)
y=V_D/2
1/6
y=V_Hr(Q)
0
0
1
STRONG
WEAK
PROPORTION OF THE PARAMETER SPACE
SELECTION IN HAPLOPHASE (Q)

(This qualitative result also can be seen in figure II.3 where, with increasing reinforcing selection, the horizontal width of the region permitting polymorphism decreases monotonically.) Consequently, any reinforcing selection will reduce the probability of polymorphism. Polymorphism is lost under reinforcing selection, because selection in haplophase disrupts the equilibrium obtained under heterozygote advantage in diplophase. In addition, reinforcing selection never results in polymorphism that would not otherwise exist in the DM.

The effect of opposing selection, on the other hand, depends on the strength of selection in haplophase. The volume of the space permitting polymorphism under opposing selection is

$$V_{Ho} = \frac{Q}{2} - \frac{Q^3}{6} - \frac{Q^2}{6}. \qquad (5)$$

(See Appendix C for proof.) When opposing selection in haplophase is very strong [i.e., $Q \leq (\sqrt{2} - 1) \simeq 0.414$], the space permitting stable polymorphism, V_{Ho}, is less than $V_D/2$ (fig. II.8B). Here the loss in polymorphism due to selection within haplophase overwhelms any gains due to balancing selection between the phases.

For a broad range of selection intensities in haplophase [i.e., $1 > Q > (\sqrt{2} - 1)$], however, V_{Ho} is greater than $V_D/2$ (fig. II.8B). Consequently, the probability of polymorphism may be enhanced under opposing selection, if $s_H < (2 - \sqrt{2})$. Further, the potential for enhancement is at its maximum when $Q \simeq 0.72$. (This result also is reflected in figure II.3, where the horizontal width of the region permitting polymorphism reaches a maximum at intermediate levels of opposing selection.) Thus, intermediate levels of opposing selection

($s_H \simeq 0.28$) have the most potential to enhance the probability of polymorphism, relative to the DM. Polymorphism is gained under opposing selection because balancing selection between the phases produces a stable internal equilibrium, where none would exist under the DM. This gain in polymorphism more than offsets the loss due to disruption by haplophase selection of the equilibrium under heterozygote advantage in diplophase.

The role of dominance in diplophase in the HDM suggests that to the extent that dominance evolves, the potential for maintaining polymorphism in haplodiplontic populations should increase. That is, as the relative fitness of the heterozygote increases (upward motion in the unshaded region of fig. II.7A), the more likely it is that the diplophase fitness regime falls within the parameter space supporting polymorphism under opposing selection (i.e., the shaded region of fig. II.7C). Moreover, if most mutations are either lethal recessive or deleterious semi-recessive in their diplophase expression (as suggested by Charlesworth 1979; Klekowski 1988), the potential for polymorphism is particularly great if they also happen to confer an advantage in haplophase. Under opposing selection, the proportion of homozygous lethal recessive and deleterious semi-recessive fitness combinations that fall within the polymorphism space of the HDM (fig. II.7C) reaches a maximum at $Q \simeq 0.72$ (fig. II.8B). Thus, opposing selection has the potential to retain alleles that would ultimately be lost under selection in diplophase alone.

Opposing selection is a type of balancing selection between the discrete haploid and diploid stages of the life history (Haldane and Jayakar 1963). As such, it may be viewed as a special case of

antagonistic pleiotropy (Rose 1982). In both the HDM and Rose's model, dominance has the effect of enhancing the probability of polymorphism. The models differ, however, in that reversal of the relative fitness of alleles occurs between different developmental stages of the same ploidy in antagonistic pleiotropy, but between differing ploidy levels in opposing selection. Thus, opposing selection represents a unique mechanism for retaining genetic variability in populations of haplodiplonts.

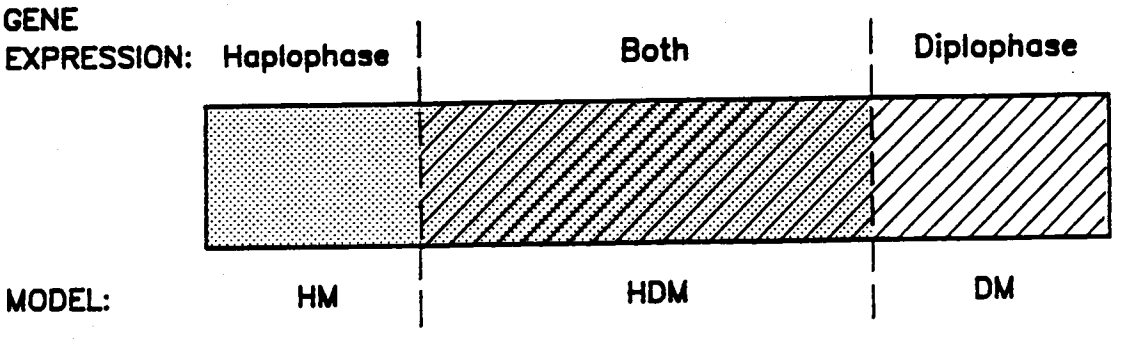
EVIDENCE FOR HDM DYNAMICS IN NATURAL POPULATIONS

The importance of HDM dynamics for reducing or maintaining genetic variation in natural populations of haplodiplonts is almost entirely unexplored. Three conditions govern the potential effect of HDM dynamics on polymorphism: The first two--that a gene is expressed in both haploid and diploid phases and that alleles are not selectively neutral--are necessary conditions for the HDM to apply. The third condition--the relative sign and magnitude of selection in the two phases--determines whether selection will tend to eliminate or retain genetic variability within a population. These conditions rarely have been documented in natural populations.

Gene expression in both phases is a necessary condition for HDM dynamics to apply (fig. II.9). Overlap in gene expression should be greater, and more of the genome should be subject to HDM dynamics, in taxa in which the gametophytic and sporophytic phases are similar in morphology and physiology. Expression of certain loci in both phases has been documented for isomorphic algae (Cheney and Babbel 1978) and pteridophytes (Gastony and Gottlieb 1982, 1985; Haufler and Soltis 1984; Haufler 1985), but the extent of overlap in gene expression between the phases has not been quantified. The little quantitative information available on gene expression in the two phases derives from studies of angiosperms (reviews in Heslop-Harrison 1980; Mulcahy and Mulcahy 1987). Quantitative estimates of overlap in gene expression between male gametophytes (pollen) and sporophytes range from 34 to 72% for plants grown in greenhouse or laboratory (*Lycopersicon esculenta*, 58%, Tanksley et al. 1981; *Tradescantia*

Figure II.9. A schematic representation of gene expression in the haplodiplontic genome, indicating the regions of applicability of the HM (shaded), the DM (hatched), and the HDM (both) (after Heslop-Harrison 1980). Gene expression in both phases is a necessary condition for the HDM. If a locus is not expressed in one phase, its alleles are effectively neutral in that phase (Hartl 1970). The HDM then reduces to either the HM or the DM, depending on whether the locus is silent in diplophase or in haplophase, respectively.

Figure II.9


GENE
EXPRESSION:
Haplophase
Both
Diplophase
MODEL:
HM
HDM
DM

paludosa, 34-56%, Willing and Mascarenhas 1984; and *Zea mays*, 72%, Sari-Gorla et al. 1986). Thus, even among these plants with a highly reduced haplophase, the first necessary condition exists for HDM dynamics to apply, because a significant proportion of the genome is expressed in both phases.

A second necessary condition is that selection occurs in both phases. Although selection studies are lacking for bryophytes, pteridophytes, and multicellular algae, studies of angiosperms have demonstrated that pollen competition (review in Mulcahy and Mulcahy 1987; also see contributions to Mulcahy et al. 1986) and pollen selection (e.g., Searcy and Mulcahy 1985) may affect the frequency of traits expressed in the sporophyte. Moreover, the third condition governing HDM dynamics has been explored in studies demonstrating the sign of correlations in fitness between the two phases. A positive correlation in fitness (i.e., reinforcing selection) between gametophytic and sporophytic traits has been found in studies of pollen (Mulcahy and Mulcahy 1987; Mulcahy et al. 1986; Searcy and Mulcahy 1985). This evidence of reinforcing selection presumably reflects selective elimination of inferior variants in the gametophytic stage. In contrast, negative correlations in fitness (i.e., opposing selection) between gametophytes and sporophytes have been observed in studies of non-Mendelian transmission during plant life cycles (e.g., Muntzing 1968, Clegg et al. 1978, Clegg and Epperson 1988). This evidence of opposing selection was detectable, in part, because traits deleterious in diplophase persist (Heslop-Harrison 1980). To evaluate the importance of HDM dynamics in natural populations, studies are needed that document the relative magnitude,

as well as the sign, of selection in both phases.

Several factors complicate the study of HDM dynamics in higher plants. Studies of pollen competition, for example, have detected only reinforcing selection between the phases. Further, special care must be taken to eliminate non-genetic causes (e.g., maternal effects or environmental effects on pollen quality) of correlations between conditions favoring pollen competition and vigor of sporophytes (Charlesworth et al. 1987; Charlesworth 1988; Young and Stanton 1990). In addition, the frequency of pollen competition in nature is presently unknown for most taxa (Snow 1986, 1990). Studies of selective transmission of traits in both phases are complicated by the small size of gametophytes and the difficulty of replicating gametophytic genotypes. Further, the dependence of the female gametophyte on the sporophyte makes it difficult to determine whether biased transmission is due to gametophytic or early zygotic selection.

There are a number of advantages to using lower plants (algae, bryophytes, and pteridophytes) as model systems for studying HDM dynamics. In lower plants, a larger portion of the genome should be subject to HDM dynamics, because both phases undergo relatively extensive development. Both phases tend to be macroscopic and gametophytes may produce numbers of genetically identical gametes. Gametophytes of algae and pteridophytes are physiologically independent of parental sporophytes, facilitating the separation of components of selection in each phase. Finally, ecological differentiation between the phases of pteridophytes (e.g., Sato 1982) and algae (e.g., Luxoro and Santelices 1989; Olson 1990; Zupan and West 1990) suggest that the relative fitness of individuals with

certain traits may vary between the phases temporally or spatially. Thus, selection should act on the vegetative, as well as the reproductive functions of both phases. Although direct evidence for selection and HDM dynamics is scant, it is possible to test the hypothesis that the presence of a prominent haploid phase is associated with reduced levels of genetic polymorphism in natural populations.

ENZYME POLYMORPHISM IN HAPLODIPLONTIC POPULATIONS

Opposing selection between haplophase and diplophase has a presently unquantified, but potentially important, role in maintaining genetic variation in populations of haplodiplonts (Ennos 1983). If the net effect of selection in haplophase were to more rapidly eliminate alleles from a population, then there would be a negative relationship between the prominence of haplophase in the life histories of species and the occurrence of polymorphism within species' populations. We test this hypothesis by comparing levels of polymorphism among several plant divisions whose life cycles represent a continuum from dominance of the haploid phase, through isomorphy of haploid and diploid stages, to diplophase dominance.

If haplophase selection reduces genetic variability in natural populations, occurrence of polymorphism should be lowest in gametophyte-dominant algae and bryophytes, intermediate among isomorphic algae, and highest among sporophyte-dominant algae, pteridophytes, gymnosperms, and angiosperms. Estimates of polymorphism have been compiled for gymnosperms and angiosperms (Hamrick and Godt 1989). However, despite reports of high levels of polymorphism among bryophytes (Yamazaki 1981, 1984; Szweykowski 1984; Wyatt 1985; Wyatt et al. 1989b), a comprehensive comparison of polymorphism among bryophytes, algae, and pteridophytes has not been previously published. To evaluate the extent of polymorphism in populations of these taxa, we compiled data from literature published between 1970 and 1989 (table II.2). Studies were included only if a genetic interpretation of the data was possible. Thirty-two studies

Table II.2. Electrophoretic variability in haplodiplontic organisms.

Taxon	Ph[1]	Rp[2]	Br[3]	Pop[4]	Ind[5]	Loci: Number Scored	Loci: P_p[6]	Loci: H_e[7]	Alleles: Number/ Pm Loc[8]	Alleles: Number/ Locus[9]	Reference
BRYOPHYTES:											
Bryophyta (mosses):											
Climacium americanum	G	A	D	3	220	8	54.2	0.236	2.13	1.63	Shaw et al. 1987
Plagiomnium ciliare	G	S	D	13	430	14	31.3	0.079	1.98	1.35	Wyatt 1985, Wyatt et al. 1989a
Plagiomnium ellipticum	G	S	D	4	112	18	50.0	0.121	2.36	1.83	Wyatt et al. 1989b
Plagiomnium insigne	G	S	D	4	90	18	16.7	0.065	2.00	1.17	Wyatt et al. 1989b
Plagiothecium curvatum	G	S	M	8	8-34[d]	20	48.0	0.190	--	1.90	Hofman 1988
Plagiothecium denticulatum	G	S	M	2	8-34[d]	20	37.0	0.170	--	1.70	Hofman 1988
Plagiothecium ruthei	G	S	M	2	8-34[d]	20	35.0	0.160	--	1.60	Hofman 1988
Plagiothecium nemorale	G	S	D	4	8-34[d]	20	39.0	0.160	--	1.70	Hofman 1988
Plagiothecium latebricola	G	S	D	2	12	20	25.0	0.110	--	1.30	Hofman 1988
Plagiothecium undulatum	G	A	--	3	8-34[d]	20	16.0	0.090	--	1.20	Hofman 1988
Polytrichum commune	G	S	D	21	--	12	17.4	0.091	--	1.22	Derda 1989[b]
Racopilum capense	G	--	P	1	--	7	29.0	0.069	--	1.29	Bramen 1986[b]
Racopilum convolutaceum	G	--	P	2	--	8	25.0	0.102	--	1.43	Bramen 1986[b]
Racopilum cuspidigerum	G	--	P	2	--	8	50.0	0.242	--	1.71	Bramen 1986[b]
Racopilum cuspidigerum	G	A	P	2	24	10	30.0	0.135	2.40	1.50	de Vries et al. 1983
Racopilum intermedium	G	--	P	1	--	7	43.0	0.093	--	1.43	Bramen 1986[b]
Racopilum robustum	G	--	P	1	--	7	29.0	0.127	--	1.29	Bramen 1986[b]
Racopilum spectabile	G	--	P	3	--	8	45.0	0.168	--	1.62	Bramen 1986[b]
Racopilum spectabile	G	--	P	3	35	10	38.5	0.163	2.61	1.70	de Vries et al. 1983

Table II.2 (continued).

Taxon	Ph[1]	Rp[2]	Br[3]	Pop[4]	Ind[5]	Loci: Number Scored	Loci: P_p[6]	H_e[7]	Alleles: Number/ Pm Loc[8]	Alleles: Number/ Locus[9]	Reference
BRYOPHYTES (continued):											
Bryophyta (mosses) (continued):											
Racopilum strumiferum	G	--	P	3	--	8	56.0	0.180	--	1.57	Bramen 1986[b]
Racopilum tomentosum	G	--	P	3	--	8	43.0	0.174	--	1.62	Bramen 1986[b]
Sphagnum pulchrum	G	A	--	6	296	16	29.2	0.091	--	--	Daniels 1982
Hepatophyta (liverworts):											
Conocephalum conicum (A)[a]	G	S	D	5	--	28	13.6	0.044	--	1.19	Odrzykoski 1986[b]
Conocephalum conicum (J)[a]	G	S	D	2	201	11	81.8	0.167	3.22	2.77	Yamazaki 1981, 1984
Conocephalum conicum (J)[a]	G	S	D	6	1-4	11	15.2	0.167	--	--	Yamazaki 1981
Conocephalum conicum (L)[a]	G	S	D	24	--	20	8.5	0.025	--	1.09	Odrzykoski 1986[b]
Conocephalum conicum (S)[a]	G	S	D	16	--	20	4.4	0.012	--	1.04	Odrzykoski 1986[b]
Pellia epiphylla	G	S	M	6	--	13	9.1	0.026	--	1.14	Zielinski 1987[b]
Pellia borealis	G	S	M	12	--	13	5.9	0.024	--	1.07	Zielinski 1987[b]
Pellia neesiana	G	S	D	4	--	11	9.1	0.031	--	1.09	Zielinski 1987[b]
Plagiochila asplenioides	G	A	D?	5	417	3	93.3	--	2.00	2.00	Krzakowa & Szweykowski 1979
Plagiochila asplenioides	G	A	D?	20	--	18	2.5	0.008	--	1.02	Wachowiak 1986[b]
Plagiochila porelloides	G	A?	D?	8	--	18	0.0	0.000	--	1.00	Wachowiak 1986[b]
Riccia dictyospora (A)[a]	G	S	M	25	1248[c]	8	9.1	0.022	--	1.10	Dewey 1989
Riccia dictyospora (B)[a]	G	S	M	14	321[c]	8	18.1	0.062	--	1.21	Dewey 1989
Riccia dictyospora (C)[a]	G	S	M	3	37[c]	8	12.7	0.048	--	1.13	Dewey 1989

Table II.2 (continued).

Taxon	Ph[1]	Rp[2]	Br[3]	Pop[4]	Ind[5]	Loci		H_e[7]	Alleles		Reference
						Number Scored	P_p[6]		Number/ Pm Loc[8]	Number/ Locus[9]	
HETEROMORPHIC ALGAE (Gametophyte dominant):											
Rhodophyta (red algae):											
Porphyra yezoensis	G	S	--	11	605	8	40.0	0.152	1.61	1.46	Miura et al. 1979
ISOMORPHIC ALGAE:											
Chlorophyta (green algae):											
Chaetomorpha aerea	B	A	D?	1	16	9	66.7	--	--	--	Blair et al. 1982
Chaetomorpha atrovirens	B	S?	D?	1	39	16	75.0	--	--	--	Blair et al. 1982
Chaetomorpha linum	B	S	D?	2	52	17	76.5	--	--	--	Blair et al. 1982
Chaetomorpha melagonium	B	S?	D?	1	11	5	20.0	--	--	--	Blair et al. 1982
Enteromorpha linza	B	A	D?	5	1074	5	64.0	--	--	--	Innes & Yarish 1984
Rhodophyta (red algae):											
Eucheuma acanthocladum	B	A	--	1	12	8	25.0	--	--	--	Cheney & Babbel 1978
Eucheuma gelidium	B	A	--	1	29	7	28.6	--	--	--	Cheney & Babbel 1978
Eucheuma isiforme	B	S	--	3	121	11	36.4	--	--	--	Cheney & Babbel 1978
Eucheuma nudum	B	S	--	3	176	12	31.3	--	--	--	Cheney & Babbel 1978

Table II.2 (continued).

Taxon	Ph[1]	Rp[2]	Br[3]	Pop[4]	Ind[5]	Loci		Alleles		Reference
						Number Scored	P_p[6]	H_e[7]	Number/ Pm Loc[8]	Number/ Locus[9]	
PTERIDOPHYTES:											
Pteridophyta (ferns):											
Adiantum pedatum (W)[e]	S	S	--	6	186	13	56.4	0.185	2.33	1.83	Paris & Windham 1988
Adiantum pedatum (S)[e]	S	S	--	1	11	13	61.4	0.166	2.25	1.77	Paris & Windham 1988
Adiantum pedatum (S-T)[e]	S	--	Z	1	22	13	76.9	0.348	2.00	1.77	Paris & Windham 1988
Asplenium platyneuron	S	S	I	3	119	15	26.7[f]	--	--	--	Werth et al. 1985
Asplenium rhizophyllum	S	S?	O	3	49	15	26.7[f]	--	--	--	Werth et al. 1985
Asplenium montanum	S	S	I	3	56	15	13.3[f]	--	--	--	Werth et al. 1985
Asplenium bradleyi	S	S?	Z	2	54	15	20.0[f]	--	--	--	Werth et al. 1985
Asplenium pinnatifidum	S	S?	Z	2	34	15	26.7[f]	--	--	--	Werth et al. 1985
Asplenium ebenoides	S	A	Z	2	4	15	20.0[f]	--	--	--	Werth et al. 1985
Blechnum spicant	S	S	O	6	553	12	23.6	0.024	1.96	1.40	P. Soltis & D. Soltis 1988a
Bommeria hispida	S	S	O	12	≤30[g]	13	61.5[f]	0.262	3.25	2.69	Haufler 1985
Bommeria subpaleacea	S	S	O	3	<5	13	38.5[f]	0.133	2.20	1.46	Haufler 1985
Bommeria ehrenbergiana	S	S	O	1	<5	13	23.1[f]	0.103	2.33	1.31	Haufler 1985
Bommeria pedata	S	A	Z	5	<5	13	46.2[f]	0.218	2.17	1.54	Haufler 1985
Botrychium dissectum	S	S	I	3	--[h]	11	18.2	--	--	--	McCauley et al. 1985
Botrychium virginianum	S	S	I	4	184	18	16.5	--	2.17	1.20	D. Soltis & P. Soltis
Dryopteris expansa	S	S	X	9	502	11	9.6	0.032	2.00	1.11	D. Soltis & P. Soltis
Pellaea andromedifolia	S	S	O	9	146	7	63.5	--	2.07	1.68	Gastony & Gottleib 1985
Polystichum munitum	S	S	O	4	341	12	54.2	0.111	2.80	2.23	P. Soltis & D. Soltis 1987
Pteridium aquilinum	S	A	O	4	191	13	34.6	0.122	--	1.62	Wolf et al. 1988

Table II.2 (continued).

Taxon	Ph[1]	Rp[2]	Br[3]	Pop[4]	Ind[5]	Loci: Number Scored	Loci: P_p[6]	H_e[7]	Alleles: Number/ Pm Loc[8]	Alleles: Number/ Locus[9]	Reference
PTERIDOPHYTES (continued):											
Microphyllophyta (club mosses):											
Huperzia miyoshiana	S	A	O	4	70	22	15.9	--	--	--	D. Soltis & P. Soltis 1988; P. Soltis & D. Soltis 1988b
Lycopodium annotinum	S	A	O	4	35	21	11.9	--	--	--	D. Soltis & P. Soltis 1988; P. Soltis & D. Soltis 1988b
Lycopodium clavatum	S	A	O	12	165	20	12.5	--	--	--	D. Soltis & P. Soltis 1988; P. Soltis & D. Soltis 1988b
Lycopodium lucidulum	S	A	--	16	241	18	9.7	0.041	2.06	1.08	Levin & Crepet 1973
Arthrophyta (horsetails):											
Equisetum arvense	S	A	O	17	669	10-13	19.1	--	--	1.16	D. Soltis et al. 1988

Table II.2 (continued).

---

[1] Phase subjected to electrophoresis (G=gametophyte, S=sporophyte, B=both).

[2] Reproductive mode. Bryophytes: sexual = sporophytes usually present; asexual = sporophytes rare or absent. Pteridophytes and spermatophytes: sexual = reproduction by spores or seeds, respectively; asexual = reproduction largely vegetative or by asexual spores or seeds. Classification derived from original studies for bryophytes and pteridophytes (table II.2) or from Hamrick and Godt (1989) for spermatophytes.

[3] Breeding system. Bryophytes: Monoecious = male and female reproductive structures on same genet; phyllodioecious = male genets epiphytic on leaves of female genet; dioecious = separate male and female genets. Pteridophytes: Inbreeding = high levels of self-fertilization within monoecious gametophytes and among gametophytes derived from spores of the same sporophyte; outcrossing = low levels of self-fertilization. Spermatophytes: Selfing = obligately self-pollinated; mixed = both self- and non-self- pollinated; outcrossing = obligately non-self-pollinated. Classifications derived from original studies for bryophytes and pteridophytes (table II.2) or from Hamrick and Godt (1989) for spermatophytes.

[4] Number of populations surveyed.

[5] Total number of individuals surveyed.

[6] Percent polymorphic loci per population. Note that data in table may differ from those presented by the original author(s), because we recalculated P_p, when possible, to meet the criteria discussed in the text.

[7] Mean expected heterozygosity.

[8] Mean number of alleles per polymorphic locus.

[9] Mean number of alleles per locus.

-- data not available.

Table II.2 (continued).

---

[a] Sibling species within genus.

[b] Study cited in Wyatt et al. 1989b and in Stoneburner et al. 1990.

[c] Mean number of samples per locus.

[d] Number of individuals per population not listed separately by author.

[e] Populations of Adiantum pedatum (W=woodland, S=serpentine, S-T=serpentine tetraploid).

[f] Data pooled among populations by the original author(s). Thus, the value represents polymorphism at the species, rather than at the population, level.

[g] Eighteen and thirty individuals from two populations, ≤5 individuals from ten other populations.

[h] Subsample of unreported size from among 209 individuals

including 65 species met this criterion, having sampled an average of 6.0 populations per species, and 13.1 loci per species. (Studies that sampled fewer than 5 individuals per population were excluded from analyses, but are included in table II.2.)

Within each population, the percent of loci found to be polymorphic was calculated from the original data if possible. (A locus was considered polymorphic if the frequency of the most common allele was $\leq$ 99%.) Expected mean heterozygosity, H_e, and mean number of alleles per locus and per polymorphic locus are included in table II.2, if given, but were excluded from further analysis due to limited sample sizes. We averaged the percent polymorphic loci per population over all populations to generate a mean population-level rate of polymorphism, P_p (Hamrick and Godt 1989), for each species. Summary statistics (mean, standard error) were calculated for the data set as a whole; for taxa grouped by dominant phase (i.e., for bryophytes, isomorphic algae, and pteridophytes) and by plant division; and for taxa grouped by reproductive mode or breeding system. One-way analyses of variance and post-hoc contrasts among means were used to determine the significance of differences between pairs of means. The single heteromorphic algal species was excluded from analyses of variance due to the inadequate sample size in that category.

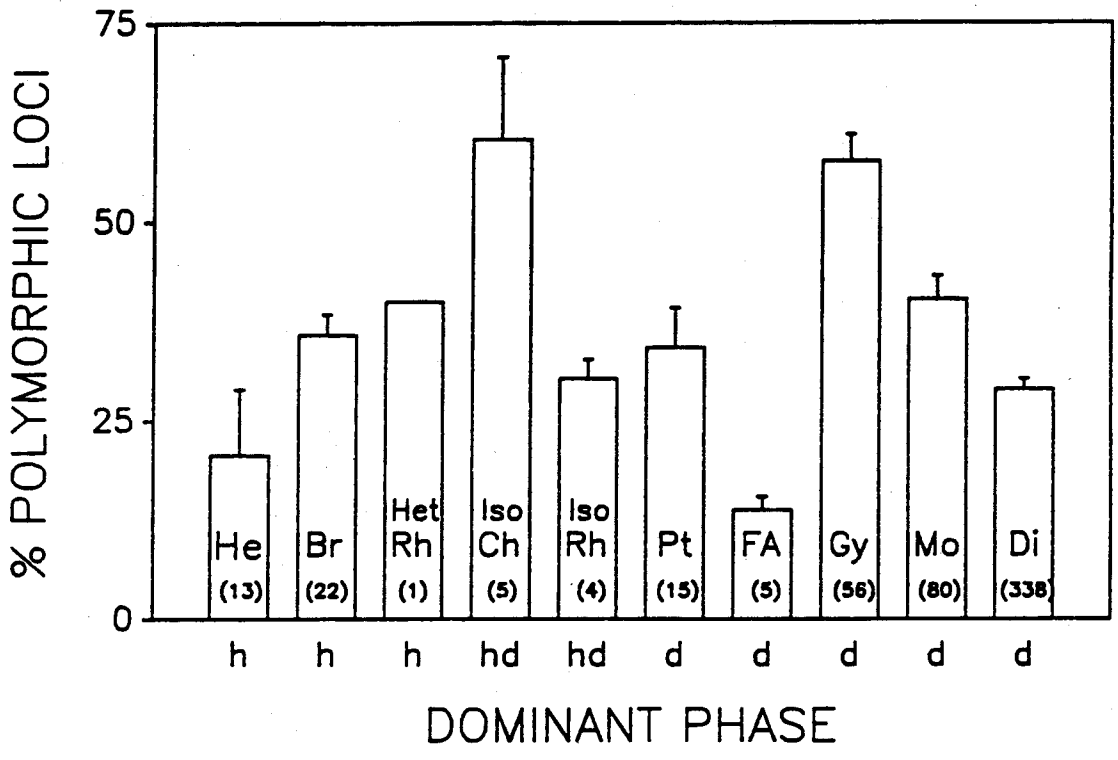
The results of our analysis do not support the notion that haplophase selection reduces polymorphism in natural populations. Rather, the occurrence of enzyme polymorphism in these 65 haplodiplontic species is similar to that observed in diploid, sporophyte-dominant gymnosperms and angiosperms and in diploid animals. Within populations, 32.3 $\pm$ 2.7(sem)% of loci were polymor-

phic, compared to 34.2 ± 1.2% for angiosperms and gymnosperms (Hamrick and Godt 1989) and to 22.6 ± 0.6% and 37.5 ± 1.1% for vertebrates and invertebrates, respectively (Nevo et al. 1984). Furthermore, enhanced levels of polymorphism do not accompany the trend toward diplophase-dominance among plant divisions.

Combining the results of the present compilation with those of Hamrick and Godt (1989), there is no apparent relationship between the level of polymorphism and the relative prominence of the phases in the life history (fig. II.10). Average levels of polymorphism were nearly identical in bryophytes where the gametophytic stage dominates the life cycle and in pteridophytes where the sporophyte is dominant (30.2 ± 3.6% and 29.1% ± 4.3%, respectively). Mean levels of polymorphism were somewhat higher in isomorphic algae (47 ± 7.7%), but means among the three groups did not differ significantly ($F = 2.625$, $p = 0.081$). Although significant differences in polymorphism exist among the six divisions we analyzed (i.e., among liverworts, mosses, isomorphic green and red algae, ferns, and fern allies, fig. II.10) ($F = 4.184$, $p = 0.003$), differences between divisions with similar life histories were as great as, or greater than, those between divisions with different life histories. For example, in post-hoc contrasts, mosses, isomorphic red algae, and ferns did not differ significantly despite extreme differences in the prominence of haplophase in their life histories. However, significantly more loci were polymorphic in mosses than in liverworts ($F = 5.055$, $p = 0.028$), in green than in red isomorphic algae ($F = 5.422$, $p = 0.023$), and in ferns than in fern allies ($F = 4.188$, $p = 0.045$), despite the similarity in life history between these pairs of taxa. Therefore, we conclude that the relative

Figure II.10. Polymorphism within plant populations that represent regions on a continuum of life history variation (from table II.2 and Hamrick and Godt 1989). Non-vascular plants: Bryophytes (Br = Bryophyta; He = Hepatophyta); and algae (Het Rh = heteromorphic Rhodophyta; Iso Ch and Iso Rh = isomorphic Chlorophyta and Rhodophyta, respectively). Vascular plants: Pteridophytes (Pt = Pteridophyta; FA = fern allies, Arthrophyta and Microphyllophyta) and spermatophytes (Gy = gymnosperms; Mo and Di = angiosperms, Monocotyledonae and Dicotyledonae, respectively). Dominant phase: h = haplophase dominant; hd = isomorphic phases; d = diplophase dominant. Sample sizes (numbers of species) given in parentheses.

Figure II.10


75
50
25
0
% POLYMORPHIC LOCI
He
(13)
Br
(22)
Het
Rh
(1)
Iso
Ch
(5)
Iso
Rh
(4)
Pt
(15)
FA
(5)
Gy
(56)
Mo
(80)
Di
(338)
h
h
h
hd
hd
d
d
d
d
d
DOMINANT PHASE

prominence of the gametophyte is not a good predictor of the level of genetic polymorphism present in a population.

Differences among taxa in mode of reproduction (i.e., sexual *versus* asexual) and in breeding system also were not consistently associated with variation in the percentage of loci observed to be polymorphic. Sexual and asexual taxa were similar, with 32.1 ± 6.3% and 31.2 ± 3.7% of loci polymorphic, respectively ($F = 0.027$, $p = 0.871$). Similarly, mode of reproduction was not related to levels of genetic variability within plant divisions or within the three groups of divisions (bryophytes, isomorphic algae, and pteridophytes) (table II.3, $p > 0.05$ in all ANOVA's). These results are consistent with those observed for higher plants where levels of polymorphism were not significantly different between sexual and asexual populations (Hamrick and Godt 1989, table II.3). Likewise, variation in breeding system was not correlated with levels of polymorphism, except in ferns where inbreeders exhibited significantly lower levels of polymorphism than outcrossers ($F = 7.285$, $p = 0.027$). Negative results such as ours must be interpreted with caution, especially in light of the relatively small sample sizes. Nevertheless, they do suggest that patterns of enzyme polymorphism among plant divisions cannot be explained by differences among divisions in the mode of reproduction or in breeding system.

An important limitation of our analysis is that we have compared polymorphism among plant divisions which differ in many ways, in addition to the prominence of haplophase in the life history. Ideally, comparisons should be made at the lowest taxonomic level possible within a plant division, i.e., between species in the same

Table II.3. Average population-level polymorphism (%) in major plant taxa, by reproductive mode and breeding system[1].

Taxon	All Species	Reproductive Mode[2]		Breeding System[2]		
		Sexual	Asexual			
BRYOPHYTES:				Monoecious	Phyllodioecious	Dioecious
Hepatophyta	20.3 (8.4) 13	17.2 (7.3) 10	47.9 (45.4) 2	11.0 (2.1) 5	--	23.5 (14.7) 5
Bryophyta	35.8 (2.6) 22	36.6 (2.7) 18	32.4 (8.0) 4	40.0 (4.0) 3	38.9 (3.3) 10	33.4 (5.7) 7
GRAND MEAN:	30.2 (3.6) 35	29.7 (3.5) 28	37.5 (13.2) 6	21.9 (5.6) 8	38.9 (3.3) 10	29.3 (6.7) 12

Table II.3 (continued).

Taxon	All Species	Reproductive Mode[2]		Breeding System[2]	
		Sexual	Asexual		
PTERIDOPHYTES:					
				Inbreeding	Outcrossing
Pteridophyta	34.2 (5.0) 15	36.8 (6.7) 11	34.6 (0.0) 1	18.7 (2.9)a 4	44.0 (7.3)b 6
Fern Allies*	13.8 (1.7) 5	--	13.8 (1.7) 5	--	14.9 (1.7) 4
GRAND MEAN:	29.1 (4.3) 20	36.8 (6.7) 11	17.3 (3.7) 6	18.7 (2.9) 4	32.4 (6.4) 10

Table II.3 (continued).

Taxon	All Species	Reproductive Mode[2]		Breeding System[2]			
		Sexual	Asexual				
SPERMATOPHYTES[1]:							
				Selfing		Mixed	Outcrossing
				Pollination System			
	34.2 (1.2) 468	34.9 (1.3) 413	29.4 (3.3) 56	20.0 (2.3)a 113	Animal:	29.2 (2.5)ab 85	35.9 (1.8)b 164
					Wind:	54.4 (8.9)c 10	49.7 (2.6)c 102

Table II.3 (continued).

---

[1] Data for bryophytes and pteridophytes are derived from table II.2 and for spermatophytes from Hamrick and Godt (1989). Mean (standard error); sample size, below. Means within a row that are followed by the same letter or by a blank are not significantly different at the $\alpha = 0.05$ level.

[2] See table II.2 caption for definitions.

-- = data not available.

* Microphyllophyta (club mosses) and Arthrophyta (horsetails).

† Coniferophyta (gymnosperms) and Anthophyta (angiosperms). Data are from Hamrick and Godt (1989).

order, family, or genus. Multicellular algae are particularly suitable for such a survey, because many pairs of closely-related taxa differ in the relative importance of the haploid and diploid phases in the life cycle (see taxa described in Tanner 1981, Pedersen 1981, West and Hommersand 1981, Bold and Wynne 1985). Unfortunately, despite increasing numbers of electrophoretic studies of algae (Cheney 1985), few have addressed the problem of genetic variability. To date, only four studies of haplodiplontic algae (table II.2) offer genetic interpretations of the data that permit comparison with studies of electrophoretic variability in other plants or in strictly haploid or diploid algae.

Future studies could test whether P_p is inversely correlated with the relative size or duration of haplophase, by determining levels of polymorphism for pairs of species that differ in the relative prominence of haplophase. It should be noted, however, that interpretation of such comparisons could be confounded by the presence of alternate asexual pathways (e.g., apogamy, parthenogenesis, and apomeiosis) (Bold and Wynne 1985) and by absence of coordination among nuclear (haploid *versus* diploid), reproductive (gametophytic *versus* sporophytic), and morphological phases (Clayton 1988; Maggs 1988). Furthermore, the life cycles of certain algae may be labile under varied environmental conditions, both in switching between sexual and asexual pathways and in the degree of coordination between nuclear, reproductive, and morphological phases. Thus, independent confirmation of the life cycle would be required for many species pairs.

Opposing selection between the phases is one mechanism that

might contribute to the maintenance of high levels of polymorphism among haplodiplonts, because it may partially counterbalance reinforcing selection and other factors that tend to reduce polymorphism. Alternative explanations for the observed rates of polymorphism in haplodiplonts include (1) neutrality of alleles (e.g., Yamazaki 1981, 1984; review in Nei 1983) or (2) balancing selection between habitats (e.g., Nevo et al. 1984), between developmental stages of the same ploidy level (e.g., Rose 1982), or between the sexes (e.g., Gregorius 1982). Unfortunately, the small sample size in our compilation does not permit further analyses of correlated ecological variables (e.g., geographic range, habitat type) that might suggest mechanisms for maintenance of this high level of polymorphism in haplodiplontic organisms. Nevertheless, there is no evidence to suggest that selection in haplophase reduces polymorphism in populations of organisms with a prominent gametophytic stage.

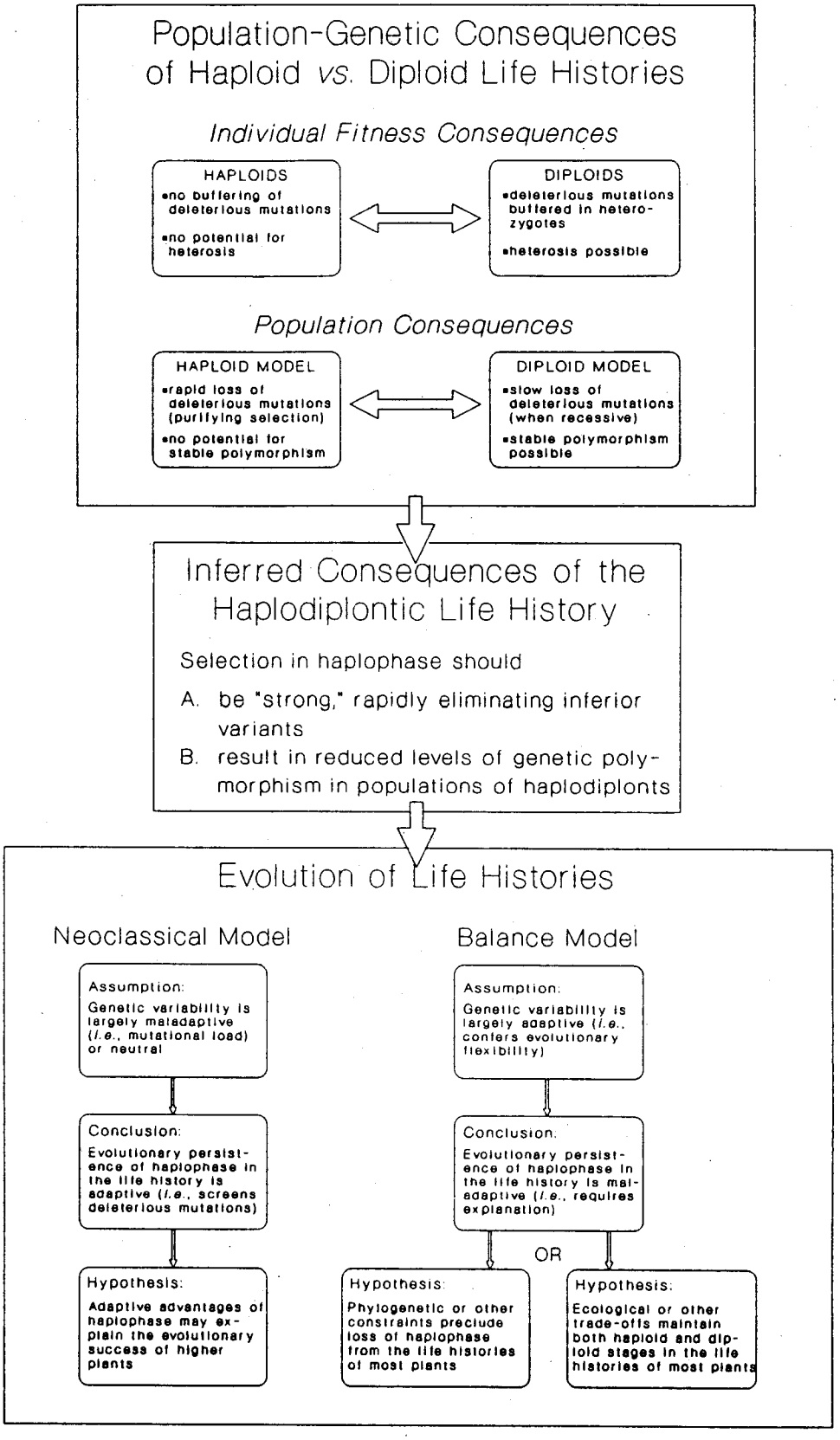
GENERAL DISCUSSION

In this paper we have examined the validity of two common-sense notions about selection during haplophase (fig. II.11, center box): (A) that it is inherently "strong" (i.e., that it rapidly eliminates inferior variants) and, consequently, (B) that it results in the maintenance of reduced levels of genetic polymorphism in populations of haplodiplonts. These two ideas are central to a loose system of arguments (review in Willson 1981) linking an understanding of the population-genetic consequences of life histories (fig. II.11, upper box) with explanations for the evolution of the haplodiplontic life history itself (fig. II.11, lower box). Our results show that these central ideas are only partially correct. Furthermore, we suggest that identifying functional or adaptive differences between haploids and diploids is only a first step in understanding both the consequences and the evolutionary causes of the haplodiplontic life history. A more comprehensive approach must also explicitly consider (1) the net effect of evolutionary processes within both phases of the life history and (2) the consequences of variation among life histories that differ in their allocation to each phase. We illustrate these points in the discussion that follows.

Inferences about the dynamics of gametophytic selection often have been based on implicit or explicit comparisons of the consequeces of haploidy *versus* diploidy (fig. II.11, upper box) at the individual and population levels (e.g., Stebbins 1950, 1960; Bonner 1965; Stebbins and Hill 1980; Yamazaki 1981, 1984; Pfahler 1983; Graham 1985; Weeden 1986; reviews in Willson 1981; Szweykowski 1984; Wyatt

Figure II.11. Outline of arguments linking population-genetic consequences of natural selection in haplodiplonts with explanations for the evolution of life histories in plants. Conclusions A and B (center box) are inferences based on comparisons of the haploid and diploid life histories (upper box). Taken together, A and B have been invoked in two lines of argument (lower box) leading to contrasting hypotheses regarding the evolution of life histories in plants. (See text for details and references.)

Figure II.11


Population-Genetic Consequences of Haploid vs. Diploid Life Histories
Individual Fitness Consequences
HAPLOIDS
•no buffering of deleterious mutations
•no potential for heterosis
DIPLOIDS
•deleterious mutations buffered in heterozygotes
•heterosis possible
Population Consequences
HAPLOID MODEL
•rapid loss of deleterious mutations (purifying selection)
•no potential for stable polymorphism
DIPLOID MODEL
•slow loss of deleterious mutations (when recessive)
•stable polymorphism possible
Inferred Consequences of the Haplodiplontic Life History
Selection in haplophase should
A. be "strong," rapidly eliminating inferior variants
B. result in reduced levels of genetic polymorphism in populations of haplodiplonts
Evolution of Life Histories
Neoclassical Model
Assumption:
Genetic variability is largely maladaptive (i.e., mutational load) or neutral
Conclusion:
Evolutionary persistence of haplophase in the life history is adaptive (i.e., screens deleterious mutations)
Hypothesis:
Adaptive advantages of haplophase may explain the evolutionary success of higher plants
Balance Model
Assumption:
Genetic variability is largely adaptive (i.e., confers evolutionary flexibility)
Conclusion:
Evolutionary persistence of haplophase in the life history is maladaptive (i.e., requires explanation)
OR
Hypothesis:
Phylogenetic or other constraints preclude loss of haplophase from the life histories of most plants
Hypothesis:
Ecological or other trade-offs maintain both haploid and diploid stages in the life histories of most plants

1985; Wyatt et al. 1989b; Ennos 1990). From these straightforward comparisons, it might be tempting to conclude that the presence of a haplophase in the life cycle should speed the loss of deleterious alleles and reduce the occurrence of polymorphism. However, our results show that this inference is only partially correct because it does not recognize the complex dynamics of selection acting in both phases of the life cycle. That is, the maintenance of polymorphism depends on the relative sign and magnitude of selection regimes in the two phases.

First, analysis of the HDM indicates that the sign of correlations in fitness of alleles between the two phases is of overriding importance in predicting the outcome of natural selection in the HDM. With reinforcing selection (positive correlation in fitness), gametophytic selection will tend to speed the elimination of deleterious alleles (fig. II.4B) or to disrupt equilibria (fig. II.4A and C), reducing the probability of stable polymorphism (fig. II.8B) and lowering mutational load, as predicted by many authors. However, under opposing selection (negative correlation in fitness), new opportunities for retaining genetic variability arise in the HDM. Opposing selection may slow or reverse the loss of alleles that are deleterious in diplophase and can result in polymorphism under conditions where none would exist in the DM (fig. II.5B and C), thus enhancing the probability of stable polymorphism (fig. II.8B). Indeed, our results show that even quite strong opposing selection [$s_H < (2 - \sqrt{2})$] may increase the probability of polymorphism in the HDM up to 25% over that in the DM (fig. II.8B).

Second, specific quantitative relationships between the two

phases in the magnitude of selection affect the qualitative outcome of selection in the HDM (table II.1; figs. II.3-II.5). That is, the intensity of haplophase selection needed to permit or preclude polymorphism depends on the selection regime in diplophase. For example, given a particular sporophytic selection regime, the qualitative outcome switches from elimination of A_1 to the maintenance of stable polymorphism (fig. II.5C) as gametophytic selection changes from weak ($w_2 \geq w_{12}$) to intermediate ($w_2 < w_{12}$) intensity. Briefly, analysis of the HDM indicates that the rate of change of allele frequencies, the existence and stability of equilibria, and the polymorphism frequency all depend on the qualitative and quantitative relationship between fitness coefficients in the two phases.

These results underscore the dynamic complexity of the HDM and highlight a previously under-appreciated mechanism (opposing selection) for retaining genetic variability in populations of haplodiplonts. Furthermore, our survey of enzyme polymorphism provides empirical evidence that levels of polymorphism are not inversely correlated with the prominence of haplophase in the life histories of plants. Consequently, we conclude on both theoretical and empirical grounds that the conventional wisdom about the consequences of gametophytic selection (fig. II.11, center box) derives from an incomplete predictive context (fig. II.11, upper box). Specifically, to adequately predict the population-genetic consequences of the haplodiplontic life history, it is insufficient to compare haploids (HM) and diploids (DM) and to infer that HDM dynamics should be intermediate. Indeed, our results illustrate that there is a non-linear relationship between life history variation (from haploid

to haplodiplontic to diploid) and variation in the potential for maintaining genetic variability, due to interaction between selective processes occurring within each phase (i.e., opposing selection). Thus, it is necessary to consider the unique dynamics of each complete life history in order to understand how the consequences of distinct life histories differ.

An appreciation of the complexity of HDM dynamics, and of their consequences for the maintenance of polymorphism, can also contribute to a better understanding of the evolutionary processes affecting the life histories of plants (fig. II.11, lower box). A bewildering array of explanations has been offered for the evolution of the haplodiplontic life history (and of the related phenomema of diploidy and sex) (e.g., reviews in Ghiselin 1974; Willson 1981; Bell 1982). We consider only two arguments (fig. II.11, lower box), each based on the presumption that gametophytic selection efficiently removes genetic variation from populations of haplodiplonts (fig. II.11, center box).

The two arguments are similar in that they consider the relative advantages of haploidy *versus* diploidy in explaining the persistence of both phases in the life histories of plants. Their predictions diverge, however, depending on whether genetic variation due to mutation is perceived as playing primarily a destructive or a constructive role in evolution (i.e., respectively, the neoclassical *versus* balance schools of population genetics, *sensu* Lewontin 1974). Specifically, some authors have suggested that haplophase is advantageous because selection can rapidly eliminate deleterious mutations (e.g., in angiosperms and pteridophytes, Mulcahy and Mulcahy

1987; Klekowski 1988; discussions in Charlesworth 1991, Kondrashov and Crow 1991, Perrot et al. 1991). Mulcahy (1979), for example, attributes the evolutionary success of angiosperms to their capacity for intensive "screening" of the genome via pollen selection.

On the other hand, some authors have viewed the presence of a haploid stage in the life cycle as detrimental, precisely because gametophytic selection has the potential to rapidly eliminate genetic variability from populations (e.g., Stebbins 1950, 1960; Bonner 1965). These arguments, based on the presumption of individual- and population-level advantages of diploidy over haploidy (fig. II.11, upper box), predict that a diplophase-dominant life history should evolve in the absence of constraints (Stebbins and Hill 1980; Graham 1985; review in Willson 1981). This prediction has led, in turn, to numerous *ad hoc* explanations for the persistence of a prominent haploid stage in the life histories of many plants (e.g., phylogenetic constraints, Stebbins 1960; Littler et al. 1987; the potential adaptive advantages of haploidy, Cavalier-Smith 1978; Lewis 1985; or tradeoffs between the haploid and diploid stages, Stebbins and Hill 1980; Keddy 1981; Willson 1981).

As discussed earlier, our theoretical and empirical results call into question the basic assumptions (fig. II.11, center box) of both lines of reasoning. That is, reduced levels of polymorphism are not necessarily predicted or observed in populations of haplodiplonts. Furthermore, we suggest that a comparative approach (similar to the one we have used to evaluate the population-genetic consequences of the haplodiplontic life history) could lead to a better understanding of the evolution of the haplodiplontic life history itself. Many

authors address the general issue of why two phases persist in plant life cycles by asking "What are the adaptive advantages of being haploid or diploid?" We argue that answers to this question are necessary, but not sufficient, for understanding the factors that drive the evolution of life cycles. Rather, the problem must be framed in a broader context: "Under what conditions should organisms alter the relative size, duration, or complexity of discrete life history stages?" (See Willson 1981 for a similar approach.) In addition to the discovery of differences and similarities between the phases, answering this question necessitates (1) increased understanding of the interplay between the phases within the life history (e.g., reinforcing *versus* opposing selection, ecological trade-offs), and (2) exploration of the theoretical and empirical links between exogenous variation (i.e., selection regimes) and variation among life histories that differ in their allocation to each phase.

This reframing of the problem has implications for the types of research needed to integrate existing knowledge and to further elucidate evolution of the haplodiplontic life history. For example, analyses of life history evolution that implicitly assume reinforcing selection between haploid and diploid stages (e.g., Kondrashov and Crow 1991, Perrot et al. 1991; discussion in Charlesworth 1991) should be extended to consider the case of opposing selection. Furthermore, theory is needed that explicitly links variation in the relative size or duration of the phases with ecological or other selection gradients. To begin to tease apart the conditions that favor one life-history variant over another, future empirical studies could take

advantage of fixed or plastic life-history variation within species (or among closely related taxa) of lower plants. By explicitly incorporating the full range of population genetic dynamics and life-history variants in future theoretical and empirical studies, progress in understanding the evolution of the haplodiplontic life history will be enhanced.

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APPENDICES

APPENDIX A

DERIVATION OF THE EQUILIBRIUM FREQUENCY, $\hat{p}$, FOR THE HAPLODIPLONTIC MODEL

At equilibrium, $f(p) = p$, so from equation (1),

$$p = pw_1[pw_{11} + (1-p)w_{12}] / D,$$

where $D = pw_1[pw_{11} + (1-p)w_{12}] + (1-p)w_2[pw_{12} + (1-p)w_{22}]$. Clearly, $p = 0$ is one equilibrium. To find the others, we divide by p. Then

$$w_1[pw_{11} + (1-p)w_{12}] = pw_1[pw_{11} + (1-p)w_{12}] + (1-p)w_2[pw_{12} + (1-p)w_{22}],$$

or, equivalently,

$$(1-p)w_1[pw_{11} + (1-p)w_{12}] = (1-p)w_2[pw_{12} + (1-p)w_{22}].$$

It is clear that $p = 1$ $(1 - p = 0)$ is also an equilibrium. We find the remaining equilibrium by dividing by $(1-p)$ and solving for p, giving

$$\hat{p} = \frac{w_2w_{22} - w_1w_{12}}{w_2w_{22} - w_1w_{12} + w_1w_{11} - w_2w_{12}} .$$

Similarly, it can be shown that the equilibrium frequency of A_2 is

$$\hat{q} = \frac{w_1w_{11} - w_2w_{12}}{w_2w_{22} - w_1w_{12} + w_1w_{11} - w_2w_{12}} .$$

Thus, we have shown that $p = 0$, $p = 1$, and $p = \hat{p}$ are the only possible equilibria.

APPENDIX B

DERIVATION OF THE CONDITIONS GOVERNING THE EXISTENCE AND STABILITY OF EQUILIBRIA FOR THE HAPLODIPLONTIC MODEL

The necessary and sufficient conditions for the existence and stability of equilibria (and, hence, stable polymorphism) in the HDM can be inferred from the shape of the function $y = f(p)$, i.e., equation (1). Equilibria, by definition, will lie along the diagonal, $f(p) = p$ (fig. B.1). Thus, for any given selection regime, equilibria will exist where $y = f(p)$ intersects the diagonal. Note that boundary equilibria ($p = 0$ and $p = 1$) always exist (Appendix A), independent of the particular selection regime. However, stable polymorphism exists if and only if $y = f(p)$ intersects the diagonal in the interval $0 < \hat{p} < 1$. Thus, the existence and stability of equilibria will depend on the slope of $f(p)$ [i.e., the first derivative, $f'(p)$] evaluated at the boundary equilibria ($p = 0$, $p = 1$).

First, rewrite equation (1) as

$$N/D = p(a+bp) \; / \; [p(a+bp) + (1-p)(c+dp)],$$

where $a = w_1w_{12}$, $b = w_1(w_{11}-w_{12})$, $c = w_2w_{22}$, and $d = w_2(w_{12}-w_{22})$. Then, $N' = a+2bp$, $D' = a+2bp-c+d-2dp$, and $f'(p) = \{N'D-ND'\}/D^2$.

If $p = 0$, then $N = 0$, $D = c$, $ND' = 0$, and $N' = a$. Thus,

$$f'(0) = \frac{a}{c} = \frac{w_1w_{12}}{w_2w_{22}} \; . \qquad \text{(B1)}$$

If $p = 1$, then $N = a+b$, $D = a+b$, $N' = a+2b$, and $D' = a+2b-c-d$.

Thus,

$$f'(1) = \frac{c+d}{a+b} = \frac{w_2 w_{12}}{w_1 w_{11}} . \qquad (B2)$$

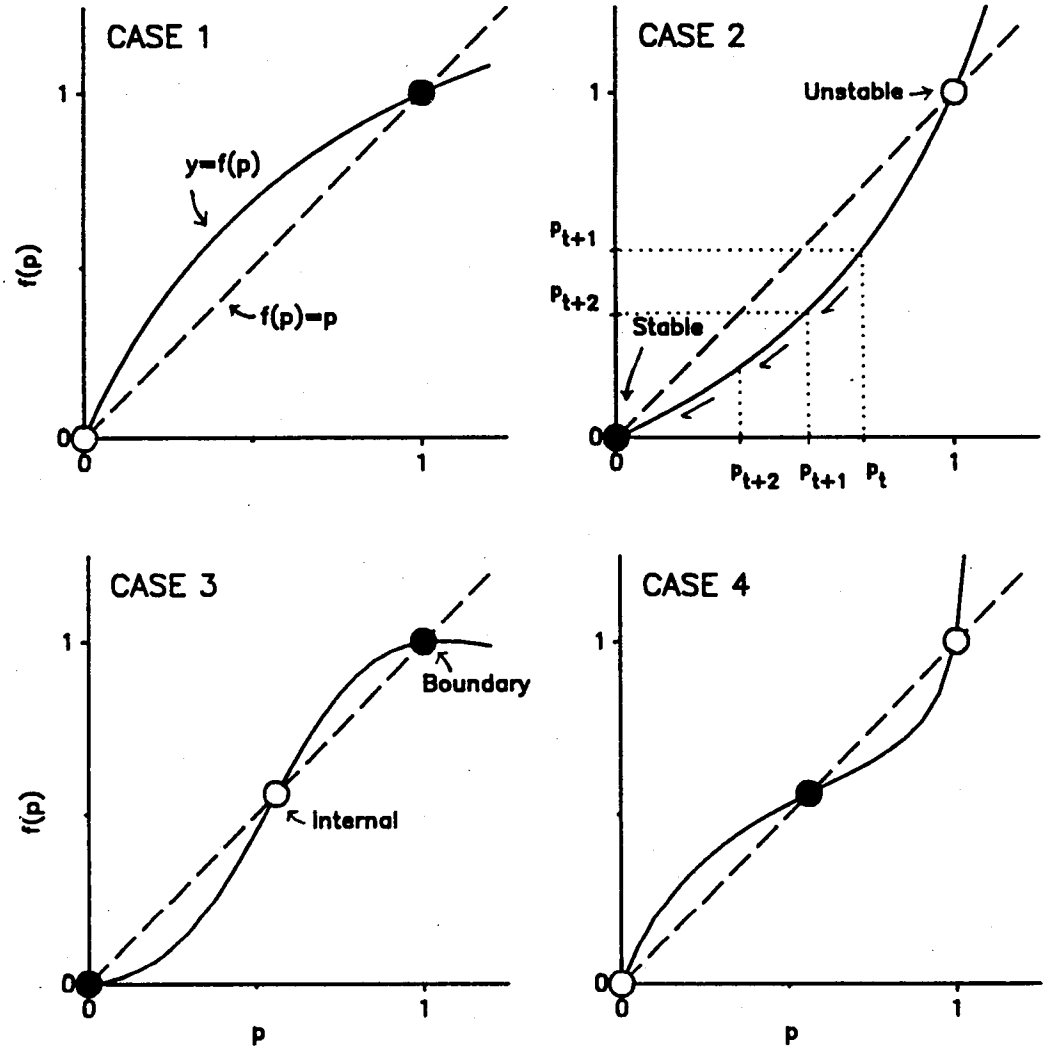
Hence, the selection regime alone determines the values of f'(p) at the boundary equilibria.

Taken together, equations (B1) and (B2) define the necessary conditions for the existence and stability of equilibria and, thus, of polymorphism (table II.1). A neutrally stable equilibrium exists for all $0 \leq p \leq 1$ when both $f'(0) = 1$ and $f'(1) = 1$ (Case 0, table II.1). An internal equilibrium does not exist either in Case 1 (fig. B.1, table II.1), where $f'(0) > 1$ and $f'(1) < 1$, or in Case 2 (fig. B.1, table II.1), where $f'(0) < 1$ and $f'(1) > 1$. However, an internal equilibrium must exist either if $f'(0) < 1$ and $f'(1) < 1$ (Case 3, fig. B.1, table II.1) or if $f'(0) > 1$ and $f'(1) > 1$ (Case 4, fig. B.1, table II.1), because f(p) must intersect the diagonal in the interval, $0 < \hat{p} < 1$. The stability of equilibria also can be demonstrated graphically (see caption, fig. B.1).

Note that under case 3, $w_{12}/w_{22} < w_2/w_1 < w_{11}/w_{12}$ implies $w_{12}^2 < w_{11}w_{22}$ or $w_{12} < \sqrt{w_{11}w_{22}}$. Likewise, under case 4, $w_{12}/w_{22} > w_2/w_1 > w_{11}/w_{12}$ implies $w_{12}^2 > w_{11}w_{22}$ or $w_{12} > \sqrt{w_{11}w_{22}}$. Therefore, a necessary, but not sufficient, condition for stable polymorphism is that the fitness of the heterozygote be greater than the geometric mean of the fitnesses of the two homozygotes.

Figure B.1. A graphical approach to inferring the qualitative selection regimes governing the existence and stability of equilibria in the HDM. Equilibria lie along the diagonal dashed line, $f(p) = p$; selection regimes are represented by the curve, $y = f(p)$. Boundary equilibria exist at $p = 0$ and $p = 1$ (Cases 1-4); an internal equilibrium is defined if $f(p) = \hat{p}$ and $0 < \hat{p} < 1$ (Cases 3 and 4). The stability of equilibria is illustrated graphically for Case 2: The initial allele frequency (p_t) is indicated on the abscissa. The allele frequency in the next generation (p_{t+1}) is found by projecting this point to the curve $y = f(p)$ and reading its value on the ordinate. This value, plotted on the abscissa, is then used to predict the frequency in the subsequent generation (p_{t+2}), and so on. The sequence of points moves along the graph of $y = f(p)$ toward stable equilibria (solid symbols) and away from unstable equilibria (open symbols), as indicated by the arrows in each panel.

Figure B.1


CASE 1
1
y=f(p)
f(p)
f(p)=p
0
0
1
CASE 2
1
Unstable
p_{t+1}
p_{t+2}
Stable
0
0
p_{t+2} p_{t+1} p_t
1
CASE 3
1
Boundary
Internal
f(p)
0
0
1
p
CASE 4
1
0
0
1
p

APPENDIX C

COMPARISON OF THE PARAMETER SPACE SUPPORTING POLYMORPHISM IN THE DIPLOID AND HAPLODIPLONTIC MODELS

The unit cube (figs. II. 7A and C.1) denotes the parameter space of the DM (i.e., $x = w_{11}$, $y = w_{22}$, $z = w_{12}$, $0 \leq w_{ij} \leq 1$). The proportion of the parameter space supporting polymorphism (i.e., $w_{12} > \max(w_{11}, w_{22})$ is $V_D = 1/3$ (fig. II.7A). Next we determine the proportion of the points (x, y, z) in the unit cube that satisfy the conditions for polymorphism in the HDM, i.e.,

$$w_{12}/w_{22} > w_2/w_1 > w_{11}/w_{12}. \qquad \text{(C1)}$$

First, assume $0 \leq w_i \leq 1$ and $w_1 < w_2$. Let $w_2/w_1 = R \geq 1$ and $Q = 1/R \leq 1$. Then (C1) can be rewritten

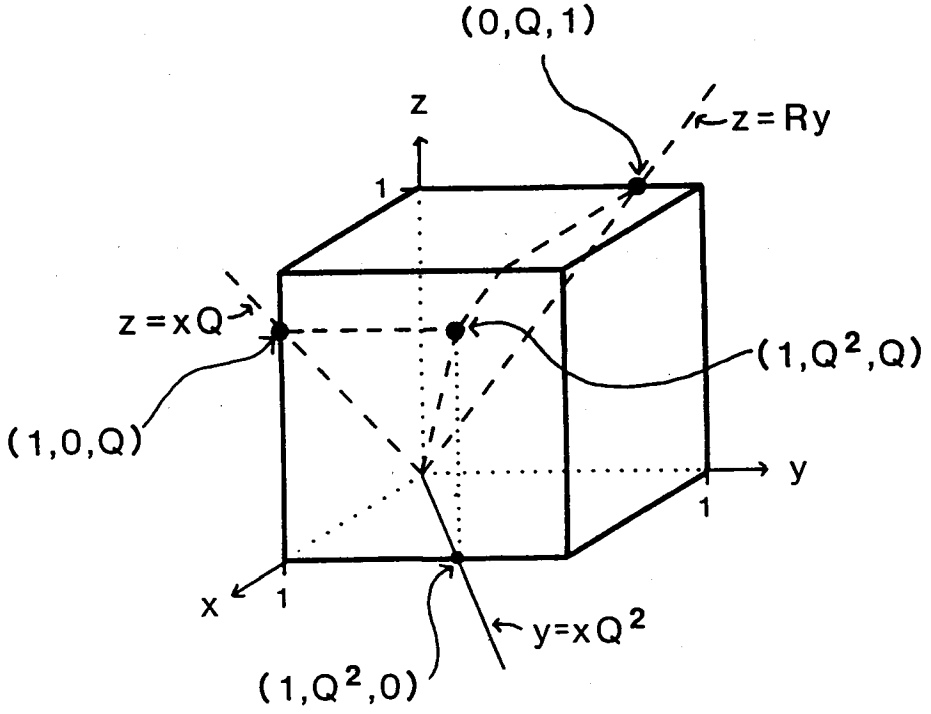
$$\{z/y > R > x/z\} \quad <=> \quad \{z > x/R = Qx \text{ and } z > Ry\}.$$

Thus, the volume of the space supporting polymorphism is defined by two planes, $z = xQ$ and $z = Ry$, which intersect along the line $z = xQ = Ry$ (fig. C.1). The projection of this line in the xy plane is $xQ = Ry$ or $y = xQ^2$ (figs. C.1, C.2A). The regions of integration are shown in figure C.2A. The volume, V_H, above the two planes, I and II, is thus

$$V_H = \int_I (1 - xQ)\, dA + \int_{II} (1 - Ry)\, dA$$

Figure C.1. Parameter space of the HDM, showing planes that define the volume of the space permitting stable polymorphism, V_H.

Figure C.1



$$V_H = \int_0^1 \int_0^{xQ^2} (1 - xQ)\, dy\, dx + \int_0^1 \int_{xQ^2}^{Q} (1 - Ry)\, dy\, dx.$$

Performing the integration and keeping in mind that R = 1/Q,

$$V_H = \frac{Q}{2} - \frac{Q^3}{6}.$$

Note that $V_H = 1/3$ if $Q = 1$ (i.e., if $w_1 = w_2$). Thus, in the absence of selection in haplophase, the volume of the parameter space supporting polymorphism in the HDM is identical to that in the DM. In addition, as a function of Q, V(Q) reaches a local maximum at Q = 1 (fig. II.8A) for all defined values of Q.

COMPARISON OF THE PARAMETER SPACE SUPPORTING POLYMORPHISM UNDER REINFORCING AND OPPOSING SELECTION

The diagonal plane x = y divides the parameter space into regions representing reinforcing and opposing selection. Because we assume at $w_2 > w_1$ the outset, $w_{22} > w_{11}$ or $y > x$ implies reinforcing selection. The regions of integration for reinforcing and opposing selection are shown in figure C.2B. Under reinforcing selection, the volume of the parameter space supporting polymorphism is thus

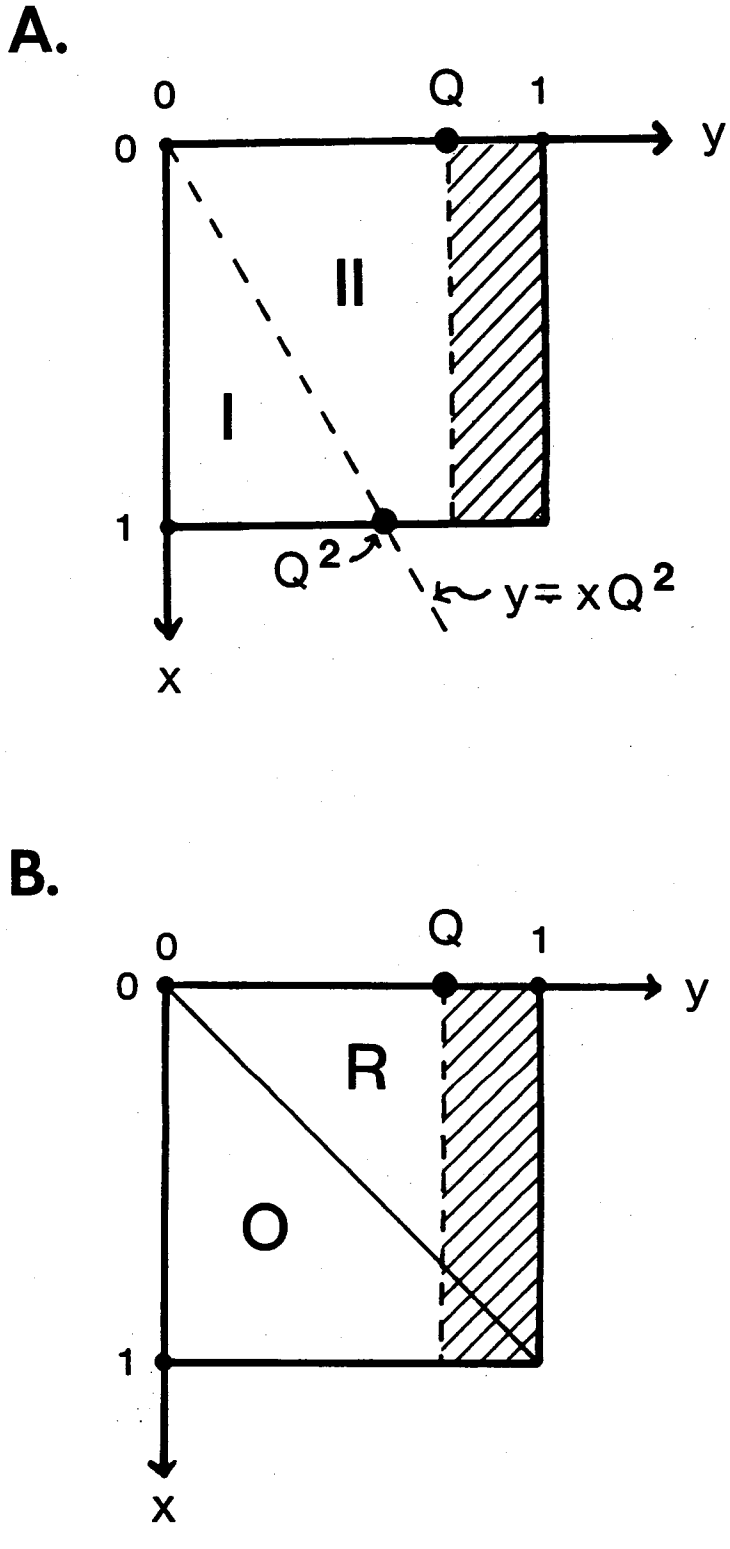
$$V_{Hr} = \int_0^Q \int_x^Q (1 - Ry)\, dy\, dx.$$

Again, performing the integration and recalling that R = 1/Q,

$$V_{Hr} = Q^2/6.$$

Figure C.2. Regions of integration in the xy plane. A. for V_H and B. for V_{Hr} and V_{Ho}.

Figure C.2



Under opposing selection, the volume of the parameter space supporting polymorphism is $V_{Ho} = V_H - V_{Hr}$, or

$$V_{Ho} = \frac{Q}{2} - \frac{Q^3}{3} - \frac{Q^2}{6}.$$

Chapter III

DESICCATION AND HERBIVORY INTERACT TO REGULATE THE UPPER LIMIT OF AN INTERTIDAL RED ALGA

ABSTRACT

Physical factors are presumed to determine the upper limits of most intertidal organisms, but the relative importance of biotic factors is poorly understood. I manipulated both desiccation and grazers (limpets) in a factorial experiment designed to evaluate their separate and joint effects on the upper intertidal limit of a perennial red alga, *Iridaea cornucopiae*. Desiccation inhibited upward vegetative growth. A significant desiccation-by-grazer interaction affected both reproduction and recruitment. In dry plots, grazers inhibited recruitment; in moist plots, grazers enhanced vegetative growth of *Iridaea*. Thus, *Iridaea* appears to be grazer-limited in dry, but grazer-dependent in moist environments.

Microalgae may mediate these effects on recruitment. Limpets often remove competing microalgae. In moist plots this probably enhances establishment of *Iridaea*. In dry plots, where microalgal production is likely to be lower, limpets may switch to *Iridaea*. Thus, both physical and biotic factors appear to set the upper limit of this alga.

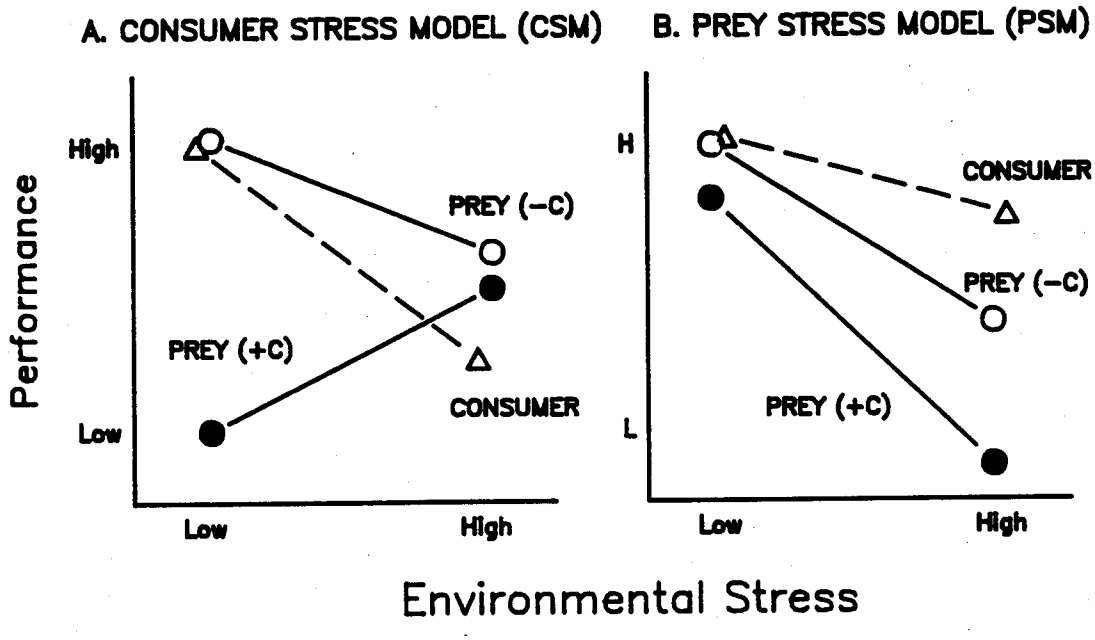
INTRODUCTION

Limits to species' distributions are often correlated with gradients in environmental harshness. Such correlations may arise because abiotic factors impose direct physiological limits on species. However, abiotic factors may also indirectly affect species' distributions by altering the outcome of species' interactions such as competition or predation. Recent conceptual advances in community ecology focus on the interplay between physical factors and species' interactions. Specifically, environmental stress models (ESMs; Menge and Olson 1990) predict how gradients in environmental stress limit the abundance of prey (animals or plants) by altering the effects of consumers (carnivores or herbivores). Two alternative sub-models (see below), each supported by an impressive array of empirical evidence, make contrasting predictions regarding the effects of environmental stress on species' distributions. Because they predict that the consequences of stress may vary, depending on species' interactions, ESMs are significant for understanding the effects of natural and anthropogenic environmental change on species' distributions. The object of this study is to evaluate ESMs in light of experimental evidence from a marine algae-molluscan herbivore system.

Two ESM sub-models reflect the likelihood that interacting species will respond differently to a given stress. In the two sub-models, the specific effect of environmental stress on a species' abundance and distribution depends on the differential responses to stress of consumers and prey (fig. III.1). The consumer stress model (CSM; Menge and Olson 1990) assumes that environmental stress

Figure III.1. Contrasting assumptions and predictions of the consumer stress and prey stress models (CSM and PSM, respectively). Assumptions (open symbols) include the direct physiological or behavioral effect of stress on consumers (open triangles, △) and on prey in the absence of consumers (open circles, ○). Predictions (solid symbols) include the indirect effect of stress on prey, mediated by consumers (solid circles, ●).

Figure III.1.


A. CONSUMER STRESS MODEL (CSM)
B. PREY STRESS MODEL (PSM)
Performance
High
Low
PREY (−C)
PREY (+C)
CONSUMER
Low
High
H
L
CONSUMER
PREY (−C)
PREY (+C)
Low
High
Environmental Stress

disproportionately affects the numbers or foraging efficiency of consumers, relative to its direct effect on the performance of prey (fig. III.1A; open symbols) (reviews in Connell 1972, 1974, 1975, 1985, Menge and Sutherland 1987, Menge and Farrell 1989). Thus, the CSM predicts that the effect of consumers on prey will be negatively correlated with stress--prey performance in the presence of consumers should improve with increased stress (fig. III.1A; solid symbols). That is, in benign conditions, prey should be limited by consumers, but where environmental conditions are too harsh for effective consumer foraging, prey should find a refuge from consumers and should be limited instead by their physiological tolerances. Classical demonstrations of this model are found in the work of Paine (1984, Paine et al. 1985) and Connell (1961a, b, 1970) in rocky intertidal systems where prey (mussels and barnacles, respectively) escape predation at elevations too high for effective foraging by consumers (seastars and whelks, respectively).

In contrast, the prey stress model (PSM; Menge and Olson 1990) assumes that environmental stress diminishes the performance of the prey more than that of consumers (fig. III.1B, open symbols). Accordingly the PSM predicts that the effect of consumers on prey will be positively correlated with stress (fig. III.1B, solid symbols), because stress increases prey susceptibility to consumer attack (reviews in Mattson and Addy 1975, Mattson 1980, White 1984, Waring and Schlesinger 1985, Louda 1988). Thus, prey are expected to persist in benign environments, but to be limited by consumers where conditions are harsh, even where levels of stress otherwise might be tolerated. Numerous studies report a positive correlation between

plant stress factors and frequency of attack by insect herbivores (e.g., White 1969, 1974, Webb 1981, Louda 1988). Others experimentally demonstrate higher rates of attack (e.g., Larsson et al. 1983, Louda and Rodman 1983, Mitchell et al. 1983, Waring and Pitman 1985) or increases in feeding preference (e.g., Lewis 1979, 1982, 1984, Hughes et al. 1982) for plants subjected to "high stress" treatments.

To test the predictions of ESMs, it is necessary to separate the direct effects of stress on prey species from its indirect effects mediated by species' interactions. In the present study, I attempted to experimentally tease apart the separate and joint effects of desiccation stress and molluscan herbivory in setting the upper intertidal limit of a marine red alga. Intertidal communities are good model systems for assessing the direct and indirect effects of environmental stress on species' distributions, because the elevational limits of both consumers and prey are often juxtaposed with steep gradients in physical factors (Lewis 1964). In particular, intertidal elevation and, thus, the vertical limits of species tend to be correlated with desiccation stress. Furthermore, the spatial and temporal scales of dominant processes make rocky intertidal communities particularly amenable to experimental investigations (Connell 1974). Consequently, experimental studies of intertidal zonation historically have been important in elucidating how abiotic and biotic factors regulate species' distributions (reviews in Connell 1972, 1974, Chapman 1973, 1974, Underwood and Denley 1984, Underwood 1985).

Both CSM and PSM dynamics have been suggested to explain the

vertical limits of intertidal species. Many experimental studies in intertidal systems lend support to the CSM scenario (review in Menge and Farrell 1989): Both consumers and prey tend to decrease in abundance and/or activity near their upper limits (e.g., Dayton 1971, Seapy and Littler 1982). However, because many consumers appear to be more susceptible than their prey to the stresses associated with emersion, prey may escape consumption at elevations presumed to be too stressful for effective consumer foraging (e.g., Connell 1961a, b, 1970, Dayton 1971, Menge 1978a, b, Paine 1984, Paine et al. 1985). Thus, consistent with the CSM, the lower limits of prey species tend to be set by consumption (or other biotic factors), while their upper limits are thought to be set by physical factors (Connell 1972).

Ample experimental evidence supports the contention that consumers have the potential to limit their prey at lower intertidal elevations (e.g., Menge 1976, Lubchenco 1980, Menge and Lubchenco 1981, Menge et al. 1986). Evidence that physical factors set the upper limits of prey species, however, is less compelling. Three types of evidence support the CSM prediction that upper limits are set by physical factors (reviews in Underwood and Denley 1984, Underwood 1985): First, the importance of physical factors may be inferred from a lack of response of prey to manipulations of predation and competition near their upper limits (e.g., Menge 1978a, b, Raffaelli 1979, Paine 1984). Second, transplants of organisms above the normal limits of distribution of the species (e.g., Schonbeck and Norton 1978) may demonstrate that mature individuals are intolerant of physical conditions, although recruitment limitation cannot be ruled out by these studies (Underwood and Denley 1984). Third,

experimentally ameliorated environmental conditions may raise the upper limit of some species (e.g., Castenholz 1961, Dayton 1971, Wethey 1984).

Relatively few studies in intertidal systems reveal a positive correlation between stress and predation or herbivory, consistent with the PSM. However, some experimental studies have demonstrated that grazing may in part explain the upper intertidal limits of some algae (Hay 1979, Underwood 1980, Cubit 1984). Because manipulation of abiotic factors was not attempted (Hay 1979, Cubit 1984) or was confounded by artifact (Underwood 1980; see Methods, below), the precise nature of the interaction between stress and herbivory was not elucidated in these studies.

In the present study, I evaluated how desiccation stress affected limpet grazing near the upper limit of a perennial red alga, *Iridaea cornucopiae* Postels & Ruprecht (Rhodophyta: Gigartinaceae) (henceforth, *Iridaea*). The objectives of this study were (1) to assess whether desiccation stress would alter the effect of herbivory on *Iridaea*; (2) if so, to determine whether the effect was consistent with the CSM or the PSM; and (3) to evaluate whether desiccation of *Iridaea* affected the feeding preferences of grazers. In a long-term field experiment, I altered both rock-surface moisture (during low tide) and limpet abundances, to evaluate their effects (separately and in combination) on the performance of *Iridaea* near its upper intertidal limit. I also conducted short-term feeding experiments in the field to determine the effect of plant condition on limpet feeding rates.

The CSM predicts that the deleterious effects of herbivores

should decline with increased desiccation and that the upper limit of *Iridaea* should set by desiccation. In contrast, the PSM predicts that the effects of herbivory should increase with stress and that herbivory should set the upper limit of *Iridaea*. Results of the present study are consistent with the ESMs, in that the effects of limpet grazing depended on the desiccation regime. Furthermore, the deleterious effects of herbivory were positively correlated with desiccation, consistent with the PSM. However, by some measures, the performance of *Iridaea* appeared to be grazer-enhanced under moist, but grazer-limited under dry, conditions. This result--not predicted by either the CSM or the PSM--suggests that more complex models may be needed to fully define the dynamics of this system.

NATURAL HISTORY

Beds of *Iridaea* dominate the high intertidal, 2.0-4.6 m above mean lower low water (MLLW), on many wave-exposed rocky shores of the northeast Pacific (Lebednik and Palmisano 1974, Kozloff 1983, Olson 1985, Hannach and Waaland 1986, Leigh et al. 1987). Short blades (usually < 5 cm in length) form a dense turf arising from a persistent basal crust (Abbott and Hollenberg 1976) that may occupy 25-40% of the substratum (Olson 1985). A canopy of blades averages 50-75% cover in undisturbed areas (Olson 1985). Blades of *Iridaea* species tend to have determinate development. A period of vegetative growth is followed by reproduction, senescence, and dehiscence of blades (Hannach and Waaland 1986, A. M. Olson, personal observation). Reproduction is correlated with declining growth rate and breakdown of the cuticle, a structure that deters grazing by some invertebrates on *Iridaea cordata* (Gaines 1985). The basal crust is a perennating structure--if it is killed, vegetative recovery is precluded. However, when the crust remains intact following experimental or natural defoliation, it may initiate new blades after conditions improve (Olson 1985, personal observation). Thus, *Iridaea* may assume its dominance by vegetatively pre-empting space.

The rather discrete upper boundary of *Iridaea* beds is a convenient local distributional limit for study. At the upper limit, canopy cover declines abruptly from >75% in some areas to 0% over a vertical distance of several centimeters. It is not unusual to see vigorously growing patches of *Iridaea* with 100% cover extending up to its extreme upper limit.

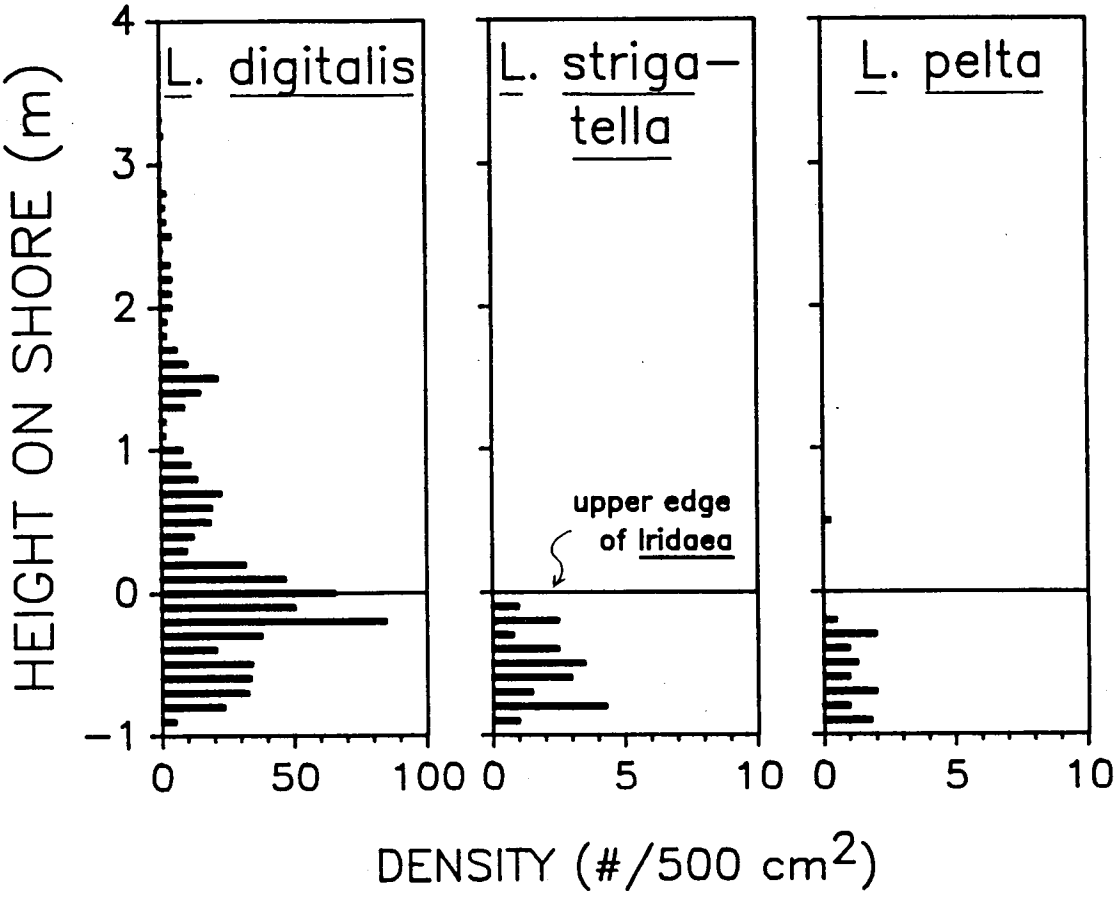
Where *Iridaea* occurs on steep, north-facing slopes, limpets are the dominant herbivore. Limpet densities typically exceed 400/m^2 in *Iridaea* beds at these sites (Olson 1985). On horizontal surfaces, however, limpets are relatively rare, due to avian predation (Frank 1982, Marsh 1986). In experimentally denuded areas within established beds, limpet grazing enhances the recruitment of *Iridaea* sporelings, presumably by removing competitively superior early and mid-successional algae (Olson 1985, Paine 1983). Thus, recruitment of *Iridaea* within established beds is grazer-dependent.

Several observations suggest that desiccation and limpet grazing may each play a role in determining the upper limit of *Iridaea* on steeply sloping surfaces. In more desiccating microsites, *Iridaea* is less abundant. From northwestern Washington to its southern limit in northern California, beds of *Iridaea* tend to be restricted to north-facing slopes; *Iridaea* occurs on horizontal or south-facing slopes only in areas of extreme wave-exposure. In contrast, beds on north-facing slopes are wider, higher, and extend farther into sheltered locations. Both the elevation and extent of *Iridaea* beds decreases from north to south over this range (A. M. Olson, personal observation and unpublished data). In addition, following bouts of prolonged aerial exposure, blades of *Iridaea* appear bleached, and this damage is more pronounced near the upper limit of *Iridaea* beds. Eventually the damaged portions of blades are removed by wave action and grazers. If previous damage to the blades exposes the basal crust to insolation, it may also become bleached and dislodge from the rock (Olson 1985).

Limpet grazing may also prevent the expansion of *Iridaea* above its normal limit and may help explain the relatively discrete upper

Figure III.2. Vertical distribution of limpets on the shore near the upper limit of the *Iridaea* bed. Density is given for contiguous 10 cm x 50 cm horizontal quadrats monitored in April 1987. Data for *Lottia digitalis* include small individuals (< 6 mm shell length) of all three species that are not readily identifiable to species.

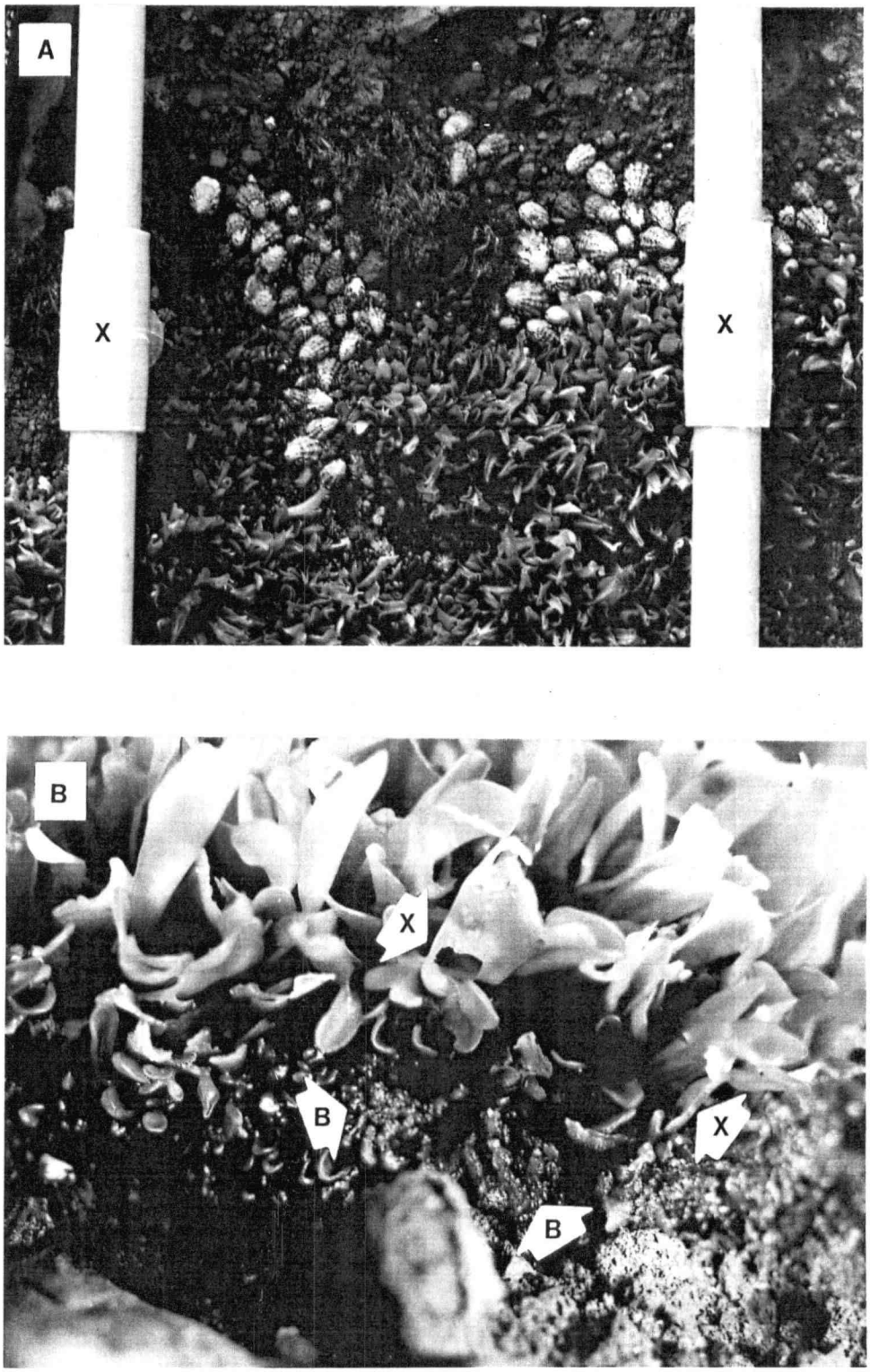
Figure III.2.


L. digitalis
L. striga-tella
L. pelta
upper edge of Iridaea
HEIGHT ON SHORE (m)
4
3
2
1
0
−1
0
50
100
0
5
10
0
5
10
DENSITY (#/500 cm2)

boundary of *Iridaea* beds on north-facing slopes. In winter, the most abundant limpet, *Lottia* (=*Collisella*) *digitalis*, ranges high in the splash zone above the *Iridaea* beds (A. M. Olson, personal observation), foraging on diatoms and ephemeral algae (Castenholz 1961, 1963, Frank 1965, Cubit 1984). In late spring, as wave heights decline and drier weather ensues, desiccation increases and microalgal productivity declines in the splash zone (Cubit 1984). Concurrently, *Lottia digitalis* moves down in the intertidal (Frank 1965, Breen 1972, A. M. Olson, personal observation), presumably to avoid desiccation or to forage for alternative foods. As a consequence of this behavior, individuals of *Lottia digitalis* aggregate along the upper margin of *Iridaea* beds in late spring (figs. III.2 and III.3A) and limpet abundances within the bed are higher in dry than in wet months (Olson 1985 and personal observation). At high densities, limpets damage blades at the edges of *Iridaea* clumps (fig. III.3B) and remove entire blades from newly recruited plants (Olson 1985 and personal observation). Thus, limpets may prevent lateral vegetative growth and establishment of sporelings above the normal limit of the species.

Figure III.3. Aggregations of limpets (A) and grazing damage (B) near the upper limit of *Iridaea*. A. *Lottia digitalis* (most in the 6-9 mm shell length class) aggregated at the upper limit of *Iridaea* bed. In such aggregations, limpets are occasionally "stacked" two or more deep on the rock. Scale: 15 cm between X's marked on photo framer. B. Damage to outer blades of *Iridaea* clump located near upper limit of *Iridaea* bed. X = holes and excavations due to limpet grazing; B = bases of blades that have been removed by grazing.

Figure III.3.



METHODS

Desiccation x Herbivory Experiment

Manipulations

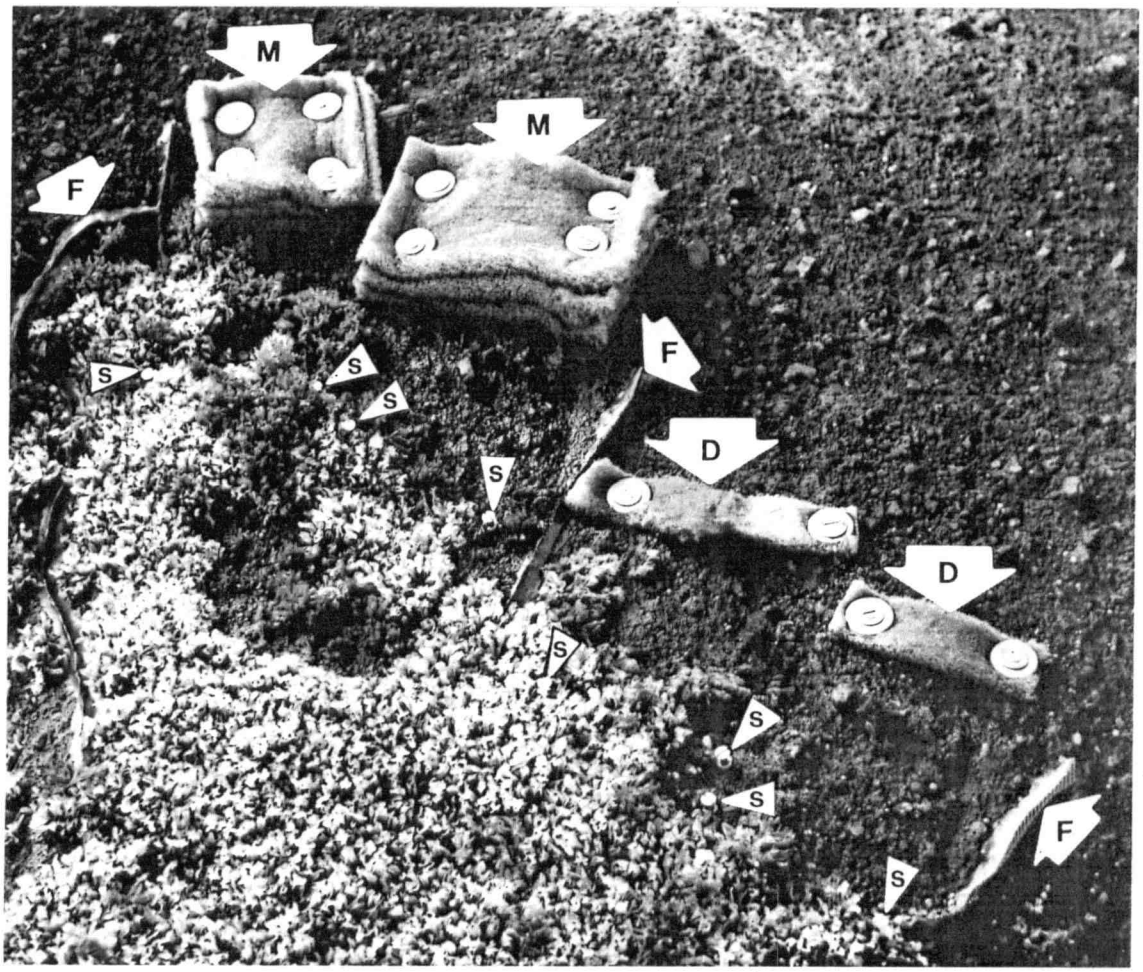
To test whether the upper limit of *Iridaea* is determined by desiccation, limpet grazing, or a combination of the two, I manipulated both rock-surface moisture and limpet densities in a field experiment, using a factorial, randomized block design. I evaluated the effects of the treatments on four indicators of plant performance--change in canopy cover, vegetative advancement of the upper limit of *Iridaea*, reproduction, and sporeling recruitment and survival.

This experiment was conducted on a basaltic headland at Whale Cove, approximately 23 km north of Newport on the central coast of Oregon (Olson 1985). Here *Iridaea* beds lie at elevations greater than +3 m MLLW on a north-facing wave-cut bench above the level of mussel beds. Cliffs immediately to the south rise approximately 10 m above the bench, shading the study site for portions of the day throughout the year. I permanently established 24 vertical plots (15 cm x 30 cm) by placing two stainless steel screws 15 cm apart, along the upper limit of the *Iridaea* bed, to mark each plot (fig. III.4). Thus, the upper 225 cm^2 half of each plot lay largely above the upper limit of *Iridaea*, while the lower half lay mainly within the *Iridaea* bed. I established eight plots in each of three replicates (blocks), but only four plots per block were used in the experiment reported herein.

I altered the local desiccation regime, adding moisture to half

Figure III.4. Experimental treatments for moisture addition x limpet removal experiment. M = moisture addition treatment (stacked sheets of polyester); D = dry control treatment (narrow strips of polyester); F = fences to limit lateral movement of limpets between plots. Two of the four possible treatment combinations are shown: Moist -Limpets (two plots on the left) and Dry +Limpets (two plots on the right). Scale is 15 cm between screws (S) marking mid-line of each plot (initial upper limit of *Iridaea*).

Figure III.4.



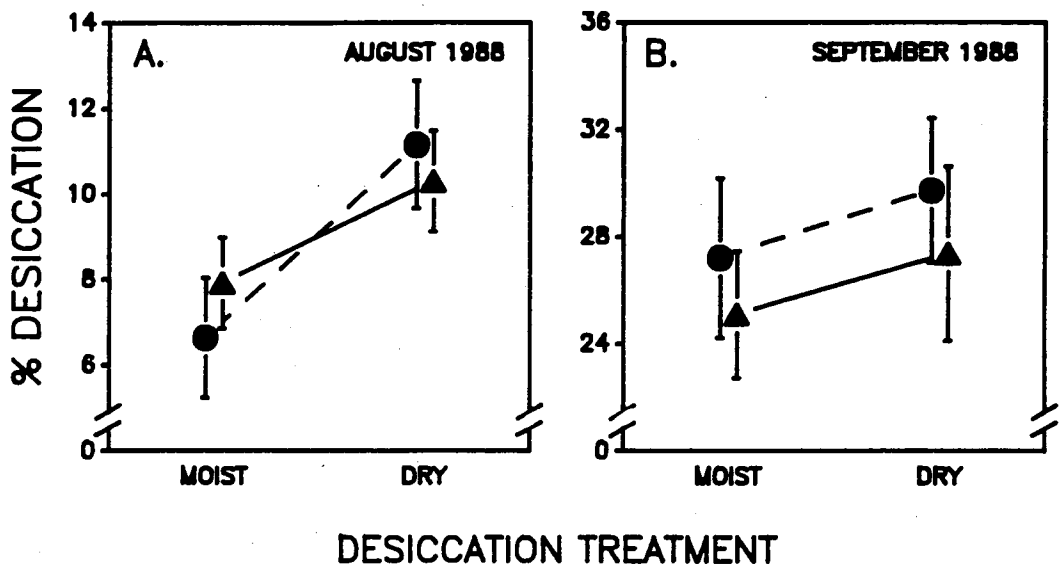
the plots (moist plots) by attaching three stacked layers of a sponge-like polyester material (each 2 cm thick and 15 cm wide) to the rock with stainless steel screws immediately up-slope from each moist plot (fig. III.4). The polyester mimics patches of algae by retaining water at high tide and releasing it across the entire width of the subtending plot for up to several hours after the tide has receded. The polyester is strong enough to withstand heavy wave action and it is biologically inert. (Cellulose sponges, in contrast, were consumed by littorinid snails in preliminary trials.) On days when the polyester was not wetted at high tide (e.g., during periods of calm seas and neap tides), I manually poured seawater over the polyester above the moist plots at least once per day.

Because the polyester potentially restricted limpet movement into or out of the plots, I attached a single, narrow layer of polyester (4 cm wide) up-slope from the control (dry) plots (fig. III.4). These control strips retained little moisture and dried rapidly, so they had relatively little effect on the moisture regime in the dry plots. The moist and dry treatments were maintained in the "dry season" (July to October 1987 and May to October 1988) and removed prior to the onset of winter storms.

I altered limpet densities by manually removing limpets from half the plots (-L) and adding limpets to the other half (+L), approximately biweekly from May to October 1987 and every 2 to 4 wk from May to October 1988. Movement of limpets between plots was restricted with small epoxy-putty ridges (fig. III.4), topped with plastic mesh fences and/or copper-based antifouling paint. Moisture addition potentially could attract limpets, confounding the limpet

Figure III.5. Desiccation of *Iridaea* blades in experimental plots. Data are mean (± standard error of the mean, SEM) for n = 3 replicate blocks. Three sub-samples from each plot were pooled prior to calculating treatment mean and SEM. A. August 1988. B. September 1988. +Limpets, solid triangles (▲); -Limpets, solid circles (●). See text for explanation of treatments.

Figure III.5.


A.
AUGUST 1988
B.
SEPTEMBER 1988
% DESICCATION
14
12
10
8
6
0
36
32
28
24
0
MOIST
DRY
MOIST
DRY
DESICCATION TREATMENT

density manipulation (e.g., Underwood 1980). To remove this potential confounding effect, I adjusted densities monthly to 10 large (> 9 mm) and 25 small (6-9 mm) limpets in limpet addition plots. Occasional mid-winter manipulations were made as weather and wave conditions permitted. To assess the effectiveness of the limpet removal treatment, I counted limpets monthly, from June to September 1987 and May to September 1988, and subjected the data to a two-factor ANOVA.

Treatment effectiveness

To assess the effectiveness of the moisture addition treatment, I measured the relative moisture content of *Iridaea* blades in each of the treatment groups on 9 August and 3 September 1988. Near the end of the period of emersion, I collected 3 blades from within 1 cm of the upper limit of *Iridaea* in each plot. Each blade was immediately placed in a sealed 0.5 ml microfuge tube, labeled, and stored in the dark on ice for transport to the lab. Within 1.5 to 5.5 hr, I determined the field mass (F) of each blade by weighing it immediately after removing it from its microfuge tube. Blades were then rehydrated to constant mass (~12 hr) and reweighed to determine their fully rehydrated mass (R). Subsequently, blades were dried in an oven at 50 C to constant mass and reweighed to determine their dry mass (D). I then calculated percent desiccation of each blade as D% = [(R-F)x100]/[R-D]) (Schonbeck and Norton 1979). Analysis of covariance was used to assess the main effects and two-way interaction of the moisture addition and limpet removal treatments. Dry mass of blades was included as a covariate, after determining that there were no

significant treatment by covariate interactions (i.e., parallel slopes, Sokal and Rohlf 1981).

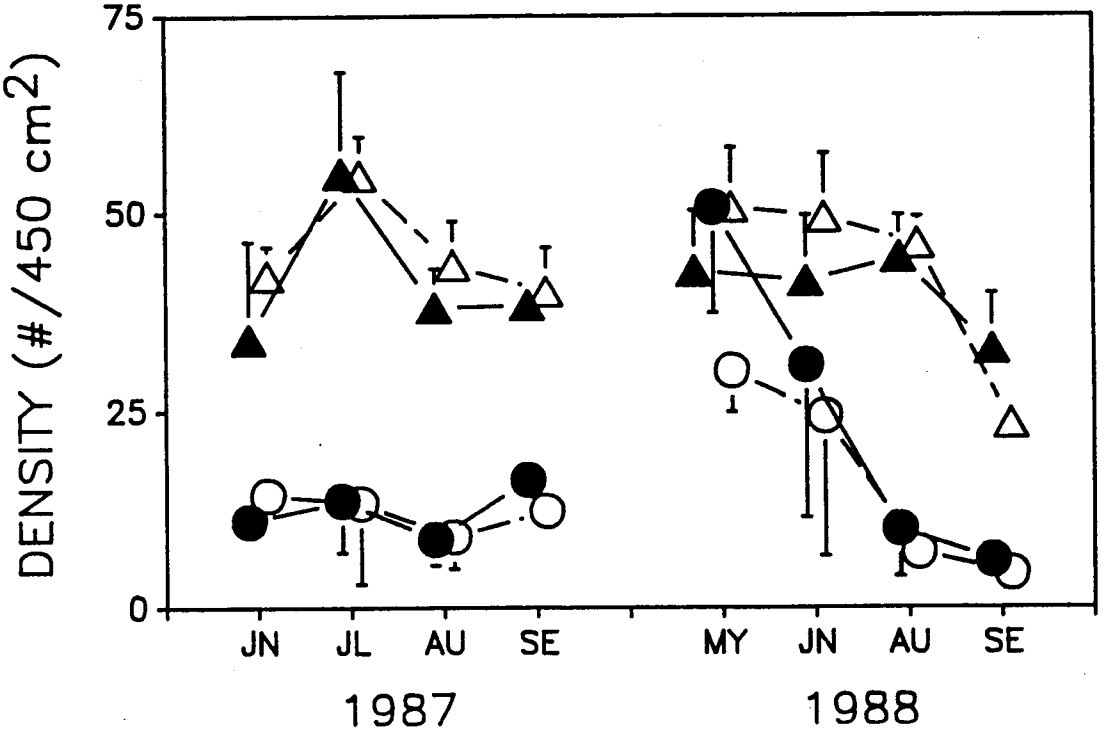
The moisture addition and limpet removal treatments were effective in reducing desiccation and limpet densities, respectively, and manipulations of desiccation and herbivores were independent. Blades in moisture addition plots were significantly less desiccated (D%) than those in dry plots on 9 August (a cool, foggy day) (fig. III.5A; main effect of moisture addition, $p < 0.01$; F-test, ANOVA). A similar pattern on 3 September (a dry, but overcast day) was not significant (fig. III.5B; $p > 0.10$). Desiccation of *Iridaea* was not affected by the limpet removal: Neither the main effect of limpet removal nor the two-way interaction between limpet removal and moisture addition significantly affected blade moisture status ($p > 0.10$). Limpet densities were significantly lower in limpet removal than in limpet addition plots on most dates (fig. III.6; main effect of limpet removal, $p < 0.01$ on all dates except May and June 1988). Limpet abundance was not affected by the moisture addition: Significant variation in limpet densities could not be attributed either to the main effect of moisture addition ($p > 0.10$) or to the two-way interaction ($p > 0.05$), for any date. Thus, effects of the two experimental factors on plant performance were not confounded.

Measures of plant performance

The effects of the treatments on plant performance were monitored in the field or from photographs. Reproduction and recruitment were assessed in the field. Reproduction (the ripening and release of spores) was limited to brief periods in late fall and

Figure III.6. Limpet densities in experimental plots. Data are mean (± SEM) for all limpet species in whole (15 cm x 30 cm) plots. Moist +Limpets, solid triangles (▲); Dry +Limpets, open triangles (△); Moist -Limpets, solid circles (●); Dry -Limpets, open circles (○).

Figure III.6.



early winter, after which vegetative growth resumed. I periodically estimated the relative reproduction of *Iridaea* in each treatment group by the following method. Over the lower half of each plot, I placed a 15 cm x 15 cm vinyl quadrat on which were painted 34 uniformly spaced dots. The proportion of dots lying over *Iridaea* blades is an estimate of the total canopy cover of *Iridaea*; the proportion lying over reproductive blades is an estimate of reproductive cover. I calculated the relative reproduction as the ratio of reproductive to total canopy cover. Initial recruitment into the upper half of each plot was estimated in the field by counting sporelings in January 1988.

Other measures of plant performance were assessed from photographs. I periodically photographed each plot, using a framer with holes that fit over the screws (fig. III.4) marking the mid-line of the plot. From the photographs, I monitored changes in total canopy cover of *Iridaea*, vegetative advance or retreat of the upper limit of *Iridaea*, and survival of sporelings in each treatment group. Canopy cover and vegetative growth were measured using a digitizer. Change in total canopy cover was calculated separately for the upper half of each plot. Because blades of *Iridaea* obscure the extent of the basal crust in photographs, vegetative advance or retreat was defined as a change in the upper limit of blades visible in photographs. Survival of sporelings that had recruited into the upper half of each plot was determined by tracking the fate of small plants visible in the photographs taken in June 1988.

Feeding Experiments

The feeding preferences of limpets were studied in field experiments. The study site was located on vertical sandstone walls at Boiler Bay, approximately 28 km north of Newport, Oregon. In the first set of experiments, choices of reproductive vs. non-reproductive blades of *Iridaea* were installed at six feeding stations where limpets were abundant. At each station, four pre-weighed blades (two reproductive and two non-reproductive) were clamped under the edge of a flexible plastic washer (a film-cannister cap) attached to the rock with a stainless steel screw and washer. Adjacent to each feeding station, a control was installed that consisted of similarly sized blades attached within a limpet exclosure of copper-based anti-fouling paint. Limpets were allowed to feed for 7 to 10 d. The percent change in mass of the blades was used to estimate feeding. Two trials of this experiment were conducted in August and September 1987. Because the limpets were free-ranging, they had access to alternative foods, but other perennial algae were essentially absent from the rapidly eroding sandstone surface (Farrell 1988).

In the second set of feeding experiments, limpets were offered desiccated and non-desiccated blades of *Iridaea*. Limpets were confined on a shady vertical wall in 30 cm x 40 cm arenas consisting of plastic mesh fences attached to the rock with epoxy putty. The outside edge of each arena was painted with copper-based antifouling paint to further inhibit limpet movement into or out of the arena. An equal number of control arenas did not contain limpets.

In the lab, blades of *Iridaea* were weighed, then assigned

randomly to the desiccation (+D) or non-desiccation (-D) treatment. Desiccated blades were held overnight (~8 h) in a drying oven (35 C in the first trial, 27 C in the second, and 30 C in the third), then rehydrated before use in a feeding trial. Non-desiccated blades were held in seawater in a refrigerator (4 C) or cold room (12 C) for the same period. Blades in each desiccation treatment were randomly assigned to one of eight arenas--four with limpets (+L) and four without limpets (-L). Next, all blades were arranged in a randomly determined order in plexiglass brackets. Each bracket consisted of two 3.7 cm x 17.7 cm sheets of plexiglass between which a sheet of polyurethane rubber and four to eight algal blades were clamped. The bases of blades were held firmly in each bracket, while the distal portions protruded to allow feeding by limpets. The blades, mounted in brackets, were then transported in a cooler to the field and bolted to the rock within the experimental and control arenas. *Lottia digitalis* were permitted to feed for 12 d in the first trial (July 1988) and 23 d in the second (August 1988); *Lottia pelta* were permitted to feed for 3 d in the third trial (September 1988).

Following each feeding trial, blades were returned to the lab for re-weighing and evaluation of herbivore damage. Herbivore damage was evaluated by examining each blade under a dissecting microscope and scoring damage in one of 7 subjective damage classes (see caption, fig. III.13). Change in mass of blades was used to estimate feeding.

Analyses

Experimental results were subjected to Chi-square analysis, analysis of variance (ANOVA), or analysis of covariance (ANCOVA), using SYSTAT@ software. If, and only if, significant heterogeneity of variances existed among ANOVA cells (F_{max}, Sokal and Rohlf 1981), data were transformed prior to analysis. For ease of interpretation, untransformed data are plotted in all figures. Transformations are indicated in the table captions.

For number of recruits, the mean and variance of one treatment combination was zero. In such cases, transformation cannot correct the heterogeneity of variances. To determine whether the qualitative result of the ANOVA was altered by this uncorrectable heterogeneity of variance, a second ANOVA was conducted. A small artificial variance was introduced, such that the mean for the treatment combination remained zero, but the F_{max} test was not significant. Results of this ANOVA were qualitatively the same as that without the artificial variance.

RESULTS

Desiccation x Herbivory Experiment

Canopy cover in the upper half of the experimental plots changed during the study period (fig. III.7). Although the pattern of change suggests that the effect of limpet grazing was dependent on the moisture regime, the two-way interaction term in the ANOVA was not significant for either period tested ($p > 0.10$, F-tests). Patterns of change in canopy cover, however, integrate the effect of the experimental treatments on vegetative advance, reproduction, and recruitment of *Iridaea*.

Vegetative growth of *Iridaea* from May to October 1987, was enhanced by moisture addition (fig. III.8A, table III.1A). *Iridaea* advanced farther up the rock in moist plots with limpets than in the other treatment groups ($p < 0.05$, Newman-Keuls post-hoc comparison of means). Vegetative growth from October 1987 to April 1988 (when the treatments were not maintained) (fig. III.8B, table III.1A) and the cumulative vegetative advancement from May 1987 to April 1988 were not significantly affected by the treatments (table III.1A).

Reproduction of *Iridaea* near its upper limit began in early fall (fig. III.9, solid symbols) and tapered off in early spring. The effect of limpet removal on the onset of reproduction of *Iridaea* (October 1987) depended on the moisture regime (fig. III.10), as indicated by the significant interaction term (table III.1B). The interaction reflected a pattern of grazer-induced reduction of reproduction in dry plots, but treatment means were not significantly

Figure III.7. Change in canopy cover of *Iridaea* in upper half (225 cm^2) of experimental plots. A. June 1987 to June 1988. B. June 1987-September 1988. See fig. III.5 caption for explanation of symbols.

Figure III.7.

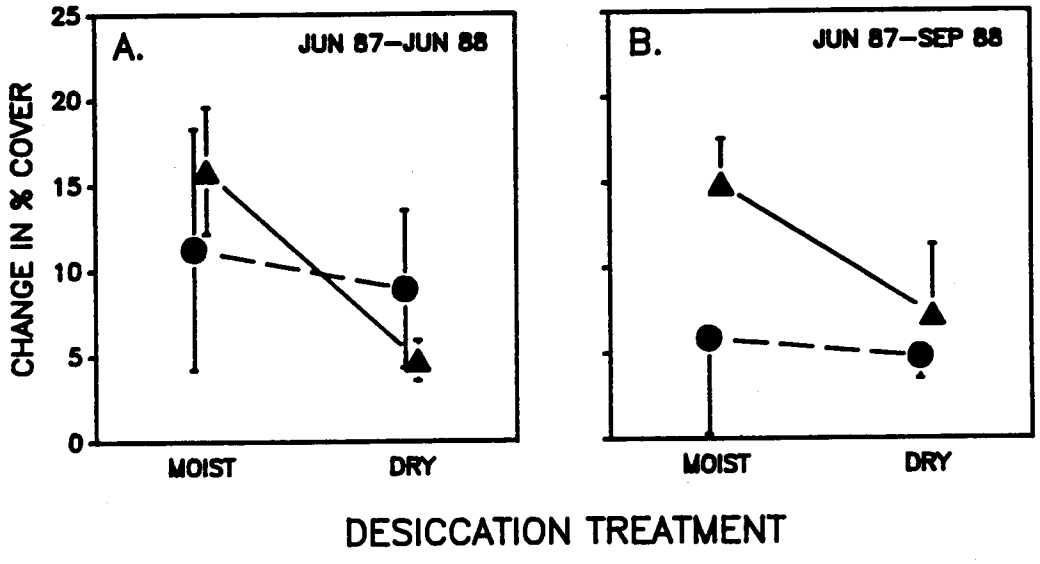

A.
JUN 87–JUN 88
B.
JUN 87–SEP 88
CHANGE IN % COVER
25
20
15
10
5
0
MOIST
DRY
MOIST
DRY
DESICCATION TREATMENT

Figure III.8. Vegetative advance of the upper limit of *Iridaea*. A. May 1987 to October 1987. B. October 1987 to April 1988. See fig. III.5 caption for explanation of symbols.

Figure III.8.

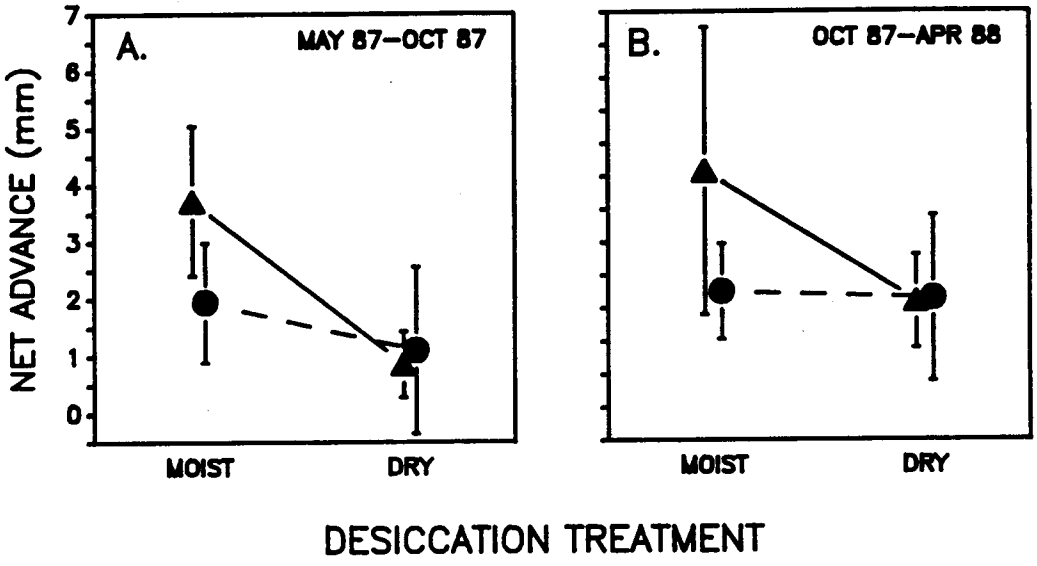

A.
MAY 87–OCT 87
B.
OCT 87–APR 88
NET ADVANCE (mm)
0
1
2
3
4
5
6
7
MOIST
DRY
MOIST
DRY
DESICCATION TREATMENT

Figure III.9. Average reproduction and number of recruits in all experimental plots. Data are mean (± SEM) for n = 12 plots. Relative cover (%) of reproductive blades, left axis, solid symbols (●); number of sporelings that recruited during winter, 1987-1988, right axis, open symbols (○).

Figure III.9.

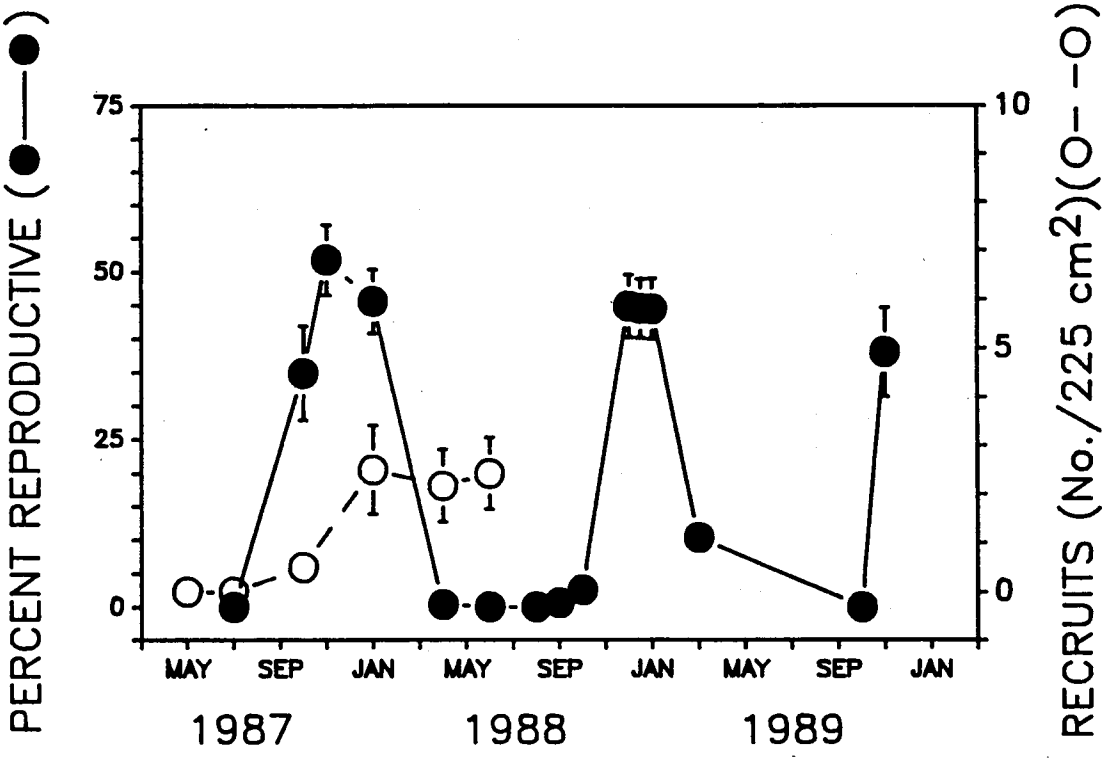
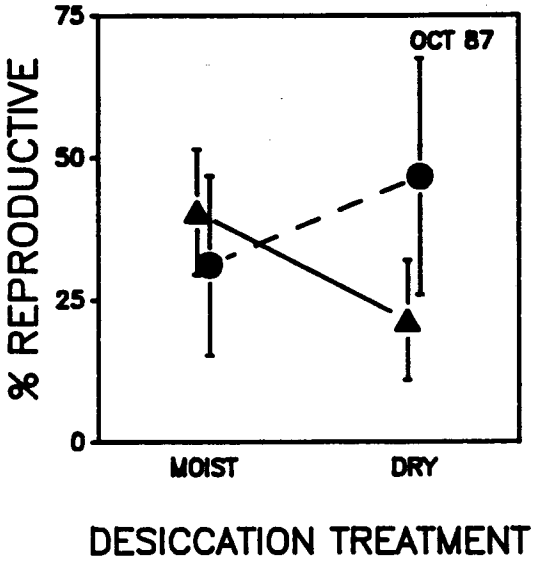

PERCENT REPRODUCTIVE (●—●)
RECRUITS (No./225 cm2)(O- -O)
75
50
25
0
10
5
0
MAY
SEP
JAN
MAY
SEP
JAN
MAY
SEP
JAN
1987
1988
1989

Figure III.10. Reproduction of *Iridaea* in experimental plots. See fig. III.5 caption for explanation of symbols.

Figure III.10.



different ($p > 0.05$, Neuman-Keuls). A similar pattern was observed throughout the 1987-88 and 1988-89 reproductive seasons, but the interaction term in the ANOVA was not significant on any other dates.

Visible recruitment of sporelings began in Fall 1987 (fig. III.9, open symbols). The effect of limpet removal on the number of sporelings recruiting in January 1988 depended on the moisture regime (fig. III.11, table III.1C). In moist plots, limpets tended to enhance the recruitment of *Iridaea*. An average of 5.00 sporelings recruited to moist plots with limpets, while only 2.33 sporelings recruited to moist plots without limpets, although these means did not differ in a post hoc comparison ($p > 0.05$, Newman-Keuls). In contrast, in dry plots, *Iridaea* did not recruit in the presence of limpets, but limpet removal permitted recruitment of an average of 2.67 sporelings per plot ($p < 0.05$, Newman-Keuls). Following initial recruitment, limpet grazing removed sporelings from moist plots. By June 1988, all sporelings that had recruited to limpet removal plots (moist or dry) remained visible in photographs, while only 63% of sporelings persisted in moist limpet addition plots. Thus, by June 1988, the number of recruits did not differ among the three treatment combinations in which recruitment initially occurred (dry -L, moist -L, moist +L; $p > 0.05$, one-way ANOVA).

Significant block effects were observed for three measures of plant performance--vegetative advance, onset of reproduction, and recruitment (table III.1). Blocks were established within 1 m elevation along a horizontal gradient of relative wave-exposure, from sheltered (Block 1) to exposed (Block 3). Other differences in environmental conditions also occurred among the blocks. For example,

Figure III.11. Recruitment of *Iridaea* in experimental plots. See fig. III.5 caption for explanation of symbols.

Figure III.11.

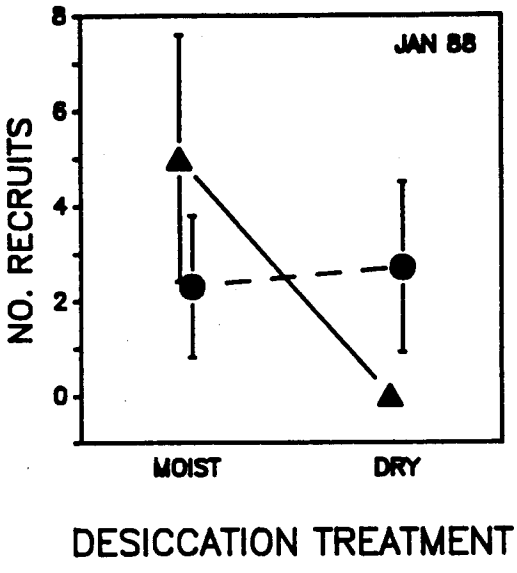


Table III.1. Effects of moisture and herbivore manipulations on vegetative advance (A), reproduction (B), and recruitment (C) of *Iridaea*. Table cells contain F-ratios based on ANOVA. Degrees of freedom: block = 2, main effects of moisture addition and limpet removal = 1, two-way interaction = 1, error = 7. Significance tests: +, $0.05 \leq p < 0.10$; *, $p < 0.05$, **, $p < 0.01$; ***, $p < 0.001$.

	Experimental Effects					
Dependent Variable	Block	Moisture Addition	Limpet Removal	Two-way Interaction	MSE	r^2
A. Vegetative advance						
5/87 - 10/87	19.263**	14.398*	2.498	4.324+	0.007	0.909
10/87 - 4/88	0.152	0.472	0.337	0.375	0.070	0.199
5/87 - 4/88[a]	2.795	3.184	0.958	1.474	0.025	0.651
B. Reproduction						
10/88	17.869**	0.066	1.391	6.817*	131.195	0.880
C. Recruitment						
1/88[b]	6.921*	6.772*	0.499	7.722*	0.254	0.828

[a] Transformed data: ln[(change in % cover) + 1]

[b] Transformed data: ln[(no. sporelings) + 1]; small artificial variance added to ANOVA cell with mean and variance of zero.

block position was correlated with relative insolation. Because all three blocks had a northerly aspect, steeper slopes resulted in less insolation. At this site, wave-sheltered plots happened to be steeper (table III.2A) and, thus, received less insolation (table III.2B) than wave-exposed plots. In addition, the steeper plots of Block 1 were shaded for longer periods of the day by cliffs rising to the south. These differences in solar input were reflected in mean rates of desiccation (table III.2C). Furthermore, limpet abundances declined along the gradient of increasing wave exposure and insolation (table III.2D). Finally, vegetative advance, reproduction, and recruitment were highest in the sheltered, shady block (table III.2E-G).

Feeding Experiments

In the feeding experiments, limpet feeding was not affected by senescence (reproductive status) or desiccation history of *Iridaea* blades. During the 1987 feeding trials (fig. III.12), limpets appeared to prefer reproductive to non-reproductive blades in the first trial (fig. III.12A), but the term for the interaction of limpet feeding and reproductive status was not significant for either trial ($p > 0.10$, F-ratio for two-way interaction, ANOVA). Trials in 1988 involving desiccated and non-desiccated blades of *Iridaea* also were inconclusive. As measured by change in mass of blades, neither *Lottia digitalis* nor *Lottia pelta* displayed a measurable preference by desiccation status ($p > 0.05$, F-ratio for two-way interaction, ANOVA).

Subjective assessments of herbivore damage, however, were associated with desiccation treatments in trials 1 and 2 (fig. III.13A

Table III.2. Characteristics of blocks (replicates). Tables cells contain mean (± SEM) of n = 4 plots/block. Slope in degrees from horizontal (=0). Insolation proportional to that received by a horizontal surface at 45 N latitude, for a given slope and aspect (B.G. Smith, unpublished program).

	Block		
Variable	1	2	3
A. Slope			
Top of plot	48.2 (2.0)	39.5 (4.0)	32.3 (6.6)
Bottom of plot	53.0 (2.9)	57.2 (5.5)	40.0 (10.7)
B. Insolation			
Top of plot	0.59 (0.02)	0.65 (0.04)	0.75 (0.04)
Bottom of plot	0.56 (0.01)	0.52 (0.02)	0.67 (0.06)
C. Desiccation (%)			
8/88	7.3 (1.0)	9.3 (1.4)	10.4 (1.1)
9/88	27.9 (2.4)	29.5 (2.2)	24.5 (2.5)
D. Limpet Density (6/88)			
<6 mm limpets	34.2 (5.8)	23.0 (4.8)	22.2 (5.0)
≥6 mm limpets	22.2 (4.4)	19.5 (3.7)	9.2 (2.8)
Total limpets	56.5 (5.8)	42.5 (7.8)	31.5 (5.8)
E. Vegetative Advance (mm)			
5/87 - 10/87	6.6 (0.8)	-0.1 (1.0)	4.0 (1.8)
10/87 - 4/88	13.3 (4.0)	4.5 (0.7)	8.4 (1.9)
F. Reproduction (%)			
10/87	62.6 (9.5)	23.7 (7.0)	18.2 (4.0)
1/88	59.4 (2.3)	31.1 (8.0)	46.1 (7.4)
10/88	9.7 (5.7)	4.2 (2.6)	0.1 (0.1)

Table III.2 (continued).

Variable	Block 1	Block 2	Block 3
G. Recruitment (#)			
1/88	4.2 (2.2)	3.0 (1.3)	0.25 (0.25)

Figure III.12. Effect of reproductive status of *Iridaea* on feeding by free-ranging limpets. Data are mean (± SEM) for six replicate feeding stations, triangles (▲), and six controls (limpet exclosures), circles (●).

Figure III.12.

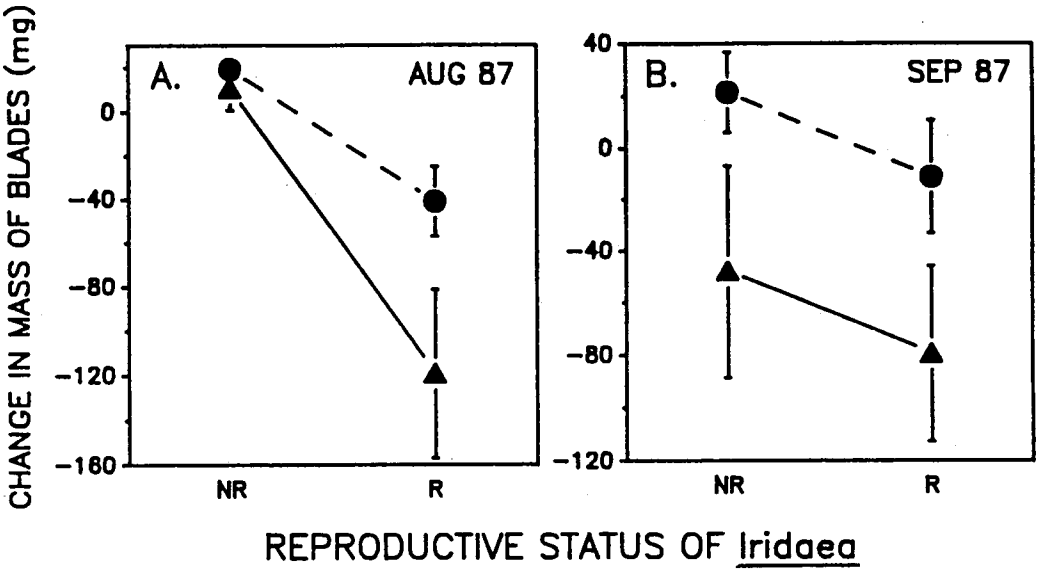
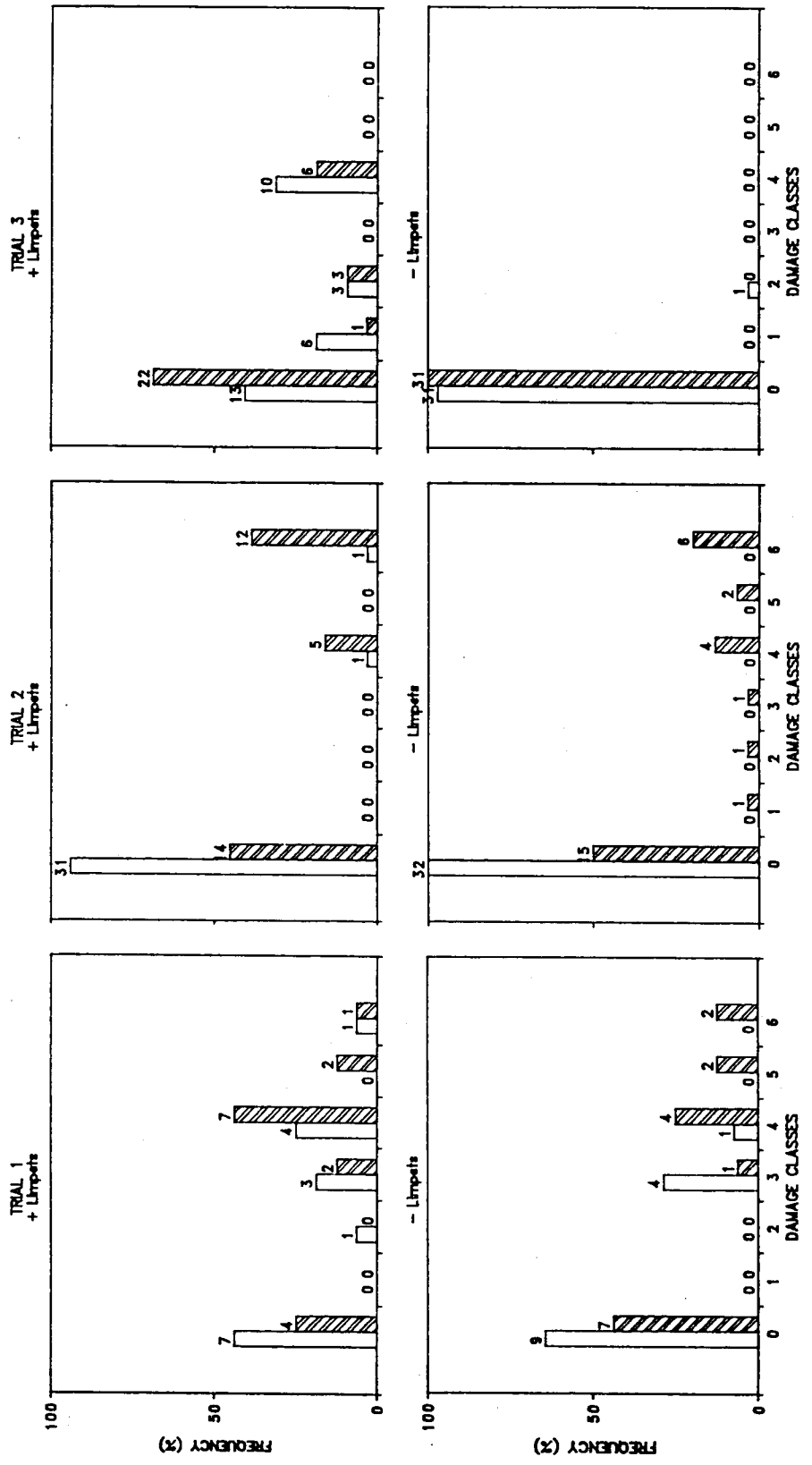


Figure III.13. Association of desiccation status of *Iridaea* with herbivore damage. Data are percent frequency of blades in subjective damage classes (numbers of blades are given above bars). Damage classes: 0 = intact (no visible damage), 1 = superficial grazing tracks (< 0.5mm deep), 2 = small holes and excavations on surface (< 0.1 mm diameter), 3 = small nicks on edge (< 1 mm diameter), 4 = large "chewed areas (> 2 mm diameter), 5 = >50% of blade removed (grazing marks visible on remaining blade, 6 = base of blade present in clamp, but protruding portion of blade removed. Trial 1, *Lottia digitalis*, reproductive blades, 12 d duration, n = 62; trial 2, *L. digitalis*, non-reproductive blades, 23 d duration, n = 126; trial 3, *L. pelta*, non-reproductive blades, 3 d duration, n = 127. Non-desiccated blades, open bars; desiccated blades, hatched bars.

Figure III.13.



and B), but not in trial 3 (fig. III.13C). In trials 1 and 2, desiccated blades were significantly more likely than non-desiccated blades to suffer substantial tissue damage (damage classes 4-6, see fig. III.13 caption), while non-desiccated blades were more likely to have minimal tissue loss (damage classes 0-3), in both limpet arenas and controls (table III.3). These results suggest that grazing by non-limpet herbivores (e.g., littorinid snails or dipteran larvae) may account for some of the damage to desiccated *Iridaea* blades, and may confound long-term field studies of limpet feeding preferences.

Table III.3. Association of herbivore damage with desiccation treatment. Table cells contain Pearson χ^2 statistics for a 2 x 2 model of desiccation x damage, with 1 degree of freedom (n = number of blades in parentheses). For χ^2 analysis, the seven subjective damage classes (see caption, fig. III.13) were collapsed into two classes: 0 = minimal tissue loss (classes 0, 1, 2, and 3); 1 = substantial tissue loss (classes 4, 5 and 6). Significance tests: +, $0.05 \leq p < 0.10$; *, $p < 0.05$, **, $p < 0.01$; ***, $p < 0.001$.

	Feeding Trials[a]		
Limpets	1	2	3
Present	2.95+ (32)	17.49*** (64)	1.27 (64)
Absent	5.93* (30)	14.87*** (62)	0.00 (63)

[a] See fig. III.13 caption for details of trials.

DISCUSSION

Predictions of the Models

Desiccation alters the effects of limpet grazing on the reproduction and recruitment of *Iridaea* at this site, and it appears to have a similar (but non-significant) effect on vegetative growth and canopy cover. Thus, it is likely that desiccation alone does not set the upper limit of *Iridaea*--limpet grazers probably also play a role. However, the interaction between desiccation and grazing is more complex than that predicted by either the CSM or the PSM (fig. III.1). Specifically, *Iridaea* appears to be grazer-limited in dry, but grazer-dependent in moist, microsites. These results suggest that a two-species model such as the CSM or PSM is insufficient to explain the interaction of desiccation and herbivory. Furthermore, these results and those of the feeding studies are not consistent with the mechanisms proposed by either model to explain correlations between stress and intensity of herbivory.

The CSM and PSM make contrasting predictions (Menge and Olson 1990) about the effect that reduced desiccation stress (i.e., moisture addition) should have on herbivory. The CSM predicts that moisture addition should exacerbate the effect of limpet grazing (fig. III.1A); the PSM predicts that it should ameliorate the effect of herbivory (fig. III.1B). Moisture addition reduced the negative effects of grazers on *Iridaea*, in particular, by permitting recruitment in the presence of grazers that was precluded in dry plots--results consistent with PSM. However, grazing by limpets tended to enhance

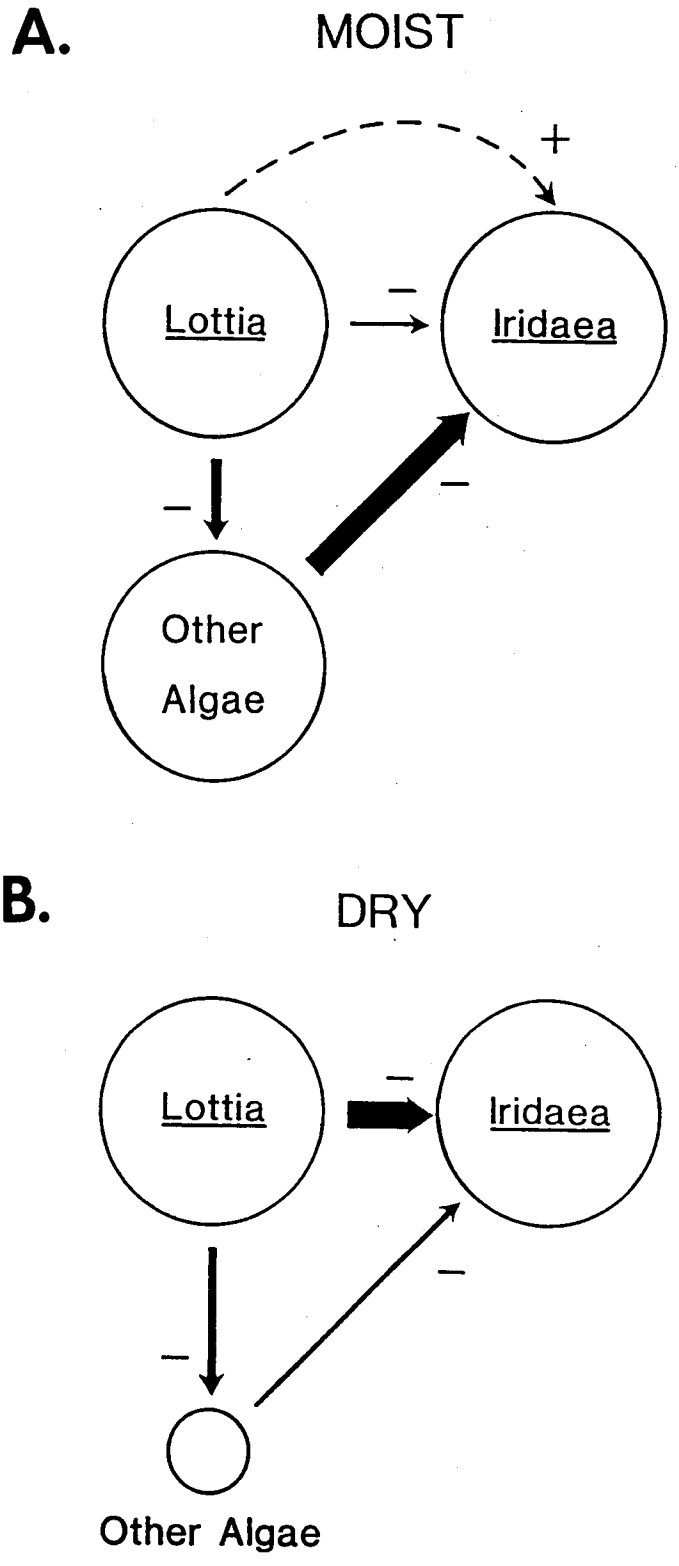
plant performance in moist plots, by increasing vegetative advance above the initial upper limit--a result not predicted by either model.

A simple two-species model, such as PSM, is probably not adequate to explain the beneficial effects of grazing under moist conditions observed in this study. It is likely that competitive interactions with microalgae (which may foul mature red algae, D' Antonio 1985; and inhibit germination of spores and growth of sporelings, Huang and Boney 1984, 1985) mediate the grazer-dependence of *Iridaea* in moist plots (fig. III.14A). *Lottia digitalis*, for exammple, preferentially feeds on microalgae and small-bodied ephemeral algae (Castenholz 1961, Frank 1965). Predation or grazing should increase the abundance of competitively inferior prey (e.g., *Iridaea*), if competitive dominants (e.g., microalgae) are preferentially attacked (Lubchenco 1978). In moist plots, where productivity of both *Iridaea* and microalgae should be greater, limpets may primarily remove microalgae, facilitating recruitment of *Iridaea* (fig. III.14A). A similar effect of molluscan grazers has been demonstrated in this (Paine 1981, Olson 1985) and other systems (e.g., review in Lubchenco and Gaines 1981). Thus, in the absence of limpets, moisture addition may have little effect on the performance of *Iridaea*, because gains in potential production are offset by losses due to competition.

Where desiccation suppresses the productivity of microalgae, limpets may feed more intensively (Castenholz 1961, 1962, Cubit 1984), including in their diets more spores and sporelings of *Iridaea*, inhibiting its growth and recruitment (fig. III.14B). During a series of feeding studies in 1987, limpets ate less *Iridaea* at naturally

Figure III.14. A conceptual model for a hypothetical effect of desiccation regime on interactions between limpets (*Lottia*) and *Iridaea*, mediated by competing algae. A. In moist environments, high productivity of other algae provides *Lottia* with an alternative food source reducing direct grazing (direct effect) on *Iridaea* and indirectly benefitting *Iridaea* by removing competitors. B. In dry environments, low productivity of other algae reduces competitive inhibition of *Iridaea*, but direct limpet herbivory on *Iridaea* is increased.

Figure III.14.



moist, shady feeding stations (where a visible standing stock of diatoms and ephemeral algae persisted throughout the summer) than at dry, sunny stations (where the rock appeared bare). The strong effect of moisture addition in the presence of limpets may be mediated by the response of limpets to the availability of their preferred microalgal food. Thus, where desiccation is low and productivity is high, limpets may subsist on microalgae (and release *Iridaea* from competition) (fig. III.14A); where desiccation is high and productivity low, limpets may begin to consume *Iridaea* and inhibit its recruitment (fig. III.14B). Thus, desiccation may alter limpet herbivory on *Iridaea* indirectly via its effects on the availability of alternative algal foods.

Causal Mechanisms

Several proximal mechanisms potentially explain the predicted association of herbivore impact with environmental stress (fig. III.15). The CSM and PSM identify certain of these mechanisms (figs. III.15A and D1); results of this study suggest other factors that may also contribute to positive or negative correlations between stress and herbivory (figs. III.15B, C, and D2).

Herbivore abundance

Decreasing herbivore abundance or effectiveness with stress (fig. III.15A) is usually invoked to explain the negative correlation of herbivory (and the positive correlation of plant performance) with stress predicted by the CSM (review in Menge and Olson 1990). Harsh conditions are consequently hypothesized to provide prey with a refuge

Figure III.15. Explanatory mechanisms potentially accounting for correlations between environmental stress and the effect of consumers on prey. The consumer stress model (CSM) predicts a negative correlation, the prey stress model (PSM), a positive correlation, between stress and the impact of consumers. Cells A and D1 reflect mechanisms usually associated with the respective models.

Figure III.15.

EFFECTS OF STRESS ON

	CONSUMERS	PREY
CSM	A. Decreased abundance or effectiveness (prey refuge)	B. Decreased palatability
PSM	C. Increased abundance (in consumer refuge)	D.1. Increased quality/decreased defense 2. Decreased recovery

from herbivory. The preditions of the CSM would also hold if prey palatability declined with stress (fig. III.15B) (regardless of changes in consumer abundance or effectiveness) as when herbivores prefer young, vigorous leaves (e.g., Coley 1983, Rauscher 1981).

In the present study, limpet abundance was negatively correlated with desiccation intensity on a large scale, a pattern expected under the CSM. Significant block effects in several analyses (table III.2) were associated with a gradient of increased insolation and desiccation, from block 1 (which is steeper and more shaded by cliffs to the south) to block 3 (which is more nearly horizontal and less shaded). Despite biweekly additions, total limpet abundances were higher at the shady than at the sunny end of this gradient in midsummer. Similarly, Louda and Rodman (1983) observed a negative correlation of herbivore damage with elevation in subalpine populations of a native mustard that appears, on a local scale, to be more susceptible to grazers when stressed by low soil moisture. In this study, the cline could be produced by desiccation-induced limpet mortality or migration (e.g., Wolcott 1973) or by bird predation in more horizontal plots (e.g., Frank 1982, Marsh 1986), but the relative contribution of each of these and other factors is not known. Within blocks, among treatments, however, the interaction of desiccation and herbivory was consistent with the PSM.

Plant susceptibility

Under the PSM, the predicted positive correlation of herbivore damage with stress has usually been attributed to a stress-induced changes in plant susceptibility to herbivory (fig. III.15D1). Stress

may induce changes in plant quality (Mattson and Addy 1975), such as increased nutrient availability (White 1984) or decreased defense (Waring and Schlesinger 1985), that lead to higher rates of feeding on stressed plants. For example, Lewis (1979, 1982, 1984) found that grasshoppers preferred wilted, senescent, or previously damaged leaves of sunflower species to vigorous, undamaged leaves. Hughes et al. (1982), also observed increased rates of feeding by Mexican bean beetles on soybean leaves that had been stressed by exposure to SO_2.

In the present study, nutrient availability and plant defenses were not directly measured. However, results of the feeding studies do not support the hypotheses that senescence (due to reproduction) or desiccation increase the susceptibility of *Iridaea* to limpet grazing. During feeding trials, reproductive blades were senescent. In the absence of limpets, non-reproductive blades appeared vigorous and tended to grow, while reproductive blades either failed to grow or lost mass. However, limpets did not preferentially feed on reproductive blades. Furthermore, desiccation treatments also did not result in measurably higher rates of feeding by limpets in repeated trials.

These results are not consistent with the hypothesis that desiccation affects plant susceptibility to limpets. However, they should not be considered conclusive for several reasons. First, the effect of chronic, non-lethal desiccation was not investigated nor were spores, small blades, or crusts used in feeding trials. Only acute, simulated desiccation damage to mature blades was tested. Results of the moisture addition X limpet removal experiment, however, suggest that the effect of desiccation on the vulnerability of spores

and small plants may differ from its effect on susceptibility of larger plants to grazers. Thus, desiccation stress may influence the likelihood that a sporeling will survive to attain a size-escape from predation (e.g., Paine 1976, Lubchenco 1983).

Second, artificially desiccated blades may not be comparable to naturally desiccated blades, which appear to become infested by micro-organisms. Following prolonged aerial exposure, blades normally become bleached, then within a few days the bleached tissue becomes "slimy." Both limpets and littorinid snails appear attracted to these damaged thalli; all the necrotic tissue is usually removed within several days, provided further desiccation does not occur. Artificially desiccated blades, on the other hand, became bleached, but tended to remain firm and intact (unless eaten) throughout the feeding trials. Thus, the effect of severe desiccation damage on herbivore feeding preferences may depend on micro-organisms (see White 1984 for a review of evidence for links between stress, pathogens, and susceptibility to grazers in vascular plants). Studies employing naturally desiccated blades, with control for infestation by microorganisms, could further resolve this question.

Third, subjective estimates of herbivore damage suggest that some unidentified members of the herbivore guild prefer desiccated to non-desiccated blades of *Iridaea*. If so, their feeding may have introduced uncontrolled variability into tests of limpet feeding preferences, particularly in the longer-term trials (1 and 2) involving *L. digitalis*. Nevertheless, desiccation of mature blades did not markedly change limpets' feeding preferences, suggesting that

other factors may account for the interaction of desiccation and herbivory observed in the long-term experiment.

Plant recovery

Recovery from herbivory may be inhibited by stress, resulting in a positive correlation of herbivory with desiccation (fig. III.15D2), consistent with the PSM, independent of changes in plant susceptibility to grazing. For example, Chater (1931) noted that isolated gorse plants vigorously sprouted from basal nodes after rabbit grazing, while those in competition with grasses failed to sprout and often died. In a prospective study, Webb (1981) found that the potential for Douglas-fir and white fir twigs to recover from tussock moth defoliation was positively correlated with starch content prior to attack (an indicator of plant vigor).

Although the present study does not address the effects of stress on recovery of *Iridaea*, preliminary results of other studies (A. M. Olson, in preparation) suggest that experimentally defoliated *Iridaea* loses less basal area and recovers canopy faster in moist than in dry treatments. For clonal organisms, with the potential to respond vegetatively to herbivory, this effect of stress on recovery from herbivory may be as important as stress-induced changes in initial susceptibility to herbivory.

Herbivore movement

Additional mechanisms that potentially result in the positive correlation between stress and herbivory predicted by the PSM are factors that directly or indirectly affect herbivore abundance or behavior (fig. III.15C), independent of their effects on plant quality

and recovery. For example, Huffaker and Kennett (1959), hypothesized that the thermal requirements of leaf beetles restrict foraging on St. Johnswort to sunny habitats, where plants may experience more heat and desiccation stress. The retreat of consumers to refuges to avoid physiological stress (Menge 1978a, b) may create high consumer densities in some microhabitats during stressful episodes (fig. III.15C). For example, *Lottia digitalis* often aggregates during daytime low tides (Frank 1965, Millard 1968, Gallien 1985) and migrates downward during summer months (Frank 1965, Breen 1972, A.M. Olson, personal observation). Thus, in consumer refuges, high environmental stress would be temporally correlated with herbivore abundance and perhaps with feeding activity.

Observations of limpet behavior lend support to the notion that desiccation magnifies the detrimental effects of grazing, in part, because limpets limit their foraging to areas close to the moist refuge provided by *Iridaea* beds. For example, in this study, limpets tended to stay within the *Iridaea* bed in dry plots; in moist plots they aggregated near the moisture-retaining polyester (A. M. Olson, personal observation). Thus, limpet foraging is probably concentrated nearer to patches of *Iridaea* or other algae under more desiccating conditions.

To understand spatial variation in prey abundance and performance it is necessary to distinguish between the pattern of consumer effects and the mechanism that produces the pattern. The impact of herbivory may increase with stress as predicted by the PSM, independent of changes in plant quality and grazer feeding rate. Plant recovery may be inhibited, or herbivore activity locally

intensified, by stress. On the other hand, stress-induced changes in consumer abundance or effecctiveness are not necessary for the impact of consumers to decline with stress. For example, when herbivores prefer vigorous tissue, plant susceptibility may decline with stress (the "plant vigor hypothesis" of Price 1991). Future empirical work should thus focus on the mechanisms which mediate the effects of stress on consumer-prey interactions.

In particular, a key issue seems to be the conditions under which either consumers or prey are relatively more affected by physical factors. The preponderance of support for CSM comes from freshwater and marine environments (reviews in Menge and Sutherland 1987, Menge and Farrell 1989), while that for PSM is mainly from terrestrial insect-plant systems (e.g., Waring and Schlesinger 1985). This observation suggests that perhaps when plant and herbivore are immersed in the same medium, CSM may apply, while PSM dynamics may be more relevant when stress factors affecting plants (e.g., soil moisture) differ from those affecting herbivores (e.g., air temperature). If this pattern holds, sub-surface (soil) plant-herbivore interactions might be expected to follow the CSM model.

Defining the domains of the CSM and PSM is not a trivial endeavor. Distributions of species predicted under each of these models will differ in specific ways from those expected on the basis of single-species models. Single-species models often will be inadequate to predict species' responses to environmental change. Consequently, identifying the domains of the models has important implications for predicting the responses of species to anthropogenic effects such as pollution or climate change (Lubchenco et al. 1991).

For environmental decision-makers, it may be critical to know whether the CSM or the PSM holds in a particular situation, because the CSM makes the counter-intuitive prediction that prey species' abundances may increase with stress, while the PSM predicts that species may be excluded (even from regions where anthropogenic stress is physiologically tolerable) by the combined effect of consumers and stress. The differences in these predictions suggest that setting acceptable levels of a pollutant, or forecasting the effect of climate change on species distributions, will require more than an assessment of the physiological responses of individual species. Instead, scientists and decision-makers will need to consider the interplay between stress and the interactions among a suite of species in order to predict, understand, and prepare for natural and anthropogenic environmental change.

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Chapter IV

COMPETITION IN SEAWEEDS: LINKING PLANT TRAITS TO COMPETITIVE OUTCOMES

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INTRODUCTION

Competition for resources among seaweeds is potentially important at several levels of organization. Competition may influence community-level patterns (e.g., species diversity, succession, and stability) both directly and by mediating the effect of other structuring agents, such as herbivory and physical disturbance (Lubchenco and Gaines 1981). At the population level, competition may affect size and age structure and other determinants of population growth. Finally, competition may influence individual survival and reproduction (fitness), with potential evolutionary consequences. In natural systems, community-, population-, and individual-level processes are intricately interwoven, making it difficult to disentangle the potential causes and consequences of

competition. We will focus on the consequences of seaweed traits for the outcome of competitive interactions.

Historically, culture and field studies have followed separate but parallel lines of inquiry. As a result, we currently lack a rigorous understanding of the consequences of particular seaweed traits for competition and of the trade-offs involved in competition and other biotic and abiotic interactions. Culture studies have tended to focus on the physiological, morphological, or life history characteristics that potentially affect competition--directing attention to the way these plant traits affect resource capture and how environmental variation affects their expression. However, most culture studies stop short of experimentally demonstrating the consequences of plant traits for competitive outcomes, simply assuming that differences in traits will result in competitive differences. On the other hand, field studies of competition have tended to focus on competitive outcomes--the fates of competing populations under differing environmental conditions (e.g., Paine 1990). The emphasis has been on the way that variation in stress (e.g., desiccation, high or low temperature), disturbance (e.g., log-bashing, sand-scour), or herbivory determines whether competition occurs and, if so, the sign or magnitude of competitive interactions. However, mechanistic explanations, often involving trade-offs at the individual level (e.g., between competitive ability and susceptibility to herbivory) have not been tested by measurements of physiological costs and benefits. Thus, the causal relationships between plant traits and competitive outcomes remain a crucial gap in our understanding of competition among seaweeds. To bridge this gap, we see a need to (1)

establish rigorously the competitive consequences of variation in traits (among and within species) observed in culture studies and (2) evaluate the hypothesized mechanisms of competition (and other ecological interactions) proposed as a result of field studies.

The contributors to this series of minireviews highlight a set of familiar and novel plant traits and suggest hypotheses regarding their significance for competitive interactions: Carpenter (1990) focuses on traits associated with the capture of space, light, carbon, and nutrients. He shows how morphological traits--such as growth form, thickness, degree of branching and surface texture--and physiological traits--such as photoadaptation, alternate carbon fixation pathways, and nutrient uptake and storage strategies--interact to determine the internal resources available for allocation to competitive interactions, as well as to other plant functions. Next, Paine (1990) offers a wide-angle view--from the individual to the community levels--of plant traits that may interact to alter competitive interactions. He reviews field observations of (1) thallus fusion or redirected growth following contact with other thalli that may represent "cooperation" within and among species, (2) epithallial sloughing or antibiotics serving as "defenses" against epiphytes, and (3) resistance to herbivory and the associated grazer-dependence of competitive outcomes. Finally, Maggs and Cheney (1990) narrow the focus to thallus fusion a novel seaweed trait also discussed by Paine. They review laboratory observations of coalescence, secondary pit connections, and fusion cells between sporelings differing in relatedness, ranging from genetically identical sporelings to those differing in ploidy or species. In this

introduction to the series, we briefly review theoretical and empirical approaches to competition and suggest research strategies for linking the traits and fates of seaweeds.

DEFINING COMPETITION

Although the early competition models were very simple, their assumptions and predictions reflect much of our common sense understanding of competition. The Lotka-Volterra model translates the deleterious effect of a competitor into a cost expressed in terms of population growth (Roughgarden 1979). This cost is proportional to the ratio between inter- (α_{ij}) and intraspecific (α_{ii}) effects for each species. According to the simplest form of the model, the outcome of competition (i.e., whether there is a winner and, if so, which species wins) depends both on the cost of competition and on the carrying capacity (K_i, or number individuals of each species that can be supported in a given environment in the absence of competition). If the carrying capacities of the two species are equal (i.e., $K_1 = K_2$), one species (e.g., species 1) will dominate only if the competitive effects are asymmetrical--that is, if α_{21} (the effect of species 1 on species 2) is greater than α_{22} (the effect of species 2 on itself) and, simultaneously, if α_{12} is less than α_{11}. Thus, a species' competitive position depends on its ability to harm its competitor (e.g., by preempting space) or to reduce the deleterious effects of its competitor (e.g., by preventing colonization or overgrowth). However, when carrying capacities are not equal (e.g., $K_1 > K_2$), the likelihood of coexistence is reduced and the balance is tipped in favor of the species with higher K. Thus, a species with greater efficiency of resource use (e.g., nutrient assimilation) may exclude its competitor, even when the balance of intra- vs. interspecific effects favors the competitor (Roughgarden 1979).

Modern competition theory continues to evolve as a result of the interplay between theoretical and empirical studies (see reviews in Pacala 1989, Kareiva 1989). Problems that arise in applying the Lotka-Volterra model to plants (Schaffer and Leigh 1976, Pacala 1989) have stimulated refinement of existing theory and development of new theoretical approaches. In the following paragraphs we present four examples of problems with the Lotka-Volterra model that are particularly relevant to seaweeds, noting some recent theoretical developments and some outstanding problems.

(1) The Lotka-Volterra model assumes that the environment is spatially homogeneous and that resource limitation or crowding can be expressed in terms of K, the maximum density of individuals in a population. However, because seaweeds and other plants are attached to the substratum, their environments are not homogeneous, the intensity of interactions among plants varies with the spatial arrangement of competitors (Pacala 1989). In addition, the number of individuals is a poor measure of crowding in plants (Schaffer and Leigh 1976). Indeterminate growth and variation in plant architecture may result in increased crowding, despite decreasing numbers of individuals. Thus, interactions among seaweeds depend upon the position, biomass, architecture, and potential for vegetative expansion of competitors, as well as on their population density. Spatially explicit models of interactions among plants have been developed (review in Pacala 1989), but these need to be linked to models of clonal growth and reproduction (e.g., Bell 1984, Caswell 1985).

(2) The Lotka-Volterra model also assumes that the cost of

competition (α_{ij}/α_{ii}) is constant and independent of density (i.e., the effects of species on each other do not change). Thus, interacting populations lack age or size structure, genetic variation, and phenotypic plasticity (i.e., all individuals are identical). Empirical studies (see "Detecting Competition," below) suggest, however, that competitive effects vary considerably with the age or size at which species interact. Although modern competition models have incorporated age or size structure (reviews in Pacala 1989, Kareiva 1989), theory that predicts the effects of genetic or plastic variability on competitive interactions is presently lacking (Kareiva 1989). (3) The Lotka-Volterra model lacks density-independent sources of mortality, such as herbivory or extreme environmental conditions. Models incorporating consumers (e.g., Caswell 1978) more realistically portray the dependence of competitive outcomes on grazing regimes (e.g., Paine 1990). (4) Unique traits of seaweeds, including isomorphic life histories and somatic polyploidy (Goff and Coleman 1986), as well as thallus fusion, suggest areas for future elaboration of plant-specific theory.

DETECTING COMPETITION

Experimental detection of competition is achieved by manipulating the abundance of competing species or the resource. The strength of competition is measured by the effect of experimentally varied plant density on abundance (e.g., density, percent cover) or on rates affecting abundance (e.g., fecundity, growth, mortality, or physiological condition) (Connell 1983, Schoener 1983). Harper (1977), Connell (1983), Underwood (1986), and Denley and Dayton (1985) provide useful discussions of appropriate experimental designs that may be applied in laboratory, mesocosm, or field settings.

Competition experiments ideally should be conducted in the field with adequate replication and controls (Connell 1983, Schoener 1983), in order to evaluate competition as a natural process. Competitor-removal experiments and transplants can be an effective way to manipulate the density of larger sporelings and established seaweeds (e.g., Schonbeck and Norton 1980; also see reviews in Denley and Dayton 1985, Chapman 1986). However, the microscopic spores of seaweeds make the field study of competition difficult for the earliest stages of development. For these stages, alternative approaches include experiments in the laboratory (Russell and Fielding 1974, Fletcher 1975) or in semi-natural tank culture (mesocosms), "seeding" spores (Dion and Delepine 1983) of competing species at different densities onto artificial substrata for later outplanting, or applying spore suspensions directly to natural substrata (L. Druehl, *pers. comm.*).

Competition will not be detectable in nature, however, if

resources are superabundant or if herbivory, low recruitment, or physical factors (e.g., storm damage, desiccation) reduce the density of potentially competing populations. Thus, it is frequently necessary to vary the context in which competition experiments are conducted, for example, by simultaneously manipulating herbivores (see Sih et al. 1985 for design suggestions) or by replicating field experiments along gradients of wave force or desiccation (e.g., Lubchenco 1986), in order to determine the conditions under which competition occurs. Alternatively, laboratory competition experiments can be made more realistic by including herbivore treatments or by mimicking desiccation (e.g., Luxoro and Santelices 1989) or water motion (e.g., Denny 1988) regimes. Such improvements in experimental design and technique will yield valuable information on the relative importance of competition for seaweeds under different conditions (Lubchenco 1986).

In the following examples we illustrate several factors that can affect the outcome of competition in the field. First, Fujita (1985a, b) suggests that the pattern of nutrient availability can determine the competitive dominant. When nutrients are continuously available, *Enteromorpha* spp., by virtue of their faster uptake rate, can out-compete *Gracilaria tikvahiae* (e.g., fig. IV.1A). However, *Gracilaria* has a greater nutrient storage capacity. Consequently, when the nutrient supply is pulsed and the interval between pulses exceeds the storage capacity of *Enteromorpha*, *Gracilaria* is the competitive dominant.

Second, competitive interactions in the mid-intertidal zone in New England illustrate the importance of timing and grazers on the

Figure IV.1. A schematic representation of some mechanisms of competition (Schoener 1983) in seaweeds. A. Consumption of nutrients mediates the interaction between *Gracilaria tikvahiae* and *Enteromorpha* spp. in the field (Fujita 1985a, b). B. A dense turf of *Enteromorpha intestinalis* preempts space, preventing colonization by spores of *Ulothrix pseudoflacca* in culture (Hruby & Norton 1979). C. *Pseudolithophyllum muricatum* overgrows *Lithothamnion phymatodeum* in the field on a smooth, artificial surface in the absence of grazers (Paine 1984). D. An alga uses allelochemicals to exclude a competitor (hypothetical interaction).

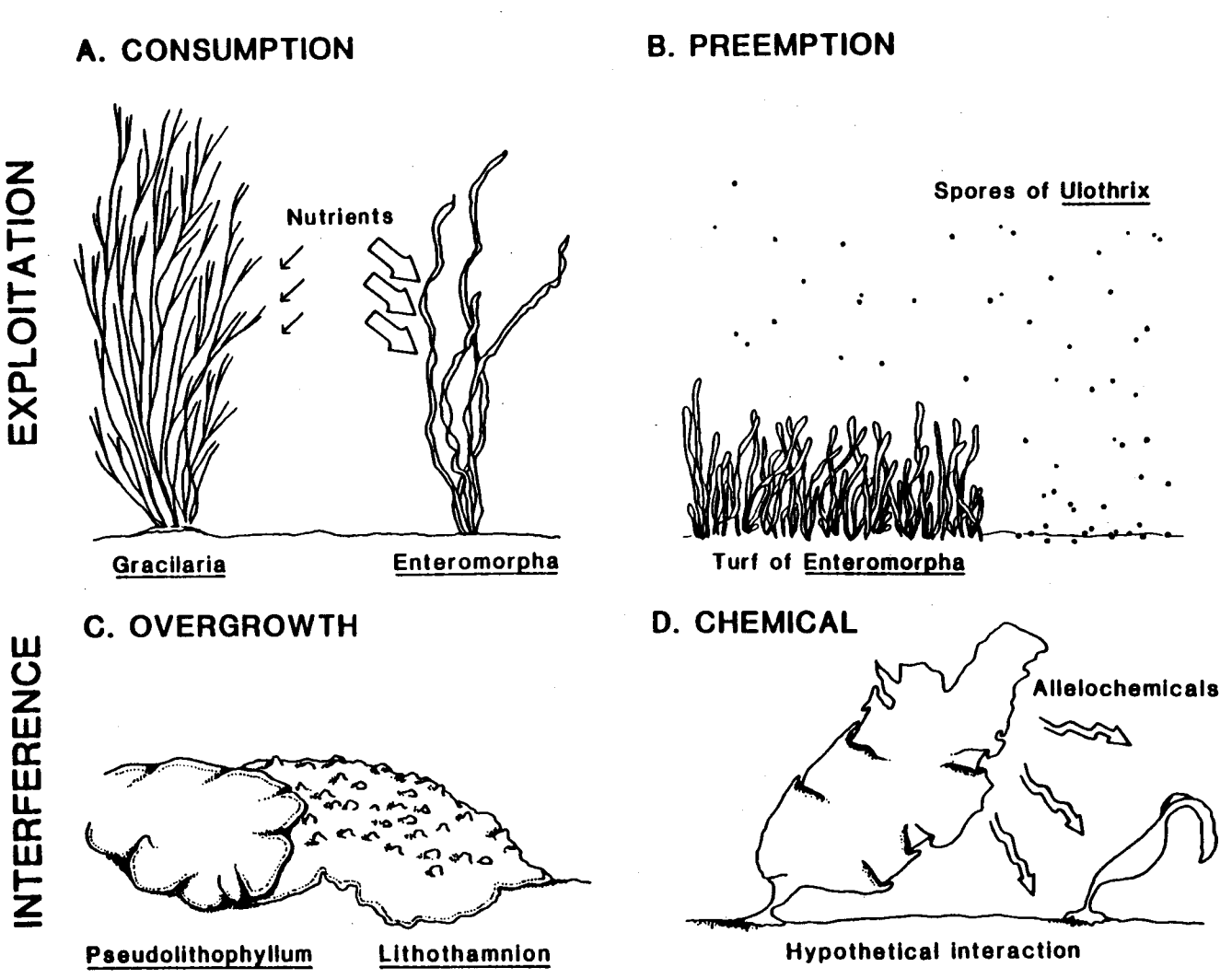
A. CONSUMPTION
B. PREEMPTION
EXPLOITATION
Nutrients
Gracilaria
Enteromorpha
Spores of Ulothrix
Turf of Enteromorpha
C. OVERGROWTH
D. CHEMICAL
INTERFERENCE
Allelochemicals
Pseudolithophyllum
Lithothamnion
Hypothetical interaction

Figure IV.1.

outcome of competition. *Fucus vesiculosus* colonizes freely in the presence of grazers that selectively remove *Enteromorpha* spp. (Lubchenco 1983). In the absence of grazers, however, *Enteromorpha* initially outcompetes *Fucus* germlings early in succession, presumably by its faster growth rate. Because grazers are usually effective, *Fucus* becomes established and overtops *Enteromorpha*. Over the long term, *Fucus* excludes *Enteromorpha* from the rock surface by preempting space, although *Enteromorpha* can occur as an epiphyte on *Fucus* when mesoherbivores are absent or ineffective. This example illustrates two effects of timing in competitive interactions: First, the outcome of competition depends on the developmental stages that are competing (i.e., germling vs. germling or germling vs. adult). Thus, a single trait, such as rapid growth, that confers superiority on *Enteromorpha* when germlings compete is not effective when competing against adult *Fucus* for attachment space. Second, the arena of competition changes during succession, expanding to include competition for light by epiphytes, as well as for attachment space on the rock surface.

The above example also illustrates the potential importance of trade-offs between competitive ability and other demands on plants' resources. In this case, the outcome of competition is grazer-dependent, because competitive ability is negatively correlated with susceptibility to herbivory. Currently, we know little about the physiological mechanisms underlying such trade-offs. In the following section, we suggest research strategies that link seaweed traits to competitive outcomes in a way that may be helpful in understanding the physiological and morphological bases of trade-offs.

CONSEQUENCES OF PLANT TRAITS AND THE MECHANISMS OF COMPETITION

Different plant traits may be associated with competitive dominance, depending on the mechanism of competition (fig. IV.1). Exploitation mechanisms include consumption (depletion of resources) and preemption (passive prior occupation of space) (Schoener 1983). Where consumption is the mechanism, higher rates of resource capture (Carpenter 1990) may afford competitive superiority. If the interaction is preemptive, then larger size, spreading habit, and the ability to perennate may be associated with dominance. Interference includes overgrowth (including epiphytic interactions), and chemical (toxic or hormonal) mechanisms (Schoener 1983). Rapid lateral growth, ability to raise the growing edge off the substratum, and production of toxins are traits that may affect the outcome of interference interactions. It is often difficult to identify a single mechanism--for example, consumption of light interferes with other species by shading, preemption may be accompanied by chemical effects. Finally, asymmetry is to be expected in the mechanism, as well as in the strength of competitive interactions. For example, *Fucus* may preempt space, preventing subsequent colonization of the rock surface by ephemerals, whereas ephemerals interfere with *Fucus* by growing on it as epiphytes and increasing the drag on *Fucus* (Lubchenco 1983).

The association of seaweed traits with competitive mechanisms, however, is largely hypothetical. The ecological and fitness consequences of particular traits await experimental analysis. Which seaweed traits are associated with competitive dominance? How does variation in a single trait affect competitive performance? We

suggest that a research strategy that explicitly focuses on the functional significance of plant traits could provide substantial insights into competition among seaweeds.

Several studies have quantified variation in a suite of morphological and physiological traits both among (e.g., Littler et al. 1983, Hay 1986) and within (e.g., Hanisak et al. 1988) seaweed species and have identified possible trade-offs between potential growth rate and a variety of other traits. We suggest that this correlative approach could be made more rigorous and definitive by simultaneously conducting competition experiments to determine species competitive rankings (e.g., Harper 1977, Gaudet and Keddy 1988). Seaweed traits and competitive ability could then be linked by multiple regression techniques (Gaudet and Keddy 1988). This approach would be particularly useful in identifying potential trade-offs between seaweed performance in competition and other ecological interactions, if experimental tests of susceptibility to herbivores, physiological stress, or mechanical disturbance (e.g., Koehl 1986) were also included in the analysis.

It is a somewhat different problem to determine the effect on competition of variation in a single trait. One must manipulate not only the densities of competing species, but the trait of interest. Sometimes it is possible to manipulate a trait directly, for example, by pinning down the upper branches of a plant to test the effect of height (Benjamin 1984). In other cases the investigator can take advantage of natural or induced (mutant) variation in a trait. For example, to understand the significance of thallus fusion for competitive outcomes, the performance (e.g., growth rate, ultimate

size, or reproduction) of fused and non-fused thalli must be tested, alone and in the presence of a competitor. If fusion has consequences for interspecific competition, performance of the fusion chimera should be better than that of non-fused thalli in the presence of the competitor. Thallus fusion may also affect competition indirectly--for example, by increasing resistance to desiccation or herbivory.

A remaining question is how any ecological benefit of thallus fusion may be distributed among the individual members of a fusion chimera. The interaction between members of a chimera may range from mutualism (both members benefit) to somatic parasitism (one member benefits at the expense of the other). Both mutualistic and parasitic intraspecific interactions have been observed in fungi and sessile invertebrates (e.g., Buss 1981, 1982, Weissman et al. 1988). The costs and benefits of these interactions depend on the genetic relatedness of the participants (Weissman et al. 1988, Grosberg and Quinn 1988). Formation of pit connections and fusion cells can be associated with parasitic or aggressive interactions in algae (e.g., Goff and Coleman 1985, Koslowsky and Waaland 1984). The potential that, in some circumstances, thallus fusion may represent parasitism needs to be explored by evaluating the fitness consequences of fusion for both members of the chimera. Further investigation of physiological integration between fused sporelings would be facilitated by use of modern molecular techniques, including tracer studies of photosynthate and nutrients, monoclonal antibody labeling to track transport of growth factors and other hormones, and molecular probes for genes or gene transcripts unique to one member of the pair.

CONCLUSIONS

In conclusion, we would like to emphasize the following points:

1. Ecological theory can be useful in identifying critical factors in competitive interactions and in predicting the logical consequences of variation in those factors. We see a need to incorporate recent theory into our thinking about competition in seaweeds and to evaluate the implications of unique seaweed traits for future theoretical treatment.

2. Because the traits of seaweeds have evolved in a context of multiple selection pressures, the consequences of traits will vary with environmental conditions. Thus, to link the traits of seaweeds with the outcome of competition, it is essential to demonstrate competitive effects in the context of environmental gradients in herbivory, stress, and disturbance.

3. A focus on the functional significance of seaweed traits can help integrate laboratory and field studies, by directing our attention to the ecological consequences of traits and to the underlying mechanisms of ecological patterns. (Similar recommendations regarding terrestrial systems have been made by Arnold 1983, McGraw and Wulff 1983, and Ehleringer et al. 1986.)

4. Seaweeds have much to offer as model systems for the study of competition: studies of seaweeds have contributed to a general understanding of the trade-offs between morphological and physiological traits and of the relative importance of competition for communities. Incorporating novel seaweed traits (e.g., coalescence) into studies of competition will put our understanding on a broader

evolutionary basis. Areas needing further investigation include the importance for competitive interactions of allelochemical interactions, of vegetative reproduction, and of variation in ploidy and morphology within the life history.

As demonstrated in this series of mini-reviews, the study of competition in seaweeds is at a crossroads. By linking the techniques of laboratory and field studies, we have a unique opportunity to develop an integrated view of seaweeds in their environments.

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QUESTIONS

Question (Carpenter): You have recommended the incorporation of simple ecological models as one basis for further experimentation to examine competition within and between algae. Given the demonstrated variability in the carrying capacity of an environment, due to either environmental changes over short time scales and/or to physiological plasticity exhibited by algae, how useful will such simple models be in predicting competitive relationships?

Answer: We view the simplest competition models as a useful framework for organizing a discussion of competition. More sophisticated models, however, make predictions that can be tested in order to further both empirical and theoretical understanding of competition.

All ecological models simplify complex phenomena, making it possible to explore the logical consequences of varying some set of factors, assuming a given biological background. Theoretical models can contribute to empirical studies by suggesting the kinds of factors that should affect competitive outcomes. Toward this end, Kareiva (1989) lists ten critical experiments suggested by modern theoretical developments. Your question regarding the effect of environmental variation on competitive interactions has been addressed in models by Chesson (e.g., 1986) that make several explicit predictions. These predictions remain to be tested (Kareiva 1989) and seaweeds may provide good model systems for doing so.

Ecological theory benefits from empirical feedback, as well. Theory necessarily makes its assumptions explicit. As "consumers" of

theory, empiricists are especially sensitive to whether particular assumptions are warranted in a given system. As you point out, real systems often violate the Lotka-Volterra assumptions of constant environment and identical individuals. Recognizing these and other limitations of the simplest models, theorists have elaborated existing theory and constructed entirely new theory that is more realistic (reviews in Pacala 1989, Kareiva 1989).

Question (Paine): To what extent are seaweed traits, expressed under laboratory conditions, accurate reflections of possible conditions or even responses in the "real world"?

Answer: Some algal traits are notoriously variable. This variation is probably expressed in both the laboratory and the field. In the past variation has either been ignored or treated as "noise", but intraspecific variation potentially has important ecological as well as evolutionary implications. Understanding the causes and consequences of such variation represents an important challenge. Both field and laboratory approaches are appropriate: In the field, transplants between habitats and experimental alteration of habitats permit evaluation of environmental effects on seaweed traits. Laboratory studies can explore the relative contribution of genetic and plastic variation that sets boundaries on the ecological responses of seaweeds in nature.

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