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Is provitamin D a UV-B receptor in plants?

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Abstract

An hypothesis is presented that provitamin D (dehydrocholesterol and/or ergosterol) can act as a UV-B receptor in plants and algae. We also propose that the proportions between provitamins D, previtamins D, and vitamins D (D₂ and D₃), after calibration, can be used to evaluate UV-B exposure of phytoplankton and terrestrial vegetation.

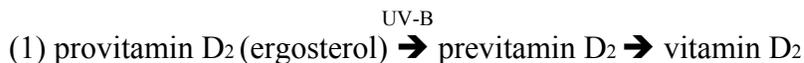
Key words: Dehydrocholesterol, Ergosterol, Photoreceptor, Provitamin D, Ultraviolet, UV-B, Vitamin D

Introduction

There is an enormous literature on the medical aspects of vitamin D (see Feldman et al. 1997; Holick 1999). The present contribution presents a possible function of the provitamin/previtamin/vitamin D system in algae, plants and fungi, namely as an ultraviolet-B photoreceptor system. Our discussion is based mostly on literature data published by other workers. We will also discuss some own findings in a general way, while details will be published elsewhere. We shall start by introducing vitamin D and related compounds and their formation in various organisms.

Vitamin D has several functions in the human body and in other terrestrial vertebrates. It was discovered as the agent which prevents rickets, a disease of the skeleton (Mellanby 1918; Steenbock & Black 1924; Hess & Weinstock 1924), and one of its most important functions is still in the regulation of calcium ion absorption from the food. The only well-documented case of a mammal not requiring vitamin D from external sources or internal production is the damara mole rat, *Cryptomys damarensis* (Buffenstein et al. 1991; Pitcher & Buffenstein 1994a, b), which seems not to regulate calcium uptake from the intestine (Pitcher et al. 1992; Pitcher & Buffenstein 1995), although it can synthesise vitamin D₃ if artificially exposed to sunlight (Pitcher et al. 1994). The situation is probably the same for the related mole-rat *Heterocephalus glaber* (Pitcher & Buffenstein 1995), and possibly for many other burrowing animals feeding from underground plant parts, and therefore lacking any obvious source of vitamin D. There are two well-known types of vitamin D, i.e. vitamin D₂ and vitamin D₃. Vitamin D₁ does not exist; it turned out that what was first named vitamin D₁ was a mixture of compounds. In amphibians and reptiles there exist other, related compounds which probably have analogous functions. Vitamins D are formed from provitamins D via intermediates called previtamins D. The conversion from provitamin to previtamin is a photochemical process requiring ultraviolet-B radiation and taking place with a high quantum yield: for provitamin D₂ and provitamin D₃ photoconversion quantum yields of 0.20 to 0.31 have been reported (Pfoerter & Weber 1972; Havinga et al. 1973; Pottier & Russell 1991); 0.26 being a value often used in various computations.

We thus have the reaction sequences, which are not enzyme-catalysed:



Provitamin D₃ is also called cholecalciferol.

Even at human body temperature the conversion of previtamin to vitamin is a slow process, requiring days to approach completeness. At the lower temperature of most organisms, the conversion is even slower. Provitamin D₃ (but not D₂) is formed in human skin, and we can form vitamin D₃ after exposure to ultraviolet-B radiation. A well-known food source for vitamin D₃ is cod-liver oil; the product first shown to prevent rickets (Mellanby 1918). The vitamin is not synthesised by the fish, but by the plankton forming the

beginning of the marine food-chain (Sugisaki *et al.* 1974, Sunita Rao & Raghuramulu 1996a, b; Takeuchi *et al.* 1991).

Table 1a. Contents of provitamins and vitamins D in phytoplankton. After Sunita Rao & Raghuramulu (1996) (a) and Takeuchi *et al.* (1991) (b). Amounts are expressed as microgram per gram of dry matter.

Source of phytoplankton	Provit. D ₂	Provit. D ₃	Vit. D ₂	Vit. D ₃
Hussain Sagar (India) (a)	3.9	23.6	0.0525	0.8035
Biwa Lake (Japan) (b)				
August	10.1	14.5	0.043	0.1473
October	2.9	3.6	0.0189	0.0496
December	2.6	3.4	–	0.0217

Occurrence of provitamins D and formation of vitamins D in algae

Provitamin D₂ (ergosterol) is present in many algae from very different groups, but not in all algae. The following have been shown to contain ergosterol: Several species of *Chlorella* (Chlorophyceae) (Patterson 1971), *Chlamydomonas reinhardtii* (Ehrenberg) (Chlorophyceae) (Patterson 1974), *Skeletonema menzeli* (Greville) (Bacillariophyceae) (Holick 1989), *Emiliania huxleyi* (Lohm.) (Prymnesiophyceae or Haptophyceae) (Holick 1989), *Ochromonas danica* (Wyssotzki) (Chrysophyceae) (Stern *et al.* 1960; Gershengorn *et al.* 1968, and others).

Source of phytoplankton	D ₂ ratio x1000	D ₃ ratio x1000	D ₃ ratio / D ₂ ratio
Hussain Sagar (India) (b)	13.5	34.0	2.5
Biwa Lake (Japan) (d)			
August	4.3	10.2	2.4
October	6.5	13.8	2.1
December	–	6.4	

Table 1b. Ratios of vitamins D to provitamins D (multiplied by 1000). Code letters for references as in Table 1a.

In Table 1a we have collected literature data on provitamins and vitamins D for phytoplankton collected in India and in Japan, and in Table 1b results of our own calculations on these data. The latter table shows the following:

- (1) The ratio of vitamin to provitamin is always higher for the D₃ type than for the D₂ type (more than twice as high). Thus vitamin accumulation from provitamin D₃ is more efficient than formation from provitamin D₂ under these natural conditions. This may at first seem surprising, since the quantum yield measured for conversion in solution is almost the same for provitamins D₂ and D₃. Different explanations are possible for this apparent discrepancy, such as faster conversion from provitamin to vitamin with less provitamin disappearing in side reactions, or slower breakdown of the vitamin D₃ in vivo. It may somehow be related to the fact that only vitamin D₃ reaches the highest trophic levels.

- (2) More provitamin is converted to vitamin in Hussain Sagar Lake in India (latitude ca 18° N), than in Lake Biwa in Japan (latitude ca 35.3° N). The UV-B radiation is, of course, stronger at the lower latitude, and this may be reflected in the accumulation of vitamin.
- (3) In Japan the vitamin accumulation is less efficient in December than in August or October, reflecting the change in UV-B exposure over the year.

Although the data are limited we propose that determinations of provitamins, previtamins and vitamins D could be used as an internal dosimeter to evaluate the exposure of phytoplankton to ultraviolet-B radiation. Calibration could be carried out with controlled exposures of the organisms. Determination of radiation exposure under natural conditions is otherwise almost impossible, as the plankton moves up and down in the water column. Galkin & Terenetskaya (1999) have discussed the use of provitamin D₃ in vitro for dosimetry, and Webb et al. (1988) have compared provitamin D₃ conversion in vitro with that in skin under different daylight conditions.

There are no corresponding data for macroalgae in the literature, but we have found provitamins and vitamins D₂ and D₃ in the brown macroalga, *Fucus vesiculosus* L. The ratios of vitamin to provitamin were higher for material from the Swedish west coast, latitude 58.3° N than for material from the Norwegian west coast, 68.1° N (both collected within twelve days in September). In this case, however, the ratios were higher for the D₂ than for the D₃ form.

Effects of provitamin D₂ and vitamins D on algae

We would like to refer to an interesting investigation by Fries (1984). She added provitamin D₂, vitamin D₂ or vitamin D₃ to the growth medium of the brown macroalga *Fucus spiralis* L. At the lowest concentration, 10⁻⁸ M, vitamin D₃ (but not the other two compounds) had a large growth-stimulating effect. At a tenfold higher concentration, also vitamin D₂ had a growth-stimulating effect, while the stimulation by provitamin D₂ was much smaller.

Occurrence of provitamins and vitamins D in higher plants

Plants produce provitamins D, vitamins D and related compounds in their leaves (Napoli et al. 1977; Wasserman 1975; Prema & Raghuramulu 1994, 1996; Zucker et al. 1980; Rambeck et al. 1981; Horst et al. 1984).

In the case of ergosterol and vitamin D₂ one has to be cautious in assigning substances found in the analysis of plants to synthesis by the plants themselves. Many plants, among them many grasses, harbour endophytic fungi (Clay 1990; Redlin & Carris 1996; Siegel et al. 1987), and fungi regularly produce ergosterol as their major sterol. The content of ergosterol in plant tissue has been used as a measure of fungal contamination (Gessner & Schmitt 1996).

It is a widespread misconception in the literature that plants produce only provitamin D₂ and vitamin D₂ (e.g., Buddecke 1980). Often as much provitamin D₃ and vitamin D₃ are produced (Zucker et al. 1980, Prema & Raghuramulu 1996). Even 1,25-dihydroxy vitamin D₃ has been found in plants (Napoli et al. 1977), as well as a glycoside of this compound, sometimes at concentrations high enough to poison grazing animals (Wasserman et al. 1976).

We have confirmed a UV-B dependent synthesis of vitamins D₂ and D₃ in the leaves of the tomato plant. An interesting observation is that the provitamin D₃ content of tomato leaves is not reduced by growing plants under UV-B radiation, although a substantial amount of vitamin D₃ is formed (Table 2). This points to a feedback mechanism regulating the amount of the provitamin.

Table 2. Contents of provitamins and vitamins D₂ and D₃ in tomato (*Lycopersicon esculentum* Mill). Tomato plants were grown in a greenhouse with or without UV-B radiation (0.85 kJ plant weighted UV-B radiation per m² and day).

Organism	Micrograms per gram dry weight			
	Provit. D ₂	Provit. D ₃	Vitamin D ₂	Vitamin D ₃
Tomato (-UV-B)	1.83	0.61	0	0
Tomato (+UV-B)	2.23	0.76	0.087	0.28

Recently Curino et al. (1998) made the startling discovery that *Solanum glaucophyllum* cells are able to synthesise vitamin D₃ and its derivatives in darkness. This is the only documented case of vitamin D₃ synthesis in the absence of UV-B. *Solanum glaucophyllum* is a very special plant which accumulates large amounts of dihydroxy vitamin D₃ as a protection against grazing mammals. Mechanisms for nonphotochemical formation of vitamin D have been proposed by Norman & Norman (1993).

Effects of vitamins D on plants

Vitamin D applied to herbaceous and woody plants stimulates initiation of adventitious roots (Buchala & Schmid 1979; Jarvis & Booth 1981; Moncousin & Gaspar 1983). Vitamin D₃ (10⁻⁹ M) inhibits root elongation in *Phaseolus vulgaris* and promotes germination of light sensitive lettuce seed in darkness (Buchala & Pythoud 1988). Thus vitamin D has a number of physiological effects.

Intracellular localisation of provitamin D

In human skin cells provitamin D₃ occurs in the outer cell membrane. After conversion to vitamin D₃ an OH group extends from the membrane to the intercellular compartment, where it attaches to a carrier protein and the vitamin is transferred to the blood stream.

In most fungi ergosterol (provitamin D₂) is the major sterol in the outer cell membrane. Upon irradiation with ultraviolet radiation under aerobic conditions it disappears, and the corresponding spectral change can be observed both in intact yeast cells and in isolated cell membranes (Arami et al. 1997a, b). It is not known whether the provitamin D present in plants is located to the cell membranes, but this appears likely, and we have started experiments to find out whether this is the case or not.

The role of provitamins and vitamins D in plants

Although provitamins and vitamins D (both D₂ and D₃ forms) occur in many, perhaps most, algae and plants, nothing is known about their possible function.

We would like to propose here a function which has not been considered by other authors, i.e., that the provitamin/vitamin D system acts as a sensor for ultraviolet-B radiation.

Several processes in plants are regulated specifically by ultraviolet-B radiation. The action spectra for some such processes have been determined and show peaks at about 295 nm (reviews by Beggs et al. 1994 and Björn 1999). Also some algae can sense the radiation level: prysemniophytes and dinoflagellates are able to adjust the content of radiation-screening mycosporine-like amino acids according to need (Hannach & Sigleo 1998). The action spectrum for pigment formation in a fungus has peak near 295 nm (Hsiao & Björn 1982). An action spectrum for mycosporine induction in a cyanobacterium has a rather different shape with a peak at 310 nm and a long tail towards longer wavelength (Portwich & Garcia-Pichel 2000). In the latter case there is some evidence for the role of a pterin as photoreceptor chromophore, and this as also been suggested by several researchers for the higher plant photoreceptor.

The action spectrum for photochemical conversion of provitamin D to vitamin D has been determined only for human skin and in this case also exhibits a peak at 295 nm (MacLaughlin et al. 1982).

Provitamin D is suitable as a radiation sensor because of the very high quantum yield for photoconversion. The latter is 0.26 for conversion of provitamin D₂ to previtamin D₂ at 0 °C both at 254 nm and 313 nm (Havinga 1973), and the yield for provitamin D₃ conversion is of a similar magnitude (Pottier & Russell 1991).

The sterol composition of plant cell membranes affects ATPase activity and proton pumping (Grandmougin-Ferjani et al. 1997), and in model experiments affect water permeability and ordering of acyl chains (Schuler et al. 1991). In yeast the photochemical removal of ergosterol causes a proportionate reduction in ATPase activity and changes in the activities of other plasmamembrane-bound enzymes (Arami et al. 1997a, b). Thus the effects of ultraviolet-B radiation on photoconvertible sterols such as provitamins D₂ and D₃ could form the start of a signal transduction chain.

Photoinactivation of plant plasma membrane ATPase has an action spectrum peaking at 290 nm (Imbrie & Murphy 1982, 1984). However, when native lipid vesicles containing ATPase are investigated, the action spectrum has much more of a tail towards longer wavelengths than what is compatible with a UV-B receptor, and direct UV action on ATPase is therefore ruled out as a UV sensing reaction. Infection of a plant with an endophytic fungus (Cheplick & Clay 1988) increases the content of ergosterol. If conversion of ergosterol is important for reactions of plants to ultraviolet-B radiation, one would presume that infected plants react to ultraviolet-B radiation in a different way from uninfected plants. In fact, Newsham et al. (1998) found that in *Lolium perenne* a certain treatment with ultraviolet-B decreased the number of spikes, the number of seeds, and the seed weight by 70–75% , but only if the plants were infected by the fungus *Neophytium lolii*.

Conclusion

Plants and some algae are able to perceive ultraviolet-B radiation and regulate chemical processes and morphogenesis in a radiation-dependent manner, and are thought to have an ultraviolet-B specific photoreceptor. Provitamins D₂ and D₃ are present in leaves of land plants and in some algae, and are converted, with a high quantum yield, to previtamins D and vitamins D upon exposure to ultraviolet-B radiation. The action spectrum for several ultraviolet-induced phenomena in plants (Björn 1999) and for provitamin D conversion in human skin peak at the same wavelength. Photodestruction of provitamin D is known to change the activity of membrane-bound enzymes in yeast cells. We have pointed to the possibility that provitamins D act as ultraviolet-B photoreceptors for UV-B induced regulatory reactions in plants, and proposed that the proportions between provitamins, previtamins, and vitamins D can be used to evaluate the UV-B exposure of phytoplankton and plants.

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Mammals need vitamin D for several processes. Because of low levels of ultraviolet-B radiation in the Arctic, vitamin D could be in limiting supply for terrestrial mammals there, such as these reindeer. But what could be the role of vitamin D in plants, algae, and lichens, and how could it be affected by the UV-B level? (Photograph by Lars-Olof Björn)