Long-term dynamics of aquatic vegetation and the state of ecosystems of soda lakes in southeastern Transbaikalia

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Abstract. The cyclical nature of long-term changes in the annual amounts of atmospheric precipitation in Transbaikalia controls most of the processes in ecosystems. The paper briefly describes the long-term vegetation dynamics of soda lakes in the southeast of Transbaikal territory. These dynamics are driven by changes in abiotic parameters of the lakes, mainly water salinity and pH values. When the values of these indicators increase, the perennial succession series of vegetation of higher plants is as following: Helophytes + Neustophytes + Hydatophytes $\rightarrow$ Helophytes + Hydatophytes $\rightarrow$ Helophytes. The succession series of macrophytic algae is as following: Stigeoclonium sp. or Spirogyra sp. $\rightarrow$ Cladophora fracta + Charophyta $\rightarrow$ Enteromorpha intestinalis.

1. Introduction
Southeastern Transbaikalia is rich in brackish and soda-salt lakes [1]. The formation of lakes is favoured by a hilly relief with many depressions and a semi-arid climate, which facilitates evaporation of surface waters [2]. The lakes are usually shallow, the maximum depth of the largest lakes in the Torey group reaches 3-8 m, while most of the lakes have a depth of about one meter [3]. The peculiarity of the soda lakes in the study area is their relatively low mineralization, which distinguishes them from saline and hypersaline alkaline water bodies in other regions [4]. The cyclical regime and the amount of atmospheric precipitation [5] in combination with different sizes of catchments lead to periodic fluctuations in the water areas, depth, and hydrochemical indicators. In the study area, soda-type lakes are more common, possessing a relatively high concentration of $\text{HCO}_3^- + \text{CO}_3^{2-}$, pH values, and wide variability in water salinity [6]. Long-term observations of the hydrochemical state of the lakes have shown that water dilution occurs during wet periods, and, on the contrary, increasing the salt concentration occurs during dry periods. According to average estimates, over 20 years, salinity increased by 5 times in oligo- and mesohaline lakes, and more than 10 and 100 times in poly- and hyperhaline lakes. Salinity increased to 15 g/l in lakes with a volume of water mass from 1 to $10^{-3}$ km$^3$ and reached 50 g/l or even more in lakes with smaller water volumes [7].

Long-term changes in environmental parameters contribute to the rearrangement of the structural and functional organisation of the lakes’ ecosystems [8]. The ecosystems of the salt lakes are structurally simple. Aquatic vegetation (macrophytes) in soda lakes is not the main producer of organic matter. However, it is one of the environment-forming components of the lake ecosystem that largely determines biodiversity and the functioning of ecosystems. Macrophytes, being sensitive to physical and chemical changes in the environment, can serve as good indicators of its condition.

The purpose of this work is to establish the long-term dynamics of the aquatic vegetation and the ecosystem of soda lakes in the southeast of Eastern Transbaikalia.
2. Materials and methods
The studies were carried out in the semi-arid area of southeastern Transbaikalia (figure 1) during the dry period (1999, 2003, 2007, 2011) and at the beginning of the wet one (from 2012, 2014, 2018). During these years, about 8-20 lakes were surveyed annually. Water quality was characterised by pH values, salinity, oxygen content, and temperature. In total, about 100 measurements were carried out. Hydrobotanical work was carried out in July using generally accepted methods, as well as those previously tested by the authors in the water bodies of Transbaikalia. Plant communities were examined during a route walk along the perimeter of a water body, if necessary with profiling deep into a water body. Two profiles were laid connecting opposite shores in larger water bodies with developed aquatic vegetation; a separate profile was laid in overgrown bays. The sampling phytomass was carried out using a gammarid quantification device (coverage area 0.25 m²), which is used by the authors in the study of aquatic plant communities in other water bodies. In total, about 80 samples of phytomass were collected.

Figure 1. The schematic map of the studied area [8]. The lakes are shaded in grey. The dashed line indicates the border between Russia and Mongolia.
3. Results and discussion

Long-term observations of the vegetation and the ecosystem of soda lakes allowed us to describe the successional changes in the vegetation. In lakes, as the water level decreases, mineralization increases, the boundaries of the littoral zone shift, which causes a decrease in the biodiversity of macrophytes. The composition of higher aquatic plants ranges from 2 to 17, macrophytic algae – 1-3 species. In the high-water level phase, the vegetation is represented by thickets of the emergent vegetation (helophytes), submerged (hydatophytes) plants, and plants with leaves floating on the water surface (neustophytes). Macroscopic algae are developed in the coastal zone and comprise *Cladophora fracta* (Müll. ex Vahl) Kütz., and *Stigeoclonium tenue* (Ag.) Kütz. inhabiting on rooting higher aquatic plants as well as flooded terrestrial vegetation.

When the mineralization increases and the water salinity reaches 1 g/l, neustophytes visually disappear because only propagules keep staying alive but fall in dormancy, the areas occupied by hydatophytes and helophytes decrease simultaneously. Reduction in the area of *Phragmites australis* (Cav.) Trin. ex Steud. is accompanied by the herbage density increasing, while the plant height is decreasing. At the same time there is an increase in some morphometric parameters of plants (e.g., the number of leaves on the stem, the length of leaves, and panicles) (figure 2a). *Stuckenia chakassiensis* (Kaschina) Klinkova grows in water bodies with higher mineralization, and *Stuckenia pectinata* (L.) Börner – in water bodies with lower salinity.

![Figure 2](image-url)  
*Figure 2.* The vegetation of the bed of Lake Barun-Torey in 2011 and 2018.  
Stage 1: a – *Phragmites australis* on a dry bed; b – temporary freshwater body.  
Stage 2: c – temporary bulk water body; d – temporary freshwater body.

When the littoral area declines, the phytomass of aquatic plants increases and it decreases when the mineralization reaches 5 g/l. Macroscopic algae *Cl. fracta* form massive accumulations in the surf zone; when the water mineralization values reach 4-5 g/l, the species is replaced by *Enteromorpha intestinalis* (L.) Link. However, in most water bodies, *C. fracta* and *E. intestinalis* coexist, occupying different parts of the lake littoral. A decrease in the water depth leads to expanding warmed-up shallow areas of the lake, where charophytes germinate.
When the salinity value in soda lakes reaches 8 g/l, only scattered and weakened individuals of helophytes can occur. Temporary overgrown lakes are formed on the drained lake beds (figure 2). The lakes can be divided into 2 types according to the peculiarities of their origin and intensity of vegetation development. The first type is temporary water bodies formed as a result of the groundwater discharge (e.g., temporary lakes in the basins of lakes Tsagan Nor, Baim Bulag). The community *Zannichellia pedunculata* Rchb. + *Chara* sp. + *Spirogyra* sp. is developing in these water bodies (figure 2b). The water bodies disappear with a decrease in underground recharge. When the volume of water supply is maintained (for example, on the northern edge of the bed of Lake Barun-Torey), water bodies overgrow and a pronounced belt of the emergent and submerged plants appears (figure 2d). These water bodies are characterized by the highest biodiversity. In 2018, 12 species were registered in the bed of Lake Barun-Torey, which were the representatives of both freshwater and brackishwater flora. The second type of water body is bulk water bodies, formed in the depressions of the basin as a result of the accumulation of atmospheric precipitation (figure 2c). They exist during a rather short period and provide good conditions for the development of *Ph. australis* and *S. pectinata*. These water bodies can be freshwater or brackish. Planktonic and non-benthic organisms are the last to develop.

The general pattern of replacement of the dominant macrophyte species is as follows: during the period of high water level, communities of helophytes + neustophytes + hydatophytes develop. In the intermediate period of a decrease in the water level, the pattern is as follows: helophytes + hydatophytes + charophytes + *C. fracta* and *E. intestinalis* f. *prolifera*. Only helophytes occur during the low water period. The early period of high humidity is characterized by the emergence of temporary water bodies with high species diversity, including both freshwater and halotolerant species.

Changes in water salinity affect not only the lacustrine vegetation but also contribute to alteration in the entire ecosystem. The values of 1, 4-5, and 8 g/l were recognised as milestone ones, causing obvious changes in the biodiversity of plant communities. The distinguished boundaries of salinity are consistent with the concept of relativity and multiplicity of barrier salinity zones, articulated by N Aladin [9] within the framework of the V V Khlebovich school. Studies of the estuaries of the Baltic Sea indicate that salinity of 5-8 ‰ acts as an ecological boundary, which is a physiological and evolutionary barrier to biodiversity [10].

When salinity reaches 8 g/l, planktonic organisms and prokaryotic microorganisms – cyanobacteria and anoxygenic phototrophic bacteria (APB) – are involved in the creation of primary production in the ecosystem. They provide energy supply to the ecosystem by different mechanisms of chemolithotrophy and two types of phototrophy. Under stressful conditions, unicellular organisms need adaptation only at the molecular and cellular level of organisation, while multicellular animals and plants have to adapt to a changing environment at the tissue and organismal levels [11]. When salinity increases, the role of phytoplankton in the production of organic matter decreases, but the role of APB increases, since water is not used as a proton donor (for example, purple bacteria use hydrogen sulphide and do not produce oxygen) for anoxygenic photosynthesis using bacteriochlorophylls. Some anoxygenic phototrophs are not primary producers and do not consume CO₂ but obtain carbon from organic matter. In this case, the efficiency of the synthesis of organic matter increases, because light energy is used for the synthesis itself. Anoxygenic photosynthesis requires a light intensity about 4 times less than an oxygenic one.

As studies show [4, 12], the productivity of soda water bodies remains high until the turbidity of water bodies significantly increases. At the same time, the benthic type of development of autotrophs is prevalent.

The ratio of ions in water is crucial for chemical processes along the salinity gradient. Increased values of Na⁺, Na₂CO₃ adversely affect the turgor of the cells of higher aquatic plants. A decrease in the content of free carbon dioxide combined with an increase in mineralization and pH leads to eliminating species unable to consume HCO₃⁻ from phytoplankton [13]. The changes in the chemical composition of lake waters and a decrease in water transparency contribute to the elimination of light-dependent algae of phytoplankton and higher aquatic plants. An increase in the total amount of dissolved salts and salt composition of water harms osmoregulation [14]. The mineralization limit is 5 g/l for crucian carp, and 8 g/l for carp.
4. Conclusion
Thus, in the long-term dynamics of the soda lakes vegetation, the cyclical nature of the long-term dynamics of annual precipitation in southeastern Transbaikalia is clearly manifested. Mineralization of water and pH values are the main factors in the transformation of the lakes’ ecosystems.

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