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# IMPACTS OF CLIMATIC CHANGE ON THE BIOSPHERE

## CIAP MONOGRAPH 5 PART 1 - ULTRAVIOLET RADIATION EFFECTS (Chapters 4 through 10)



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FINAL REPORT

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TABLE 8.1. Examples of Rapid Evolution Resulting from Recent Environmental Changes

Evolutionary change	Organism	Reference
Industrial melanism	Lepidoptera (~50 spp.) Coleoptera (2 spp.) Arachnida (4 spp.)	Kettlewell (1961) Creed (1966) Berry (1972)
Heavy metal tolerance	Bacteria, Fungi, Algae, Mosses, Liverworts, Vascular plants	Antonovics et al. (1971)
Insecticide resistance	Mosquitoes, house-flies crop pests (~250 spp.), mites	Brown (1960)
Infective multiple drug resistance	Bacteria	Anderson (1968)
Co-evolution of disease resistance and avirulence	Rabbits and Myxomatosis Virus	Fenner (1971)
Warfarin resistance	Rats	Drummond (1970)
Fungicide tolerance	Fungi	Georgopoulos et al. (1967)

CHAPTER 8

PREDICTING EVOLUTIONARY RESPONSE OF NATURAL POPULATIONS TO INCREASED UV

RADIATION

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The ecological responses of a species to environmental change are generally interpreted in terms of the physiological reaction norms of that species to the relevant environmental parameters. As a consequence, it is generally accepted that, by accurately understanding the physiology of a species, we will be able to predict how it will be affected by a given environmental change. This general principle is often extended to the community and ecosystem to give us a powerful means of anticipating the biological effects of pollution, climatic change, and other environmental disturbances. The major obstacle to predictability seems to be the complexity of ecosystem processes; if these can be resolved by detailed studies, by modeling of complex systems, and by coordinated efforts of many scientists with a goal-oriented approach, we will have a sure footing for environmental management. These have been the major tenets behind projects such as the International Biological Program and the present study on the biological effects of UV radiation.

There is, however, a serious complication that is often underestimated or even totally ignored in such a line of reasoning. Ecological response is not solely determined by the physiological responses of the component species; it is also determined by their evolutionary responses. The existence of an evolutionary component to ecological amplitude has been known for many years (particularly since the work of Turesson, 1922 in Europe and Clausen et al., 1940 in the United States), but it has generally been considered a "second-order" response of minor consequence. It is only recently that the reality and dynamics of this fact have been brought home to us by many examples of recent rapid evolution, much of it in response to man's impact on his environment [see table 8.1 for major examples and Berry (1972) for review].

In the light of these many examples, it is disturbing that relatively large-scale studies on the impact of environmental changes on ecosystems, such as the large-scale study of the effects of radiation on a tropical rain forest (Odum & Pigeon, 1970), make no attempt to assess possible evolutionary reactions of the component species. The reasons for this are worth exploring before returning to the specific subject of resistance to UV radiation.

Opinions as to the predictability of evolutionary responses range from (a) the view that, since the raw materials of evolution are random mutations, we are dealing with a totally unpredictable process, to (b) a pan-selectionist view that organisms are capable of evolving in reaction to many alterations in the environment.

The first view is based on the naive assumptions that an organism is capable of mutating in an infinite number of random directions and that selection acts directly on these single gene mutations. Very simplistic considerations show that this is not the case. Although a plant may mutate to produce an extra row of petals, it is hardly likely to produce an extra pair of arms. The reason is that a mutation can only occur within the context of a given developmental pathway; the whole developmental pathway could only be switched by an event in which mutations are numerous, occur simultaneously and occur harmoniously--in probabilistic terms this is essentially impossible. The subject has been discussed at length in regard to animals by Waddington (1957) and is familiar to plant breeders as Vavilov's Law of Homologous Variation (Vavilov, 1949). The other assumption, namely that selection acts directly on single gene mutations, clearly ignores the importance of recombination among existing genes as a means of generating variability. If we can study the stored (and extant) genetic variation, we may clearly be able to predict what new variation recombination can produce. This point may seem obvious, but it is surprising how many biologists (not to mention non-biologists and nonscientists) still view a new mutation as a prerequisite for any kind of adaptation.

The pan-selectionist view is partly a philosophical reflection of the achievements of evolution. There are relatively few environments on earth that cannot support some form of life.

Some algae, such as *Sphaerella nivalis*, grow and multiply on the surface of alpine snows, that is, at temperatures close to 0° C, while *Bacillus megaterium* and the fungus *Sporobolomyces* grow in Antarctica in saline pools at -23° C, the lowest temperature at which active life has been recorded. Some algae living in the outflow from the hot springs in Yellowstone Park have an optimal temperature range of 50-55° C but can still grow at 73-75°; some bacteria grow there at 80-85° C and can tolerate a temperature of 91° C, which is only 2° below the boiling point of water at the elevation where they live. The bacterium *Thiobacillus thiooxidans* grows in strongly acid media, whereas the alga *Plectonella noctocorum* tolerates an alkalinity of pH 13 (Skinner, 1968). A species of *Delphinium* (Larkspur) grows on Mt. Everest at 20,340 feet, and some spiders even exist at 22,000 feet, feeding apparently on springtails and other insects, also living there or blown in by winds. (Dobzhansky, 1970)

Perhaps a more relevant example is *Micrococcus radiodurans*, which can endure up to half a million rads (5,000 J/kg) (Kewcombe, quoted in Dobzhansky, 1970). It also seems that "normal environments" are only so judged as such because organisms have become resistant to and/or dependent on them. Oxygen is believed by some to have been a toxic byproduct of early plant life; UV radiation that does not normally penetrate to the earth's surface is generally harmful, whereas wavelengths that do penetrate are used in a variety of ways by plants and animals. Therefore, why should we not expect general evolutionary adjustment to new environments? In recent years, the pan-selectionist view has received considerable experimental support. Populations have been shown to be highly polymorphic genetically, showing genetic variation in up to 50 percent of their loci; examples of rapid evolutionary adjustment to recent environmental changes have already been cited; and breeders can seemingly produce an endless variety of forms; some just curiosities, some bred for specialized purposes. As an illustration, table 8.2 lists recorded responses to artificial selection in *Drosophila melanogaster*. It is not an exhaustive list, yet it seems that *Drosophila melanogaster* is capable of a great number of evolutionary responses. While many of them may seem totally artificial, the Hawaiian *Drosophila* are testimony to the fact that, given appropriate circumstances, many of these responses can occur in nature (Carson et al., 1970). The *Drosophilidae* of Hawaii consist of at least 500 largely endemic and closely related species; their external phenotypes are often bizarre, with protruding eyes; blotched wings with extra veins; missing, extra, and highly modified bristles; and modified mouthparts.

Obviously, the pan-selectionist view of evolution as an all-powerful force is also simplistic. It ignores the time factor, which is clearly important in all predictive formulations; evolutionary potential may be very large, but the time scale involved is often enormous. It predicts that ecotones and species distributions should have little constancy. It contradicts the frequent observation that drastically changed environments result in a much lower species diversity since only a small proportion of the species can adjust to the changed conditions.

TABLE 8.2. List of Characters That Have Shown Response to Artificial Selection in a Single Species, *Drosophila melanogaster*, the Fruit Fly

Sources: Complete references have not been listed in the reference list but can be traced from the author, date, and journal; D.I.S. refers to *Drosophila* Information Service, and Hershowitz refers to Hershowitz, I.H., Bibliography on the genetics of *Drosophila*.

**Morphology**

- Stornopleural bristle number (Davies and Workman, 1971, Genetics)
- Abdominal bristle number (Davies and Workman, 1971, Genetics)
- Scutellar bristle number (Fraser, 1970, Genetics)
- Wing vein bristle number (Orr and Sheldon, 1970, Genetics)
- Body weight (Martin, 1958, Hershowitz)
- Wing length (Tantawy and Tayel, 1970, Genetics)

**Behavioral Traits**

- Geotaxis (Dobzhansky and Spassky, 1967, D.I.S.)
- Phototaxis (Hadler, 1964, D.I.S.)
- Activity (Ewing, 1963, D.I.S.)
- Mating speed (Manning, 1959, Hershowitz)
- Escape reaction (Grant and Mettler, 1969, Genetics)
- EGG aggregation (Del Solar, 1968, Genetics)
- Duration of copulation (MacBean and Parsons, 1967, Genetics)

**Life History**

- Fecundity (Brown and Bell, 1961, D.I.S.)
- EGG-adult viability (Sankaranarayanan, 1967, Genetics)
- Developmental rate (Clarke, Maynard Smith and Sondhi, 1961, Hershowitz)
- Competitive ability (Antonovics, 1967, Heredity)

**Meiotic Events**

- Recombination frequency (Kidwell, 1972, Genetics)

**Modifiers of Following Mutants**

- Bithorax (Waddington, 1954, D.I.S.)
- Crossveinless (Milkman, 1956, D.I.S.)
- Scute (Bendel and Sheldon, 1960, Hershowitz)
- Witty (Whitten, 1968, Heredity)
- Bar (Waddington, 1966, Genetical Research)
- Wing 4th vein (Scharloo, 1970, Genetics)

**Resistance to Toxic Substances**

- Cyanide (Harrison, 1954, D.I.S.)
- Hexachlorocyclohexane (Dresden and Oppenorth, 1952, D.I.S.)
- Parathion (Kikkawa, Ogaki and Tsukamoto, 1953, D.I.S.)
- X-rays (Strimnacs, 1952, D.I.S.)
- Nicotine (Tsukamoto and Ogaki, 1954, D.I.S.)
- Dipterex (Tsukamoto, 1956, D.I.S.)

TABLE 8.2. (Cont'd)

Sodium chloride	(Miyoshi, 1958, D.I.S.)
Dieldrin	(Oshima, 1959, D.I.S.)
DDT	(Merrell, 1960, D.I.S.)
BMC	(Dresden and Oppenorth, 1953, D.I.S.)
PTC	(Ogita, 1957, Herskowitz)
Phenylurea	(Ogita, 1957, Herskowitz)
E.D.T.A.	(Robertson, 1966, Genetical Research)
Formalin	(Antonovics, 1966, unpublished)
Peppermint	(Watson, 1972, unpublished)
Heat resistance	(Tantawy and Mallah, 1957, D.I.S.)

The answers clearly lie somewhere between these two extreme philosophies. How do we arrive at a more balanced picture regarding the predictability of evolutionary events, and how can we relate evolutionary responses to physiological responses to produce a more general predictive base?

8.1 COMPONENTS OF EVOLUTIONARY RESPONSE

Genetic variability, in its broadest sense, is not just an intra-specific concept, but can be regarded as being spread over species and diverse taxa. This is easiest to consider in terms of a linear scale of some single hypothetical variable or character (say degree of genetically determined UV resistance). This variable, in all likelihood, will itself be a compound of individual characters, and the environment to which it is adaptive may be equally complex. This linear scale is shown on the horizontal axis of fig. 8.1. The vertical axis has been added to illustrate the contrast between visible and hidden (or potential) genetic variation. Each population is represented by Mather's "icebergs" of genetic variability (Mather, 1964), emphasizing that only a small fraction of the potential genetic variation is visible at any moment (the tips of the "icebergs"). A group of populations forms each species, and the tips of each species represent the visible genetic variation. This visible genetic variation is also some indication of the hidden genetic variability, but only very approximately. As we move toward the bases of the pyramids, we see the levels of resistance that could be produced by less and less likely recombinational events or that are introduced by raw mutations. These events are clearly more unpredictable; we cannot see the shape or extent of the icebergs under water, but we do know their approximate position from the visible portion. Let us consider what would happen with increasing UV radiation, represented by the truncation lines  $E_1$ ,  $E_2$ ,  $E_3$ , and  $E_4$ . Under a very slight increase in UV radiation ( $E_1$ ), we may see no obvious effects; certain classes of mutations that are particularly sensitive may be eliminated faster and contribute less to the recombinational pool, but that is all. At moderate levels of UV ( $E_2$ ), certain obviously physiologically sensitive taxa would probably be eliminated, but some members may respond by developing resistant forms of mutation or recombination. Other taxa may respond as predicted from their physiological responses. At yet higher levels ( $E_3$ ), most

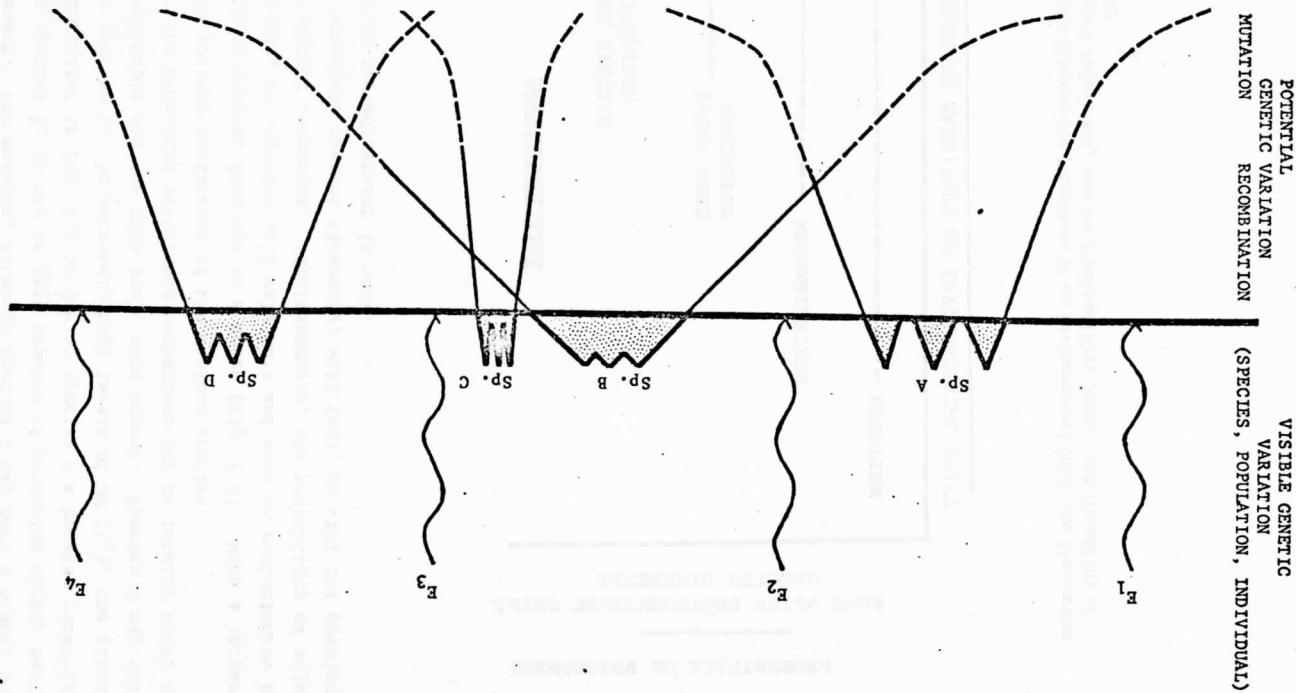


FIGURE 8.1. Schematic Diagram Illustrating the Concept of Visible (Shaded Peaks) and Potential Genetic Variation Available Through Recombination and Mutation (Areas Under Solid Line). The visible genetic variation is much smaller than the potential variation, and is a poor indicator of the magnitude of such variation or the potential for evolutionary change.

8.2 EVIDENCE FOR EVOLUTIONARY RESPONSE TO UV RADIATION

Ultraviolet radiation has undoubtedly had a profound influence on the evolution of living organisms. The presence of UV repair systems in as wide a range of organisms as bacteria, blue green algae, yeasts, higher plants, and mammals, including man, emphasizes that many organisms have evolved mechanisms to cope with UV radiation (see section 3.5). It has even been suggested by Sagan (1973) that the eukaryote cell was evolved as a response to high levels of UV in the early atmosphere of the earth. Sagan suggests that the packaging of the DNA within a nuclear membrane in the center of the cell and surrounded by initially inert RNA may have been an early shielding mechanism that enabled the ancestors of eukaryotes to take advantage of light as an energy source.

Differences between various groups of organisms in their response to UV radiation are well known and form much of the subject of this volume. Often, these differences appear to be correlated with the level of UV radiation in the environment of the organism, but whether this is directly related to UV resistance or related to the general fact that organisms generally exposed to greater amounts of UV are also exposed to greater overall radiation is not clear. For example, cave-dwelling fishes, subterranean castes of termites, soil organisms such as springtails, and endoparasitic larvae often lack protective pigmentation, but it is possible that the lack is simply due to the absence of visible light and, therefore, no need for, say, cryptic coloration. It has also been shown that cultures of microorganisms epiphytic on stems are more resistant to UV than epiphytic organisms on roots (Shirokov, 1959).

Better evidence for evolutionary response to UV radiation in natural populations comes from correlations with different levels of UV radiation found in different latitudes or altitudes. Gloger's rule, an ecogeographic rule proposed in the late 19th century and well known to zoologists, states that animals in more equatorial regions have more pigmentation. No satisfactory explanation for this has yet been produced, and the phenomenon may well be related to UV radiation levels. The different levels of pigmentation in various human populations provide a good example of Gloger's rule; the selection pressures bringing about these differences have been discussed in chapter 4. In spite of attempts to demonstrate that high altitude races of plants are more resistant to UV radiation (Caldwell, 1967; Brödführer, 1955) no clear-cut differences between mountain and lowland races or species have emerged. However, it has been reported that alpine plants have a higher flavone concentration (Shibata et al., quoted in Cline & Salisbury, 1966) and that mountain strains of yeast-like organisms are particularly UV resistant (Solntseva, 1967). However, specific examples often contradict these trends. For example, in the only extensive study of anthocyanin variation with altitude within a plant species, *Potentilla glandulosa* (Clausen & Hiesey, 1958), it was observed that anthocyanin content decreased with increasing altitude (table 8.3). Lichens, organisms which often grow in very exposed conditions, are known to contain a wide range of substances that strongly absorb UV (table 8.4), and

species are eliminated unless they can produce recombinants or mutations that are resistant to these higher levels. At this point, their overt physiological responses become less and less relevant. For example, although species C may have a higher physiological resistance than species B, it may be less capable of producing highly resistant types. This has been indicated in fig. 8.1 by giving species B a broader potential range of variation than species C. At extremely high levels of UV ( $E_4$ ), the situation would become more unpredictable and the time scale more urgent. Species D may well adapt more readily, but the necessary resistance mechanisms may be totally novel and totally unrelated to the present resistance of the various species.

We can summarize these general findings in a chart (fig. 8.2). With a larger and larger environmental change, an organism will rely more and more on evolutionary and less and less on physiological responses. Simultaneously, the probability of adjustment (and consequently, the immediate species diversity) will fall, as will the predictability and rate with which any adjustment is made.

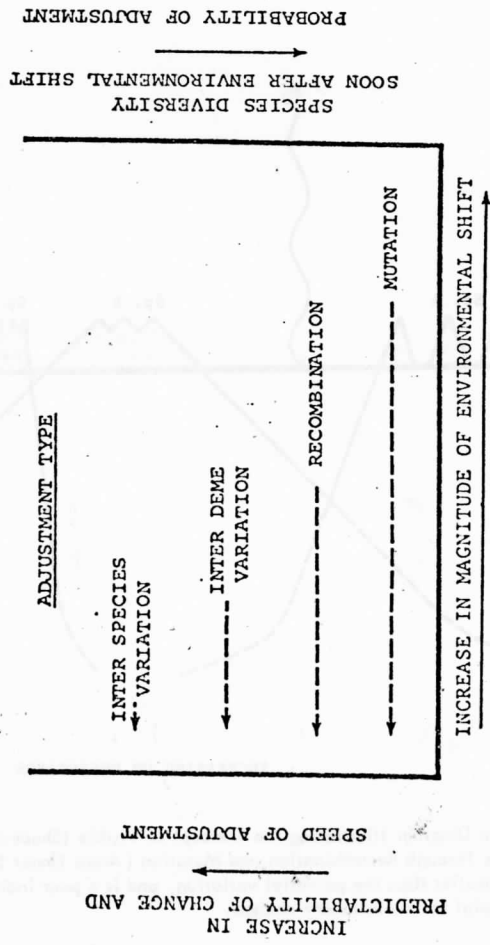


FIGURE 8.2. Relationship Between the Magnitude of an Environmental Shift, the Mechanism of Genotypic Adjustment, and the Predictability, Speed, and Probability of Adjustment

TABLE 8.3. Number of Plants With a Given Anthocyanin Score (Green, Intermediate, Dark) in Different Populations of *Potentilla glandulosa* Taken From an Altitudinal Gradient and Crown Under Standard Garden Conditions in Stanford, California (Altitude 30 m)  
Source: Clausen & Hiesey, 1958

ALTITUDE m	SUBSPECIES*	ANTHOCYANIN SCORES		
		GREEN	INTERMEDIATE	DARK
60	T		56	4
250	R			60
275	T	31	6	
750	T			
910	R		9	38
1060	R		13	20
1190	R		6	41
1400	R	24	36	29
1400	H	24	9	
1650	R	47	51	
1830	H	45	14	
1950	H	54	6	
2040	H	52	7	
2100	H	58		
2190	H	49	5	
2440	H	2	4	
2478	H	1	4	
2530	H	47	1	
2590	N	57		
2740	N	57		
2910	N	26		
3170	N	53		
3350	N	46		

\* T = typica, R = reflexa, H = hanseni, N = nevadensis

TABLE 8.4. UV-Absorbing Substances Largely Restricted to Lichens (after Huneck, 1968)

Compound	Max. absorbance wavelength, nm. (log E in parenthesis)
<b>Depsides</b>	
Planaic acid	250(3.85), 284(3.81)
Merochlorophaeic acid	260(4.2), 300(3.8)
Tumidulin	259(4.2), 318(4.1)
Lecanoric acid	270(4.3), 307(4.2)
	268(4.2), 304(4.0)
Cryptochlorophaeic acid	260(4.2), 295(3.8) (shoulder)
Atranorin	239(4.06), 285(3.78) (shoulder)
	262(4.25) (inflexion), 280(4.35), 386(3.51)
Squamatic acid	244(4.78) (shoulder), 306(4.49)
<b>Depsidones</b>	
4-O-Methylphysodic acid	211(4.67), 260(4.15)
Norlobaridone	270(3.96)
Grayanic acid	258(4.10), 300-310(3.5) (shoulder)
Physodic acid	256(4.2), 330(3.5) (shoulder)
Diploicin	270(3.79), 325(3.04) (inflexion)
Virensic acid	240(4.47), 308(3.68)
Vicanicin	270(3.94), 324(2.48) (inflexion)
Hypotocetraric acid	216(4.59), 262(4.09)
Protocetraric acid	256(4.14), 314(3.55)
Salazinic acid	238(4.44), 312(3.68)
	239(4.3), 312(3.8)
<b>Depsones</b>	
Picrolicheninic acid	225(4.55), 250(4.38) (shoulder), 280(3.8)

it has been shown in *Cladonia subtenuis* by Rundel (1969) that the content of one of these substances, usnic acid, is directly related to the light intensity in which the lichen is growing (fig. 8.3).

Attempts to select for UV resistance have been largely confined to micro-organisms. Mutants of the bacterium, *Escherichia coli*, resistant to UV radiation, have been frequently isolated (Witkin, 1947; see fig. 8.4) and extensively characterized (Crunow & Geissler, 1970; for review see Kalle & Sivasubramaniam, 1967). Blue-green algae, which are believed related to the bacteria, can also develop UV-resistant strains (Kumar, 1963, 1968; Singh, 1968; Srivastava, 1970). Ultraviolet-resistant strains are also known in yeast (Kilbey, 1970). Selection for UV-resistant strains in fungi usually results in selection of forms with darkly pigmented spores (Markert, 1953, see fig. 8.5; Parmeter & Hood, 1962).

Studies of evolutionary response to UV in higher organisms have been virtually non-existent, apart from those of adaptation to solar radiation by melanin pigmentation in different races of man. Repair mechanisms have also been extensively studied (see section 3.2) but there is no clear evidence they have greater efficiency in regions of high UV radiation. There is evidence that *Drosophila melanogaster* can evolve resistance to X-rays (see table 8.5), but the mechanism is unknown.

TABLE 8.5. Resistance of *Drosophila melanogaster* to X rays Before and After Selection for X-ray Resistance (after Strommaes, 1952). The selection technique consisted of mating the progeny of males giving the highest hatchability in each generation to their first cousins.

Selection Line	Z hatchability after X-ray irradiation of males with 2,300 roentgens.	
	Foundation stock	After 12 generations selection
a	60.38	67.86
b	56.12	72.16
c	59.12	72.74
d	59.69	72.00

### 8.3 PREDICTORS OF EVOLUTIONARY RESPONSE

Basically, we can recognize two types of predictors of evolutionary response. The first relates to the speed with which genetic variability can be generated in a changing environment, i.e., the degree to which hidden genetic variability can be conserved and released. This class of predictors we will call the classical, neo-Darwinian predictors of evolutionary response. The second kind refers to specific characteristics of a group

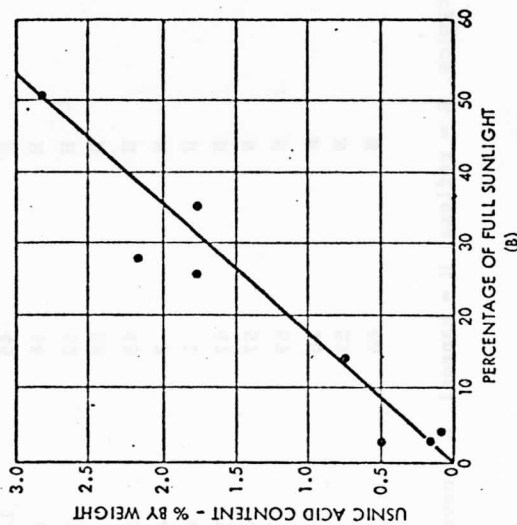
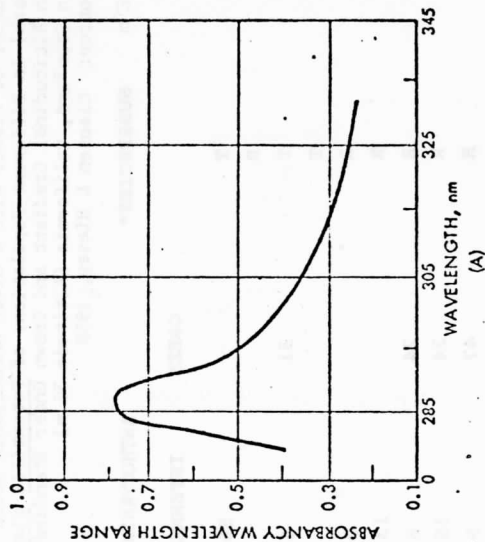


FIGURE 8.3. Absorbance of Usnic Acid from the Lichen *Cladonia subtenuis* (a) and Its Concentration in Lichens Taken from Habitats With Different Levels of Insolation (b)  
Source: Adapted from Rundel, 1969

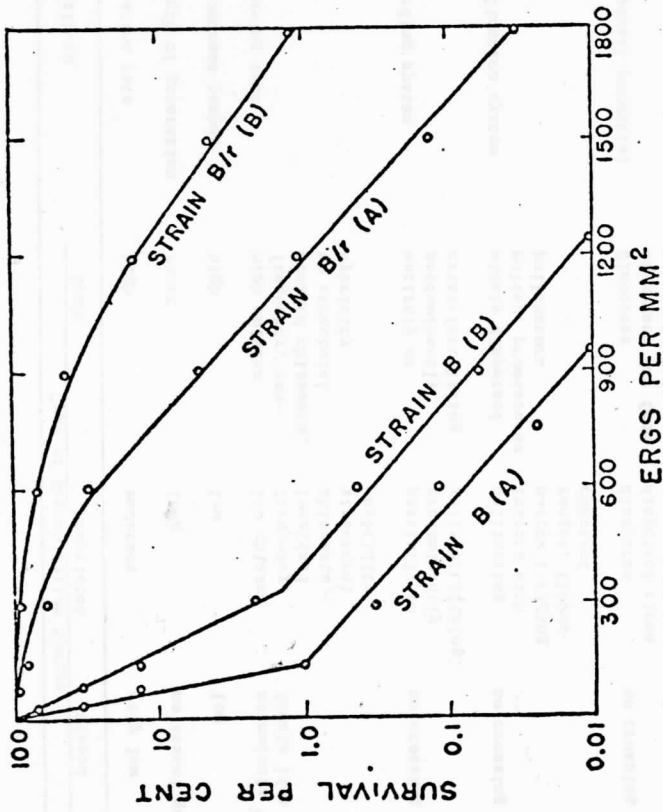


FIGURE 8.4. Resistance to Ultraviolet 254nm in the Bacterium *Escherichia coli*. (A) Bacteria irradiated on surface of solid medium. (B) Bacteria irradiated in liquid suspension. Strain B = normal strain; B/r = resistant strain (1 erg/mm<sup>2</sup> = 0.1 J/m<sup>2</sup>). Source: Witkin, 1947

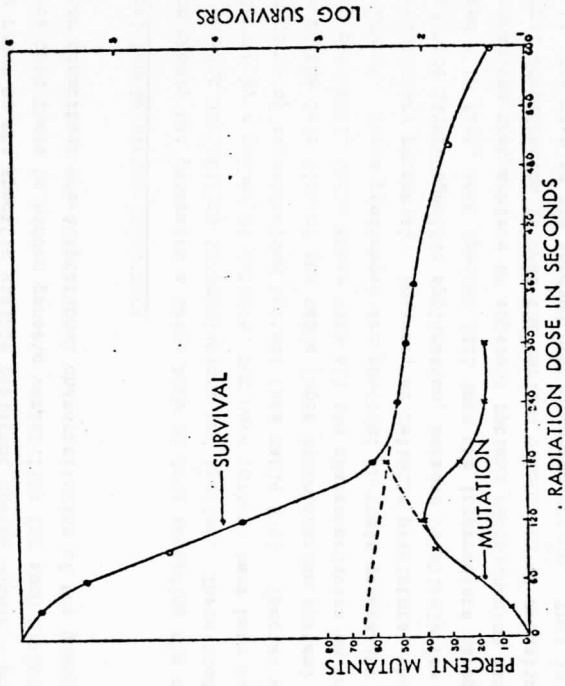


FIGURE 8.5. (a) Effects of UV (254 nm UV, 4.77 W/m<sup>2</sup>) on Survival and Mutation to UV Resistance in *Glomerella Cingulata*; (b) Resistant Spores in UV Resistant Strains of *Glomerella Cingulata*. (Left) Resistant pigmented spores germinating after exposure to 1,500 sec of UV radiation. (Right) Unirradiated colorless sensitive spore germinating Source: Markert, 1953



that might pre-adapt them to coping with a particular environmental change; these characteristics may refer to the specific visible resistant traits within a group or to specific evidence that there is hidden genetic variability for such traits. This latter type of predictor constitutes pre-adaptational characteristics of the group in question.

### 8.3.1. Classical Neo-Darwinian Predictors

Modern evolution theory has generated a large body of data regarding the source and maintenance of genetic variability in populations and species. These ideas have been considered at length by a number of authors, but have perhaps best been summarized by Grant (1958) in terms of recombination systems (see table 8.6). Species with all the characteristics on the left side of the table (open recombination system) have the highest evolutionary potential, while those with all the characteristics on the right side would have the lowest. These predictors are powerful in their generality and relate well to long-term evolutionary potential. However, as reliable predictors, they are very weak, since they have little specific application, because relatively few categories are distinguished. In fact, most species fall into the intermediate category or have compensatory mechanisms that achieve an apparent optimum recombination rate (Grant, 1958).

An additional complication is that the various components of recombination systems may themselves be sensitive to the imposed environmental change. This is particularly the case with UV radiation. Ultraviolet radiation can increase the mutation rate, in general, or the mutation rate to UV resistance (see figs. 8.4 and 8.5). It can cause chromosome aberrations and disturb chiasma distribution (Swanson & Sandler, 1955; Wolff, 1972). It may also influence cross-pollination by insects and thereby disturb breeding systems.

### 8.3.2. Pre-Adaptational Characteristics

Evidence for differences between various groups of organisms in their response to UV radiation has already been mentioned. No attempt will be made to review the literature. Clearly, organisms with efficient repair mechanisms, protective pigments and epidermal tissues, or appropriate behavioral responses will be preadapted to survive increased UV levels (see section 3.5).

There is also considerable evidence of intraspecific differences in response to UV radiation or in the factors that may give UV protection. For example, different races of *Arabidopsis* (Brödfuhrer, 1955; see fig. 8.6) and different races of potatoes (Nilsen, 1971) differ in their UV sensitivity. Genetic variation in anthocyanin content (see table 8.7) and cuticular structure (Martin & Jennifer, 1970; Barber, 1965) is also well known. Among animals, genetic variation in radiation resistance is known to exist in wild populations of *Drosophila melanogaster* (Parsons et al., 1969) and between different strains of mice (Grann, 1958), but no studies have been carried out specifically with UV radiation. Differences in UV resistance have been detected between pigmented and unpigmented strains of protozoa (Giese, 1963).

TABLE 8.6.

Attributes of Recombination Systems That Conserve Large Amounts of Genetic Variability Which Would Be Expected to Give Rapid Evolutionary Responses (Open) vs. Characteristics of Recombination Systems, Conserving Little or Very Small Amounts of Genetic Variability, and Which Would Be Expected to Give Slow or Limited Evolutionary Responses (Restricted, Closed)  
Source: Grant, 1958

Attribute	Type of Recombination System		
	Open	Restricted	Closed
Mutation rate	high	moderate	very low
Length of generation	short	long	no sexual generations
Chromosome number	high	low	low
Crossing over	high chiasma frequency, randomized chiasmata, no structural hybridity	low chiasma frequency, localized chiasmata, structural hybridity	no meiosis in female line
Breeding system	entirely or predominantly cross-fertilizing	partially to predominantly self-fertilizing	no crossing
Pollination system	widely dispersed pollen, promiscuous pollinators	pollinating insects with narrow foraging ranges, flower constant	no crossing
Dispersal potential	diaspores dispersed far from parental plant	diaspores dispersed close to parental plant	no crossing
Population size	large continuous populations, margins of smaller populations	small colonial populations	asexual clones
Geographical & ecological pattern	numerous, partially isolated, ecologically diverse populations	ecologically diverse but isolated or continuous but ecologically uniform	restricted geographically and ecologically
Isolation	related species, sections or general isolated	related species strongly isolated	no hybridization

TABLE 8.7. List of Plant Species that Exhibit Genetic Variation in Anthocyanin Content of Green (nonflowering) Tissues. (Ecological relationships of contrasting anthocyanin types mentioned in parentheses if known.)

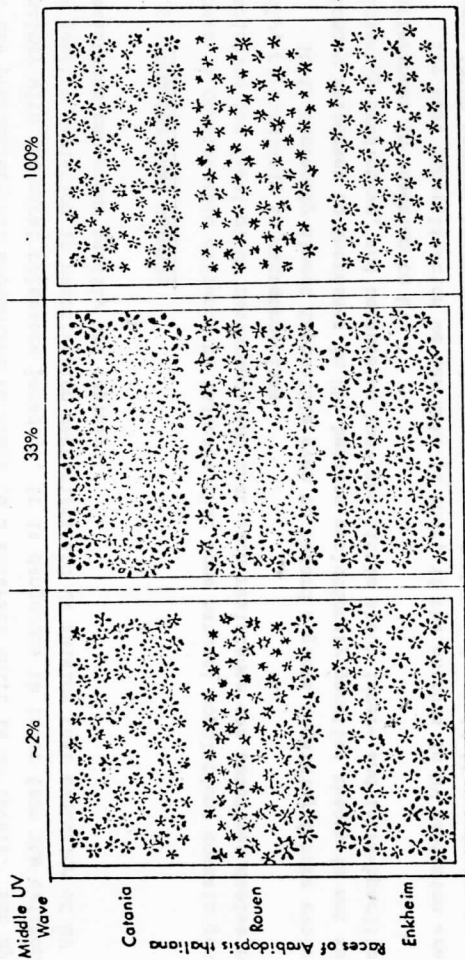
<i>Crepis capillaris</i>	Clausen & Hiesey, 1958
<i>Geranium robertianum</i> (beach type red, woodland type green)	Clausen & Hiesey, 1958
<i>Ceum urbanum/rivale</i> (woodland form green, stream form red)	Clausen & Hiesey, 1958
<i>Geum coccineum</i> (alpine, green)	Clausen & Hiesey, 1958
<i>Plantago major</i>	Clausen & Hiesey, 1958
<i>Potentilla glandulosa</i>	Clausen & Hiesey, 1958
<i>Chloris gayana</i>	Bogdan, 1963, Heredity
<i>Agrostis stolonifera</i>	Antonovics, unpublished
<i>Arrhenatherum elatius</i>	Antonovics, unpublished
<i>Lolium perenne</i>	Griffiths, 1950
<i>Trifolium repens</i>	Davies, 1963

Although specific studies of genetic differences between strains and individuals in UV resistance are few, it is clear from the studies that have been done and from the variations in repair and protective mechanisms that there must be considerable genetic variation for UV resistance within species. This view is supported by evidence of natural and artificial selection for UV resistance, reviewed earlier.

#### 8.4 CORRELATED RESPONSES AND AN ANALOGOUS EXAMPLE OF ENVIRONMENTAL CHANGE

It is essential to emphasize that the evolution of UV resistance will almost certainly result in correlated changes in other characteristics. Even the single gene mutants responsible for UV resistance in microorganisms have correlated effects: for example, in *E. coli*, the resistant B/r strain is also more resistant to X-rays and antibiotics, but has a slower overall growth than the nonresistant strain and is eliminated, presumably by competition, in aging cultures (Witkin, 1947). Similar results have been obtained with blue-green algae (Kumar, 1963). In general, evolution of UV resistance will be accompanied by associated metabolic changes that may have secondary effects very relevant to the survival of the strain.

We can also imagine situations where there is a complex interplay of features determining UV resistance and other factors. Perhaps an oversimplified but somewhat realistic example will best illustrate this. Melanism in moth species (e.g., *Biston betularia*) is well known as an adaptation to urban areas. In these areas, black forms are at a cryptic advantage since they are not as easily detected by predators against lichen-free and soot-blackened tree trunks (Kettlewell, 1961; Owens, 1961). Surely then, moths could develop melanic forms that would survive increased UV doses. This is certainly true in urban industrial areas, but in woodland districts melanic forms are



Size of rosettes on June 27. The plants were 46 days old and were under these experimental conditions for 15 days. Drawn from a photograph.

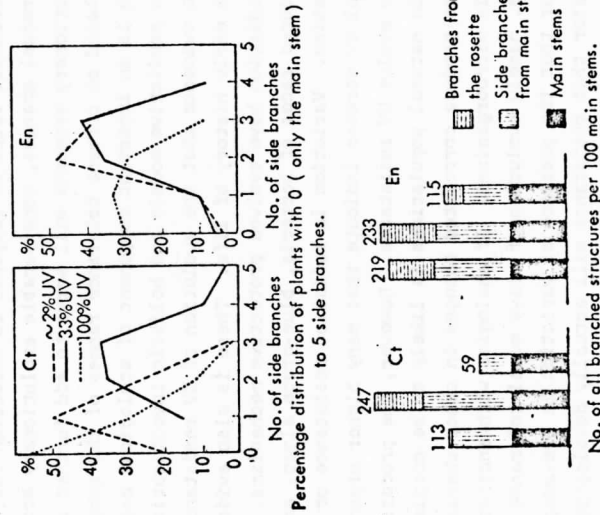


FIGURE 8.6. Differences in UV Response in Races of *Arabidopsis thaliana* grown at 3 Natural UV Intensities at 1575 m Above Sea Level. Source: Brodführer, 1955

at a great selective disadvantage. Therefore, an increase in UV radiation in this hypothetical example would lead to a drastic reduction in the population, or even to an elimination of the species in woodlands, even though all the preadaptational characteristics for UV resistance are present.

The complexities of each individual example of UV resistance can only be guessed at, since few studies bear directly on the problem. Nevertheless, considerable information is available on adaptation by natural populations to increased levels of heavy metals, a situation that provides an example of environmental change very analogous to UV resistance (see Antonovics et al., 1971, for review). High concentrations of heavy metals are toxic to plants and animals, since, like high levels of UV radiation, they have a high affinity for and readily interact with many organic substances, such as proteins, amino acids, carbohydrates, and nucleic acids. Both heavy metal ions and UV are mutagenic. At the same time, at moderate levels, heavy metals are involved in normal metabolism and constitute essential trace elements that are constituents of heme groups and many enzymes.

Therefore, it would seem that an organism could readily evolve metal tolerance, using genetic variability in metal metabolism as a source of resistance. But this is not the case; what actually happens is of considerable interest. Only a relatively few species have evolved tolerance to high levels of heavy metals, even on natural outcrops that have been in existence for thousands or even millions of years. Studies on cobalt and copper outcrops in Rhodesia, Katanga, and Zambia show a peculiar flora of relatively low species diversity. In areas of recent mining, one of the most obvious signs of toxicity is the "weed-killer effect," i.e., only a few species are able to evolve tolerance and survive; and because they have few competitors, they are abundant and form extensive stands of only a few or even just one species. It is also interesting that some species can evolve tolerance, but only to a certain limited extent. There seems to be a limit to developing more and more resistance in some forms. Perhaps equally relevant is the mechanism of tolerance to these metals. Seemingly, the mechanism does not involve the normal metabolic processes, or any kind of extensive general tolerance. Instead, a "new" mechanism has developed whereby (in several species at least) the metal is bound to the pectate fraction of the cell wall and thereby prevented from reaching the more sensitive parts of the cell. The mechanism is not only novel, it is also metal-specific: tolerance to one metal does not give tolerance to another. Very few so-called "co-tolerances" have ever been reported. All this makes some sense. It is precisely because metals interact with so many biological processes that it is unlikely an organism would produce (by recombination plus mutation) generalized tolerance in all the multifaceted enzymes and processes affected by heavy metals. A specialized mechanism that protects these processes is evolved instead; but apparently, this is only possible in a few species.

Therefore, given our present state of knowledge, the evolutionary effects of increased UV radiation are likely to be unpredictable. It may be possible for organisms to use preadaptational mechanisms to adapt to a moderate shift in UV levels. But by analogy with the metal tolerance paradigm, it is dangerous to infer from the existence of genetic variation in reactivation mechanisms and UV shields that evolution of UV resistance can occur readily and rapidly.

#### 8.5 PROGNOSIS AND SUMMARY

There is considerable evidence to indicate that some natural populations contain genetic variation for level of UV resistance and that such resistance can sometimes evolve rapidly, particularly in microorganisms.

It is currently almost impossible even to hazard a guess regarding future evolutionary responses to increases in UV, because evolutionary genetics theory is not sufficiently predictive, and because we know too little about inter- and intra-specific differences in reaction to UV.

The best generalization we can make is that, if the changes in UV radiation are large (>100 percent increase), and if the rate of change is rapid (i.e., it occurs over tens rather than hundreds or thousands of years), then there will probably be a large number of extinctions and extensive changes in community composition due to differential sensitivity and differential rates of response to selection for UV resistance. Yet, with smaller, more gradual changes, considerable evolutionary accommodation may occur. In either case, evolutionary response will serve to add further uncertainty to ecological predictions based on current tolerance ranges of the component species. Evolutionary response is an important component of ecological amplitude, but one that is often neglected in predictive models and holistic investigations of ecosystems.

There is considerable evidence that the evolution of UV resistance has been an important step in the early history of life. There is also evidence that species exposed to high UV radiation have evolved protective mechanisms. Artificial screening experiments have produced races of bacteria, blue-green algae, and fungi resistant to shortwave UV radiation. Variation in radiation resistance or genetic variation in levels of potential UV screens indicate that many higher organisms should also have the potential to evolve UV resistance. However, the process of adaptation to increased UV levels in natural populations is likely to be complex. Evolution of UV resistance is known to produce correlated changes in other characteristics and reduce competitive ability in microorganisms. If analogies with another well-studied evolutionary response, namely evolution of heavy metal tolerance in plants, can be drawn, it would appear that the presence of variation in pre-adaptational traits is usually a poor indicator that resistance will actually develop in a natural situation. Evolutionary adjustment would be easier if the increase in UV radiation was small and the rate of increase low. More research on selection for resistant forms is needed, particularly in higher organisms. Ideally, such studies should be combined with long-term exposure of segments of ecosystems to artificially increased UV radiation.

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