



Discussion

Fitness decline and adaptation to novel environments in ex situ plant collections: Current knowledge and future perspectives



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ARTICLE INFO

Article history:

Received 16 May 2015

Received in revised form 12 October 2015

Accepted 21 October 2015

Available online 10 November 2015

Keywords:

Ex situ conservation

Botanic gardens

Artificial selection

Genetic drift

Adaptive evolution

ABSTRACT

The conservation of rare plant species as living collections in botanic gardens and arboreta has become an established tool in the battle against worldwide species' extinctions. However, the establishment of ex situ collections with a high conservation value requires a sound understanding of the evolutionary processes that may reduce the suitability of these collections for future reintroductions. Particularly, risks such as fitness decline of cultivated plants over time, trait shifts and loss of adaptation to the original habitat due to changes in selection regimes have rarely been addressed so far. Based on a literature review and results of our own project we show that genetic drift can lead to fitness decline in ex situ cultivated plants, but these drift effects strongly depend on the conditions and cultivation history in the ex situ facility. Furthermore, we provide evidence that shifts in traits such as germination and flowering time, and a decrease in stress tolerance to drought and competition can reduce the conservation value of ex situ collections. These threats associated with ex situ conditions require more attention by researchers, curators and conservationists. We need to increase knowledge on traits that are subject to novel selection pressures in ex situ collections, and to define population sizes that prevent genetic drift. Establishing conservation networks with replicated collections across gardens and balancing the seed contribution of mother plants to the next generation within a collection are suggested as first steps to increase the conservation value of ex situ plant collections.

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1. Introduction: ex situ plant collections — potential and challenges

Safeguarding at least 75% of threatened plant species in ex situ collections (that is outside their natural environment either in seed banks, cryopreserved, as tissue cultures, or as living collections in botanic gardens) is one of the goals of the “Global Strategy for Plant Conservation” (Secretariat of the Convention on Biological Diversity (SCBD), 2010) with at least 20% of these species to be used for recovery and restoration purposes. Especially in cases where in situ conservation cannot be guaranteed, for example due to habitat destruction or land-use change, ex situ collections in botanic gardens and seed banks may be the appropriate method to ensure species survival and maintain genetic variation that can be utilized as a source for reintroduction and restoration. Conservationists and botanic gardens have therefore recognized the potential of botanic garden facilities to preserve the genetic resources of threatened plant species as well as to breed species for reintroduction and restoration programs (BGCI, 2012; Donaldson, 2009; Hardwick et al., 2011; Heywood, 2011). Consequently, reintroduction

programs were launched and networks to facilitate ex situ conservation efforts have been established worldwide (e.g. Burkart et al., 2005; Faggi et al., 2012; James, 2004; Maunder, 1994; Sharrock and Jones, 2011). At the same time, problems and risks of ex situ cultivation were recognized. Amongst those problems are 1) the genetic representation of wild populations in ex situ collections, i.e., the appropriate population sampling strategies across the species range (Guerrant et al., 2004; Hoban and Schlarbaum, 2014; Saura et al., 2008), 2) genetic erosion and divergence of ex situ collection from their wild source population over time (Enßlin et al., 2011; Lauterbach et al., 2012; Rucinska and Puchalski, 2011), 3) fitness decline in putatively bottlenecked ex situ collection due to genetic drift and inbreeding depression (Havens et al., 2004; Vitt and Havens, 2004), and 4) adaptation to the ex situ environment and loss of adaptations to the original natural environment, respectively (Enßlin et al., 2011; Havens et al., 2004). While for many temperate plant species with their often dormant seeds the establishment of seed banks may be the preferred option to reduce the risks listed above (Hay and Probert, 2013), the general principles and threats do also apply for seed banks as stored seeds also need to be regenerated regularly due to a decrease of seed viability over time (Godefroid et al., 2010; Nagel et al., 2009; Schoen and Brown, 2001). Furthermore, there is still a huge need for effective management of living plant collections,

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e.g. for many tropical plants with recalcitrant seeds (Li and Pritchard, 2009). As a result, first studies were conducted to explore the conservation value of living ex situ collections (Cibrian-Jaramillo et al., 2013; Enßlin et al., 2011; Kozłowski et al., 2011; Maunder et al., 2001). Particularly, the appropriate level of genetic representation of the wild population in the ex situ collection has received increased attention in recent years (Brütting et al., 2012; Christe et al., 2014; Hoban and Schlarbaum, 2014; Namoff et al., 2010; Yokogawa et al., 2013). However, important issues such as adaptation to novel artificial environments, loss of adaptations to the natural environment and subsequent fitness decline under natural conditions have received less attention.

In this perspective, we first (1) present a general state-of-the-art summary of fitness decline and (2) loss of adaptations in ex situ living collections in botanic gardens and show data of our own studies that add to the current knowledge. We then (3) suggest research needs that may help to fill existing knowledge and finally (4) propose some management recommendations that we derive from the literature review and our own results.

2. Fitness decline in ex situ collections

Population genetic theory predicts a high probability of decline in fitness for small and isolated plant populations (Ellstrand and Elam, 1993; Falk and Holsinger, 1991). Processes such as genetic drift reduce genetic variation and randomly fix alleles, while inbreeding increases homozygosity in small populations (Ellstrand and Elam, 1993). In wild plant populations, the link between small population sizes and lower average fitness has been often observed (for reviews see Leimu et al., 2006; Reed, 2005). For animals kept in captivity in small numbers, models have been used to predict their fitness decline (Ford, 2002; Robert, 2009) and actual fitness decline has been demonstrated for species in zoos (Boakes et al., 2007) as well as in supportive breeding programs (e.g. Araki et al., 2007). Although ex situ collections in botanic gardens usually meet the criteria of small and isolated populations (Schaal and Leverich, 2004) and experiences from captive breeding of animals suggest similar problems in ex situ plant collections in botanic gardens, studies addressing consequences of ex situ cultivation on performance, fitness, and trait development of plants in ex situ collections are still mostly lacking.

The few existing studies, which tested fitness differences under common garden conditions, did not find general differences in fitness between wild and ex situ populations in the two plant species tested (Enßlin et al., 2011; Lauterbach, 2012). In contrast, Schröder and Prasse (2013a) observed an increased biomass production and seed yield in commercially cultivated varieties of *Plantago lanceolata* and *Lotus corniculatus* compared with wild collected ones suggesting that garden cultivated collections may show increased performance due to positive selection on growth and reproductive traits. Thus, potential negative effects of genetic drift and inbreeding on performance and reproductive fitness may be offset by positive selection for growth and reproduction, at least under optimal growing conditions.

2.1. Performance decline in ex situ collections under garden conditions: a case study with seven botanic gardens in Germany

We experimentally assessed whether the cultivation of four native wild plant species (*Carlina vulgaris* L., Asteraceae; *Corynephorus canescens* P. Beauv., Poaceae; *Jasione montana* L., Campanulaceae; *Melilotus officinalis* L., Fabaceae) in seven botanic gardens in Germany for different time spans affects their performance compared with plants from wild populations. To be able to derive strong inferences about performance changes due to cultivation, we collected the wild plants from the original wild source population of each of the ex situ collections (wild and corresponding ex situ collection are hereafter called “population pairs”). We collected the seeds in 2009 from 14 accessions in seven botanic gardens in Germany and from their 14 wild source populations,

respectively (Table 1). The cultivation time of the plants in the botanic gardens varied between three and 31 years (Table 1). We grew all plants of each species (ex situ and wild origin) in each of the species' ex situ collections (botanic gardens), to study their performance and fitness while excluding a potential home-site advantage of plants from one particular ex situ collection. In spring 2010, we planted seedlings in a randomized block design in each target botanic garden directly into garden beds. After one full growing season (in July 2011), we harvested all plants individually aboveground, dried them at 72 °C for three days and weighed them. For *C. vulgaris*, *J. montana* and *M. officinalis*, we also recorded the number of flowering stems as a fitness-correlated measure. We used nested analyses of variance (ANOVA) to analyze the effects of wild or garden origin, population pair, and time of cultivation on aboveground biomass production and number of flowering stems for each species separately. As we based our sampling design on comparing the ex situ collections with their original wild population, we were interested in whether there was a general difference in performance between wild and ex situ plants (origin effect) or whether the response of the ex situ plants to cultivation was different in the different population pairs (origin × population pair interaction), which would indicate differences due to genetic drift. Detailed information about the experimental design and the analyses is given in the Appendix A.

We found that in all four species, under botanic garden conditions, biomass and number of flowering stems generally did not differ between plants from ex situ origin and plants from wild origin (no origin effect). However, in all species, the difference between ex situ and wild origin depended on the population pair (significant origin × population pair interaction, $F_{2-3,46-545} = 2.1-9.6$, $P < 0.1$; Table A1 in Appendix A). When each population pair was tested separately, we found both significantly higher and lower performance of wild plants compared to the ex situ plants in half of the comparisons (seven out of 14, $F_{1,9-148} = 5.7-9.6$, $P < 0.05$, Fig. 1a–d), suggesting that opposing responses across the population pairs offset a general difference between ex situ and wild plants. Consequently, we also found only weak indications that the decline in fitness in ex situ collections increased with the cultivation time of the plants (only for the number of flowering stems in *C. vulgaris*, $F_{1,6} = 6.1$, $P < 0.05$, Fig. 2).

Our results show that differences in performance and fitness related traits between ex situ and wild plants can be found, but the direction of the effect was mainly dependent on the specific pair of botanic garden and original wild populations. However, in six out of seven significant differences within the population pairs, ex situ plants showed a lower fitness than the plants from their wild source population (Fig. 1), suggesting that the problem of fitness decline in ex situ collection exists and should be taken into consideration. This is supported by the negative relationship of the number of flowering stems with cultivation time found in *C. vulgaris* (Fig. 2). All species in our experiment were short-lived perennials, which, under favorable conditions, flower every second year, resulting in approximately 10–15 generations of the plants in the ex situ collections. Hence, the phenotypic differentiation observed in our population pairs must have taken place within these 10–15 generations. Havens et al. (2004) noted that effects of drift and inbreeding become most obvious after 25–100 generations, but changes due to selection can occur much faster, depending on the strength of the selection (e.g., Burgess et al., 2007). Selection by gardeners is usually directed to high vigor, growth, and larger flowers and seeds (Havens et al., 2004), while genetic drift randomly fixes alleles within the population, particularly in small ones (Willi et al., 2006), thus potentially resulting in both positive and negative impacts on plant performance in the short run. In our study, all wild populations were larger than the ex situ collections (Table 1) and in some cases, ex situ collections contained less than 10 individuals enhancing the probability of genetic drift in these collections. The regeneration method varied between the botanic gardens: five out of the 14 collections were artificially propagated in the garden, i.e., gardeners germinated and

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