Landscape Genomics: An Emerging Discipline That Can Aid Forest Land Managers with Planting Stock Decisions

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The Issue

Forest land managers must frequently contend with identifying appropriate planting stock for many needs, from reforestation following harvest or disturbance, to habitat restoration and conservation plantings. Difficult enough in the best of times, such decisions are complicated today by anticipated global climate change and decades of fire protection that have altered, in some cases, our understanding of what constitutes historical species assemblages. Indeed, much thought is now being given to the concept of assisted migration, or the deliberate movement of planting stock of forest tree species far from their location of origin, to ensure species survival in the event conditions in the native range become intolerable. Regardless of the specific need, the goal of a land manager is to ensure that planting stock used for reforestation is adapted and grows well. Deciding what to plant requires an intimate knowledge of the environments intended for planting and the genetic makeup of the planting stock. The emerging field of landscape genomics may soon provide tools to aid the land manager in making those decisions.

Landscape genomics is a newly emerging discipline that combines the fields of population genetics and landscape ecology to study patterns of demographic and adaptive genetic variation across highly diverse landscapes. The science of landscape genomics is driven by the merger of rapidly developing technologies in both genomics and GIS (Geographic Information Systems). Landscape ecology has been described as the science of studying and improving relationships between ecological processes and particular ecosystems. (http://en.wikipedia.org/wiki/Ecological_geography). Genomics is the simultaneous study of an organism's complete genetic complement. With the ability to characterize genetic diversity and map environmental variation better than ever before, the science of landscape genomics promises to bring an entirely new set of precise, diagnostic tools to the land manager (Fig.1).

Before we proceed much further with the introduction of landscape genomics, it is worth taking a bit of time to reflect on the more traditional methods used to identify adapted planting stock, where tree improvement programs do not exist. While the science

Figure 1. Species assemblages develop across the landscape as a function of demographic, environmental and genetic factors. Landscape genomics seeks to identify which environmental and genetic factors most influence adaptation (Wheeler and Neale, 2013).

of landscape genomics is just developing, land managers have long sought to match planting stock to environment to ensure their forests are thrifty. These techniques found favor because of rather bad experiences with maladapted planting stock in early reforestation efforts. Today, foresters rely principally on seed zones for guiding their decisions on reforestation needs (Fig.2). Simply stated, stock used to replant a site in a given seed zone should have originated from that zone. Zones are roughly identified by geography, elevation, drainage, climate, and so forth. This approach is sure to provide planting stock with a generally accepted level of adaptation and performance, though it does not address issues that could arise due to rapidly changing environments. For that matter, trees growing across the landscape today may not even be optimally adapted to current conditions.

Figure 2. Forest tree seed zones of California.

The provenance, or common garden trial, provides a more empirical means of identifying seed sources that perform well and are adapted to various environments. Though provenance trials first appeared several hundred years ago in Europe, they were only widely adopted in America by forest geneticists in the middle of the last century and remained popular for a relatively short period of time, from about 1960 to 1980. A typical provenance trial may include seed collections from a few trees from each of many populations (e.g., 50 to 100 or more) across the species natural range. Seedlings are raised in a common nursery, and

out-planted to replicated plantations established on many field test sites, again, distributed across the species range. In some cases, such trials are exported beyond the species natural range, or even overseas. Species such as Sitka spruce, Douglas-fir and lodgepole pine, for instance, are now widely planted in the UK, Europe, New Zealand and Scandinavia as a result of such trials having identified the best sources for the new environments.

While provenance trials can be very informative they have a number of limitations. They require a great deal of time and money to plan, establish, and maintain for long periods of time. Administering these long-term projects requires a dedicated and committed staff with constant funding. Plantations need to be replicated across the landscape, reaching to extremes of the natural range, and perhaps beyond. For such reasons, provenance trials have been established for relatively few, generally highly valued, species.

The most informed decisions regarding seed source movement across the landscape are provided by intensive tree improvement programs. Extensive and expensive genetic field trials provide excellent empirical evidence of adaptability and phenotypic plasticity in varying environments. With the rapidly developing genomic resources for a few species, tree breeders are now developing a growing understanding of which genes are contributing to performance and adaptation traits. Landscape genomics seeks to extend this intimate knowledge of genetics to the full range of tree species for which breeding programs do not exist.

The Science of Landscape Genomics

Simply stated, landscape genomics attempts to explain which genetic and environmental factors play a role in how organisms adapt to their surroundings. Environmental factors like precipitation, temperature, soil chemistry, water holding capacity, insects and disease, etc., determine which tree species, and individuals within species, survive and thrive in a given environment. They do so by acting on the natural genetic variation within the species. Trees with the best combination of genes will succeed and adapt; those with less favorable combinations will eventually perish.

Consider the scenario shown in Figure 3, representing a timeline of 200 years. In this progression, a recently deforested landscape, scarred by fire, is naturally regenerated with a genetically diverse group of seedlings from one or more species of forest trees. Colors represent trees with various combinations of genes that confer more or less cold tolerance. In the beginning, they are relatively evenly distributed, as one might expect from seed
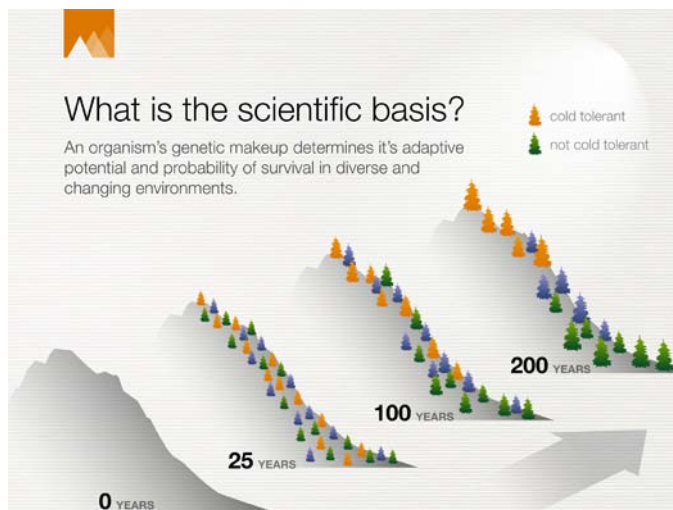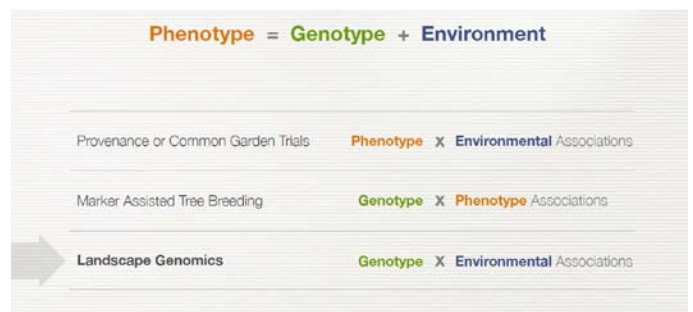
Figure 3. Hypothetical development of tree populations following disturbance (Wheeler and Neale, 2013).

distributed according to environmental variation because those traits affect fitness. All approaches have utility, and may be used in complementary fashion, but come with different costs and constraints. In contrast to genetic tests and provenance trials, costs for landscape genomics are largely front-loaded, without the burden of long-term trials. Furthermore, landscape genomics can provide basic information that would be valuable across time and space, and study of one species may lend itself to application in other species.

Figure 4. Contrasting approaches to identifying stock adapted to planting site (Wheeler and Neale, 2013).

that fies into the valley on strong winds from nearby populations. Orange trees, with gene combinations that confer cold tolerance, eventually become dominant at higher elevations while green trees, lacking cold tolerance, become dominant at lower elevations. Landscape genomic approaches can identify those suites of genes that confer adaptedness and the environmental factors driving selection.

Another way of illustrating the fundamental basis of landscape genomics is to contrast approaches to identifying adapted planting stock, with respect to the classic equation used by forest geneticists to describe the relationships between phenotype, genotype, and environment (Fig.4). The phenotype of a tree is what we can see or easily measure. It is determined by the individual tree's genotype at literally thousands of genes, and the environment in which the tree grows. Typically, phenotype has been the unit of selection. With provenance trials one seeks to identify associations between phenotypes and environments. For instance, it might tell you that trees from higher elevation, or more northern latitudes, in general, have later bud fush and are more cold hardy than those from lower elevations. By contrast, tree breeders seek to understand the association between genotype and phenotype. For traditional programs genotype is defned by pedigreed families. For intensive tree improvement programs with genomic resources such as genetic markers, breeders seek to reveal associations between specifc genes, and their alleles, with specifc phenotypes like cold hardiness. Landscape genomics differs from these approaches by seeking to identify associations between environments and genotypes, where genotypes are defned by knowledge of specifc genes and their alleles. The premise of landscape genomics is that phenotypic traits are

The scientifc goals of a landscape genomics project can be generally described by noting major steps in the experimental process. The frst step in the process is to characterize the genome of the species of interest. That is, identify all the genes, their putative function, and their genic or allelic diversity. This process, though seemingly impossible only a few years ago, is becoming increasingly tractable, both technically and fnancially. Analysis of these data will allow one to identify those genes under natural selection from environmental factors, both biotic and abiotic in nature. The next step is to characterize the spatial distribution of allelic diversity across the landscape and lastly, test for associations between tree genotypes and environmental traits tree genotypes and phenotypes. The results of these analyses may be used to predict or model which trees or populations are best suited for placement in areas requiring reforestation or restoration.

An Example

The science and application of landscape genomics may best be illustrated by example. In 2010, Eckert et al. published a paper that described how their team identifed an array of genes that appeared to be strongly associated with bioclimatic variables. The team gathered climate data from the WORLDCLIM 2.5-min geographical information system (GIS) layer and overlaid this on distribution maps of over 900 loblolly pine trees with known genotypes for over 3000 genes. Monthly minimum and maxi-

mum temperatures, monthly precipitation, and 19 other bioclimatic variables were evaluated. The temperature and precipitation data were used to estimate potential evapotranspiration (PET) and an aridity index was defned as the ratio of precipitation to PET. This was done on a quarterly basis. The pattern of aridity observed across the Southeastern United States is illustrated (Fig. 5) for the second quarter of the calendar year.

Environmental association analysis identifed fve genes associated with aridity gradients. The primary functions of gene products encoded by these loci were abiotic and biotic stress responses, as determined in previous studies. The relationships between genotypes and aridity are shown (Fig. 5) for four of the genes. The genotype is defned here by letters on the x-axis of the graphs, while the Y axis is a measure of aridity. The letters designate the combination of alleles that an individual tree possesses at a given gene. Take for example the left-most graph, showing the gene identifed as a photosystem II protein. Of the 900+ trees in the study, some proportion of them had two C alleles (CC), some, one A and one C allele (AC) and some two A alleles. Collectively those groups occurred more or less frequently in areas of differing aridity, implying they contributed to the adaptation of those trees to those sites. While no single gene contributed dramatically to adaptation to arid conditions, the cumulative effect of all genes detected can approximate the total genetic variability (additive genetic variation) in a species. The results of this study could be easily used as a basis for Marker Assisted Selection for trees best suited for more arid landscapes. Furthermore, knowledge of which genes are associated with aridity in this species can likely inform which genes should be evaluated in other species for the same trait.

Summary

Landscape genomics offers the potential for land managers to fne-tune their decision making process with regards to reforestation, habitat restoration, and conservation. The knowledge gained from the study of forest tree genomes, coupled with enhanced understanding of our changing environments and landscapes, will guide decision making for seedling deployment in a fexible, sustainable manner for broad geographic regions. Common garden trials can, and probably should be employed to validate landscape genomic prescriptions, though their drawbacks must be weighed carefully. Common garden trials are expensive and time-consuming to establish and must be maintained for many years. In situations where planting materials are drawn exclusively from seed lots obtained from local seed zones, landscape genomic tools could signifcantly improve survival and productivity in a changing landscape.

References

Eckert, Andrew J., Joost van Heerwaarden, Jill L. Wegrzyn, C. Dana Nelson, Jeffrey Ross-Ibarra, Santıago C. Gonzalez-Martınez, and David B. Neale. 2010. Patterns of population structure and environmental associations to aridity across the range of loblolly pine (*Pinus taeda* L., Pinaceae). Genetics 185: 969–982. Supporting information is available at http://www.genetics.org/cgi/content/full/genetics.110.115543/DC1.

Wheeler, N. and D. Neale. 2013. Landscape genomics [Online Learning Module]. Pine Reference Sequence. eXtension Foundation. Available at: http://www.extension.org/pages/67919
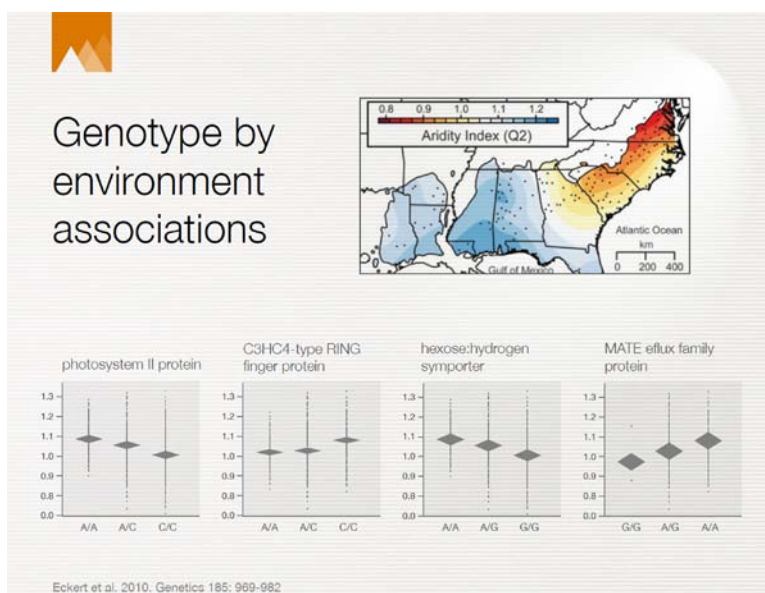
Figure 5. An example of genotype by environment associations discovered in loblolly pine (Wheeler and Neale, 2013).