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Photobiological Characteristics of Vitamin D_2 in Agaricus bisporus and Its Clinical Bioavailability in Humans

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Abstract: Mushrooms exposed to sunlight or ultraviolet (UV) radiation serve as an excellent dietary source of vitamin D_2 due to their high content of ergosterol (provitamin D_2), the precursor of vitamin D. Upon UV irradiation, ergosterol is converted to previtamin D_2, which rapidly undergoes thermal isomerization to form vitamin D_2 via a mechanism analogous to the transformation of previtamin D_3 to vitamin D_3 in human skin. Continuous UV exposure further generates two photoproducts: lumisterol$_2$ and tachysterol$_2$. Research shows that lumisterol$_2$ concentrations remain stable for up to 24 hours after biosynthesis in Agaricus bisporus.

Keywords: Vitamin D; Vitamin D_2; *Agaricus bisporus*; 25-hydroxyvitamin D; Ultraviolet irradiation; UVB.

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1. Introduction

A human bioavailability comparative study demonstrated that daily ingestion of 1800 IU vitamin D_2 derived from UV-irradiated Agaricus bisporus exerts equivalent efficacy in elevating and maintaining serum 25-hydroxyvitamin D (the gold-standard biomarker for assessing human vitamin D nutritional status) compared with identical doses of supplemental vitamin D_2 or vitamin D_3. Accordingly, mushrooms represent a rich dietary source of vitamin D_2, and their consumption sustains serum 25-hydroxyvitamin D concentrations within a healthy physiological range.

2. Phylogenetic and evolutionary overview

It is hypothesized that vitamin D originated from the earliest life forms on Earth over 900 million years ago. Primitive organisms were continuously bombarded by solar UV radiation, which damages UV-sensitive DNA, RNA, and proteins within cells. Ergosterol (provitamin D_2) absorbs UV light at wavelengths of 240–

320 nm, functioning as a natural photoprotectant. Phytoplankton and zooplankton capable of synthesizing ergosterol gain resistance to UV-induced nucleic acid damage and successfully transmit their genes to progeny [1,2].

As early as 500 million years ago, phytoplankton species including *Emiliania huxleyi* synthesized ergosterol. Upon UVB irradiation, ergosterol converts to previtamin D_2, which subsequently undergoes thermal isomerization to yield vitamin D_2. Higher trophic-level marine animals acquire vitamin D through ingestion of phytoplankton and zooplankton.

Terrestrial vertebrates rely on vitamin D to maintain serum calcium homeostasis and bone metabolism. The skin of poikilothermic animals contains multiple provitamin D species, dominated by 7-dehydrocholesterol (7-DHC, provitamin D_3). The epidermal provitamin D_3 concentrations of northern grass frogs and anole lizards are 1–2 orders of magnitude higher than those in humans, endowing them with an extraordinary capacity for cutaneous vitamin D_3 synthesis. This evidence indicates that skin-mediated vitamin D biosynthesis played a pivotal evolutionary role in terrestrial poikilothermic vertebrates.

3. Historical research background

Vitamin D deficiency is linked to multiple skeletal disorders, among which rickets is the earliest well-documented clinical manifestation. At the beginning of the 19th century, rickets reached epidemic proportions across Europe and the United States, with a particularly high prevalence in northern industrial cities. Autopsy investigations conducted in Boston (USA) and Leiden (the Netherlands) in the late 19th century revealed that 80–90% of children suffered from rickets. Etiological factors of rickets encompass vitamin D insufficiency, inadequate calcium intake, as well as congenital and acquired disorders disrupting vitamin D, calcium, and phosphorus metabolism. Typical clinical manifestations include growth retardation, muscle weakness, skeletal malformations, stunted stature, and bowlegs.

In 1822, Polish physician Sniadecki observed a markedly higher incidence of rickets among children residing in densely populated Warsaw relative to rural children with abundant sunlight exposure, and first proposed the critical role of solar irradiation in bone health. In 1861, French physician Trousseau postulated that rickets arises from combined insufficient sun exposure and dietary defects, and successfully treated affected patients with cod liver oil.

In the early 20th century, German physician Huldschinsky administered UVB-emitting mercury vapor quartz lamp phototherapy to children with rickets. After six weeks of intervention, skeletal radiographs demonstrated significant improvements in bone mineralization [3]. In 1921, Hess and Unger verified that 3–4 weekly sessions of direct natural sunlight exposure ameliorated both clinical and radiological manifestations of childhood rickets; meanwhile, cod liver oil proved effective for rickets prophylaxis and treatment in adolescents.

3.1. Research progress of vitamin D in food

In 1918, Mellanby first confirmed that dietary cod liver oil prevents the onset of rickets in puppies [4]. In 1924, Steenbock and Black discovered that UV-irradiated foods confer antirachitic activity when fed to experimental animals [5]. In 1925, Cowell demonstrated that bovine milk irradiated under a mercury vapor lamp for 20 minutes alleviates rickets in adolescents upon consumption [6]. Over the subsequent two decades,

a broad spectrum of foods and beverages were fortified with vitamin D. These findings collectively validated the antirachitic bioactivity of vitamin D in humans and animals.

Vitamin D_2 and vitamin D_3 share highly homologous molecular structures, differing exclusively in two structural features: vitamin D_2 bears a carbon-carbon double bond between carbons 22 and 23, and a methyl group attached to carbon 24 of the side chain.

4. Photobiological mechanisms of vitamin D_2 biosynthesis in Agaricus bisporus

Agaricus bisporus (Large) Sing., commonly named white button mushroom, belongs to the family Agaricaceae, genus Agaricus. Its fruit bodies are medium-sized with caps ranging 5–12 cm in diameter, initially hemispherical before flattening out; the cap surface is white and smooth, gradually turning pale yellow when dry, with involute margins in immature specimens. The flesh is thick and white, developing faint reddish discoloration upon bruising, and emits the characteristic aromatic odor of mushrooms. As early as 1994, Mattila et al. extracted ergosterol from wild mushrooms, confirming the presence of vitamin D precursors in edible fungi and drawing widespread academic attention to their nutritional benefits [7].

Commercial Agaricus bisporus are cultivated under complete darkness, resulting in negligible intrinsic vitamin D_2 content: fresh mushrooms contain 56.3 μg ergosterol per 100 g fresh weight, with only 0.11 μg endogenous vitamin D_2 per 100 g fresh weight [8]. Artificial UV irradiation induces massive vitamin D_2 synthesis in mushrooms, a technology widely adopted by the mushroom industry to enhance the vitamin D_2 content of commercial products.

The photobiological pathways governing cutaneous vitamin D_3 synthesis in poikilotherms and humans have been thoroughly characterized, whereas the reaction kinetics of UV-triggered vitamin D_2 production in mushrooms remained poorly elucidated prior to this study.

4.1. Photochemical generation of previtamin D_2 in mushrooms

This study employed UV-irradiated Agaricus bisporus as the experimental matrix to dissect the synthetic pathway of vitamin D_2, with methanolic ergosterol solution (50 μg/mL, sealed in borosilicate ampoules) serving as the positive control. A Xenon RC-500B pulsed UV curing system was utilized for 5-minute irradiation, with samples positioned 3.5 inches from the lamp source. Tissue cores with a diameter of 0.5 cm and depth of 0.1 cm were collected at serial time points over a maximum 96-hour incubation period.

Tissue samples were homogenized in 6 mL pure methanol, followed by centrifugation; the supernatant was harvested and evaporated to dryness under nitrogen flow. Dried residues were reconstituted in hexane containing either 0.3% or 0.8% isopropanol, then separated via an Agilent 1100 diode-array high-performance liquid chromatography (HPLC) system. Two silica stationary-phase columns were sequentially applied to resolve ergosterol, its photoderivatives and vitamin D_2:

(1) Zorbax RX-SIL column (mobile phase: 0.8% isopropanol in hexane): separation of lumisterol$_2$ and previtamin D_2;
(2) Zorbax CN column (mobile phase: 0.3% isopropanol in hexane): separation of tachysterol$_2$ and vitamin D.

Concentrations of individual photoproducts were quantified via external standard calibration curves.

Immediately following 5 minutes of UV irradiation, ergosterol in Agaricus bisporus was photoconverted to a chromatographic peak eluting at 6.7 min with a maximum UV absorbance (λmax) of 260 nm, consistent

with the spectral signature of previtamin D_2. The peak at 10.6 min (λmax = 265 nm) corresponds to vitamin D_2. The chromatographic profiles of irradiated mushroom extracts were identical to those of irradiated ergosterol standard ampoules, validating prior findings reported by Kalaras et al [9].

A 96-hour time-course experiment tracked the conversion kinetics of previtamin D_2 to vitamin D_2 in irradiated mushrooms and methanolic ergosterol standards, revealing a time-dependent accumulation of vitamin D_2. At 6 hours post-irradiation, 24% of previtamin D_2 in mushroom tissue had undergone isomerization to vitamin D_2, compared with merely 10% conversion observed in the methanolic standard solution. At 11.5 hours post-irradiation, 50% of mushroom-derived previtamin D_2 converted to vitamin D_2, while only 19% conversion occurred in the organic solvent matrix.

This kinetic pattern closely mirrors the transformation of 7-DHC in methanol and cutaneous previtamin D_3 synthesis in UV-exposed lizard skin [10]. The results demonstrate that thermal isomerization of previtamin D_2 to vitamin D_2 proceeds substantially faster in mushroom tissue than in pure organic solvents, following a membrane-facilitated catalytic mechanism analogous to that observed in lizard epidermis.

4.2. Photogeneration profiles of lumisterol$_2$ and tachysterol$_2$

Gradient UV irradiation durations (1, 2, 3, 4, 5, 10 min) were applied to Agaricus bisporus at a constant temperature of 25°C. Two distinct photoproduct peaks emerged after 5 minutes of irradiation:

(1) Retention time = 7.3 min, λmax = 272 nm: lumisterol$_2$;

(2) Retention time = 11.7 min, λmax = 281 nm: tachysterol$_2$.

Identical peaks of previtamin D_2, lumisterol$_2$ and tachysterol$_2$ were detected in irradiated ergosterol standard ampoules, consistent with published literature.

Previtamin D_2 and lumisterol$_2$ were detectable after only 1 minute of UV exposure; tachysterol$_2$ became detectable upon 3 minutes of irradiation. A photoequilibrium state among previtamin D_2 and its photoderivatives was achieved at 4–5 minutes of irradiation. Prolonging exposure beyond 5 minutes increased the total yield of all photoproducts without altering their relative molar ratios. No previtamin D_2, photoderivatives or vitamin D_2 were detectable in non-irradiated control mushrooms.

4.3. Stability of lumisterol$_2$ and tachysterol$_2$ in mushroom tissue

Serial sampling over a 24-hour incubation period was performed to characterize the stability of previtamin D_2 photoproducts in Agaricus bisporus. All samples received standardized 5-minute UV irradiation, with tissue harvested every 2 hours for 24 hours. Previtamin D_2 concentrations declined progressively over time, accompanied by a corresponding rise in vitamin D_2 levels. A supplementary 336-hour stability trial assessed photoproduct persistence in methanolic solution, confirming that lumisterol$_2$ and tachysterol$_2$ remain chemically stable for over 300 hours in methanol.

Within irradiated mushroom tissue, lumisterol$_2$ concentrations remained constant throughout the 24-hour monitoring window. In contrast, tachysterol$_2$ concentrations decreased continuously and fell below the limit of detection within 24 hours post-irradiation.

5. Vitamin D_3 production in mushrooms

Prior academic consensus held that UV irradiation exclusively induces vitamin D_2 synthesis in mushrooms. Prompted by the discovery of vitamin D_4 biosynthesis in fungal species, this study re-evaluated mushroom

extracts to identify additional provitamin D congeners.

Reverse-phase HPLC analysis of shiitake mushroom extracts identified a peak at 11.5 min corresponding to provitamin D_4, alongside a peak at 10.8 min with a UV absorption spectrum matching that of 7-dehydrocholesterol (7-DHC, provitamin D_3), confirmed via co-chromatography with authentic standards. The elution order of the three provitamin D species was determined as: provitamin D_4 (9.6 min), provitamin D_2 (10.8 min), provitamin D_3 (11.5 min). Concentrations of 7-DHC and provitamin D_4 in shiitake gill tissue were 5.8-fold and 2.6-fold higher, respectively, relative to concentrations in the outer cap epidermis.

Shiitake mushrooms were irradiated for 5 minutes with gill surfaces oriented upward, and metabolites were separated on a C18 HPLC column. Previtamin D_3 eluted at 6.3 min under normal-phase chromatographic conditions. Following thermal isomerization, the resultant vitamin D species eluted at 5.1 min (vitamin D_2) and 6.1 min (vitamin D_3), both exhibiting a characteristic λmax of 265 nm. These data confirm that UVB irradiation of shiitake mushrooms simultaneously produces vitamin D_2, vitamin D_3 and vitamin D_4.

6. Human bioavailability of mushroom-derived vitamin D_2

Food fortification with vitamin D has been practiced in the United States for over 70 years, as naturally vitamin D-rich foods are scarce in conventional diets. Milk, orange juice, bread, dairy products, and selected breakfast cereals are routinely fortified with supplemental vitamin D. UV-irradiated mushrooms constitute a superior natural dietary source of vitamin D_2. Multiple clinical trials have verified that vitamin D_2 and vitamin D_3 from fortified foods effectively elevate serum 25-hydroxyvitamin D, the gold-standard biomarker for evaluating human vitamin D nutritional status.

6.1. Summary of preceding clinical trials

(1) Biancuzzo et al.

Oral consumption of orange juice fortified with 1000 IU vitamin D_2 or vitamin D_3 produced equivalent elevations in total serum 25-hydroxyvitamin D compared with identical doses of oral vitamin supplements. The magnitude of increase in serum 25(OH)D_2 and 25(OH)D_3 did not differ between juice-fortified and capsule-supplemented treatment arms [11].

(2) Natri et al.

Bread fortified with vitamin D_3 elevated serum 25-hydroxyvitamin D concentrations in adult women with equivalent efficacy to standalone vitamin D_3 capsules [12].

Two independent clinical trials have specifically investigated the in vivo bioavailability of vitamin D_2 from UV-irradiated mushrooms:

(1) Urbain et al. (2011)

A 5-week single-blinded randomized controlled trial enrolling 26 Caucasian healthy adults with baseline serum 25(OH)D < 20 ng/mL [13]. Subjects were randomized to three intervention arms:

- Group 1: Mushroom soup containing 28,000 IU mushroom-derived vitamin D_2 + placebo, administered four times weekly;

- Group 2: Soup containing non-irradiated mushrooms (60 IU endogenous vitamin D_2) + 28,000 IU liquid synthetic vitamin D_2 supplement;

- Group 3: Non-irradiated mushroom soup + placebo supplement.

After four weeks of intervention, serum 25(OH)D concentrations increased significantly in Group 1 and Group 2, with mushroom-sourced vitamin D_2 demonstrating equivalent potency to identical doses of synthetic supplemental vitamin D_2 for raising circulating 25(OH)D levels.

(2) Stephenson et al. (2012)

Subjects consumed one standardized mushroom serving daily alongside meals for six weeks, allocated to four parallel groups: control (non-irradiated mushrooms), low-dose irradiated mushrooms (352 IU vitamin D_2), high-dose irradiated mushrooms (684 IU vitamin D_2), synthetic vitamin D_2 supplement (1128 IU) paired with non-irradiated mushrooms [14].

All treatment arms except the control exhibited significant increases in serum 25(OH)D_2. Mild reductions in serum 25(OH)D_3 (mean decrease = 0.32 ng/mL) were observed in the high-dose mushroom and synthetic supplement groups, offset partially by a 0.40 ng/mL rise in 25(OH)D_2, yielding a minor net reduction in total serum 25(OH)D. This observation sparked academic controversy: several publications claimed vitamin D_3 exerts superior potency for maintaining circulating 25(OH)D concentrations relative to vitamin D_2, and even suggested vitamin D_2 intake may reduce total serum 25(OH)D. However, multiple investigations led by Holick, Biancuzzo, and collaborators demonstrated equivalent efficacy of equimolar vitamin D_2 and vitamin D_3 for elevating and sustaining total serum 25(OH)D. Weekly high-dose supplementation with 50,000 IU vitamin D_2 for up to six years reliably elevates total serum 25(OH)D and represents a safe therapeutic strategy for the prevention and treatment of vitamin D deficiency.

6.2. Present clinical trial design

6.2.1. Trial objective

To compare the efficacy of daily oral administration of 1800 IU vitamin D_2 extracted from Agaricus bisporus (MRVD2), synthetic 1800 IU vitamin D_2 capsules, synthetic 1800 IU vitamin D_3 capsules, and maltodextrin-matched placebo capsules in elevating and maintaining human vitamin D nutritional status.

6.2.2. Subjects

40 healthy adult participants (21 males, 19 females; mean age = 38.5 years). All subjects received daily oral capsules throughout a 3-month winter intervention period. Vitamin D content of all capsules was quantified via HPLC with a tolerance error margin of ± 10%. All 40 participants completed the full trial protocol.

6.2.3. Randomization groups

10 subjects per arm: mushroom vitamin D_2 group, synthetic vitamin D_2 group, synthetic vitamin D_3 group, placebo group. Serum samples were collected weekly, and concentrations of 25(OH)D_2, 25(OH)D_3, and total 25(OH)D were quantified via liquid chromatography-tandem mass spectrometry (LC-MS/MS).

6.3. Clinical trial outcomes by treatment group

6.3.1. Mushroom-derived vitamin D_2 group

(1) Baseline serum 25(OH)D_2: 0.6 ± 0.3 ng/mL; endpoint at week 12: 18.6 ± 1.4 ng/mL ($p < 0.0001$).

(2) Baseline total serum 25(OH)D: 20.6 ± 2.4 ng/mL; endpoint at week 12: 30.1 ± 2.6 ng/mL ($p < 0.001$).

6.3.2. Synthetic vitamin D_2 supplement group

(1) Baseline serum 25(OH)D_2: 1.5 ± 1.2 ng/mL; endpoint at week 12: 13.3 ± 2.0 ng/mL ($p < 0.001$).

(2) Baseline total serum 25(OH)D: 19.4 ± 2.3 ng/mL; endpoint at week 12: 29.2 ± 2.0 ng/mL ($p < 0.01$).

6.3.3. Synthetic vitamin D_3 supplement group

(1) Baseline serum 25(OH)D_3: 16.3 ± 0.6 ng/mL; endpoint at week 12: 34.4 ± 1.3 ng/mL.

(2) Baseline total serum 25(OH)D: 17.1 ± 1.4 ng/mL; endpoint at week 12: 34.4 ± 1.3 ng/mL ($p < 0.05$).

6.3.4. Placebo group

(1) Baseline serum 25(OH)D_2: 1.5 ± 1.2 ng/mL; endpoint at week 12: 1.6 ± 1.4 ng/mL ($p < 0.001$).

(2) Baseline total serum 25(OH)D: 20.4 ± 2.3 ng/mL; endpoint at week 12: 20.2 ± 2.0 ng/mL ($p < 0.01$).

Baseline total serum 25(OH)D concentrations were not statistically different across the three active treatment groups. Serum 25(OH)D concentrations reached a plateau at week 7 and remained stable for the subsequent 5 weeks of intervention. At the 12-week endpoint, no statistically significant intergroup differences in total serum 25(OH)D were detected among active arms: synthetic vitamin D_3 group (34.4 ± 1.1 ng/mL), synthetic vitamin D_2 group (29.2 ± 2.0 ng/mL), mushroom vitamin D_2 group (30.1 ± 2.6 ng/mL). Total serum 25(OH)D levels remained essentially unchanged in the placebo group over the 12-week trial period.

(3) Trial conclusion: Daily oral intake of mushroom-derived vitamin D_2 significantly elevates and sustains circulating total serum 25(OH)D concentrations, exhibiting equivalent efficacy for improving and maintaining vitamin D status relative to identical doses of synthetic supplemental vitamin D_2 and vitamin D_3.

7. Conclusions

Vitamin D deficiency constitutes a global public health crisis, increasing population-level risk of skeletal disorders and multiple chronic non-communicable diseases. Three core strategies support maintenance of physiological vitamin D concentrations: moderate solar UV exposure, consumption of naturally vitamin D-dense foods, and oral vitamin D supplementation.

For over 500 million years, marine phytoplankton have biosynthesized vitamin D_2 using ergosterol as the primary precursor. The phytoplankton species Emiliania huxleyi contains 1.0 μg ergosterol per gram wet weight, serving as a fundamental source of vitamin D_2 for marine food webs over geological timescales. Fungi, analogous to phytoplankton, accumulate high ergosterol reserves and undergo robust vitamin D_2 biosynthesis upon UVB irradiation.

UVB irradiation triggers photolysis of ergosterol in mushroom tissue to generate previtamin D_2, which undergoes secondary UV absorption to form two photoproducts: lumisterol$_2$ and tachysterol$_2$. Thermal isomerization of previtamin D_2 to vitamin D_2 proceeds far more rapidly within mushroom tissue than in pure organic solvents, driven by a membrane-catalyzed acceleration mechanism conserved in lizard and human skin.

Mechanistic rationale: The planar molecular conformation of 7-DHC and ergosterol enables intercalation between triglyceride acyl chains and polar head groups of cell membranes. UVB photons excite the conjugated 5,7-diene moiety to generate previtamin D, which exists in two stereoisomeric conformations:

the thermodynamically favored trans-cis (tZc) conformer (biologically inert for isomerization) and the less stable cis-cis (cZc) conformer (capable of rearranging to active vitamin D). In pure organic solvents, 90% of previtamin D adopts the inactive tZc conformation, requiring multiple days to equilibrate to the reactive cZc form. The lipid membrane microenvironment in mushrooms shifts the stereoisomeric equilibrium toward cZc, drastically accelerating vitamin D formation; this membrane-mediated regulatory pathway has evolved over hundreds of millions of years.

Historical literature assumed UV irradiation only induces vitamin D_2 production in mushrooms. This study confirms that numerous edible fungal species synthesize provitamin D_4, while shiitake mushrooms additionally accumulate 7-DHC. Accordingly, selected mushroom species generate a mixture of three bioactive vitamin D congeners (vitamin D_2, D_3, D_4) following UVB exposure.

UVB-irradiated mushrooms represent an ideal natural vitamin D_2 source for vegan and vegetarian populations. The 3-month controlled clinical trial presented herein validates that daily intake of 1800 IU mushroom-derived vitamin D_2 elevates circulating total 25(OH)D with equal potency to synthetic vitamin D_2 and D_3 supplements, consistent with findings from food fortification trials and long-term high-dose vitamin D_2 therapeutic studies. Consumption of UV-treated mushrooms provides an effective nutritional intervention to correct suboptimal vitamin D status, with the unique added benefit of concurrent dietary delivery of vitamin D_3 and vitamin D_4 in selected fungal varieties.

Disclosure statement

The authors declare no conflict of interest.

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