

Limits to Local Sourcing in Herbaceous Plant Restoration

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ABSTRACT

The appropriate collection zone for seeds and transplants is a key concern for plant restoration ecology, with local sourcing thought to be the “gold standard.” Local sourcing is based on the premise that most plant species are genetically adapted to the local environment through the action of natural selection, and that non-local ecotypes will disrupt this adaptation. However, a number of factors may allow practitioners to expand sourcing. These include genetic variation that is non-adaptive, phenotypic plasticity, climate change, disturbance, and a host of practical issues. These factors are reflected in the range of collection zone protocols that have been developed by practitioners, ranging from local sourcing to bypassing species identity in favor of function. In addition, phenotypic plasticity, because it allows a single genotype to produce different phenotypes in response to environmental variation, may also allow for a broadened collection zone. Little is known about the degree of genetic variation and local adaptation for most plant species. More evidence-based sourcing could result from collaboration between researchers and practitioners, including tracking seed and plant sources, their performance at restoration sites, and conducting reciprocal transplant studies. Inferring the degree of gene flow based on morphological characters has also shown some promise for inferring genetic variation among populations. Research that includes more robust sampling of populations within species would lead to more precise estimates of gene flow in relation to plant traits.

Keywords: genotype, local ecotype, phenotypic plasticity, seed sourcing

Restoration Recap

- Local sourcing has been the “gold standard” for obtaining plant material for restoration, and continues to have a place in restoration protocols.
- Genetic and ecological considerations, as well as practical issues suggest that in many cases sourcing can be expanded beyond a strictly local scope. This is reflected in the wide range of sourcing protocols used by restoration practitioners.
- Restoration sites are well-suited for incorporating research that can help answer questions related to genetic variation, local adaptation, phenotypic plasticity and how these may vary with plant traits related to gene flow, and ultimately provide the basis for more evidence-based sourcing.

The Case for Local Sourcing

Local sourcing is based on the premise that most plant populations are genetically adapted to their local environment through natural selection acting on genetic variation (Breed et al. 2013). Specifically, local ecotypes are defined as genotypes that perform better at their home sites compared to distant sites (Linhart and Grant 1996, Hufford and Mazer 2003, McKay et al. 2005). If natural selection

leads to most plant species developing local ecotypes, using non locally-sourced material in restoration projects may disrupt local ecotypes through outbreeding depression and genetic swamping.

The offspring of crosses between local and non-local genotypes may result in outbreeding depression, manifest in two ways. First, crosses between local and non-local genotypes may result in offspring with intermediate genotypes that do not perform as well as the local parent genotype, resulting in, for example, reduced seed production or reduced fitness of the progeny (Hufford and Mazer 2003, McKay et al. 2005). Secondly, outbreeding depression may be manifest in the breakup of co-adapted gene complexes, defined as genes from multiple loci that interact and result

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in greater fitness, where, again, crosses may underperform compared to local genotypes (Hufford and Mazer 2003, McKay et al. 2005). At the opposite end of this spectrum, a highly successful non-local genotype could perform too well, or swamp local populations either numerically or in fitness advantage, resulting in loss of genetic diversity in the local population (Falk 2001 et al., Handel et al. 1994, Hufford and Mazer 2003, McKay et al. 2005).

Formation of locally-adapted ecotypes requires at least four conditions: 1) that there is genetic variation, 2) that different genotypes have different relative levels of success or fitness, 3) that the direction of selection is strong, consistent and cumulative (Bazzaz and Sultan 1987, Kawecki and Ebert 2004), and 4) that gene flow is insufficient to homogenize the population (Falk et al. 2001, Loveless and Hamrick 1984). In their review of cases involving small-scale genetic differentiation (less than 1 m to 1000 m), Linhart and Grant (1996) highlighted differentiation associated with human-caused environmental conditions such as toxic soils (e.g., mining, heavy metals, chemicals), fertilizers, herbicides, mowing, and grazing, as well as salt, wind, and strong gradients of moisture, temperature and elevation, herbivory, and predation and parasitism. They concluded that this variation could be attributed to natural selection, though they did not use the term local ecotype to describe this outcome.

In addition, a more conservative or local collection zone has been recommended for species that have low gene flow, which is associated with increased among-population genetic divergence (Loveless and Hamrick 1984, Falk et al. 2001). Traits associated with low gene flow include self-fertilization and gravity dispersal (Loveless and Hamrick 1984). Low gene flow can also occur in species that are rare, endemic, occur in an historically fragmented landscape, or are part of an old and stable landscape, and that may, therefore, also require local sourcing (Loveless and Hamrick 1984, Havens et al. 2015).

The Case for Expanded Sourcing: Genetic, Ecological and Practical Factors

Non-Adaptive Genetic Factors

Genetically distinct populations can also arise from processes that are not related to natural selection and adaptation (Hufford and Mazer 2003, Kawecki and Ebert 2004). The resulting among-population genetic differentiation cannot, therefore, be considered adaptive to the local environment (Hufford and Mazer 2003, Kawecki and Ebert 2004). Non-adaptive genetic processes include genetic drift, the random fluctuation of allele frequencies in small populations (reviewed by Heywood 1991, Hufford and Mazer 2003), and founder effects, where a new population is founded by a few individuals representing a small portion of the original population's genetic

variation, ultimately leading to differentiation between the two populations (Falk et al. 2001, Hufford and Mazer 2003). In sum, even when among-population genetic variation has been detected, it does not always result from selection and translate into the superior performance of local versus non-local genotypes (Bishoff et al. 2010).

Phenotypic Plasticity

Phenotypic plasticity, defined as the capacity for the same genotype to produce different phenotypes under different environmental conditions (Sultan 1987, Bazzaz and Sultan 1987), may fully or partly mask genetic variation (Kramer et al. 2015, de Villerereuil et al. 2016, Altrichter et al. 2020). Research suggests that plasticity is pervasive among plant species (Bradshaw 1965, Bazzaz and Sultan 1987, Sultan 1987, Berg and Ellers 2010, de Villemereuil et al. 2016, Sultan 2017, Yurkonis and Harris 2019) and has been described as “one of the most common phenomena characterizing the living world” (Pigliucci 2005). For example, a common plant response to low light is to produce large leaves in order to maximize surface area for light capture, while decreasing leaf thickness (Sultan 2003 and references therein).

Plasticity arises when plant species experience environmental conditions that are both variable and unpredictable in time and space, so that rather than strong and consistent selection pressure, there is variation in the direction and strength of selection (Sultan 1987, Bazzaz and Sultan 1987, Kawecki and Ebert 2004). Important sources of this variation include nutrients, temperature, light, moisture, herbivores, maternal effects, and other plants (Schlichting 1986, Bazzaz and Sultan 1987, Sultan 2017). As a result of this variation, no single genotype produces a consistently favored phenotype that is then favored by selection (Sultan 1987).

Although not often considered in the restoration literature (but see Golay et al. 2013, Kramer et al. 2015, Altrichter et al. 2020), plasticity research is receiving renewed attention among researchers in ecology, evolutionary genetics, evolutionary development and related fields (Bossdorf et al. 2008, Ellers and Stuefer 2010, Sultan 2017, Baker et al. 2018). Specifically, studies at the molecular and developmental level are revealing that genes themselves respond in complex ways to environmental cues. For example, environmental cues can turn regulatory genes off and on and alter hormonal and developmental feedback loops, which can in turn alter the phenotype of ecologically significant traits such as flowering time, leaf size and structure, and root diameter and depth (Bossdorf et al. 2008, Sultan 2010, Baker et al. 2018). In short, plasticity is now viewed as a general property of organisms that arises by complex interactions between the genome and environmental cues (Sultan 2017).

Climate Change

There is growing recognition of the need to give restored plant populations resilience in the face of changing climate, and that local populations may not have the genetic variability to adapt to these changing weather patterns (Johnson et al. 2004, Breed et al. 2013, Handel 2013, Havens et al. 2015, Bucharova et al. 2019). The long-term resiliency of restored populations may be addressed by a regional collection approach that ensures a diversity of genotypes are introduced to restoration sites (Saari and Glisson 2012, Herman et al. 2014, Bucharova et al. 2019), or even purposefully moving populations beyond their current range (predictive provenancing) in order to be proactive in response to climate change (Havens et al. 2015).

Disturbance

If restored sites are highly altered or degraded by disturbance, local sourcing may not be called for because locally-adapted populations may not be available, or are no longer suited to the altered environmental conditions associated with highly disturbed sites (Lesica and Allendorf 1999, Jones and Monaco 2007, Breed et al. 2013, Havens et al. 2015), particularly when the disturbance is both intense and extensive (Lesica and Allendorf 1999). The potential for local populations that remain after such disturbances to be inbred or bottlenecked is also a concern (Breed et al. 2013). Instead, recommendations are for a regional collection approach similar to the approach above with climate change (Lesica and Allendorf 1999, Havens et al. 2015).

Practical Challenges to Local Sourcing

While local ecotype seems straightforward in concept, practitioners have found it challenging to use in many on-the-ground restoration projects (Saari and Glisson 2012, Altrichter et al. 2017). One challenge is lack of a definition or agreement on what constitutes “local”. Plant species vary widely in distribution of genetic diversity (Falk et al. 2001), with the implication that collection zones will be species-specific (Havens et al. 2015). However, we don’t know the actual distribution of genetic diversity for most species (Millar and Libby 1989, Johnson et al. 2004, McKay et al. 2005, Saari and Gleason 2012, Herman et al. 2014, Havens et al. 2015), and practitioners must make sourcing decisions in the face of this uncertainty. The question can be succinctly summarized as “How local is local?” (McKay et al. 2005). For example, variation in what is considered local was evident in a survey of restoration practitioners in the Chicago, U.S. region, where practitioners defined local ranging in scale from “within a county border,” “between 20–25 miles,” to “on-site” (Saari and Glisson 2012).

Other practical concerns include lack of local source populations for many species of interest in restoration or, when source populations are available, low seed production for species of interest (Houseal and Smith 2000, Saari and

Glisson 2012, Herman et al. 2014, Altrichter et al. 2017, Breed et al. 2018, Harrison et al. 2020). Quantities of local seed may also be limited because lack of demand for local material makes it economically infeasible for growers to invest in production (Herman et al. 2014, Altrichter et al. 2017). This is especially the case for rare or uncommon species (Herman et al. 2014, Havens et al. 2015). Lack of local source material has led to cancelled restoration efforts (Saari and Glisson 2012), has required seeding to be phased over several years (Houseal 2008, Breed et al. 2018), or resulted in high seed costs (Herman et al. 2014, Altrichter et al. 2017, Harrison et al. 2020).

High demand for seeds can also lead to shortages (Breed et al. 2018, Harrison et al. 2020), particularly for restoration projects following wildfire or other large scale disturbances (Harrison et al. 2020). In addition, the seed that is available may not represent the range of genetic characteristics found in the wild, and therefore may not be suitable for the wide range of projects where they are needed (Harrison et al. 2020)

Collection Zone Implications

Given the issues described above, and given the lack of information on the nature of genetic variability and local adaptation for virtually every species that could be included in restoration projects (Millar and Libby 1989, Johnson et al. 2004, McKay et al. 2005, Saari and Gleason 2012, Herman et al. 2014), it is not surprising that there is a wide variety of sourcing policies among restoration workers. This variety also reflects how highly debated sourcing policies have been (Falk et al. 2001, Burton and Burton 2002, Saari and Glisson 2012). However, rather than being considered a problem or a source of controversy, an alternative viewpoint may be to see flexible policies as a way to avoid a one-size-fits-all approach, and to give practitioners the ability to vary policies according to the factors above, as well as by habitat type, project goals, seed availability and other factors (Saari and Glisson 2012). In fact, practitioners frequently mention the need for flexibility (Jones and Monaco 2007, Saari and Glisson 2012, Herman et al. 2014, Altrichter et al. 2017).

Collection Zone Approaches

I include the approaches below not as an exhaustive list of sourcing strategies, or to evaluate the pros and cons of each, but to illustrate how wide ranging strategies and their rationales can be (see Havens et al. 2015 for a comparison of the benefits and risks of five sourcing strategies ranging from local to predictive provenancing, e.g., range expansion).

- 1) Local approach: This approach limits seed collection to an area on-site or “near” the restoration planting site (Hufford and Mazer 2003, McKay et al. 2005),

although, as noted above, there is no single criteria for what constitutes “local.”

- 2) Ecological or environmental distance approach (Bower et al. 2014): This approach seeks to source plant material from regions with similar environmental conditions. For example, temperature and moisture data have been used to divide the United States into 64 zones (Bower et al. 2014). In another example, the long-standing Iowa Ecotype Project divides the state into three zones based on the differences in rainfall from north to south (Houseal and Smith 2000). Including sufficient genetic diversity to adapt to climate and other environmental changes may also be a component of the ecological distance approach (Houseal 2008, Herman et al. 2014).
- 3) Adaptive genotype or fine-tuning approach (Burton and Burton 2002): This approach centers on the goal of including a diversity of genetic material, rather than minimizing genetic variation. It is based on the fact that well-mixed genotypes have long resulted from historical events, such as glaciation, biome shifts, climate change and altered disturbance regimes (Yurkonis and Harris 2019). By including source material beyond the local site, over time the site will filter or “select” appropriate genotypes, thereby giving species the opportunity to respond to climate change and other stressors (Falk et al. 2001, Burton and Burton 2002, McKay et al. 2005, Yurkonis and Harris 2019).
- 4) Restoration gene pool (RGP) concept (Jones and Monaco 2007): This is a hierarchical approach that combines local, regional and even broader approaches. With this approach the collection zone depends on availability of source material and the degree of damage to the ecosystem or the “stress” it is under. RGP can range from a “primary gene pool” (restoration site or genetically connected metapopulation) up to a “quaternary gene pool”, which includes species other than the desired taxon but are similar in life form and function (Jones and Monaco 2007).
- 5) Phenotypic plasticity: Plasticity does not represent a stand-alone sourcing strategy, but it likely has implications for sourcing (Kramer et al. 2015, Breed et al. 2018, Altrichter et al. 2020) because it has the potential to increase the size of collection zones. For example, in my work in central Iowa, U.S., I could detect genetic differences between individuals from a local population and those from a population 250 km distant, but three years following transplantation in one region these differences disappeared (trait measurements converged) as phenotypic plasticity allowed both local and non-local populations to adjust to the environment (Sultan 1987, Altrichter et al. 2020). In short, if, due to plasticity, plants are able to express the appropriate phenotype required by differences in

environment between the source and restoration site, then it would be possible to source from a larger geographic area (Kramer et al. 2015, Breed et al. 2013, Altrichter et al. 2020). It should be noted that the degree to which this may expand sourcing zone size will require applied research efforts (see below).

There are also other proposed approaches, but the examples above cover a span of strategies from local sourcing to inclusion of species not native to the restoration site but considered functionally equivalent. To help define sourcing protocols, practitioners also use experience, knowledge of plant species and species biology, restoration goals and priorities, budget, site conditions and quality, location of sites relative to native populations, state and county lines or a pre-set maximum distance, trusted authorities and professional training (Jones and Monaco 2007, Saari and Glisson 2012, Breed et al. 2013, Bower et al. 2014, Herman et al. 2014, Altrichter et al. 2017).

A Way Forward: Collaboration between Research and Restoration

The literature frequently notes that we lack knowledge about the scale and degree of genetic variation and local adaptation for most species, and therefore, the size of seed collection zones (Millar and Libby 1989, Johnson et al. 2004, McKay et al. 2005, Saari and Gleason 2012, Herman et al. 2014, Havens et al. 2015). Ongoing restorations are frequently noted as the most feasible option for developing more evidence-based sourcing guidelines (Millar and Libby 1989, Rice and Emery 2003, McKay et al. 2005, Saari and Glisson 2012, Golay et al. 2013). Practitioners effectively “test” (albeit uncontrolled and unreplicated tests) the suitability of various transfer zones each time sourcing decisions are made (McKay et al. 2005, Kramer et al. 2015).

If we documented sources of seeds and transplants, tracked the location of plants at restoration sites, and monitored survival and comparative performance of fitness-related traits, we could potentially develop sourcing protocols based on performance of plants collected both near and more distant to the restoration site (Millar and Libby 1989, Saari and Glisson 2012, Golay et al. 2013, Havens et al. 2015).

We could also obtain data on genetic variation and phenotypic plasticity through reciprocal transplant studies (e.g., common garden studies located at both the local and non-local site) incorporated into restoration sites (Hufford and Mazer 2003, Kawecki and Ebert 2004, de Villemereuil et al. 2016). If local plants outperform non-local plants, then we can conclude that there is evidence for local adaptation (also often referred to as home-site advantage) (Hufford and Mazer 2003, de Villemereuil et al. 2016). In contrast, if the relative performance of local and non-local plants shows yearly variation in response to environmental

conditions, or initial genetic differences converge over time we can conclude that we are observing morphological characters that change plastically (Altrichter et al. 2020).

While fruitful, to incorporate research and monitoring into restoration projects can be a time and labor intensive process (Millar and Libby 1989, Saari and Glisson 2012), and limited funding and staffing impose barriers for many organizations (Dettman and Mabry 2008). Greater collaboration between researchers and practitioners may be a way forward. For example, researchers could develop an experimental design template of a common garden study, removing the need for practitioners to decide on planting arrays, sample sizes, what traits to measure and how to analyze the data.

The extent of gene flow is not known for most species (Breed et al. 2013), but one hope is that plant traits related to it could be used to help guide sourcing strategy (Herman et al. 2014, Mabry 2017). In an extensive review, Loveless and Hamrick (1984) found that traits related to low gene flow were associated with among-population genetic differentiation, particularly self-fertilization, pollination by small bees, gravity dispersal, and asynchronous flowering phenology (Loveless and Hamrick 1984). For many species there can be substantial variation in outcrossing rates and therefore in gene flow because estimated rates have been based on just one or two populations (Whitehead 2018). Research that includes more robust sampling of populations within species may lead to more precise estimates of the extent of gene flow in relation to plant traits and other attributes.

Conclusion

Local sourcing is based on the premise that natural selection produces locally-adapted populations at relatively small scales, and is intuitively appealing with its clear prescription. As restoration has matured as a field, however, strictly local sourcing has become less scientifically supported. We have also learned more about how sourcing interfaces with other genetic and ecological considerations, along with more practical facets of restoration projects. These factors have widened sourcing perspectives, but have also raised dilemmas and uncertainties about how to source. The community of researchers and practitioners are grappling with these, and are addressing them. One way to view the current state of affairs is as analogous to medicine. Both are concerned with complex systems, with complex interactions among the parts of the system, and without all interactions even known. Both are a combination of science and “art”, in that we use the best science that we have, but we also must use judgement because we don’t have all the science that we need, and we have pragmatic constraints of logistics and budgets, along with meeting variable goals of projects, individuals, and sites.

Acknowledgments

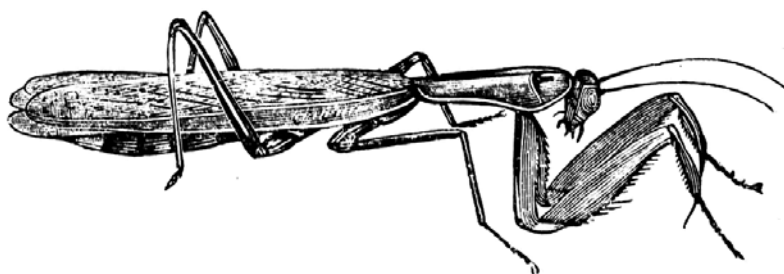
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The praying mantis is named for the posture it assumes when watching for prey. Source: Worthington Hooker, *Natural History* (New York:Harper and Brothers, 1882), The Florida Center for Instructional Technology, fcit.usf.edu.