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Original article

The value of small habitat islands for the conservation of genetic variability in a steppe grass species

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ABSTRACT

The habitat loss and fragmentation due to agricultural land-conversion affected the steppe throughout its range. In Ukraine, 95% of steppe was destroyed in the last two centuries. Remaining populations are confined to few refuges, like nature reserves, loess ravines, and kurgans (small burial mounds), the latter being often subject to destruction by archeological excavations.

Stipa capillata L. is a typical grass species of Eurasian steppes and extrazonal dry grasslands, that was previously used as a model species in studies on steppe ecology. The aim of our research was to assess genetic diversity of *S. capillata* populations within different types of steppe refuges (loess ravines, biosphere reserve, kurgan) and to evaluate the value of the latter group for the preservation of genetic diversity in the study species.

We assessed genetic diversity of 266 individuals from 15 populations (nine from kurgans, three from loess ravines and three from Askania-Nova Biosphere Reserve) with eight Universal Rice Primers (URPs).

Studied populations showed high intra-population variability (I: 0.262–0.419, PPB: 52.08–82.64%). Populations from kurgans showed higher genetic differentiation ($\Phi_{ST} = 0.247$) than those from loess ravines ($\Phi_{ST} = 0.120$) and the biosphere reserve ($\Phi_{ST} = 0.142$). Although the diversity metrics were to a small extent lower for populations from kurgans than from larger refugia we conclude that all studied populations of the species still preserve high genetic variability and are valuable for protection. To what extent this pattern holds true under continuous fragmentation in the future must be carefully monitored.

1. Introduction

Habitat destruction and fragmentation are the major threats to biodiversity worldwide (Secretariat of the Convention on Biological Diversity United Nations Environment Programme, 2014; Haddad et al., 2015). These threats pose a serious challenge for nature conservation and are subject to intense ecological research throughout the World (Wilcox and Murphy, 1985; Young and Clarke, 2000; Fahrig, 2003; Niebuhr et al., 2015).

One of the most important indirect, but irreversible implications of habitat fragmentation is the loss of genetic diversity in rare species due to the division of continuous populations into smaller, genetically isolated subpopulations (Lienert, 2004; Barr et al., 2015; Ortego et al., 2015). In some plant species, isolation can lead to decrease of genetic diversity (Buza et al., 2000; Gustafsson, 2000; Wallace, 2002; Lauterbach et al., 2012). In other plant species, negative effects have not been detected yet, possibly due to biological traits, such as long life-span, outcrossing and ability for long-distance gene-flow (Kaljund and Jaaska, 2010; Lander et al., 2010; Winkler et al., 2011; Dzialuk et al., 2014).

Steppe is one of the most transformed biomes of the world (Henwood, 1998). Hence, the research on fragmentation effects in steppe plant populations is particularly important. In south-eastern Europe, in the westernmost part of the Eurasian steppe belt, fragmentation has been particularly intense (Chibilyov, 2002; Parnikoza and Vasiluk, 2011). Steppe is a natural, zonal vegetation in Ukraine that originally covered approximately 40% of the country. From the north to the south of the Ukrainian steppe belt different types of steppe vegetation are distinguished: meadow steppe, herb-grass steppe, grass steppe and desert steppe (Chibilyov, 1990). Similarly as in other parts of Eurasia the Ukrainian steppe was used as pastoral land by nomadic tribes since ancient

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times. Change in the steppe management began 200 years ago, when the intensive farming has been introduced in the region. As a result 95% of the Ukrainian steppe has been converted to crop land (Burkovsky et al., 2013). Today, steppe persists in few refuges. The best preserved grass steppe vegetation refuge is Askania-Nova Biosphere Reserve, where the steppe ecosystem has been preserved in its primary natural form on an area of 110 km^2 (http://askania-nova-zapovidnik.gov.ua). The steppe vegetation has also been preserved in places with difficult access (i.e. loess ravines, slopes of river valleys, outcrops, saline soil, etc.) where the vegetation occupies an area of intermediate size. The last type of steppe refugium are kurgans. They are small in size, but more numerous in the landscape than both previously mentioned types of enclaves.

Kurgans are burial mounds of earth and stone, of 1–15 m height and 10–110 m width (Mozolevskiy and Polin, 2005). They are objects interesting from an archeological point of view as they have been built by ancient cultures (Yamna, Catacomb and other Bronze Age cultures, Scythians, medieval nomads; Chernyakov, 1993) and harbor archeological artifacts. In Ukraine the number of kurgans reaches 150,000 (formerly there were around 0.5 million of them; Chernyakov, 1993).

The historical value of kurgans has been known for a long time (Chernyakov, 1993; Mozolevskiy and Polin, 2005). Recent research of Ukrainian kurgans has also shown their great importance as refuges of steppe vegetation (Moysiyenko and Sudnik-Wójcikowska, 2006; 2010; Sudnik-Wójcikowska and Moysiyenko, 2006; 2010). These observations as well as other studies indicate that kurgans, which are situated in the midst of large-area arable cropland, can serve as refuges for natural vegetation in the radius of many kilometers and as habitat islands surrounded by a strongly altered, anthropogenic landscape (Deák et al., 2016; Dembicz et al., 2016). However, the small size and spatial isolations of these objects makes kurgan populations of plants vulnerable to inbreeding and stochastic extinction (Dembicz et al., 2016). Furthermore plowing and archeological excavations are significant threats despite legal protection of kurgans in Ukraine as a cultural monuments (On Protection of Cultural Heritage Act, 2000). Following archeological excavation the steppe vegetation typically does not return to the site and the kurgan is overgrown by ruderal and agricultural weed species (Sudnik-Wójcikowska and Moysiyenko, 2012).

The richness of the kurgan flora, especially the presence of rare steppe plant species is surprising considering their small size and the long period of isolation (about 100–200 years; Lisetskii, 1992). To what extent kurgans can sustain viable steppe plant population under continuous fragmentation in the future has been poorly explored. Resolving this question is not only relevant to Ukraine but other regions, like western Russia where the steppe was converted to crop land on a massive scale.

Feathergrasses (*Stipa* spp.) are perennial tussock grasses that dominate many steppe vegetation types (Mordkovich, 2014). Due to their adaptation to a dry continental climate they play a large role in supporting the pastoralism in arid areas (Werger and van Staalduinen, 2012). In recent years they are being increasingly used to restore natural areas degraded by drought or inappropriate farming (Hu et al., 2014). Relatively long development and life-span of those grasses, as well as their resistance to harsh and variable habitat conditions could enhance survival of small populations even despite long-lasting isolation due to strong anthropogenic habitat fragmentation. Nevertheless these species are vulnerable to gradual loss of genetic variability impeding sometimes their sexual reproduction and successful existence in a location (comp. Eckert, 2001). This is crucial for self-incompatible species where sexual reproduction becomes impaired or unreachable, but also bears fitness costs for self-compatible species (like many *Stipa* species) making them prone to stochastic loss of genetic diversity and subsequent extinction (Heinicke et al., 2016; comp. Loveless and Hamrick, 1984). This phenomenon may be especially pronounced on very small habitat islands which harbor small populations.

The analysis of molecular fingerprints has become a standard method to assess the effects of small population size and isolation on the genetic diversity (Haig, 1998). In this paper we present our results on the genetic structure of *Stipa capillata* L. a frequent species of steppe vegetation in Eurasia that was used by several previous studies as a model organism (Wagner et al., 2011; Durka et al., 2013; Peng et al., 2015 and cited literature).

The majority of previous research on the genetic variability of *S.capillata* and closely related species were conducted at a large spatial scale (distances between studied populations of tens or hundreds kilometers); in many cases, studied populations were very large (Krzakowa and Michalak, 2007; Hensen et al., 2010; Wagner et al., 2011). Small-scale studies on fragmented feathergrass populations are scarce (Sui et al., 2009; Han and Zhao, 2011). Closing this knowledge gap is not only important for nature conservation efforts in the Ukraine but also for land management in other regions, where large habitats were reduced to small patches. Hence, we pursued two objectives: 1) To assess the genetic variability and genetic structure of *S. capillata* in the grass steppe zone of the southern Ukraine, 2) To compare the value of kurgans in preserving the genetic variability of this species against larger types of steppe vegetation refugia.

2. Materials and methods

2.1. Study species

Stipa capillata is a perennial, long-lived (estimated life span of 30–40 years, Gorchakova and Zhivechkov, 2009), tetraploid (Skalińska et al., 1968) tussock grass. The height of its generative shoots varies between (30) 40 and 90 (130) cm. In Ukraine, the species flowers from June to July (Prokudin, 1977). It represents a clonal growth type, but with very limited spread, only in the immediate vicinity of the tussocks, therefore each tussock represents one separate genet (Klimešová and Klimeš, 2013) and generative reproduction prevails (Hensen and Müller, 1997). The species is facultatively cleistogamous, with chasmogamous flowers being wind-pollinated (Ponomarev and Zvorygina, 1949). Caryopses are provided with awns 12–18 cm in length, on apices of lemmas that enable seed dispersal by animals (epizoochory), humans and wind (Hensen, 1997). The species forms a transient soil seed bank (Kleyer et al., 2008). Under natural conditions, only few produced seeds survive and develop into mature plants (Vorontzova and Zaugolnova, 1985). The range of this species extends from Spain in the west to eastern Mongolia and Yakutia in the east, however the areas where *S. capillata* is one of the dominant species of the zonal vegetation include steppe zone from southeastern Europe to Central Asia (Hensen et al., 2010). Due to massive habitat loss, the species is included in the Red Data Book of Ukraine (Didukh, 2009).

2.2. Research area and field sampling

We conducted field sampling within the Black Sea Lowland in the Kherson region, southern Ukraine (Fig. 1). The area is located within the West Pontic grass steppe zone (Bohn et al., 2004). The landscape is dominated by vast plains, sometimes slightly wavy. In response to erosion of thick loess sediments loess ravines evolved along river valleys. Climate of this region is continental with an average annual precipitation of 350–400 mm and a mean annual temperature of 9–11 °C. Most of the annual rainfall is in spring (mainly May–June) and autumn (mainly October), with droughts