THE MECHANISM OF THE NH$_4$ ION OSCILLATORY TRANSPORT ACROSS THE EXCITABLE CELL MEMBRANE

ABSTRACT: This paper presents results on typical oscillations of the membrane potential induced by the excitation of the cell membrane by different concentrations of the NH$_4$Cl solution. The existence of four classes of oscillations of the membrane potential and several different single and local impulses rhythmically occurring were determined. It is known that the oscillatory processes of the membrane potential are in direct dependence on oscillatory transport processes of NH$_4$ and Cl ions across the excitable cell membrane. A hypothesis on a possible mechanism of oscillatory transport processes of NH$_4$ and Cl ions across the excitable cell membrane is also presented.

KEY WORDS: plant cell membrane, excited state, membrane potential, oscillatory transport, NH$_4$ ion

INTRODUCTION

It is generally known that movements, phenomena and processes occurring oscillatory and rhythmically can be found within almost all fields of physics, chemistry and biology. Oscillations are such movements and processes at which, magnitudes of physical quantities determining them, occur at exactly or approximately equal periods of time. Hence, any system disturbed from equilibrium starts to oscillate under certain conditions. Systems with one
or two degrees of freedom are the basis for the analysis of oscillations. Regardless of different types of oscillatory processes, each oscillatory system can be described by a physical quantity whose displacement from its equilibratory value depends on coordinates and time.

The unique mathematical model is used in description of all oscillatory processes, but, homogenous differential equations of the second order with constant coefficients are mainly applied for discrete systems, while partial differential equations with variable coordinates and time are applied for continuous systems (Andronov et al., 1966, Crawford, 1984; Tihonov et al., 1972).

Oscillations and rhythms are one of the principal characteristics of living organisms. A rhythm, as a type of the regularity and autoregulation, with a patterned increase and decrease of certain parameters in the curse of time, has been detected at all levels of organization: molecules, cells, tissues, organs, organisms and the population (Bjunning, 1964, Bioteux et al., 1977).

In recent times the occurrence of oscillations of the membrane potential has been more systematically studied and analysed and therefore it is a very actual and contemporary scientific topic (Koljs et al., 1993, Kraisinski et al., 1981, Žabotinskij, 1974).

Furthermore, overall bioelectric studies on plant models contributed to a discovery of the phenomenon of the membrane oscillatory potential (Vorobljev et al., 1967, 1968, Radenović, 1974). The actual and genuine phenomenon of the membrane oscillatory potential on the excitable cell membrane (plasmalemma and tonoplast) of intact plant cells was discovered at the end of 1960s (Radenović et al., 1968, Volkov et al., 1968, Vučinić et al., 1973, 1987). The excitation of the plant cell and its membranes was performed under the influence of selected factors (concentration, mechanical, temperature, luminous, etc.) under which the oscillations of the membrane potential are generated (Radenović and Penčić, 1970, Radenović and Vučinić, 1987, Vuletić et al., 1987). To that effect, the same or similar is related to the membrane oscillatory potential induced by concentrations of monovalent cations (Radenović et al., 1977, Radenović and Rataković, 1982). There are no integral papers on the membrane oscillatory potential studied at different NH₄ ion concentrations in the available literature. In this paper we report, for the first time, a more detail investigation of the membrane oscillatory potential induced by different NH₄ ion concentrations, the same as the explanation of oscillatory transmembrane transport across the excitable cell membrane.

MATERIALS AND METHODS

The bioelectrical experiments for producing oscillations of the membrane potential at different NH₄ ion concentrations were performed on living cells of the fresh-water alga Nittela. Growing conditions and the standard preparation of Nittelle cells for bioelectric measurements had already been described in our

All chemicals were of the pa. grade, prepared fresh prior to experiments.

Single and local impulses and complete oscillations of the membrane potential were registered after the method with a microelectrode technique, which was also previously described, in principle and details, (Radenović et al., 1968; Radenović and Penčić, 1970, Radenović et al., 1976, 1977).

RESULTS

1. Obtained results of bioelectric standard measurements prior to recording of oscillations of the membrane potential induced by the NH₄Cl solution

Living cells of Nittela grown on the 1% nutrient agar (0.1 mM KH₂PO₄, 1.0 mM NaHCO₃, 0.4 mM CaCl₂ 6H₂O and 0.2 mM Mg(NO₃)₂ x 6H₂O) prior to recording of oscillations of the membrane potential were stabilised by the standard solution for 60 min. Ordinary measurements (membrane stationary potential, cyclosis) were performed by using the standard solution (Table 1) as an external solution. Once the values of bioelectric parameters were within the limits of the normal physiological state of a stabilised living cell, oscillations of the membrane potential can be induced and recorded at different NH₄Cl solution concentrations.

Tab. 1: Bioelectrical parameters of the cell state of alga Nittela prior to inducement of oscillations of the membrane potential with the solution with NH₄Cl.

<table>
<thead>
<tr>
<th>Membrane stationary level (( \Psi_m ), mV)</th>
<th>Cyclosis (( \mu \text{sec}^{-1} ))</th>
<th>Standard solution for initial bioelectrical measurements</th>
</tr>
</thead>
<tbody>
<tr>
<td>Standard levels:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>—90</td>
<td>45</td>
<td>0.1 mM HCl + 1.0 mM NaCl</td>
</tr>
<tr>
<td>—120</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td>—150</td>
<td>52</td>
<td></td>
</tr>
</tbody>
</table>

2. Oscillations of the membrane potential induced by different NH₄Cl solution concentrations

When the standard solution was exchanged for the NH₄Cl solution in the external solution, the excitement of Nittela was made and oscillations of the membrane potential were possible to be induced and registered in plasmalemma and tonoplast. The results of 11 typical oscillations of the membrane potential induced by different NH₄Cl concentrations are presented. The stated oscillations can be grouped into four classes and as such shall be presented in this paper:
2.1. The first class of oscillations of the membrane potential induced by the lowest NH$_4$Cl concentration (1 mM)

Figure 1 and Table 2 present the results of oscillations of the membrane potential induced by the solution of the lowest concentration (1 mM NH$_4$Cl). This typical oscillation is characterised by a pre-oscillatory period with the occurrence of only six single impulses. The possible local impulses or failed oscillations occurred soon after the second single impulse. The irregularity became more pronounced in further observations of oscillations. The end of oscillating passed into chaos.

![Fig. 1: First class of oscillations. Abbreviations: x — axis: time (min), y — axis: electric potential (mV), arrow start of oscillatory process, $\tau_\text{osc}$: total duration of oscillations, $\tau_{\text{p,osc}}$: duration of preoscillatory period, $\tau_{\text{osc}}$: duration of oscillatory period. For parameters see Tab. 2](image)

<table>
<thead>
<tr>
<th>Conc. (mM)</th>
<th>Duration of membrane potential oscillation (min)</th>
<th>Duration of preoscillatory period (min)</th>
<th>Duration of oscillatory period (min)</th>
<th>Frequence of singular oscillation appearance (osc/min)</th>
<th>Relative amplitude of oscillation (mV)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>13.64</td>
<td>4.36</td>
<td>9.28</td>
<td>0.37</td>
<td>27.5  19.0</td>
</tr>
</tbody>
</table>

2.2. The second class of oscillations of the membrane potential induced by low NH$_4$Cl concentrations (3—7 mM)

The results of oscillations of the membrane potential are presented in Figures 2 (A-D), while their characteristics are encompassed by Table 3. Oscillating induced by the solution of 3 mM NH$_4$Cl (Figure 2 A, Table 3 A) is a somewhat different than the previous one. It had two impulses in the process of depolarisation and seven in the process of repolarisation of equilibration. Possible local impulses could have been observed among single impulses. Oscillating ended in a monotonous stationary state, Figure 2 A, Table 3 A.
Fig. 2: Second class of oscillations. A: NH$_4$ ion concentration: 3 mM, B: NH$_4$ ion concentration: 5 mM, C: NH$_4$ ion concentration: 6 mM, D: NH$_4$ ion concentration: 7 mM. For parameters see Tab. 3
Tab. 3: Second class of membrane potential oscillations

<table>
<thead>
<tr>
<th>Conc. (mM)</th>
<th>Duration of membrane potential oscillation (min)</th>
<th>Duration of preoscillatory period (min)</th>
<th>Duration of oscillatory period (min)</th>
<th>Frequency of singular oscillation appearance (osc/min)</th>
<th>Relative amplitude of oscillation (mV)</th>
<th>Segment of oscillogram</th>
</tr>
</thead>
<tbody>
<tr>
<td>A 3</td>
<td>25.6</td>
<td>0.09</td>
<td>25.51</td>
<td>0.35</td>
<td>40.35</td>
<td>—</td>
</tr>
<tr>
<td>B 5</td>
<td>23.49</td>
<td>0.31</td>
<td>23.18</td>
<td>0.55</td>
<td>30.42</td>
<td>—</td>
</tr>
<tr>
<td>C 6</td>
<td>28.28</td>
<td>0.03</td>
<td>28.25</td>
<td>1.27</td>
<td>56.75</td>
<td>whole</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>56.75</td>
<td>I</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>25.38</td>
<td>II</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X_{av} = 21.69</td>
<td>X_{av} = 27.28</td>
</tr>
<tr>
<td>D 7</td>
<td>38.04</td>
<td>0.00</td>
<td>38.04</td>
<td>1.31</td>
<td>X_{av} = 49.67</td>
<td>—</td>
</tr>
</tbody>
</table>

Oscillating presented in Figure 2 B and Table 3 B (5 mM NH₄Cl) is very similar to oscillating in Figure 2 A. A clearly equilibrated stationary level is observed under depolarisation conditions. Only single impulses with declining amplitudes occurred in this oscillating that ended in an unsuccessful single impulse or a weak local impulse, Figure 2 B, Table III B.

Oscillating presented in Figure 2 C and Table 3 C (6 mM NH₄Cl) acquired characteristics of long-lasting oscillations with a greater number of single impulses (in the processes of depolarisation and repolarisation) up to the stationary level. Three segments can be observed in Figure 2 C. The first oscillation segment started with the single impulse of the highest amplitude and continued with relative damping. The second oscillation segment was bordered with two local impulses within which there were five single impulses of different amplitudes. The third oscillation segment was characterised by the occurrence of a local impulse, Figure 2 C, Table 3 C.

Oscillating presented in Figure 2 D and Table 3 D (7 mM NH₄Cl) also acquired characteristics of long-lasting oscillations with higher NH₄Cl concentrations. Indications of local impulses occurred in the beginning and at the end of oscillating. Oscillating was characterised by alternating and gradual ascending and descending of single impulse amplitudes. A middle part of oscillating (from the 16th to the 46th single impulse) was characterised by consistent amplitudes. At the end of oscillating (the 47th single impulse), amplitudes of single impulses significantly increased, and then gradually decreased till the end of oscillating, Figure 2 D, Table 3 D.

2.3. The third class of oscillations of the membrane potential induced by NH₄Cl concentrations of 8, 9 and 10 mM

The results of oscillations of the membrane potential are presented in Figures 3 A-C, while their characteristics are encompassed by Tables 4 A-C.
Tab. 4: Third class of membrane potential oscillations

<table>
<thead>
<tr>
<th>Conc. (mM)</th>
<th>Duration of membrane potential oscillation (min)</th>
<th>Duration of preoscillatory period (min)</th>
<th>Duration of oscillatory period (min)</th>
<th>Frequency of singular oscillation appearance (osc/min)</th>
<th>Relative amplitude of oscillation (mV)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A 8</td>
<td>35.42</td>
<td>4.26</td>
<td>31.16</td>
<td>0.56</td>
<td>$X_{av} = 41.60$</td>
</tr>
<tr>
<td>B 9</td>
<td>43.15</td>
<td>8.25</td>
<td>34.90</td>
<td>0.42</td>
<td>$X_{av} = 44.7$</td>
</tr>
<tr>
<td>C 10</td>
<td>50.72</td>
<td>0.21</td>
<td>50.51</td>
<td>1.03</td>
<td>$X_{av} = 39.02$</td>
</tr>
</tbody>
</table>

Since oscillations presented in Figure 3 A and Table 3 A (8 mM NH$_4$Cl) did not have an equal level of the stationary state, amplitudes of single impulses differed. Local impulses were pronounced during oscillating.
Oscillating presented in Figure 3 B and Table 4 B (9 mM NH₄Cl) was characterised by a pre-oscillatory period. The process of depolarisation lasted till the end of oscillating and was accompanied by single impulses with different amplitudes.

Oscillating presented in Figure 3 C and Table 4 (10 mM NH₄Cl) had characteristics of equilibrated and long-lasting oscillations with a higher number of single impulses and regular processes of depolarisation and repolarisation. However, in comparison with the fourth class of oscillations the duration of this oscillations was not long. The beginning of oscillating was accelerated, but the frequency of the occurrence of single impulses decreased with further spreading of oscillations. An indication of a local impulse occurred almost after every single impulse, Figure 3 C, Table 4 C.

2.4. The fourth class of oscillations of the membrane potential induced by the highest NH₄Cl concentrations (10 mM)

The results of oscillations of the membrane potential are presented in Figures 4 A-C, while their characteristics are encompassed by Table 5 A-C.

Oscillating presented in Figure 4 A and Table 5 A (10 mM NH₄Cl) had a pre-oscillatory period in which the indication of local impulses occurred. Besides, this oscillating in the process of depolarisation had the indication of single impulses occurrence, similar to the process of gradual repolarisation. Recor-
Oscillations of the membrane potential were interrupted between the 30th and 105th minute and the analyses were performed separately. In both segments of oscillating, local impulses were observed among single impulses, provided that the number of local impulses was much greater in the second segment. The frequency of the occurrence of single impulses declined towards the end of oscillating, Figure 4 A, Table 5 A.

Tab. 5: Fourth class of membrane potential oscillations

<table>
<thead>
<tr>
<th>Conc. (mM)</th>
<th>Duration of membrane potential oscillation (min)</th>
<th>Duration of preoscillatory period (min)</th>
<th>Duration of oscillatory period (min)</th>
<th>Frequency of singular oscillation appearance (osc/min)</th>
<th>Relative amplitude of oscillation (mV)</th>
<th>Segment of oscillogram</th>
</tr>
</thead>
<tbody>
<tr>
<td>A 10</td>
<td>156.34</td>
<td>4.72</td>
<td>151.62</td>
<td>—</td>
<td>—</td>
<td>whole</td>
</tr>
<tr>
<td></td>
<td>29.14</td>
<td></td>
<td></td>
<td>0.31</td>
<td>$X_{av} = 44.20$</td>
<td>I</td>
</tr>
<tr>
<td></td>
<td>51.34</td>
<td></td>
<td></td>
<td>0.16</td>
<td>$X_{av} = 59.25$</td>
<td>II</td>
</tr>
<tr>
<td>B 10</td>
<td>295.63</td>
<td>0.00</td>
<td>295.63</td>
<td>—</td>
<td>—</td>
<td>whole</td>
</tr>
<tr>
<td></td>
<td>24.30</td>
<td></td>
<td></td>
<td>0.37</td>
<td>$X_{av} = 72.32$</td>
<td>I</td>
</tr>
<tr>
<td></td>
<td>28.86</td>
<td></td>
<td></td>
<td>0.21</td>
<td>$X_{av} = 99.28$</td>
<td>II</td>
</tr>
<tr>
<td></td>
<td>19.18</td>
<td></td>
<td></td>
<td>0.31</td>
<td>$X_{av} = 98.28$</td>
<td>III</td>
</tr>
<tr>
<td></td>
<td>25.63</td>
<td></td>
<td></td>
<td>0.16</td>
<td>$X_{av} = 66.00$</td>
<td>IV</td>
</tr>
<tr>
<td>C 10</td>
<td>235.88</td>
<td>0.00</td>
<td>235.88</td>
<td>—</td>
<td>—</td>
<td>whole</td>
</tr>
<tr>
<td></td>
<td>26.53</td>
<td></td>
<td></td>
<td>0.38</td>
<td>$X_{av} = 78.70$</td>
<td>I</td>
</tr>
<tr>
<td></td>
<td>23.33</td>
<td></td>
<td></td>
<td>0.86</td>
<td>$X_{av} = 38.62$</td>
<td>II</td>
</tr>
<tr>
<td></td>
<td>18.59</td>
<td></td>
<td></td>
<td>0.70</td>
<td>$X_{av} = 21.61$</td>
<td>III</td>
</tr>
<tr>
<td></td>
<td>20.82</td>
<td></td>
<td></td>
<td>0.29</td>
<td>$X_{av} = 9.49$</td>
<td>IV</td>
</tr>
</tbody>
</table>

Oscillating presented in Figure 4 B and Table 5 B (10 mM NH₄Cl) was the longest registered oscillating of the membrane potential. Over 100 single impulses were generated in five hours. The frequency of generating of single impulses varied; the process of depolarisation occurred in the beginning and at the end of this oscillating, while gradual repolarisation occurred in the middle of oscillating. This oscillating was characterised by the irregular occurrence of impulses, Figure 4 B, Table 5 B.

Oscillating presented in Figure 4 C and Table 5 C (10 mM NH₄Cl) had the greatest number of generated single impulses (over 140). This oscillating started similarly to oscillating presented in Figure 8. The difference occurred in the magnitude of amplitudes of single impulses. This oscillating will also be analysed by its segments. It seems that segments II, III and IV had stable states and approximately equal amplitudes of single impulses, which is not characteristic for the majority of oscillations induced by the NH₄ ion. Oscillating ended with the occurrence of single impulses of low amplitudes and small frequencies, Figure 4 C and Table 5 C.
DISCUSSION

1. General and specific characteristics of oscillations of the membrane potential induced by different NH₄Cl concentrations

The first prerequisite for the occurrence of oscillations of the membrane potential is the excitation of the living cell and thereby its membranes. The excitation in these experiments was performed by the addition of different NH₄Cl concentrations to the external solution.

According to the obtained results, the probability for inducing oscillations of the membrane potential in experiments with high NH₄Cl concentrations (8—10 mM) amounted to 62%. As expected it was much more difficult, but not impossible, to obtain oscillations at lower and low NH₄Cl concentrations. Oscillations of the membrane potential were most often induced after the first exchange of the standard solution (Table I) for the NH₄Cl solution. In such cases oscillating of the membrane potential was the most intensive by amplitude magnitudes, number of single and local impulses, as well as by the duration and frequency of the occurrence (Tables 2—5). Furthermore, this did not exclude the possibility to induce oscillations in repeated exchange of the stated solutions. But even if they occurred, the characteristics of such oscillations were weak and numerous with single and local impulses. The duration of oscillations of the membrane potential induced by 6—10 mM NH₄Cl was very long and lasted, on the average, up to 100 min with generation of over 50 single impulses (Figures 3 C — 4 A-C), (Tables 4 C — 5 A-C). Damping of these oscillations was minimal (1.038), and the frequency of generation of single impulses was also quite low (0.74 im min⁻¹). The occurrence of local impulses was significant and gradually increased with an inevitable prolongation of the impulse intervals. However, oscillating ended with a cessation of generation of local impulses.

The longest oscillating of the membrane potential was obtained in these experiments — the excitable but living plant cell Nitelle generated over 100 single impulses in the course of five hours (Figure 4 B).

Figure 4 C presents oscillating of the membrane potential with the greatest number of generated single impulses. Over 140 single impulses were generated in this oscillating for four hours.

A certain „pre-oscillatory period” occurred in some of the stated oscillations of the membrane potential from the moment of the exchange of the standard solution for the NH₄Cl solution up to the beginning of oscillating (Figures 1, 2 C, 3 B and 4 B). The stated pre-oscillatory period lasted for several minutes (Tables 2, 3 C, 4 B and 5 B).

Single impulse amplitudes did not change to a greater extent in oscillations of the membrane potential induced by different NH₄Cl concentrations. However, its kinetics varied in the processes of depolarisation and repolarisation. Single impulses most often lasted differently, sometimes for 2 to 4 sec, and sometimes 6 to 8 sec.
2. Functional dependence of the membrane potential and transport process across the cell membrane

It is well known that the membrane potential depends on a complex ion transport across the cell membrane. This dependence is encompassed by Fick's law of diffusion, Using's criterion, Teorel, Nernst-Plank-Goldman equation (Radeno, 1974, 1998, 2001). Moreover, it is also known that two action forces: the strength of the concentration gradient and the strength of the electric gradient are considered in the case of transport processes across the cell membrane.

The ion transport across the excitable cell membrane is characterised by passive and active transport processes. The diffusion most often occurs as a dominant carrier of passive transport processes. It exhibits as simple, restricted and relieved. A simple diffusion consists of ion transport processes through the lipid bilayer of the membrane, or through pores in proteins and through pores in the lipid bilayer. A restricted diffusion occurs in the form of spatial ion process through pores with charged groups on proteins. At last, a relieved diffusion occurs in the form of ion transport processes with a movable carrier, fixed carrier and as the diffusion of the exchange. It is obvious that there are the following two initiators of the stated ion transport processes with dominant passive characteristics: the ion concentration gradient and the membrane potential gradient. Naturally, in the case of coupling of these two gradients, ion transport processes with characteristics of active ion processes across the excitable cell membrane can occur. Certainly, active transport processes occur in opposition to the chemical and electrochemical gradients (Radeno, 1998, 2001, 2003) as they require energy. These processes do not proceed independently, but always with the processes of ATP hydrolysis, i.e. on the account of energy accumulated in the macroenergetic constituents and their bonds with ATP, that is by ATPase.

Different characters of movements of proteins, lipids, pigments and other structures bound by the complex also contribute to the mechanism of total transport processes across the excitable cell membrane (Radeno, 1998, 2001, 2003). These movement characters in the excitable cell membrane can be: lateral movement (typical for proteins and lipids), rotational movement (typical for proteins specialized in ion transport processes) and so-called flip-flop movement (typical for lipids and proteins that regulate transport processes from one side of the excitable cell membrane to the other). When the degree of excitement of the cell membrane is higher, the stated characters of the movement (of lipids, proteins) are more significant in their intensity, dynamics and diversity, and the total transport processes are affected (Koys et al., 1993, Radeno, 1998, 2001, 2003).

Considering the above stated on the dependence between the membrane potential and transport processes, it is often said that the membrane potential (by its intensity and kinetics) is a measure of the total transport processes occurring across the cell membrane. Hence, when the membrane potential reaches the stationary state, then ion transport processes across the membrane are uniform by the direction, intensity and charge. Furthermore, when the mem-
brane potential changes (linearly, exponentially, or in some other pattern), the ion transport processes occur in such dependence (by the direction, intensity and sign of the ion charge). Similar can be stated for the processes of depolarisation and repolarisation (Figure 5). It seems that a Cl\textsuperscript{−} transport and a partial NH\textsubscript{4}\textsuperscript{+} transport (presented by the direction, course, intensity and charge) occurred in the case of depolarisation processes (Figure 5). In cases of repolarisation, the NH\textsubscript{4}\textsuperscript{+} transport was dominant and Cl\textsuperscript{−} transport was partial (also presented by the direction, course, intensity and charge) (Figure 5). When the membrane potential was balanced, then Cl\textsuperscript{−} and NH\textsubscript{4}\textsuperscript{+} transports were also equilibrated (by the direction, course, intensity and charge) (Figure 5). Analogously to the stated, Cl\textsuperscript{−} and NH\textsubscript{4}\textsuperscript{+} transports occurred alternately in each single impulse of the oscillation of the membrane potential.

3. Oscillatory pattern of transport processes across the excitable cell membrane

The obtained results reported in this paper point out to the fact that oscillations of the membrane potential occur under certain conditions (Figures 1—4, Tables 2—5). Furthermore, a possible dependence of the membrane potential on different forms of ion transport processes across the excitable cell membrane is indicated. Therefore, based on the results and discussion, as well as, on our gained knowledge, we propose the following hypotheses:

— Oscillations of the membrane potential occur when the plant cell and thereby the cell membrane is excitable. As a rule, the excitable cell membrane is accompanied by unstable activities of ions: K\textsuperscript{+}, Na\textsuperscript{+} and Cl\textsuperscript{−} that are no more constant in cell phases: vacuole, cytoplasm and cell wall (V o r o b l j e v et al, 1968, R a d e n o v i č, 1983, 1985a, 1986, 1998, 2001).
— When the excitation of the cell membrane is produced by NH₄Cl concentrations, proteins oscillate in the cell membrane and rhythmically perform ion (Cl⁻ and NH₄⁺) transport processes across the excitable cell membrane in the oscillatory regimes of the membrane potential (Figure 1—4). In such a state, ion (Cl⁻ and NH₄⁺) transport processes become cooperative by which conformational-functional changes of active ion channels that spread and contract are induced (in the oscillatory regime) and in such a way rhythmically change total transport processes.

— The occurrence of oscillations of the membrane potential and ion (Cl⁻ and NH₄⁺) transport processes across the excitable cell membrane inevitably produce oscillations in cell supply in energies: chemical, osmotic and electric. Likewise, the dependence of transport processes and the metabolism becomes oscillatory. This especially relates to oscillatory processes of autoregulation within the plant cell.

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REFERENCES

B j o n i n g, E. (1964): Biologiceskie casi, pp. 11—26, Mir, Moskva.
B h a t n a g r, P. L. (1979): Nonlinear waves in one-dimensional dissipative systems, pp. 9, Calendron Press, Oxford.
B i o t e u x, A., H e s s, B., P l e s s e r, T. H. and M u r r a y, J. D. (1977): Oscillatory phenomena in biological systems, FEBS Lett. 75, 1—4.
F r a n k, G. M., Z a b o t i n s k i i, A. M., M o l c a n o v, D. S., C e r n a v s k i i, S. E. and S i o l j (1966): Kolebatelnie procesi v biologiceskih i himiceskih sistemah, Izd. Nauka, Moskva.
G r e h o v a, M. T., A n t o n e c, V. A., K r i n s k i i, V. I., O s t r o v s k i i, L. A., R a b i n o v i c, M. I., J a h n o, B. G. and G o r o d e c k a j a, N. A. (1981): Avtovolnoe procesi v sistemah s difuziei, pp. 6, Izd. Instituta prikladnoi fiziki ANSSR, Gorkii.
K o l s, O. R., M a k s i m o v, G. V. and R a d e n o v i ć, Č. N. (1993): Biofizika ritmiceskogo vozburdenja, Izd. Moskovskogo univerziteta, Moskva.


Radenović, Č., Vučinić, Ž. (1976): Simultaneous measurement of the bioelectric potential of the cell wall and the vacuoles during the oscillatory response to the Nitella cell, Physiol. Plant. 37, 207—212.


МЕХАНИЗАМ ОСЦИЛАТОРНОГ ТРАНСПОРТА NH₄ ЈОНА КРОЗ ПОБУЂЕНУ ЋЕЛИЈСКУ МЕМБРАНУ

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Резиме

У овом раду дaju се резултати типичних класа осцилација мембранског потенцијала, које су изазване побуђивањем ћелијске мембране слатководне алге Nitella, са различитим концентрацијама раствора НH₄CI. Утврђено је постојање четири класе осцилација мембранског потенцијала, више различитих појединаца и локалних импулса, који се јављају у ритму. Познато је да су процеси осцилације мембранског потенцијала у директној зависности од осцилаторних транспортних процеса NH₄ и CI Јона кроз побуђену ћелијску мембрану. Осцилаторни процеси кроз живу ћелијску мембрану, изазвани NH₄ Јоном, имају специфичне параметре: дужина трајања осцилације, број импулса у осцилацији, интензитет амплитуде, фреквенција, фактор пригушења и други, у поређењу са осцилаторним процесима изазваним другим моновалентним катионима. Предложена је хипотеза могуће механизма осцилаторног начина транспорта NH₄ и CI Јона кроз побуђену ћелијску мембрану.