Possible Role of Ultraviolet Radiation in Evolution of *Cannabis* Chemotypes[1]

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The damaging effects of UV-B radiation have apparently affected the amounts of ultraviolet-absorbing secondary compounds in some plants. A similar role for Δ^9 *tetrahydrocannabinol may explain the high levels of this compound in* Cannabis *from areas of intense ambient UV-B. Further research is needed to determine whether UV-B radiation serves only as a selection pressure or if UV-B-induced stress may also directly stimulate production.*

Cannabis is a dioecious annual whose economically-important products include food and oil from its seed, fiber for rope and fabric from its stem, and a psychoactive drug from its flowers and leaves. This last characteristic caused early people to both fear and revere the plant, a condition that persists to the present day! The main ingredient responsible for most of these effects is Δ^9-tetrahydrocannabinol (Δ^9THC), an example of the cannabinoid-type compounds apparently unique to this genus (Mechoulam, 1973). Its biosynthetic precursor has been thought to be cannabidiol (Mechoulam, 1973; Shoyama et al., 1975), with the formation of these cannabinoids being enzyme mediated (Mechoulam and Gaoni, 1965; Latta and Eaton, 1975). Although some photochemical effects have been observed, careful in vitro studies (Allwardt et al., 1972) have demonstrated the conversion of cannabidiol (CBD) to Δ^9THC only at wavelengths (<280 nm) nonexistent at terrestrial levels.

The state of controversy surrounding this plant has served to stimulate the generation of a vast literature (Eddy, 1964; Waller et al., 1976), and although reports on the human use of *Cannabis* drugs are well represented, fewer studies have focused on the biology of the plant. The Δ^9THC content can account for over 5% of the dry leaf and flower weight. This results from an energy expenditure that otherwise could have been devoted to growth and reproduction. Yet there exists no detailed explanation of its raison d'être. Towards this end, the present paper attempts an initial inquiry into a subtle environmental stress apparently basic to evolutionary selection for *Cannabis* chemotypes and the biosynthesis of Δ^9THC as an appropriate protective response.

ULTRAVIOLET RADIATION

Various systems of UV classification have been proposed, but the method of Coblentz (Meyer and Seitz, 1942) will be used here. This designates radiation between 400 nm (the approximate beginning of the visible region) and 315 nm as UV-A, 315–280 nm as UV-B, and the shorter nonterrestrial ultraviolet wavelengths as UV-C. Most of the UV-B range impinges on the earth's surface and also possesses considerable biological effect, so it is the band of most concern.

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With UV-B exposure dependent on the interplay of many atmospheric, latitudinal, altitudinal, and terrestrial factors, estimation of its global distribution is indeed difficult. Schulze (Schulze and Grafe, 1969) has published the only extant world distribution map of UV-B radiation. This estimate should be regarded as approximate since it is valid only to an altitude of 1,600 m and does not account for the shorter wavelengths of the band. Although present in only minor quantities, these shorter wavelengths are disproportionately effective in their biological action. Therefore, the biological value for each region may vary somewhat from that implied by the designated wattage.

Ultraviolet radiation interferes with cellular reproduction and metabolism through its damaging effects on nucleic acids and proteins. Although peak nucleic acid absorption of UV is at approximately 260 nm, there is substantial UV-B absorbance by nucleic acids in the 290–315 nm portion of the band occurring at terrestrial levels (Rupert, 1964). The 280 nm absorbance peak that proteins exhibit is closer to the limit of terrestrial shortwave exposure, making them even more susceptible to damage in nature. Damage can also result through a nucleic acid/protein interaction (Smith, 1964).

HOW SOME PLANTS COPE WITH UV-B

Photoreactivation is a process by which some nucleic acid damage can be repaired (Rupert, 1964). This is accomplished through an enzyme-mediated splitting of UV-B formed dimers, triggered by exposure to longer wavelengths in the UV-A to shortwave visible light band (313–549 nm). Since exposure to the entire spectrum is simultaneous, DNA damage in natural circumstances is not so dramatic as that induced by experimental monochromatic UV irradiation. UV-induced DNA lesions are also repaired by other enzymatic means (Smith, 1974), although none of the above mechanisms has restorative effects on protein-involved damage.

While photoreactivation helps to repair damage done, UV-B opaque pigmentation appears to provide a means of preventing such damage. In a series of laboratory and field experiments, Caldwell (1968) demonstrated that flavonoids can fulfill this function and that their production by the plant in response to UV-B exposure can be quite marked. Both crude plant extracts and isolated compounds reveal a strong absorbance in the UV-B range (Stafford, 1965; Caldwell, 1968). Some of these compounds can be produced in darkness, but induction of others depends on exposure to UV-B or longer wavelength light (Stafford, 1965). Wellman (1976) noted a linear relationship between UV dosage and flavonoid production in various crop plants and found that a response could be triggered by either blue or far red light, depending upon the species involved and the plant part exposed. Other compounds that may protect plants from UV-B include anthocyanins, xanthophylls and cuticular waxes (Caldwell, 1971).

PROPOSED HYPOTHETICAL MODEL

Interest in the possible role of ultraviolet radiation as a selection pressure in the evolution of *Cannabis* chemotype was piqued by the casual observation that the sun-drenched areas growing the most potent *Cannabis* were populated by native peoples of the darkest complexions. This same UV-B pressure on plants

has been shown (Caldwell, 1968) to have affected the evolution of a protective flavonoid pigmentation functionally analogous to the melanization of human skin. *Cannabis* seems to employ a similar mechanism, its chemical screen being Δ^9THC. In areas with little UV-B radiation, little Δ^9THC is made from precursor CBD, and the general cannabinoid level is modest. Differences found under these circumstances are probably attributable to local factors, e.g., water stress, soil mineral balance, etc. In areas of intense UV-B, cannabinoid production is high and found predominantly as Δ^9THC. Here again, local factors play a role in the final expression of cannabinoid content. Indeed, evidence that root stunting occurs in plants grown in UV-B enriched environments (Caldwell et al., 1974), may imply a UV-B/drought stress interaction. Increased stress and selection pressure from intense insect predation in tropical areas is also probably involved. While individual plant production of this compound may be affected by environmental circumstance, the evolutionary selection of a chemotype best adapted for these conditions has also apparently taken place. UV-B selection pressures may be directed toward plant survival or reproductive success, the latter perhaps involving pollen viability or flower longevity.

The importance of this compound is underscored by the discovery (Turner and Hadley, 1973) of a Δ^9THC-rich African strain of *Cannabis* in which absolutely no CBD precursor could be found. They suggest the evolution of a bypassed step or an alternative biogenic route, neither of which would be of particular advantage if the product was of little importance. Is it only coincidence that this apparently has occurred in an area of great UV-B intensity?

Small et al. (1975) have presented evidence that Δ^9THC content differences of gender can be either substantial, as is the case for high latitude plants, or nominal for those from low latitudes. This consistently higher production may be attributable to the survival priority of the female as the seed producer. Since one male can pollinate many females, male survivorship is not quite as critical to population maintenance. In circumstances of minimal UV-B exposure, the extant gender differences in Δ^9THC content would be of little consequence. In areas of greater irradiation this selection pressure would also be brought to bear on males, a Δ^9THC production response insuring adequate male survivorship and increased flower and pollen protection. The need for this protection is implied by a demonstrated vulnerability of *Cannabis* pollen to shortwave UV radiation (Montemartini, 1926). It has been suggested that analogous carotenoid and flavonoid pigmentation may serve in such a protective capacity for many other pollens (Stanley and Linskens, 1974).

Differences in the numbers of resin-producing glands and corresponding variations in Δ^9THC content among the plant parts follow consistently with the protective function model. Surfaces covered by a corky layer, such as the lower main stem, and the roots protected from sunlight and most dessication stress by the soil, contain few cannabinoids. The reproductive structures, as more immediately essential for the perpetuation of the species, would naturally receive priority for protection over vegetative parts and have been observed to contain richer concentrations of Δ^9THC (Fetterman et al., 1971). The observations of Kimura and Okamoto (1970), concerning the increased cannabinoid content of structures protecting the pistil after fertilization at the expense of leaf content, serve to emphasize this relationship. Gender comparisons of Δ^9THC content reflect the

survival priority of the female flower parts. They eventually contain the next generation, and by virtue of their longevity must tolerate longer exposure, while the male flower exists only briefly to shed its pollen.

The biased placement of glands toward the abaxial surface of the vegetative leaves (perhaps reflecting insect predation pressure) may be at odds with their inclusion in a chemical screen hypothesis. However, other plants such as *Acer saccharinum* have light reflectant coatings similarly placed. Dense populations of glands on the upper surface might interfere with photosynthetic light absorption, particularly for *Cannabis,* since exuded resins quickly turn black upon exposure to the atmosphere (Fairbairn, 1976). Of course its usefulness as a sun screen would seem negated by such a gland distribution, but it must be remembered that UV-B radiation usually arrives at all angles via albedo and diffuse sky radiation in amounts surpassing direct insolation. Under these conditions of exposure, only 50% of the leaf will be exposed on the less protected surface, and then at levels not tremendously higher than the underside. Leaf wilt could also serve to decrease leaf surface area exposed to direct rays. Perhaps these mechanisms represent the best workable compromise between total protection with inhibited photosynthesis and no protection at all.

Finally, this model is also consistent at the chemical level. For Δ^9THC production from CBD to be evolutionarily selected, differences in their protective capabilities would have to exist. This can be inferred from the work of Grlic (1962), an investigation of identification methods for the various chemotypes of *Cannabis.* Ethanolic extracts of 3 types of *Cannabis* revealed considerably different UV absorbance properties in the crucial 285–300 nm band of highest biological activity. "Unripe" *Cannabis* extract (containing mostly cannabidiolic acid) absorbed little of this UV-B, whereas "ripe" *Cannabis* extract (containing mostly Δ^9THC) absorbed strongly. An extract of *Cannabis* intermediate in "ripeness" (CBD/THC balance) exhibited an intermediate value. While such crude extracts certainly contain compounds in addition to the cannabinoids, the latter are usually predominant.

UV-B RADIATION LEVELS AND CANNABINOID CONTENT

Cannabis for drug production has traditionally been grown in high altitude regions of the world (Bouquet, 1950). Part of the reason for this is undoubtedly political since detection and sanction of growers is more difficult in rugged terrains. However, this cannot be the entire case, since *Cannabis* raised at a higher altitude demands a higher price than that raised at a lower altitude of the same area (Anonymous, 1976). Altitude effects have been attributed to water deprivation (Bouquet, 1950), but this alone cannot account for the considerable Δ^9THC content of plants growing in moist, low-altitude, tropical regions.

In Lebanon, it has been observed that "hemp cultivated in the plains gradually loses the property of supplying active resin" (Bouquet, 1950). This altitude effect is echoed in the experience of Bergel (1965):

> When we were still working in this field we were told that the production of the active resin, in any kind of *Cannabis* plant, depends entirely on the altitude of the plantation; for example, you get rich charas or bhang in northern India only at a certain height above sea level. It was also

> reported that in order to obtain active resin one had to plant *Cannabis* in Germany near Roserheim, not far from Munich, which again is above a certain altitude.

Bouquet (1950) relates that latitude decreases can result in a natural selection for increased resin production. To illustrate this point further, he continues:

> In Egypt, when the Viceroy Mehemet Ali wished to create a navy, he got *Cannabis* seeds from Europe in order to obtain suitable fiber for cordage. New seed had to be brought periodically, because the hemp plants obtained soon became incapable of producing good textile fibers. On the other hand, they began to secrete abundant quantities of the inebriating resin.

This change from a fiber to a resin phenotype and vice versa in response to environmental factors has also been observed by Boucher et al. (1974).

The work of Small and Beckstead (1973) has indicated a substantial biosynthesis of Δ^9THC in *Cannabis* originating between 30°N and S latitudes. This is complemented by their observations of high latitude CBD-predominant strains and an intermediate chemotype from border areas. Is it only coincidence that this pattern follows latitudinal increases of UV-B, with the 30°N to 30°S belt exposed to the greatest intensities? Certain regions somewhat outside this belt that are known for their *Cannabis* products (including Morocco, Afghanistan, and Lebanon) raise their crops at UV-B enriched high altitudes. One of the samples that Small et al. (1975) investigated originated from seed of a Mexican strain raised in Mississippi at the Research Institute of the Pharmaceutical Sciences for NIMH distribution as "standardized marijuana." This strain produced only 1.5% Δ^9THC in Canada, about 50% of its content when grown in the more southerly location. While growing conditions were not carefully coordinated, and the authors attribute this difference to increased desiccation-induced leaf abscission of the Mississippi-grown plants, one plausibly might suspect the ~50% increase in UV-B exposure there.

Latta and Eaton (1975) have shown that peak Δ^9THC content in wild Kansas *Cannabis* occurs in the later part of June and early July. This is also the peak period of UV-B intensity in temperate latitudes. In addition, their data seem to indicate that Δ^9THC content approximates seasonal UV-B intensity level variations. An exception to this can be noted between the early July peak and mid-August. However, during this period the plant seemed to show a greater emphasis on the production of Δ^8THC, perhaps reflective of the water-stress conditions found in the Midwest during that time of year. The exceptions to this trend occurred during periods of high Δ^9THC production. This coincides with the observations of Haney and Kutscheid (1973), who found a Δ^8THC accumulation to be more dependent on drought stress contributing factors than for Δ^9THC, and also reported a negative correlation between the occurrence of the 2 compounds in Illinois *Cannabis*. Turner et al. (1975) have reported a pattern of Δ^9THC production similar to that observed by Latta and Eaton, but have attributed this to the maturation and sexual differentiation of the plant. It is also possible that this fluctuation could be attributed to a biosynthetic "cycling spiking" (Phillips et al., 1970) since the Δ^9THC peak is followed by high levels of its breakdown product, cannabinol (CBN).

Only infrequently have researchers expressed thoughts and speculations on *Cannabis* and sunlight. "I have long assumed that close association of the stalked glands with the developing female inflorescence suggests that the cannabinoids

may function as a protective from excessive insolation for the delicate ovaries and seeds" (Fairbairn, 1972). "A speculative and teleological explanation of the purpose of the resinous secretion is that the resin is a kind of varnish, intended to protect the leaves against the sun" (Small et al., 1975). The briefest of mentions specific to ultraviolet light are occasionally seen in the literature (Bergel and Sieper, 1965; Coutselinis and Miras, 1970; Haney and Mechoulam, 1970; Hermonn, 1971), but scientific studies relating any light effects to cannabinoid production are rare.

Davis et al. (1963) analyzed *Cannabis* from Morocco, Greece, Brazil, Canada, Switzerland, Germany, and one seizure sample believed to be of Mexican origin. Ratios of Δ^9THC and CBN to CBD were obtained and the data plotted. The tropical specimens exhibited a high Δ^9THC and CBN to CBD ratio while those from high latitudes showed the reverse, with the suspected Mexican sample giving an intermediate value. Temperature, rainfall and mean annual cloudiness data for these regions were compared and only the last of these seemed to show an unambiguous trend. Samples with the highest ratios came from regions whose sunshine was least attenuated by cloud cover, a variable affecting levels of UV-B irradiance.

Fairbairn and Liebmann (1974) attempted to evaluate environmental lighting influences on cannabinoid production. Four similar groups of Nepalese *Cannabis* were grown: one in normal greenhouse daylight only, another supplemented with additional visible light, a third supplemented with UV, and the last grown outdoors. Analysis did not indicate a significant difference between the unsupplemented greenhouse control group and those receiving additional visible light. The Δ^9THC content of the group receiving supplementary UV was increased by 20%, and that of those grown outdoors increased by over 90%. Yet the authors concluded that environmental lighting effects are of no significance, apparently based on the assumption that the plants grown outdoors served as an additional control group. This could only be valid if the UV levels in both areas were equivalent before supplementation. Since the type of glass used in most greenhouses absorbs UV-B, the greenhouse intensity levels actually could have been considerably lower than outside and only partially compensated by the lamps. These and additional complications greatly diminish the chance of reliable conclusions being reached. They include:

1. UV supplementation was provided only during the first and last 2 h of the day apparently under the assumption that the plants would be naturally irradiated between times (as with the visible light supplementation). This would create an exposure regime opposite to that of natural circumstances in which midday would be the period of greatest exposure.
2. The lamps used as the supplement (Osram 400 W) contain radiation of unnaturally short wavelengths and were apparently unfiltered.
3. Soil moisture, humidity and air circulation factors that could potentially contribute to stress were not reported as controlled.
4. Variation in intragroup Δ^9THC content accounted for differences of up to approximately 300%, so it would seem a more rigorous approach is demanded. Perhaps this could be implemented through the use of plants of identical genetic makeup, i.e., clones or cuttings from one parent.

Lastly, all samples were taken from vegetative tissue. More apparent contrasts may be revealed by sampling the delicate flower structures more susceptible to the possible effects of UV-B and the site of the highest cannabinoid production in the plant.

In pursuit of further evidence for a correlation between Δ^9THC production and UV-B irradiation levels, a preliminary examination of published research was conducted. The data of Small and Beckstead (1973) provided a cannabinoid profile survey of plants from seed of diverse and well-defined origins, grown under uniform conditions. It should be noted that only part of these data has been utilized in an attempt to eliminate spurious information. Data were eliminated if the specimen:

1. Lacked quantifiable amounts of either Δ^9THC or CBD.
2. Resulted from a breeding program.
3. Was labeled with quotation marks to indicate a particular strain or variety that may have been subjected to unnatural influences (this probably eliminated a few valid specimens as well).
4. Possessed a species name indicating that the plant was imported (e.g., *indica* or *sinensis* from a European source).
5. Was monoecious, since this represents an unusual form.
6. Resulted from an official seizure outside its country of origin.
7. Was obtained from a source intermediate to the original, except for United Nations contributions.

The remaining data are assumed to be from plants native to their respective areas or introduced long enough ago to be well adapted. This is a rather generous assumption, however, and probably accounts for much of the observed deviation in results.

The UV-B irradiation level of each origin was estimated from the map of Schulze, the x-y coordinates computer-plotted on scatter diagrams (Fig. 1, 2, and 3), and the data statistically analyzed via SAS General Linear Models and 2×2 chi-square procedures. This was done for both the absolute amounts of Δ^9THC and CBD and their relative amounts as designated by a cannabinoid ratio similar to that utilized by Davis et al. (1963), Fetterman et al. (1971), and Haney and Kutscheid (1973).

Higher levels of Δ^9THC are evident in plants from origins of intense ambient UV-B (Fig. 1). Even with the rather nonspecific data base used, the results are highly significant ($P < .0001$) and ambient UV-B levels of seed origin account for over 40% ($r^2 = .409537$) of the observed variation in % Δ^9THC content. As could be expected, there is also a corresponding negative correlation between % CBD and UV-B intensity (Fig. 2). The relative relationship of both compounds is summarized by a plot of the ratio of THC/CBD vs. UV-B (Fig. 3). Precursor (CBD) dominant plants have a ratio of 1 or less, while product (Δ^9THC)-dominant plants are plotted above this level. In this case, almost 50% ($r^2 = .493784$) of the ratio variation is predicted by the UV-B levels, at a high level of significance ($P < .0001$).

CONCLUSIONS

The results of this review appear to indicate that individuals of *Cannabis* have been naturally selected to produce large quantities of Δ^9THC in situations of high

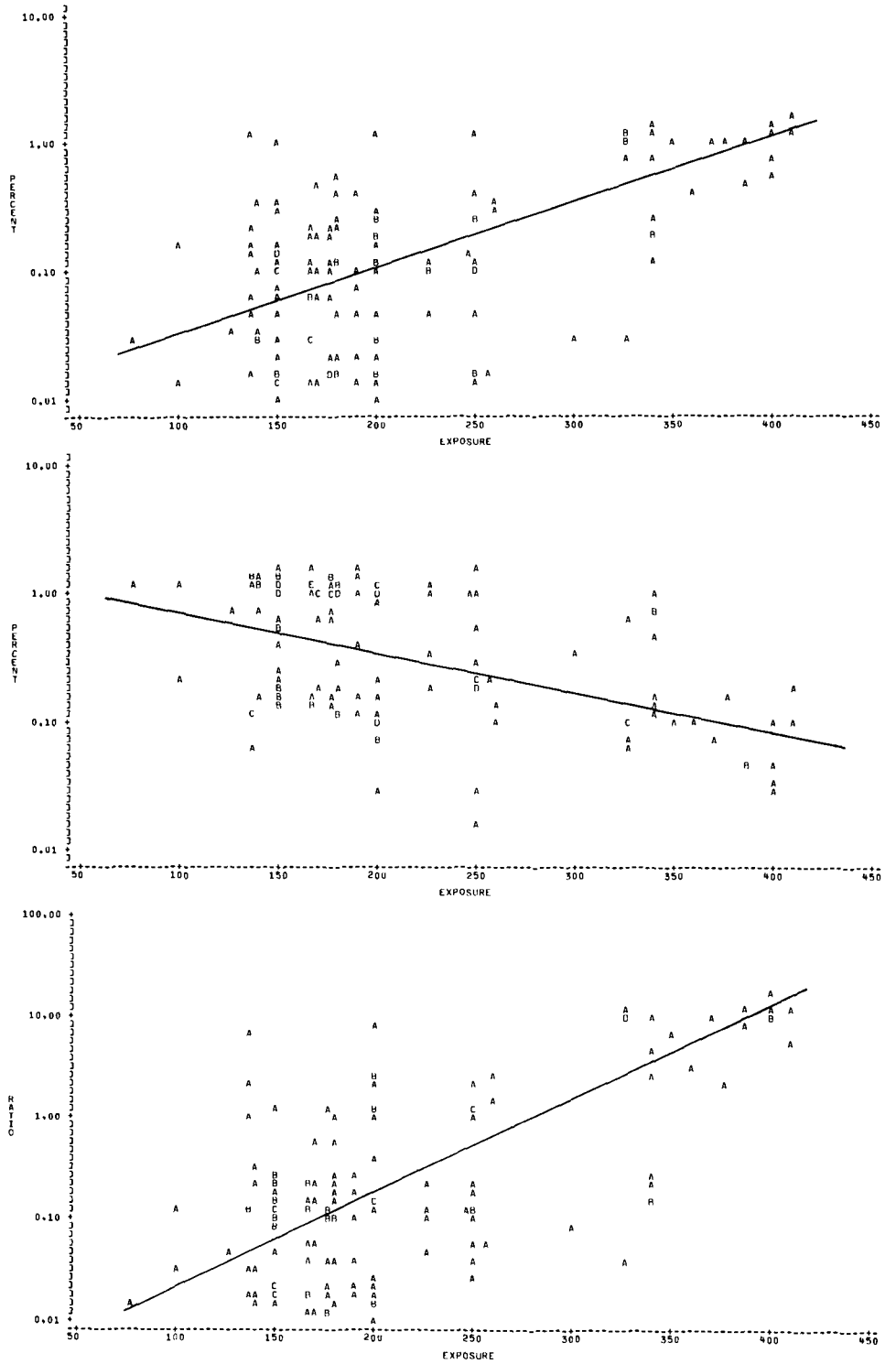

Fig. 1-3. Plots of cannabinoid content vs. annual UV-B exposure (watt-sec/cm^2) 302.5–312.0 nm. Legend: A = 1 observation, B = 2 observations, etc. Fig. 1. % Δ^9THC vs. exposure. Fig. 2. % CBD vs. exposure. Fig. 3. Ratio of THC/CBD vs. exposure.

UV-B exposure. This seems to be the consequence of an advantage conferred to the organism by the UV-B-screening properties of this compound. The utility of the cannabinoids for countering other ecological threats (Pate, 1979) may explain observations of local production variability. Further investigation of the phytochemical evolution of *Cannabis* would certainly constitute a useful study of a major economic plant, but more far reaching implications are also involved. This genus serves as a good model of an apparently widespread UV-B-coping mechanism. Pigmentation in both plants and people appears to be an important answer to an ubiquitous hazard. Indeed, the evolution of pigmentation and photoreactivation was probably a prerequisite to the successful establishment of land-based organisms.

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