

Light piping driven photosynthesis in the soil: Low-light adapted active photosynthetic apparatus in the under-soil hypocotyl segments of bean (*Phaseolus vulgaris*)



Andrea Kakuszi^a, Éva Sárvári^b, Ádám Solti^b, Gyula Czégény^c, Éva Hideg^c, Éva Hunyadi-Gulyás^d, Károly Bóka^a, Béla Böddi^{a,*}

^a Department of Plant Anatomy, Institute of Biology, Eötvös Loránd University, Pázmány P. s. 1/c, Budapest H-1117, Hungary

^b Department of Plant Physiology and Molecular Plant Biology, Institute of Biology, Eötvös Loránd University, Pázmány P. s. 1/c, Budapest H-1117, Hungary

^c Department of Plant Biology, Institute of Biology, University of Pécs, Ifjúság u. 6., Pécs H-7624, Hungary

^d Institute of Biochemistry, Biological Research Centre of the Hungarian Academy of Sciences, Temesvári krt. 62., Szeged H-6726, Hungary

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ABSTRACT

Photosynthetic activity was identified in the under-soil hypocotyl part of 14-day-old soil-grown bean plants (*Phaseolus vulgaris* L. cv. Magnum) cultivated in pots under natural light-dark cycles. Electron microscopic, proteomic and fluorescence kinetic and imaging methods were used to study the photosynthetic apparatus and its activity. Under-soil shoots at 0–2 cm soil depth featured chloroplasts with low grana and starch grains and with pigment-protein compositions similar to those of the above-soil green shoot parts. However, the relative amounts of photosystem II (PSII) supercomplexes were higher; in addition a PIP-type aquaporin protein was identified in the under-soil thylakoids. Chlorophyll-*a* fluorescence induction measurements showed that the above- and under-soil hypocotyl segments had similar photochemical yields at low ($10\text{--}55\ \mu\text{mol photons m}^{-2}\text{s}^{-1}$) light intensities. However, at higher photon flux densities the electron transport rate decreased in the under-soil shoot parts due to inactivation of the PSII reaction centers. These properties show the development of a low-light adapted photosynthetic apparatus driven by light piping of the above-soil shoot. The results of this paper demonstrate that the classic model assigning source and sink functions to above- and under-soil tissues is to be refined, and a low-light adapted photosynthetic apparatus in under-soil bean hypocotyls is capable of contributing to its own carbon supply.

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1. Introduction

Most plants have under-soil shoot region which is exposed either to low light filtered by the soil or is fully shaded. Thus the latter tissues develop in full darkness [1] and show etiolation symptoms [2]. Their chlorophyll (Chl) biosynthesis is arrested at the conversion of protochlorophyllide (Pchlde) to chlorophyllide catalyzed by the light-dependent NADPH:protochlorophyllide oxidoreductase enzyme

(LPOR; EC 1.3.1.33) [3]. Etioplasts develop, the inner membranes of which contain Pchlde forms [4]. The Pchlde forms have usually been studied in leaves [5] or stem-related organs [6] of dark-grown laboratory plants which are good models to study the Chl biosynthesis. Pchlde₆₃₃ and Pchlde₆₅₄₋₆₅₅ forms were detected in the under-soil shoot (epicotyl) segments of pea grown in pots under natural light-dark cycles [2]; the spectral properties of these forms were similar to those of etiolated plants. Close to the soil surface (at 0–3 cm depth), however, the pea epicotyls had Chl pigments in parallel with the decreasing amounts of Pchlde [2]. The under-soil segments of bean hypocotyls contained Pchlde and Chl pigments, too [7]. However, Chls were detected in hypocotyls even in 5 cm soil depths. This difference has been explained by light piping of the hypocotyl in which a central cavity develops [7]; however, the intensity of the piped light is very low - it is about 10% of the incident light.

Photosynthetic acclimation of plants grown under low light intensities is a well-known phenomenon [8,9]. Characteristic changes in the Chl-protein composition of the leaves take place: the relative amount

Abbreviations: L, leaf; AS, above-soil hypocotyl; US-1, under-soil hypocotyl segment at 0–2 cm depth; US-2, under-soil hypocotyl segment at 2–4 cm depth; Chl, chlorophyll; Pchlde, protochlorophyllide; PS, photosystem; LHC, light harvesting complex; PFD, photon flux density; ROS, reactive oxygen species; PIP, plasma membrane intrinsic protein; Y(II), photochemical quantum yield of PSII; Y(NPQ), regulated non-photochemical quantum yield; Y(NO), non-regulated non-photochemical quantum yield; Φ_{NF} , participation of non-functional PSII reaction centers in the excitation energy.

* Corresponding author.

E-mail address: bela.boddi@ttk.elte.hu (B. Böddi).

of the photosystem II (PSII) and its light-harvesting antenna (LHCII) increases [10,11] and as a consequence, the Chl-*a* to Chl-*b* ratio decreases. In the chloroplasts the grana stacks are higher and broader than those of the high-light adapted plants [12,13]. Besides of leaf photosynthesis, the contribution of the photosynthetic activity of stems – including even woody stems – is important [14,15]. The presence of chloroplasts was described in the cortex and in the pith regions of twigs [16]. Radial light transmittance was reported with decreasing photon flux density (PFD) gradient from the twig surface towards its central pith allowing photosynthetic activity; the quantum efficiency of PSII was found decreasing towards the central pith [17]. Although lengthwise light piping seems to be obvious in stems, we could not find direct measurements about this phenomenon; only microscopic observations were published [18]. The lengthwise light piping is effective in stems having hollow pith; this was described in our previous work in which chloroplast containing tissues were observed in under-soil regions of bean hypocotyl [7].

This paper supplies details of the structure and photosynthetic activity of the under-soil bean hypocotyl. The aim of this work was to investigate whether the under-soil chlorenchyma-like tissues have photosynthetic activity. The presence of stomata was detected with scanning electron microscopy, chloroplasts ultrastructure was studied with transmission electron microscopy, the chlorophyll-protein complexes were analyzed with proteomics and the photosynthetic electron transport was studied with variable chlorophyll fluorescence.

2. Materials and Methods

2.1. Plant Material

Seeds of bush bean (*Phaseolus vulgaris* L. cv. Magnum, Rédei Kertimag Ltd., Réde, Hungary) were soaked in running tap water for 2 h then pre-germinated in Petri dishes in darkroom at 23 °C. After 3 days, the seedlings had 1 cm radicle and were planted under dim green light into pots (planting depth: 4 cm) in potting soil (ASB-Greenworld, pH 5.0–6.5, Zár, Czech Republic). The plants were grown under natural light-dark cycles for 14 days in the laboratory window where the maximal daily PFD varied between 100 and 600 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. The plants were watered every second day from the bottom thus the soil structure around the shoots was undisturbed. 14 days after sowing, the plants had a 12–15 cm above-soil shoot (including a 4–5-cm-long hypocotyl part) and an under-soil hypocotyl of 7–8 cm (during the development of the root system, the root neck moved deeper into the soil). The hypocotyls were labeled at the soil surface level before the pots were transferred into darkroom where the plants were taken out from the soil under dim green light. Their under-soil hypocotyl parts were rinsed to remove soil particles. Samples were taken from the leaves (L) and from the following shoot sections: the hypocotyl section right above the soil surface (AS); the under-soil hypocotyl region at 0–2 cm depth (US-1) and between 2 and 4 cm depths (US-2). The samples were collected under the above mentioned dim green light.

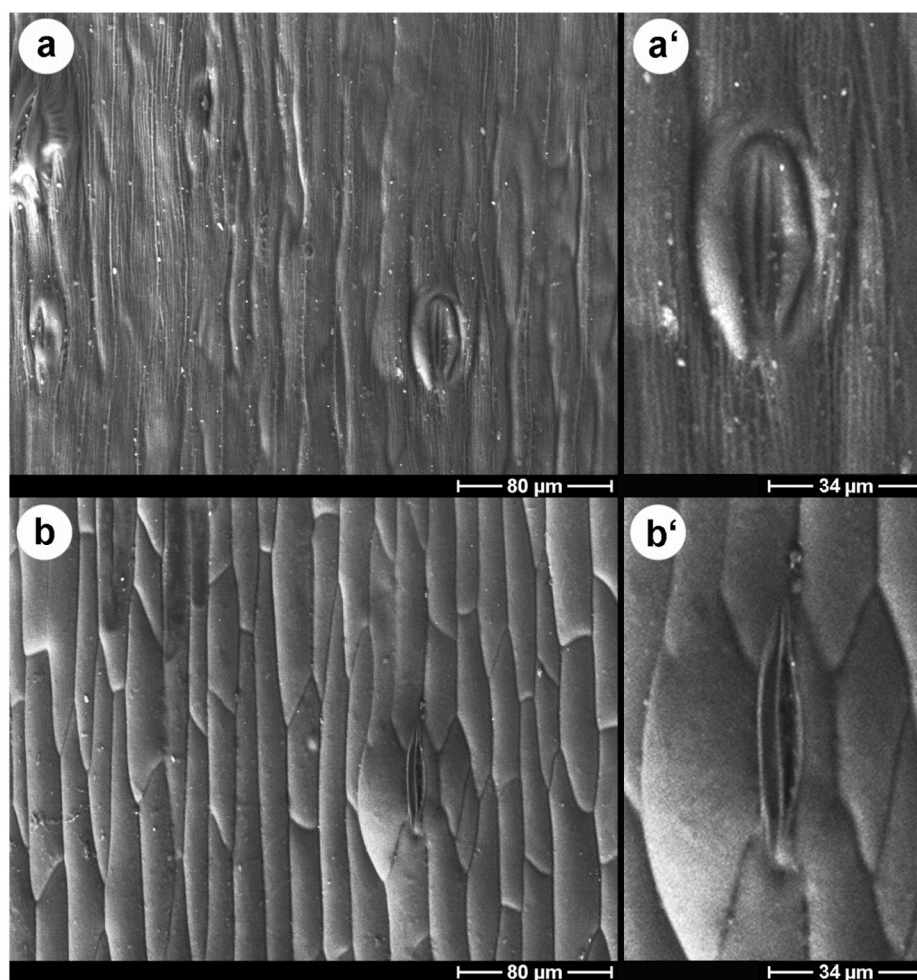


Fig. 1. Scanning electron microscopic images of the epidermis of different hypocotyl sections. The images were taken from 14-day-old bean plants grown in pot under natural light conditions. *a*: Hypocotyl section 1 cm above the soil surface (AS); *a'*: enlarged detail of (*a*) with a stoma complex; *b*: epidermis of the hypocotyl section 2 cm under the soil surface (US-1); *b'*: enlarged detail of (*b*) with a stoma complex.

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