Serine Transport and Membrane Depolarization in the Liverwort *Riccia fluitans*

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The plasmalemma of thallus cells of the aquatic liverwort, *Riccia fluitans*, is reversibly depolarized by L- and D-serine. At 0.1 mM K⁺ in the medium, the depolarization saturates at 50 mV; half-maximal depolarization occurs at 13 μM L-serine and 30 μM D-serine, respectively. Uptake of [¹⁴C]-labelled L-serine depends upon the K⁺ concentration and is sensitive to the membrane potential as indicated by its reduction through 1 mM sodium cyanide. We propose that serine binds to and is transported by an electrogenic carrier. However, an interaction of serine with K⁺ channels of the membrane seems also possible.

**Introduction**

Electrogenic membrane transport of amino acids has been shown to occur in fungi [1]. Recently, it has been proposed to occur also in higher plants; namely, H⁺-dependent cotransport has been attributed to *Avena* coleoptile [2], *Lemna* leaf [3], and suspension-cultured tobacco cells [4].

Since an electrogenic carrier contributes as well as responds to both the transmembrane electrical potential difference (\(\psi_m\)) and conductance, it seems advisable to search for it and study it on a system where both parameters can be assessed easily. This requirement is met by the thallus cells of the aquatic liverwort, *Riccia fluitans* [5]. This plant has been shown already to feature a hexose-specific electrogenic carrier [6].

**Materials and Methods**

Thalli of *Riccia fluitans* from a greenhouse pond were incubated 24 h before the experiments with the following standard test solution: 0.01 mM KCl, 0.99 mM NaCl, 0.1 mM CaCl₂, and 1.9 mM sodium phosphate buffer to adjust the pH as desired. Serine was added to this solution. For changes of the K⁺ concentration NaCl was replaced with KCl. The reported experiments were carried out at pH 5.6 under 1 W m⁻² of white light. The techniques used for measuring the electrical parameters and radiotracer fluxes across the plasmalemma of *Riccia* cells have been described previously [5]. Uptake of uniformly labelled [¹⁴C]serine was measured similarly as during a recent study of hexose uptake [6]. The given data are from representative single experiments.

**Results and Discussion**

Serine rapidly and reversibly depolarizes the plasmalemma of *Riccia* thallus cells (Fig. 1). Obviously, both the rate, \(d\psi_m/dt\), and the amplitude, \(A\psi_m\), depend upon the serine concentration. The degree of depolarization is different for L- and D-serine. Both isomers have been tested over the concentration range from 10 μM to 1 mM. The Lineweaver-Burk plot of Fig. 2 displays a common maximal depolarization \(A\psi_m\) of 50 mV and apparent \(K_m\) values of 13 μM L-serine and 30 μM D-serine, respectively. In using this plot we propose that L-serine specifically binds to the *Riccia* membrane creating *de novo* an electrogenic transmembrane pathway or/and increasing the activity of an existing pathway. The stereo-specificity argues against adsorption being the essential mechanism of serine action. Rather, the observed saturable depolarization is basically consistent with both, the operation of an amino acid-specific electrogenic carrier and an amino acid-induced increase of the permeability of the K⁺ channel. Consistent with both mechanisms is also the measured increase of the electrical slope conductance; upon addition of 0.1 mM L-serine this conductance rises from 0.3 to 0.4 S m⁻².

Evidence, although indirect, for an electrogenic carrier mechanism is provided by the reduction of serine uptake through sodium cyanide (Fig. 3). Cyanide invariably depolarizes the plasmalemma by about 100 mV, thus substantially reducing then in-

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Fig. 1. Depolarization of the plasmalemma of thallus cells of *Riccia fluitans* by different concentrations of L-serine. [K+] = 0.1 mM. Downward arrows denote the addition of the indicated concentration of serine (μM), upward arrows the exchange (wash) with the control medium.

Fig. 2. Lineweaver-Burk plot the dependence of the amplitude of depolarization (ΔΨm in Fig. 1) on the concentration of L- and D-serine, respectively. [K+] = 0.1 mM.

Fig. 3. Uptake of [14C]labelled L-serine over a 5 min-period as a function of the external K+ concentration. Uptake was measured for two serine concentrations and in the presence and absence, respectively, of 1 mM NaCN (see box).

wardly directed electrochemical driving force for any positively charged substrate. Serine could be charged by and cotransported with, for example, H+ or K+. In fact, both depolarization by and transport of L-serine depends only slightly upon the external pH, but significantly upon the K+ concentration (Fig. 3). The action of K+ is not mediated by ψm, because ψm does not change by more than 30 mV over the tested range of K+ concentration. Interestingly, the electrogenic hexose transport of *Riccia* does depend upon H+ rather than K+ [6].

The possibility of a serine-induced increase of the K+ permeability is implied by the observation that during the serine-induced membrane depolarization ψm approaches, but never exceeds the K+ equilibrium potential.

In sum, a thorough study of membrane transport and electrical activity of different amino acids in *Riccia fluitans* seems promising. In particular, *Riccia* lends itself to a current-voltage analysis [5] and to a simultaneous measurement of radiotracer fluxes of K+ and amino acids. This approach is essential to the assessment of the possible interaction of amino acids with a particular electrogenic membrane pathway.

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