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Genetic polymorphism and natural selection within populations of Haloxylon aphyllum under Kyzylkum desert salinity environments

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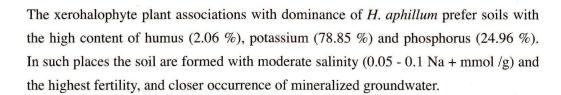
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Haloxylon aphyllum (black saxaul) is tree-like shrub with photosynthetic succulent shoots, hemixerophyte, halophyte with C4 type of photosynthesis and the main edificators of Central Asia deserts. Increase of the anthropogenic impacts on the natural and human disturbed desert ecosystems leads to negative changes in the botanical diversity of plant associations, to decreasing of species genetic diversity, and as a result reduces the productivity and functioning of arid ecosystems. A significant factor in the stability of desert woody plants is their intraspecific polymorphism. The spatial organization of populations of desert species carries important information about the results of their interaction with environmental factors and among themselves.

Under the canopy of *H. aphillum* the special soils properties are formed in comparison with the background desert soils, which lie outside of the canopy. This is related with the highest accumulation of salts, silt and humus in soils directly under the canopy of *H. aphyllum*. Influence of *H. aphillum* on the properties of desert soils due to the high ash content (30-40%) of assimilation shoots and high sodium content in the ash. In addition, the sodic soil enrichment occurs as a result of decomposition of litter, and its leaching of fallen shoots and washout from *H. aphillum* canopy. Besides of sodium and chloride, the phosphorus, sulfur, potassium and calcium ions are actively accumulated in the ash of black saxoul. *H. aphillum* is able to grow on different soils - the sand and gypsum substrates with varying degrees of salinity (from 0.01 to 0.5 Na+ mmol/g), dominating in different plant communities (xerophytic, xerohalophyte, halophytes).



It was found that in different plant associations and soils with various water-salt regime H. aphyllum produces seeds with different quality (morphologically, physiologically, and genetically). The seed formation, embryo development, fertilization and flowering in H. aphyllum are timed to certain seasons. The development of male generative structures of H. aphyllum occurs in the most favorable seasonal conditions (March-April, temperature 10-150C, >10 mm rainfall), independent of the level of soil salinity. The development of female generative structures and the process of fertilization occur in 30 - 50 days after flowering, in less favorable conditions (May-June, temperature 20-250C, 3-5 mm rainfall). With the increased stress impact (July-August, temperature 25-300C, 0 mm rainfall) the evident slowdown rate of development and differentiation of female reproductive sphere, i.e. so named "summer dormancy" is observed. During the development of female generative structures, especially at the stage of embryo (April-September) in H. aphyllum the appearance of degenerating and aberrant ovules is observed, which is considered as one of the vital elements of the survival strategy to harsh desert conditions. There was a significant difference in the stability of the female gametophyte (number of aberrant ovules) in the most stressful period (July-August) in plants from different conditions of water-salt regime of the soil. As a result, H. aphillum produces morphologically, physiologically, and genetically different seeds. Seeds, which are formed in conditions of weak and strong salinity, are characterized by small size (6.4+0.19 mm) with long-term rate of germination (9 days) and lower (50%) germination. Seeds, which are formed in moderate salinity (0.05 - 0.1 Na + mmol/g) are characterized by a larger size (8.0+0.2 mm) and accelerated rate of germination (75% germination for 5 days). Differences in seeds of H. aphillum from various conditions of water-salt regime of the soil were shown at the genetic level also. All parameters of genetic variation of H. aphillum (proportion of polymorphic loci, the expected and observed heterozygosity) were in 2 times higher under moderate salinity of soil. Such differences might be considered as an evidence of local adaptation to specific growing conditions. In addition, the difference more than 2 times in the level of heterozygosity at moderate salinity indicates optimality conditions. Thus, under natural conditions in populations of *H. aphillum* the selection in favor of homozygotes is observed on soils with weak and strong salinity. The heterozygotes are selected on soils with moderate salinity, relatively high fertility and closer occurrence of saline groundwater.

In model experiments on the effect of salinity (by NaCL) and water deficit (osmotic stress, by PEG) on the productivity and sustainability of different genotypes of *H. aphillum* it was found that heterozygous genotypes have benefits under optimal conditions (0.05 - 0.1 Na⁺ mmol/g and without water deficit). Under water deficit (PEG) advantage observed in homozygous genotypes: water use efficiency was 2.2 times higher, and the content of proline and MDA (biochemical markers of stress) were 2 times less than in heterozygotes. Thus, the most stress factor for *H. aphillum* was water deficit (in the absent of salinity) - only in the experiment with PEG the content of proline in seedlings of both genotypes increased in 2-6 times compared with the control. At the same time, under water deficit the level of MDA and proline in heterozygous genotypes was in 2 times higher than in homozygous, indicating their less resistance to this type of stress.

Thus, the conditions with different water-salt regime of the soil affect on the genetic diversity of populations of xerohalophyte H. aphyllum, leading to the formation of genetically different seeds. The germination, survival and stability of different types of seeds are timed to specific growing conditions. The optimal natural conditions for H. aphyllum are observed in xerohalophyte plant communities, on soils with moderate salinity, relatively high fertility and closer occurrence of saline groundwater. In such type of biotops, the natural selection in favor of heterozygotes of *H. aphyllum* occurs, and heterozygous genotypes have the most productivity. The homozygous genotypes more tolerant to water deficit and the natural selection in favor of them occur in xerophytic and halophytes plant associations. So, genetic diversity is the basis of adaptation to new ecotopes (biotops), confirming their stability and resilience of arid ecosystems.

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