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One hundred years into the study of ecotypes, new advances are being made through large-scale field experiments in perennial plant systems

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Abstract

A hundred years after Turesson first clearly described how locally adaptive variation is distributed within species, plant biologists are making major breakthroughs in our understanding of mechanisms underlying adaptation from local populations to the scale of continents. Although the genetics of local adaptation has typically been studied in smaller reciprocal transplant experiments, it is now being evaluated with whole genomes in large-scale networks of common garden experiments with perennial switchgrass and poplar trees. These studies support the hypothesis that a complex combination of loci, both with and without adaptive trade-offs, underlies local adaptation and that hybridization and adaptive introgression play a key role in the evolution of these species. Future studies incorporating high-throughput phenotyping, gene expression, and modeling will be used to predict responses of these species to climate change.

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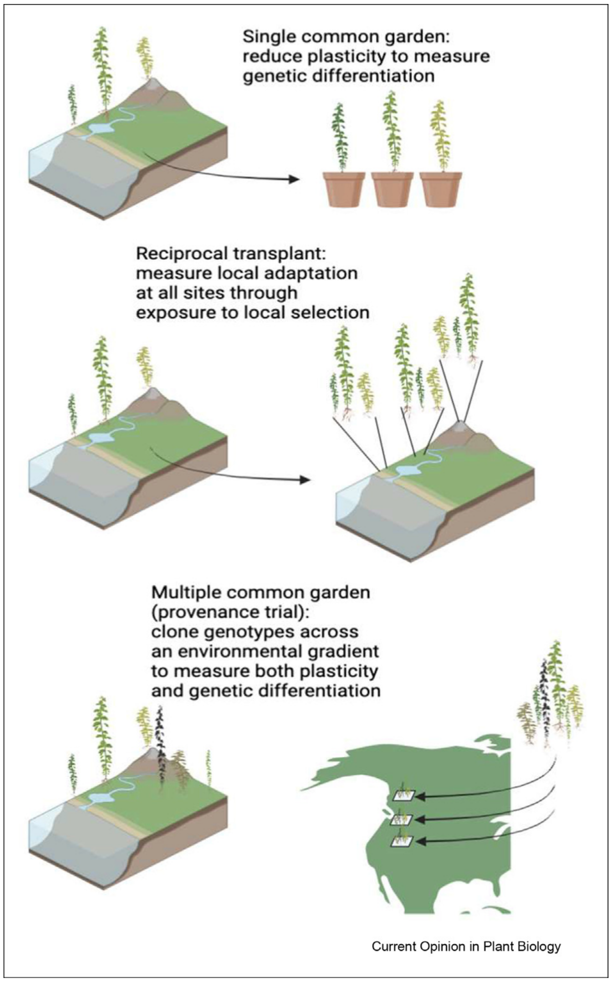
Introduction

One hundred years ago, Swedish botanist Göte Turesson [1] reported a series of observations from common garden experiments in which he found that plants of the same species collected from different habitats had distinctive genetically based differences in morphology and growth form [1]. Turesson cogently argued that the differences among populations were the result of natural selection, which was a rejection of the Lamarckian paradigm that dominated the literature up to that point [3–7]. To more clearly communicate the phenomena, Turesson coined the term ecotype in 1922 to describe distinct groups of plant populations that are locally adapted to particular habitats. These ecotypes were identifiable by having a shared suite of genetically based traits that could be observed when grown in common garden experiments. A hundred years later, plant biologists continue to build on Turesson's legacy of understanding how natural selection shapes variation within plant species through common garden experiments [8]. In this review, we highlight recent advances in understanding plant adaptations in two perennial plant species through long-term common garden experiments and outline our perspective on where the field is headed next.

Distinguishing genetic from environmentally based variation in plant species has required a rigorous development of experimental methods in plant evolutionary ecology. Turesson's compelling intellectual arguments in his publications have earned him credit for much of the early work to measure locally adaptive variation within species. However, Langlet [9] correctly pointed out that provenance trials in the field of forestry, which examine the relationship between ecology and genetics (genecology), had long recognized within species adaptive genetic variation, even if those studies had not clearly articulated their findings in an evolutionary context. Provenance trials consist of planting common gardens at multiple locations along environmental gradients to assess the relationship of fitness to distances from a home environment (Figure 1). In the middle of the 20th-century, Clausen, Keck, and Hiesey [10,11] combined

Figure 1



Three types of experiments that test different aspects of local adaptation. Poplar icons represent genotypes.

Turesson's ecotype concept with provenance trials across California to establish reciprocal transplant experiments as the gold standard for testing whether ecotypes are locally adapted to their home environments.

Today, common garden experiments have entered the population genomic era, as whole-genome data sets are becoming increasingly available for accessions planted in geographically widespread common garden experiments. A number of annual and short-lived perennial plant systems, including *Arabidopsis*, *Mimulus*, and *Boechera*, have begun to bring reciprocal transplant common garden field studies into the genomic era [12–14]. Here, we focus on two long-lived perennial systems, switchgrass (*Panicum*) and poplar trees (*Populus*), where larger networks of multiyear common gardens are being used to gain a more comprehensive understanding of local adaptation across geographic space. The results from these two systems illustrate current and emerging approaches to understanding locally adaptive allelic variation that is distributed on the scale of continents.

Understanding the role of fitness trade-offs in local adaptation in switchgrass

Switchgrass, *Panicum virgatum*, is a large perennial North American grass species that has a native range from Central America to southern Canada [15,16]. Across this range, switchgrass exhibits a wide array of genetic variation and adaptive phenotypes. Recent common garden research has leveraged a strategically constructed quantitative trait locus (QTL) mapping population and a large diversity panel to understand the genomics of adaptation from South Texas to South Dakota [17,18]. This recent work builds on historical efforts by forage grass researchers, who have long recognized that there are striking patterns of local adaptation of switchgrass across North America. Classic common garden research by Calvin McMillan [19,20] in Nebraska and Texas found strong patterns consistent with local adaptation along a latitudinal gradient stretching across the length of the Great Plains. In addition to these clinal patterns of adaptive variation, other researchers found evidence that there are several distinct ecotypes of switchgrass that likely originated through geographic isolation into distinct refugia during glaciation. Researchers generally recognized two major switchgrass ecotypes, upland and lowland. The lowland ecotype was generally associated with wetter riparian habitats in the southern United States (US), whereas the upland ecotype was thought to primarily occur in more northern regions and typically drier habitats. In the central US where these ecotypes co-occur, Porter [21] conducted a series of experiments to demonstrate strong physiological divergence between the upland and lowland ecotypes. Thus, adaptive genetic variation in switchgrass is distributed both along environmental gradients correlated with latitude and as a mosaic of more discrete ecotype variation [16].

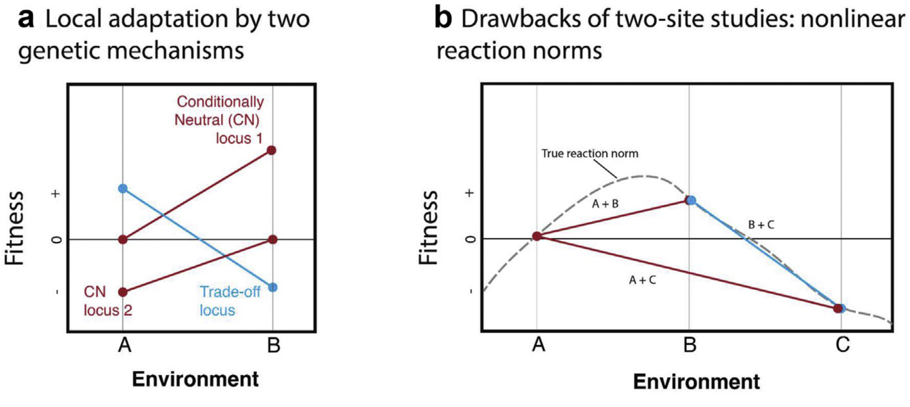
The strength of the switchgrass system in the study of ecological genetics lies in the construction of large-scale, replicated experiments. Although McMillan and Porter were able to document morphological differentiation that seemed to be adaptive across the species, modern studies have sought to directly link ecotypic variation to underlying genetic loci. To understand the genetic architecture of local adaptation between northern upland and southern lowland ecotypes, researchers developed genetic mapping populations derived from crosses between upland and lowland germplasm [22,23]. One of these upland × lowland mapping populations was clonally divided through vegetative propagation and planted into 10 field sites spanning 17 degrees of latitude from South Texas to South Dakota and Michigan in 2015 [17]. This experimental design resulted in the exact same set of genotypes being planted across 10 different environmental conditions, allowing for a comprehensive analysis of the genotype, environment, and genotype × environment contributions to trait variation and fitness. This experiment has facilitated QTL analyses across all of these sites to understand how the genetic architecture of trait variation and fitness changes across space [24–27].

Critically, the network of common gardens has allowed researchers to rigorously test a long-held prediction of evolutionary theory: that local adaptation is the result of fitness trade-offs at the individual genetic locus level [28–30]. This theoretical work suggested that the loci involved in adaptation should exhibit a fitness advantage in their home environment but a fitness cost in a foreign environment (Figure 2a), leading to increased phenotypic differentiation among habitats. However, recent studies have indicated that not all loci underlying local adaptation exhibit fitness trade-offs [31]. Most of these studies only used two field sites in a single year, which means that the lack of trade-offs could be the result of failure to measure a sufficient proportion of climate space where trade-offs might manifest (Figure 2b). With the switchgrass common garden network replicated at many sites, it was possible to determine the extent to which there are trade-offs at individual loci. Although this work detected a few loci with clear trade-offs across space, there were many more loci that had effects on biomass in one geographic region with nonsignificant effects in other regions [17]. Thus, some combination of trade-offs and conditional neutrality is responsible for the overall patterns of local adaptation, a pattern that also has been observed previously in two-site reciprocal transplant experiments [31]. Furthermore, using perennial plants for these studies provides the important context of temporal variation in selection pressure, which may be essential to understanding adaptation under climate change.

Although QTL mapping populations are powerful tools to understand the impacts of genetic loci on traits and fitness, genome-wide association studies (GWAS) offer improved precision to identify individual causal genes owing to a high number of natural recombination events [12,32,33]. To further elucidate the complement of genes contributing to local adaptation in switchgrass, researchers established a new set of common garden experiments with a diversity panel at 10 field sites (only one site was different from the study by Lowry et al. [17]) in North America and three sites in Mexico (spanning 24° of latitude) in 2018 and 2019 (Figure 3) [18]. This diversity panel is composed of 732 tetraploid genotypes of switchgrass collected from across eastern North America and clonally propagated at each field site.

As expected, the diversity panel revealed a strong signal of local adaptation, with lowland genotypes generally having higher biomass at southern field sites, whereas the upland genotypes displayed the opposite pattern [18]. Winter kill in the north has been by far the largest source of mortality in the experiment. Overwinter survival has long been known to be important in switchgrass, but it recently received increased research attention owing to it being a primary factor limiting the planting of highly productive southern lowland bioenergy cultivars in the northern US [34–38]. Many candidate genes underlying adaptive trait variation, including overwinter survival, were revealed through

Figure 2



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Detecting the genetic basis of local adaptation. (**a**). Two ways that loci can produce local adaptation: single trade-off locus increases fitness in one environment while decreasing it in another (blue reaction norm); two conditionally neutral loci can each have effects in only one environment but combine to form a local advantage (red reaction norms). (**b**). Nonlinear reaction norms can result in studies misinterpreting local adaptation patterns. In this scenario, the trade-off for the locus will only be detected if environments B and C are sampled (blue line), owing to an underlying nonlinear reaction norm (dashed gray line).

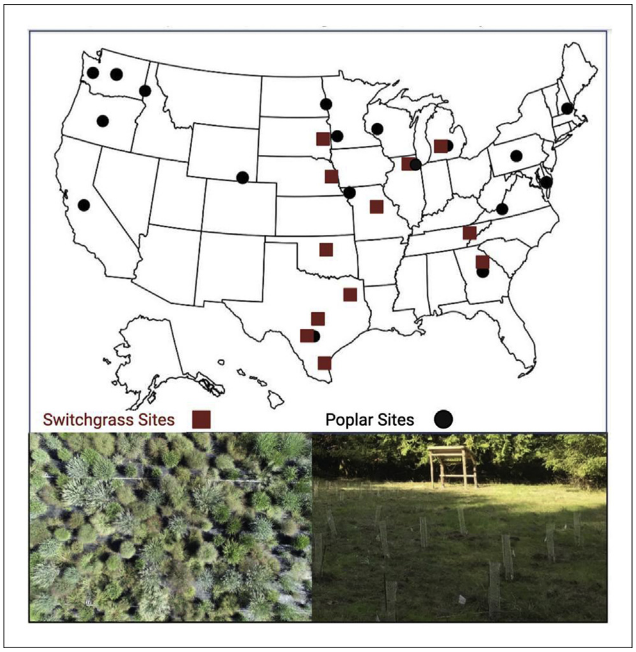
Figure 3

Representative samples of each recognized switchgrass ecotype. Bars indicate 1 m. From Lovell et al. [18].

GWAS. Further understanding of these fitness-related genes will facilitate future gene-editing efforts powered by advances in switchgrass *Agrobacterium*-mediated transformation [39,40].

One of the key results of genome resequencing in the tetraploid diversity panel was that patterns of population genetic structure were discordant with the morphological clustering of plant accessions into ecotypes [18]. Incorporating switchgrass from the eastern US revealed a third 'coastal' ecotype in addition to the previously recognized upland and lowland ecotypes (Figure 4). Population genomic analyses similarly identified three major groups, but these were surprisingly discordant from the morphological ecotypes. This finding contradicts the assumption that ecotypes exist as structure groups, where both structure in trait variation and population genetic structure are inexorably correlated across geographic space [41]. Of particular interest, numerous genotypes with the upland ecotype from the northeastern US clustered with the genetic group containing the new coastal ecotype. Haplotype-level analyses revealed regions of introgression from the mostly upland population into the mostly coastal population and further that these introgressed regions were enriched for GWAS-detected loci that enhance winter survival [18]. This result suggests that adaptive introgression from the upland population allowed coastal plants to maintain fitness along the northern Atlantic coast.

Figure 4



Switchgrass and poplar common garden experiments. Locations of PopUp Poplar Network sites (black circles) and switchgrass diversity panel planting locations (red squares) across North America. At each poplar location, two replicates of 50 poplar clones of mixed genomic ancestry between *Populus trichocarpa, P. balsamifera,* and their hybrids have been planted and maintained since 2020. Inset pictures of switchgrass gardens at Kellogg Biological Station (left) and poplar at Evergreen State University (right) (Photo Credit: Robert Goodwin and Dylan Fischer).

In the coming years, the network of switchgrass common garden experiments will facilitate a better understanding of how specific abiotic and biotic environmental factors have contributed to adaptive evolution across geographic space. For example, VanWallendael et al. [24] identified two major QTLs for resistance of switchgrass to pathogenic rust fungi. Interestingly, these QTLs both have strong effects in northern sites but were rarely detected in southern sites, suggesting that genotype × environment interactions play a critical role in shaping biotic interactions across space. In addition to research on pathogens, mutualistic microbes assist with nutrient uptake and may confer additional stress tolerance in leaves [42] and are differentially partitioned across portions of roots [43]. In switchgrass leaves, the fungal microbiome is differentially partitioned across genetic populations, a pattern that may be driven by variation in plant immune response genes [44].

Populus as a model system for ecological, evolutionary, and community genomics

Forestry, more than any other field of plant science, has used provenance trials to understand the impact of seed provenance, or origin, on traits important for growth and persistence under varying abiotic and biotic environments [9,45–47]. Indeed, the field of genecology, commonly applied within forestry, largely derives from Turesson's observations of the relationship between heritable trait variation and that of the environment, serving as foundation to the contemporary field of ecological genomics [48]. Thus, understanding the relationship between genotypic and ecotypic variation across environments provides a powerful tool to predicting the health and productivity of reforested regions across space and time [49]. Provenance trials provide invaluable resources which extend our ability to assess adaptation and evaluate populations' capacity for evolution under changing climatic conditions. With the inclusion of new whole-genome data sets, extension to new statistical approaches, and the development of new phenotyping platforms, the value of provenance trials has only increased.

Populus has become a model genus for studies of local adaptation in forest trees owing to its compact genome, rapid growth, ease of vegetative propagation, and extensive natural genomic and phenotypic variation [50,51]. Extensive surveys of range-wide genomic variation in poplar species [52,53], paired with phenotypic measurements from long-term common garden experiments [54–56], have advanced our understanding of the role natural selection has played in shaping adaptive variation within and between poplar species [57–60]. In addition, *Populus* has also become a key model leading advances in breeding and functional genomics due to the propensity of its species to form natural hybrids and the degree to which hybrids often exhibit heterosis or adaptive introgression for traits valuable in cultivation [59,61–63]. Finally, poplar is a model system for community genetics — or the study of genetic interactions among species and their abiotic environment [64,65] where heritable trait variation within poplar genotypes has measurable impact on the biotic community impacting ecosystem function [65]. Thus, research using *Populus* capitalizes on its value as a keystone species to understand a species' impact across scales of biodiversity, from genes to individuals to populations and communities.

The relatively nascent nature of commercial breeding in forest trees, where many species are only one to three generations from their wild progenitors [66], emphasizes the value that natural hybrid zones provide. Natural hybrid zones circumvent much of the challenge associated with traditional breeding in long-lived species by offering natural, replicated hybrid crosses. Moreover, where ecological differences exist between hybridizing species, zones of contact provide the opportunity to directly evaluate the role natural selection has had on admixture, which in turn provides insight into the architecture of adaptation. A unique aspect of *Populus* has been the value of comparative genomics and admixture mapping within naturally replicated contact zones between two species [59,67]. Within the context of climate change, standing genetic variation generated from natural zones of introgression provides a mechanism to facilitate adaptation to novel environments [68–70]. Notably, the contact zone between *Populus trichocarpa* x *balsamifera* indicates expansion of the range of *P. trichocarpa,* which traditionally is characterized by a maritime climate has benefitted from introgression with more continental *Populus balsamifera* [59,71]. Thus, a valuable reservoir of adaptive genetic variation may be maintained within zones of introgression with natural selection structuring range-wide genomic and phenotypic variation [55,59,68,71]. Clonally replicated poplar common garden experiments have now been established at 18 distinct environments across the US as part of the PopUp Poplar Network (Figure 5; http://popup-poplars.com). These plantings sourced a latitudinal gradient of native field-collected *P. trichocarpa, P. balsamifera,* and their hybrids spanning six replicated contact zones across the Rocky Mountains, from Washington to Alaska. This model system pairs whole genome sequences, clonally replicated common gardens, and climate modeling to understand how genotypic variation, genomic ancestry, and environmental variation interact to produce phenotypic variation important to climate adaptation and hybrid breeding. This living laboratory provides an unprecedented resource to quantify the role of hybridization in evolution and adaptation, the role of natural selection in shaping quantitative trait variation, and the role interactions between abiotic and biotic factors may have on plant fitness and community and ecosystem function.

Future directions: predicting locally adaptive responses to climate change

Current studies of switchgrass are greatly advancing researchers' understanding of how individual loci contribute to the process of evolution at the scale of a continent. One of the most consequential results of this study being conducted in multiple sites and years is that it has enabled the prediction of locus-specific effects on traits and fitness in unmeasured environments. For example, Lowry et al. [17] developed models based on the QTL results from the 10 common garden locations to predict allelic effects of loci based on a suite of local environmental conditions. From this modeling effort, it was possible to construct predictive maps across central North America of where individual alleles would be most beneficial to increasing fitness. In the future, these genetic models can be integrated with climate change models to predict how additive allelic effects will shift over time [72]. This future research will complement recent work on trait and fitness predictions for switchgrass at the cultivar level [73].

A major recent advance in predicting plant evolution in response to changed or novel environments leverages spatially informed genomic data sets with genome—environment associations to predict genotype performance across future environments [74]. These predictions, which assess the degree to which genotype—environment associations are perturbed from locally adapted fitness peaks under climate change, provide an ability to forecast the impact climate change may have on fitness [74—77]. Gougherty et al. [77] recently used genes associated with the flowering time pathway in *P. balsamifera* to characterize the impact disruptions may have on the maintenance of variation necessary for persistence across the species' range. Broadly, this landscape-level assessment identified regions across the species' distribution that may lack the variation needed to adapt to change and those that may benefit from rescue via migration [77,78]. In combination with advances in machine learning, these new forecasting approaches enhance our ability to predict maladaptation to changed conditions with practical application to restoration under current and future climates [76].

Plant breeding is increasingly incorporating high-throughput phenotyping through remote sensing of multispectral and hyperspectral data using unmanned aerial vehicles and satellites [79,80]. The incorporation of remote sensing methodologies into local adaptation studies will greatly expand in the not too distant future. These approaches will help to bridge the genome to phenotype gap for applications to breeding, evaluation of intraspecific variation essential to restoration efforts, and gaining a more general understanding of the mechanisms of local adaptation [81,82]. Furthermore, gene expression analyses within hybrid mapping populations and diversity panels will usher in a new era of expression QTL studies to understand how gene regulation contributes to local adaptation. Field expression QTL mapping has already recently been conducted in a common garden experiment of a close relative of switchgrass (*Panicum hallii*; [83]). Furthermore, gene expression analyses are now beginning to be incorporated into field reciprocal transplant experiments [13,84,85]. One hundred years after Turesson [2] first clearly articulated how ecotype variation arises from natural selection driving local adaptation, rigorous experimental studies have allowed researchers to more clearly understand the role genetics play in the generation of within-species variation, but the challenge of understanding plants' response to global climate change is a reminder that we still have much to learn.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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