



Ex situ seed collections will benefit from considering spatial sampling design and species' reproductive biology



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ABSTRACT

Collecting seed from natural plant populations is a key tool for conservation, ecological restoration, assisted migration, studying plant mating systems, and crop breeding. Many collections rely on simple, broadly-applied rules-of-thumb for minimum sample sizes, regardless of species' natural history, and are likely inadequate for obtaining sufficient genetic representation. There is a current paucity of information about how various logistical and biological factors influence seed sampling outcomes. Here we use simulated and empirical data to, for the first time, quantitatively evaluate the degree to which collection effectiveness is influenced by spatial arrangement, sampling intensity, and species' reproductive biology. We clearly and quantitatively demonstrate that collections with spatially limited or biased sampling arrangements, or collections from species with high selfing or low dispersal, will need substantially more samples than are commonly recommended, or else will fail to reach the targeted genetic diversity. We also show that the marginal gain from sampling additional maternal plants will nearly always exceed that of additional seeds. Lastly we show that random sampling outperforms "easy access" and "transect" sampling by 70% and 30%, respectively. Overall, we conclude that collection guidelines tailored to particular taxa will help facilitate optimal sampling design.

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1. Introduction

Ex situ plant collections can help conserve threatened species (Richards et al., 2006), function as a source of traits for agricultural improvement (Tanksley and McCouch, 1997; Neale and Kremer, 2011; Brummer et al., 2011), or be used to propagate large numbers of individual plants for ecosystem restoration or assisted migration (Broadhurst et al., 2008; Vitt et al., 2010; Aitken and Whitlock, 2013). Seed collections are also used for population monitoring (Shaw and Etterson, 2012). One major objective of seed collections is to maximize genetic diversity, which is known to contribute to species' adaptive potential, prevent inbreeding effects, and facilitate ecosystem stability and resilience (Reusch et al., 2005; Frankham, 2010), and may also preserve variation in genetically-based phenotypic traits (drought tolerance, phenology, growth traits, disease resistance (Volk et al., 2008; McCouch, 2013; Olsen and Wendel, 2013)). Many agencies are establishing, renewing, or supplementing their collections (FAO, 2009; Namoff et al., 2010; Echt et al., 2011a; BLM, 2012). In order to preserve genetic

diversity, the organizations and individuals involved must carefully decide how best to gather samples from wild populations, considering limited funds for expeditions, seed storage, maintenance, and other costs (Guerrant et al., 2004; Namoff et al., 2010; Cibrian-Jaramillo et al., 2013). Efficient and effective sampling protocols are crucial to ensure a broad genetic base for future use. Evaluating the expected performance (amount of genetic diversity to be captured) of potential sampling protocols prior to making a collection might help choose an optimal strategy.

A number of seed collection guidelines exist (Table 1, Supplemental Table 1), many of which are based on probability models that calculate the minimum number of individuals to sample to ensure a high probability of capturing alleles at a specified frequency. For example, Brown and Marshall (1995) estimated that sampling between 30 and 60 randomly chosen individuals will provide a 95% chance of capturing at least one copy of each allele existing at frequencies >0.05, although larger collections are recommended if the collectors desire higher probabilities (Lawrence et al., 1995; Lawrence, 2002). The simple minimum protocol of 50 samples (a compromise between 30 and 60) has been advised and implemented as a general rule-of-thumb across a diversity of species and landscapes (Brown and Briggs, 1991; Lockwood et al., 2007; BLM, 2012), as shown in Table 1. An important, implicit

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Table 1Ex situ seed collection guidelines from governmental and non-governmental organizations. References details are in [Supplemental Table 1](#).

Ref #	Number mothers	Number seeds	Spatial distribution	Cited justification
1	>50	10,000 + Total	"equally and randomly across the extent of the population"	Brown and Marshall (1995)
2	>50	–	"clusters of five (5) individuals separated by at least 25 feet"	Brown and Marshall (1995)
3	>50	10–20 seeds per mother	"throughout the population-avoid biased collection by location and phenotype"	–
4	50	20–30 seed per mother	–	Brown and Marshall (1995)
5	>50	10,000 + Total	"equally and randomly across the extent of the population" AND "throughout its dispersal season"	Brown and Marshall (1995)
6	50	~1000 seeds per tree	"at least 10 locations that are at least 1 mile apart" AND "Individual seed trees should be spaced preferably at least 300 feet, and not less than 100 feet apart"	FAO (1995)
7	>10	–	–	–
8	>20	–	Including "different growth forms"	Broome (2003)
9	15–25	–	"isolated trees or groves should be avoided because of the possibility of non-viable seed resulting from poor pollination or the possibility of excessive in-breeding"	–
10	>15	–	50–100 m between trees or clumps of trees	–
11	>50	500–10,000	"well-spaced individuals"	Falk and Holsinger (1991)
12	>3	>15 total seeds	–	Griffith et al. (2011)
13	200–300	1–4 seeds from each	"sampling should include representatives from any distinctive microhabitats in a site (e.g. topographical features or soil heterogeneity)"	Yonezawa (1985)
14	50–100	–	"sample individuals at random in each site"	Brown and Marshall (1995)
15	>50	10,000–20,000 is ideal; 500 viable is minimum	sample from large number of habitats, soil types, plant communities; stratified random; sample through whole season	Brown and Marshall (1995)

assumption of probability-based guidelines is that collections can and will capture a random subsample of the target population ([Lockwood et al., 2007](#)). Real-world collections are unlikely to be truly random due to several biological and logistical factors, and may therefore capture less diversity than predicted under naïve models. Two such factors are (1) non-random choice of plants to sample seeds from, combined with an underlying non-random spatial distribution of diversity on the landscape, and (2) shared ancestry among seeds from a chosen maternal plant.

Principally, sampling conditions and resources are often non-ideal ([Bamberg et al., 2010](#); [Oyler-McCance et al., 2013](#)) due to limited time, funds, or accessibility. Chosen plants might be spatially biased (e.g. near a trailhead, along roadsides, or at easily accessible elevations). Crucially, if the allelic diversity is also not distributed randomly in space, a spatially biased sampling strategy may also be genetically biased, neglecting the subset of diversity in un-sampled areas. Indeed, most plant populations show some nonrandom spatial distribution of alleles (spatial genetic structure, or SGS), due to low dispersal and clustering of related individuals ([Dick et al., 2008](#); [Sagnard et al., 2010](#); [Hoban et al., 2014](#)). Consequentially, proximal individuals may share substantial genetic material, while distant individuals harbor dissimilar alleles. Practically speaking this means that collecting from nearby individuals (e.g. those along a roadside) could result in a collection having many repeated copies of particular alleles, while omitting other alleles, and thereby capturing fewer distinct alleles than random sampling.

In addition, multiple seeds sampled from a given maternal plant will share genetic material due to several facets of plant mating system and reproductive biology. First, as pollen dispersal is limited in many species, multiple seeds from a given maternal plant may share a common paternal parent (making them full-siblings) or may have distinct but related (to each other or to the maternal parent) paternal contributors, as clustering of relatives is common in plants ([Heuertz et al., 2003](#)). Second, even if each paternal parent (pollen donor) is unique and unrelated, multiple seeds from a maternal plant will be half-siblings, sharing on average one-fourth their alleles. Third, self-pollination may occur, causing highly overlapping genetic material among seeds. For these reasons, a second seed gathered from a given maternal plant will likely add fewer unique alleles to the collection than the first seed

did, while further additional seeds may have rapidly decreasing probability of adding new alleles. Common probability-based recommendations dictate only a minimum "sample size" ([Brown & Marshall, 1995](#); [Lawrence et al., 1995](#); [Lockwood et al., 2007](#)), and guidelines differ in the suggested number of seeds per maternal plant ([Table 1](#)).

Thus previous guidelines likely misestimate, to some unknown degree, the expected allelic capture of real-world seed collections. Indeed, considering that multiple biological and logistical factors could affect the number of unique alleles collected, it is remarkable that seed-collection guidelines generally do not quantitatively account for the target species' life history, reproductive biology, or sampling arrangement ([Griffith et al., 2015](#)). This is particularly remarkable considering that a conceptual framework regarding the importance of biological knowledge to guide collections was developed more than two decades ago ([CPC, 1991](#); [Guerrant et al., 2004](#)). For example it has been noted in a general way that larger collections may be needed in some situations (e.g. high self-pollination), but there have not yet been developed quantitative protocols accounting for this knowledge of plant genetics and ecology ([Guerrant et al., 2015](#); [Hoban et al., 2015](#)). In addition, some sampling recommendations include spatial aspects (e.g. maternal plants should be separated by >100 m ([Guerrant et al., 2004](#); [Rogers and Montalvo, 2004](#); [Echt et al., 2011b](#))). Still, many protocols rely on [Brown and Marshall \(1995\)](#)'s suggestion of 50 samples, and few custom-tailor protocols for a species or situation ([Table 1](#)). It is possible that collectors remain unmotivated to make such considerations because the relative importance of these spatial and biological factors to a real-world conservation collection has not been quantified in any study, and it is not known whether current protocols need modification. A quantitative evaluation of the performance of realistic spatial sampling strategies and sampling intensities (numbers of maternal plants and seeds) under realistic models of spatial structure could help collectors determine when randomized collection strategies are worth the additional effort, what biological factors are most important to consider when planning collections, and how many seeds to collect from each sampled plant ([Griffith et al., 2015](#); [Hoban et al., 2015](#)).

Analytical models are one approach to quantify sampling strategy performance under simple conditions. For example, previous

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