



# Increased nutritional quality of plants for long-duration spaceflight missions through choice of plant variety and manipulation of growth conditions

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## ABSTRACT

Low levels of radiation during spaceflight increase the incidence of eye damage and consumption of certain carotenoids (especially zeaxanthin), via a whole-food-based diet (rather than from supplements), is recommended to protect human vision against radiation damage. Availability of fresh leafy produce has, furthermore, been identified as desirable for morale during long spaceflight missions. We report that only trace amounts of zeaxanthin are retained post-harvest in leaves grown under conditions conducive to rapid plant growth. We show that growth of plants under cool temperatures and very high light can trigger a greater retention of zeaxanthin, while, however, simultaneously retarding plant growth. We here introduce a novel growth condition—low growth light supplemented with several short daily light pulses of higher intensity—that also triggers zeaxanthin retention, but without causing any growth retardation. Moreover, two plant varieties with different hardiness exhibited a different propensity for zeaxanthin retention. These findings demonstrate that growth light environment and plant variety can be exploited to simultaneously optimize nutritional quality (with respect to zeaxanthin and two other carotenoids important for human vision, lutein and  $\beta$ -carotene) as well as biomass production of leafy greens suitable as bioregenerative systems for long-duration manned spaceflight missions.

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## 1. Introduction

The growing of fresh food in space, via bioregenerative food systems, has been identified as a desirable goal for future manned interplanetary missions (for a recent review, see [1]). Based on assessment of consumer preferences, such fresh food should include leafy green vegetables [2]. In addition to providing a renewable source of palatable plant food for long missions, the food produced on the spacecraft should be of high nutritional

quality to maintain optimal health. One issue that has been identified as a particular challenge for long-duration spaceflight missions is astronaut eye health. For example, even low space radiation increases the risk of cataracts [3–5]. Apart from any elevated risk for eye damage or disease during extraterrestrial flight, it is clear that maintenance of optimal eye function depends on consumption of a combination of essential nutritional factors.

First and foremost among these nutritional factors essential for vision are three carotenoid pigments needed (i) as precursors for the actual constituents of the human eye ( $\beta$ -carotene as the precursor for vitamin A, the light-absorbing component of the visual purple in the retina) and (ii) as protectors against eye damage by intense light

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(two additional carotenoids, zeaxanthin and lutein). Dietary zeaxanthin and lutein are chief protectors against cataracts and age-related blindness (age-related macular degeneration, AMD), while also conferring protection against other chronic diseases [6–8], and zeaxanthin has furthermore been shown to be required for visual acuity [9]. While both zeaxanthin and lutein function in the protection of human vision, zeaxanthin is thought to have the more important role, and lutein does not appear to be able to replace zeaxanthin [10]. For example, zeaxanthin is preferentially accumulated over lutein during the transitions from the human gut content to the blood stream and, further, to the retina of the human eye, causing the ratio of zeaxanthin to lutein to be much higher (i) in the human blood stream compared to the intestines and (ii) in the human retina of the eye compared to the blood stream [6,11,12].

Since the human body is unable to produce any of these carotenoids (zeaxanthin, lutein, and  $\beta$ -carotene), all three must thus be consumed with the human diet. While supplements are available, it appears that consumption of these bioactive factors from a whole food-based diet is highly preferable due to (i) better uptake from real foods and (ii) a more suitable, safer concentration of these carotenoids in real foods versus high-dose supplements that can actually inflict harm rather than being protective [8,13–15]. Furthermore, while zeaxanthin is of primary importance for the protection of the human eye, this particular carotenoid is much more difficult to obtain from a diet containing leafy greens than lutein or  $\beta$ -carotene.

Why is zeaxanthin not readily available from leafy greens? The green leaves of plants typically contain reasonably high, constant levels of  $\beta$ -carotene and lutein, but variable, and often very low, levels of zeaxanthin [16]. Just as in the human eye, zeaxanthin serves as the chief protector against excessively bright light absorbed by the green leaves of plants [17]. Because zeaxanthin removes, or dissipates, excessive light absorbed by plants, plants typically **only** form zeaxanthin when actually exposed to bright light, and **quickly remove** zeaxanthin (by conversion to a different carotenoid, violaxanthin, that does not remove, or dissipate, absorbed light) when exposed to less bright light that can, and should, be fully utilized in the process of photosynthesis and should thus not be removed/dissipated [17]. Therefore, the green parts of plants typically contain high levels of lutein, but retain mere traces of zeaxanthin following harvest. By the time leafy greens typically reach the table of the consumer, the levels of the dissipater zeaxanthin are thus low, while the levels of the corresponding non-dissipating carotenoid (violaxanthin)—with no known function in, or benefit for, the human eye—are high.

In contrast, constantly elevated zeaxanthin levels have been reported in plants exposed to harsh environmental conditions (such as drought or excessively high or low temperatures) that strongly inhibit plant growth and photosynthesis, and thereby create a scenario where all absorbed light needs to be safely removed at all times (for reviews, see [16,17]). The plant grower is thus currently faced with a choice between two similarly unattractive options, i.e. (i) growth of leafy greens with negligible

zeaxanthin levels (and corresponding limited health benefits) under conditions conducive for fast plant growth and high biomass accumulation or (ii) production of zeaxanthin-rich leafy greens with superior health benefits under plant-growth-retarding conditions leading to low crop yields.

The present study was thus undertaken to investigate possible novel growth conditions that may induce **augmented** zeaxanthin levels in leaves **without** major, or any, losses in plant biomass production. We investigated a range of plant growth conditions, including a novel condition with infrequent, short high-light pulses, to elucidate whether zeaxanthin retention could be triggered without subjecting the plants to stress that would lead to reduced growth. In addition, we investigated whether different plant varieties may exhibit different responses. We utilized the primary model species (*Arabidopsis thaliana*) of a fast-growing, leafy annual, and compared two lines of this species from the extremes of its geographic range, i.e. plant lines adapted to the climate of Sweden versus the climate of Italy [18]. *Arabidopsis thaliana* is not a plant grown for human consumption. However, the two varieties tested here demonstrate natural genetic differences of a well-studied model species that should be explored for application to highly nutritious crop plants. Our results can serve as proof of concept to guide future development of specific growing systems for a variety of leafy vegetables for long-duration manned spaceflight missions where both high yield of plant biomass *and* nutritional content are desirable.

## 2. Materials and methods

### 2.1. Plant material

Two ecotypes of *A. thaliana* (L.) Heynhold from the extremes of the species' geographic range, one from northern Sweden and the other from southern Italy [18], were incubated as seeds at 4 °C for 4 days (a protocol necessary for seed germination in this species), then germinated in standard six-plug trays (plug volume of 50 mL) in temperature- and humidity-controlled (75% relative humidity) growth chambers at 25 °C, ambient CO<sub>2</sub> level, and various light intensities (for further detail on the specific light conditions, see below) provided by fluorescent and incandescent light bulbs (photoperiod of 9 h light/15 h darkness). Seedlings were subsequently transferred to larger (3.35 L) pots and kept under the germination conditions described above for a re-adjustment period of 2 days.

Only fully expanded, mature leaves, all of which had emerged under the final growth conditions, of 6- to 8-week-old (warm- or cool-grown, respectively; see growth temperature and light intensity below for details), non-flowering *A. thaliana* plants were characterized. *Arabidopsis thaliana* rosettes were 20 cm in diameter and leaf blades characterized ranged between 3 and 5 cm in length (not including leaf stems). To document delayed development of plants grown under cool conditions and 400  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , 6-week-old rosettes were also evaluated for leaf area and fresh biomass.

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