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The effects of light on induction, time courses, and kinetic patterns of net nitrate uptake in barley

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ABSTRACT

Barley seedlings (*Hordeum vulgare* L.) were grown hydroponically with (induced) or without (uninduced) nitrate in a light/dark cycle with high photon flux density to determine the effects of light on time courses, induction and kinetics of net nitrate uptake. Nitrate uptake was induced by external nitrate in both light and dark and was prevented by 1 mol m^{-3} p-fluorophenylalanine. In high light, nitrate uptake was about 2-fold higher than in low light. During time course experiments the uptake rates oscillated due to daily light–dark changes. Rates of nitrate uptake also increased at about 2200 h during continuous darkness. This increase coincided approximately with the time at which the dark period started during the previous culture of the plants, indicating that it was due to a mechanism associated with an endogenous diurnal rhythm. When calculating the kinetics of nitrate uptake, a model with two saturable systems, including a high-affinity system (HATS) and a low-affinity system (LATS), gave the best fit to data in all treatments. The apparent affinity of the HATS ranged from 7·7 to 12·2 mmol m^{-3} in induced plants in all light conditions. The effect of light on the HATS was mainly an increase of apparent V_{max} in the step from low to high light. In uninduced plants the HATS operated at a very low activity which was strongly enhanced during induction. Interpretation of the calculated kinetics of the LATS was much more difficult on the basis of net uptake data. The apparent affinity of the LATS increased from 24·3 mol m^{-3} in low light up to 0·17 mol m^{-3} after acceleration in high light. These extreme changes in apparent affinity of the LATS could not be explained satisfactorily, and the nature of this system is also discussed with respect to the method used.

Key-words: *Hordeum vulgare* L.; net nitrate uptake; light (intensity); kinetic parameters; induction time courses; Poaceae.

Abbreviations: FPA, p-fluorophenylalanine; FW_R, fresh weight of the roots; HATS, high-affinity transport system; K_d, rate constant; K_m, Michaelis-Menten constant; LATS, low-affinity transport system; V_c, constant uptake rate; V_{max}, maximal uptake rate.

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INTRODUCTION

The uptake of nitrate by roots of plants not previously exposed to nitrate is usually at a low, constitutive level, but exposure to external nitrate can increase the rate by 2- to 5-fold above this constitutive level. Nitrate uptake occurs thermodynamically uphill and can be inhibited by processes which depress synthesis of ATP and proteins (for a review, see Clarkson 1986). The energy dependence of nitrate uptake is consistent with a NO_3^-: $2H^+$ symport (Glass, Shaff & Kochian 1992). Subsequent steps in nitrate metabolism, nitrate reduction and ammonium assimilation, are also inducible and energy dependent since reducing power, ATP and C-skeletons are needed. The uptake and assimilation of ammonium and nitrate require a significant amount of root respiration (Bloom, Sukrapanna & Warner 1992). Hence in an intact plant, nitrate uptake, N metabolism, C metabolism and ultimately photosynthesis are all linked. These steps in nitrogen metabolism are all life-dependent processes which are influenced by environmental factors like light, temperature or stress conditions as well as variations during ontogeny (Imsande & Touraine 1994). So, if light conditions change, a signal from the shoot, the site of light perception, to the root, the site of nitrate uptake, would be not surprising. Rideout *et al.* (1993) concluded from their experiments with soybean that carbohydrate flows from the shoot to the root may regulate nitrate uptake more than the level of nitrate in the root itself. However, the mechanistic effects of light on nitrate uptake in higher plants have not been studied as extensively as other factors such as concentrations of nitrate, temperature and inhibitors. These results were more descriptive. Rao & Rains (1976b) reported that illumination stimulated nitrate absorption in barley, and Aslam *et al.* (1979) showed that nitrate uptake was 20% faster in the light than in the dark. Clement *et al.* (1978) found that the nitrate uptake in simulated swards of ryegrass was related to diurnal, day-to-day, and seasonal changes in radiation. Delhon *et al.* (1995) recently showed that nitrate influx was down-regulated in the dark. No information is available about the effects of light on the kinetic parameters of nitrate uptake.

A 'dual uptake system' for the kinetics of nitrate uptake was first described in maize (Neyra & Hageman 1975), in barley (Rao & Rains 1976a), and in Arabidopsis (Doddema & Telkamp 1979). These and subsequent observations led