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## Genecology and Adaptation of Forest Trees

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### Introduction

Genecology is the study of intraspecific genetic variation in relation to environmental conditions. It reveals patterns of adaptation of populations to their environments that result from differences in natural selection among locations. Genecological studies are conducted for the practical purposes of: (1) determining how far seed can be moved from the collection site to a reforestation site without risking maladaptation of the trees to the planting site; (2) delineating geographic breeding zones for which a single breeding program would suffice; (3) selecting optimal provenances within the native range for nonnative (introduced) species; and, more recently, (4) predicting the ability of populations of forest trees to adapt to rapidly changing climates.

To meet these objectives, seed is collected from different provenances (geographic origins) throughout all or a portion of a species range and planted in one or more field or nursery common-garden experiments. The survival and growth of trees of different provenances are observed under the same set of environmental conditions, allowing for the separation of genetic and environmental effects. Genetic variation in resistance to biotic (e.g., insects and diseases) or abiotic (e.g., cold and drought) stresses can also be observed in different environments or tested artificially. Variation among provenances is quantified and related to patterns of geographic variation in climate

or other environmental factors. Species that show a high degree of genetic differentiation among provenances require the management of genetic resources on a more local scale than those that show relatively little genetic variation. If seed for reforestation is moved too far from the environments to which it is well adapted then losses in growth, health, and survival may result. The ability of populations to adapt to climate change will depend on current geographic patterns of genetic differentiation as well as the amount of genetic variation for adaptive traits that exists within populations.

### Background

The recognition of genetic variation among populations of trees occupying different environments is not new. A full century before both Darwin's theory of evolution was published in *On the Origin of Species*, and Johann Gregor Mendel determined the mechanics of heredity, Carl von Linné (also known as Carolus Linnaeus, the father of modern taxonomy), reported in 1759 that yew trees (*Taxus baccata*) from France were less cold-hardy than those from Sweden. Around the same time, Henri Louis Duhamel du Monceau, Inspector-General of the French navy and noted botanist, established the first forest genetic trials on record. He collected seed from Scots pine (*Pinus sylvestris*) from various locations across Europe and established plantations in France in which to compare the performance of different provenances (seed origins). Later in the eighteenth century, the importance of provenance was recognized by guidelines of the Swedish Admiralty for selection of seed sources of pine and oak, and in Germany for the use of tree species introduced from North America. Similarly, the importance of using local, well-adapted provenances was recognized in Japan centuries ago.

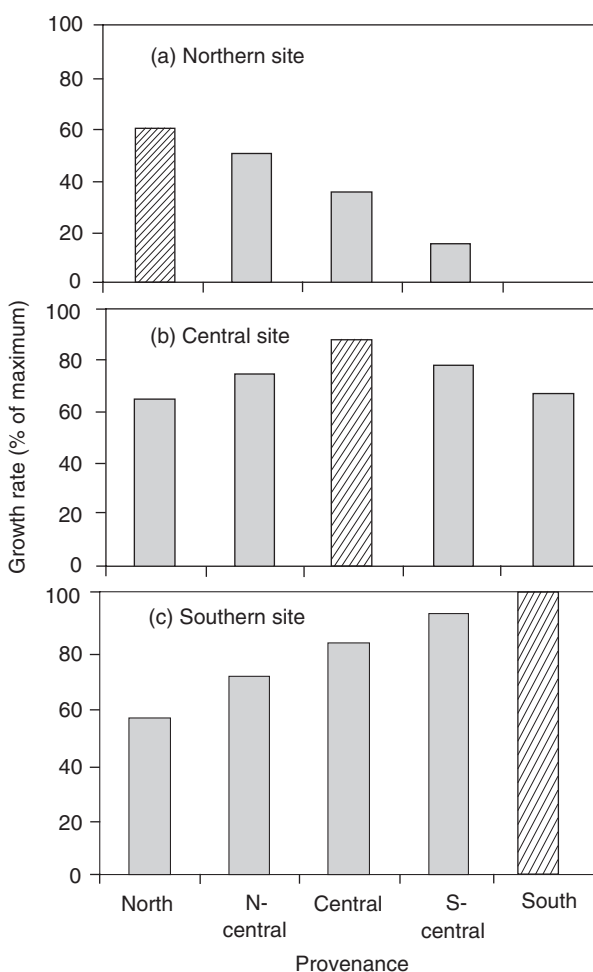
While early botanists and foresters lacked an understanding of evolution and genetics, they recognized that the survival, health, and growth of planted individuals of a tree species depended jointly on the location where seed was collected and the environment in which the resulting seedlings were planted. Maladaptation can result in slow growth, and injury or mortality due to biotic (e.g., insects, diseases, or competition) or abiotic (e.g., cold or drought) agents. When seed was planted in an environment very different or very far from the one in which it was collected, the likelihood of maladaptation was clearly high; however, nonlocal provenances sometimes outperformed local material.

Investigations of provenance variation continued through the nineteenth century, most notably for

Scots pine in France, Germany, and Switzerland, and Norway spruce (*Picea abies*) in Germany, Austria, and Switzerland. Adolf Cieslar studied variation in Norway spruce among provenances from different elevations and latitudes, and found that seed from higher latitudes and higher elevations produced slower-growing seedlings than seed from lower or more southerly locations when planted in the same location. He also suggested that the different performance of provenances was inherited.

Early provenance trials were often located in a single environment, on one site, with limited replication. Thus, while the effects of source environment of provenances could be studied, and the optimum provenance for the test plantation site determined, the effects of planting environment and interactions between source and planting environments could not, nor could the results be extrapolated to select provenances for other planting sites. Not until well into the twentieth century was the first published systematic genecological study established, involving multiple experimental sites as well as many provenances, with sufficient replication for robust statistical analysis. The focus of this study was not a tree species, but the herbaceous perennial yarrow (*Achillea millefolium*). Clausen, Keck, and Heisey collected seed from yarrow plants along an east–west transect in California from the Pacific Ocean (sea level) over the coastal range, across the Central Valley, up to the crest of the Sierra Nevada (3300 m) and down its dry eastern slope. They then established common-garden experiments, in which plants from all populations sampled were grown together in a replicated experiment, on experimental sites along the original transect sampled. Similar to earlier studies of Norway spruce, at low-elevation experimental sites the populations from higher elevations were the slower-growing. They also observed that, at each experimental site, the population that grew to the greatest size was the one from closest to the experimental site. Thus, the relative rankings of populations, from largest to smallest based on mean plant size, changed with planting environment, which has been observed since then for many tree species. This is an example of genotype  $\times$  environment interaction ( $G \times E$ ) (Figure 1). If there was no  $G \times E$ , the fastest-growing population at one experimental site would be the fastest-growing throughout.

The basic genecological experimental design used by Clausen, Keck, and Heisey was repeated for many tree species around the world in the second half of the twentieth century, very often revealing similar patterns of local adaptation: Figure 1 illustrates a typical pattern. The majority of these tests have been in temperate forest regions in Europe and North



**Figure 1** Results of a hypothetical genecological experiment illustrating typical results for widespread, temperate tree species. In this example, seed was collected from five locations (provenances or populations) along a latitudinal transect in the northern hemisphere and grown in common-garden experiments at three of those locations (north, central, and south). Growth is illustrated as a percentage of the mean of the fastest-growing provenance on the fastest-growing site. Average growth is highest at the southernmost site, and lowest at the northernmost site, but the fastest-growing provenance on any one site is local (indicated by the cross-hatched bar). There is genotype-by-environment interaction: the ranking of provenances is different at each site.

America, with fewer published studies of tropical or boreal species. While these trials were initially established to generate information for operational forestry, they have been used for new applications in recent years, including predicting response to climate change, determining the underlying genetic basis of adaptive traits (i.e., ecological genomics) and testing evolutionary and ecological theories about factors limiting the evolution of species range. The extensive body of scientific literature on local adaptation in forest trees may well exceed that for any other type of organism.

## Evolutionary Forces

The pattern of genetic variation among and within populations within a species results from the cumulative effects of five evolutionary forces: (1) mutation; (2) gene flow (migration); (3) genetic drift (random changes in allele frequencies from generation to generation due to sampling effects); (4) natural selection; and (5) mating system (the degree to which sexual reproduction occurs through self-pollination, consanguineous mating between related individuals, or mating between unrelated individuals). Genecological studies of tree species with large distributions and historically large populations reveal the efficacy of natural selection in a given environment in favoring locally adapted phenotypes (Figure 1). Patterns of genetic variation among populations often mirror environmental gradients, revealing the strong effects of natural selection despite considerable gene flow introducing alleles conferring adaptation to other environments. Genecological studies of species with small ranges, small or isolated populations, or species that have experienced major bottlenecks (e.g., during glacial periods in the Pleistocene) often reflect the effects of genetic drift to a greater extent than other evolutionary forces, and as a result have more random patterns of genetic variation among populations rather than clines along environmental gradients.

Species that show strong patterns of genetic variation among populations in growth and other adaptive traits associated with environmental gradients are referred to as adaptive specialists, while those with weak or no geographic patterns are referred to as adaptive generalists. Generalists may lack such patterns owing to one of two reasons: either they have a high degree of phenotypic plasticity, i.e., the same genotype (genetic make-up) can produce a range of phenotypes (outward appearance, performance, or physiological behavior) depending on the environment, or local adaptation has not had an opportunity to develop as natural selection has been countered either by gene flow or by genetic drift in small populations. In North America, lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*) are examples of adaptive specialists, while western white pine (*Pinus monticola*) and western red cedar (*Thuja plicata*) are generalists. Adaptive specialists require more restrictive seed transfer guidelines and smaller breeding zones than adaptive generalists, as there is a greater risk of maladaptation with seed transfer or deployment of genetically selected material. The variation among species in the degree and patterns of specialization means that provenance trial results for one species cannot be extrapolated to another.

Some species have intraspecific taxonomic structure resulting from past isolation of portions of the range leading to more abrupt genetic differentiation among regions due to both random genetic drift and natural selection. This taxonomic structure can persist after previously isolated varieties or subspecies come into secondary contact through range expansion or migration. Examples of such species include *P. contorta* comprising subspecies *contorta*, *latifolia*, *murrayana*, and *bolanderi*, and *Pseudotsuga menziesii* coastal variety *menziesii* and interior var. *glauca*. In species with intraspecific taxonomic structure, genetic differentiation resulting from both isolation and past adaptation can overlay and complicate the interpretation of variation resulting from adaptation to current or recent environments in continuously distributed populations. Hybridization resulting from secondary geographic contact between previously separated species can also produce strong geographic patterns of adaptive variation, for example, in the introgression zone between *Picea glauca* and *P. sitchensis* in the coastal mountains of British Columbia and Alaska.

## Genecological Methods

### Provenance Trials

Traditional provenance trials require five steps: (1) collection of seed; (2) growing of seedlings; (3) planting of a replicated experiment on multiple field sites; (4) measurement of traits; and (5) analysis and interpretation of results. Seed is typically collected from 10 to 25 trees per location, to ensure a representative sample of the natural population from each provenance. Parent trees sampled are usually 50–100 m (or more) apart, to minimize sampling of closely related individuals. Seeds are sometimes kept separate by seed parent (called a provenance–progeny trial), to allow for the estimation of within-provenance genetic variation and trait heritabilities as well as to facilitate some initial selection for selective breeding; however, bulk seedlots are often used, with seed pooled across parents within provenances. Seed is collected from accessible locations scattered throughout the zone of interest within the species' range, with anywhere from just a few to over 100 locations sampled, depending on the size of the area and the resources available.

Seeds are usually sown in greenhouses or nursery beds and seedlings grown in randomized, replicated blocks for 1–2 years before outplanting. Field provenance test sites are usually selected to cover the range of planting environments that are typical for a species within a given political jurisdiction,

although some trials are rangewide, particularly those coordinated by international organizations. To ensure that a range of environments is sampled for native species, sites are usually selected to cover the full range of latitude, longitude, elevation, and ecological conditions across which the target species is found or actively managed. For exotic species, sites are selected across the range of potential planting sites for that species.

Blocks are delineated within planting sites, hopefully grouping similar environments together; for example, with block boundaries following contour lines along slopes, or separating wetter and drier areas. Within blocks, a complete, randomized block design can be used where trees from individual provenances are represented by single-tree plots; a split-plot design can be used where provenances are allocated to main plots and individual-tree progenies within provenances to single-tree subplots. Where such families are identified, equal numbers of seedlings from each family represent a provenance in all blocks, and families are randomized within provenances, usually in single-tree plots.

Traits assessed in provenance trials are often limited initially to survival, height, and diameter. Tree size is used as a cumulative index of tree health and degree of adaptation, and individual tree growth is an indicator of potential stand-level productivity. As trees age, insect or disease outbreaks, and unseasonable weather events such as frost and drought offer opportunities for studying population variation in resistance to biotic and abiotic stresses. However, response to these agents is often best studied under more controlled conditions. While mortality is usually periodically recorded, differences among provenances in survival must be large or replication (blocks and sites) high for these to be statistically significant. In addition, trees can often survive a much broader range of environments than those in which they can be highly productive. In most areas of the world with a focus on industrial plantation forestry, survival is more dependent on good silvicultural practices than on the choice of provenance. Choice of the wrong provenance can reduce the realized production of a high-productivity site, just as planting an optimum provenance can increase site productivity, so growth is usually emphasized. Wood cores can be sampled from older provenance trials and wood properties analyzed including wood density, fiber length, microfibril angle, lignin content, extractives content, and other economically important traits, although within-population variation in wood properties is usually of greater interest than among-population variation.

### Short-Term Genecological Experiments

Some traits related to adaptation to specific environmental stresses can be assessed in long-term field provenance trials such as phenology (e.g., timing of bud burst, bud set, leaf abscission, pollination, and seed maturation); cold-hardiness; and drought-related traits (e.g., water-use efficiency as measured by stable carbon isotope ratios in wood samples). Adaptive traits such as these are more commonly assessed in short-term nursery, greenhouse or growth-chamber experiments under more controlled conditions. These trials have several advantages over field provenance studies. They can typically be completed in 2–3 years, can involve more uniform environments and thus have a greater ability to detect genetic differences, can be located close to laboratory facilities for repeated observations or for assessment of time- and equipment-intensive traits, and can allow the isolation, control, and testing of specific environmental factors such as temperature, moisture, photoperiod, and nutrients. Disadvantages include a lack of long-term information on survival and health in natural environments, and the inability to assess mature characteristics. Ideally, these short-term experiments are linked with long-term provenance trials containing similar genetic materials.

The experimental designs for short-term genecological experiments can be similar to or quite different from those for provenance trials. If a genecological mapping approach is taken, instead of sampling from many trees at relatively few locations, many locations are sampled with seed collected from just one or two trees per location. This method, pioneered by R.K. Campbell, allows for the fine-scale mapping of genetic variation and, using spatial analytical techniques, results in detailed spatial maps with isoclines that connect and delineate environments with similar natural selection pressures. Including progeny of two trees at some or all locations allows for the estimation of within-location genetic variation for estimation of trait heritabilities.

Short-term genecological experiments can allow the separation of temperature- and moisture-related adaptation more easily than long-term provenance trials, where factors contributing to tree injury or death may be unclear; treatments controlling environmental factors allow detailed assessments of physiological responses to these treatments. Soil-temperature treatments have been successfully created through the use of soil heating cables, and such treatments have revealed provenance  $\times$  treatment interaction in some species.

Rather than develop experimental systems to grow seedlings under different temperature regimes, most

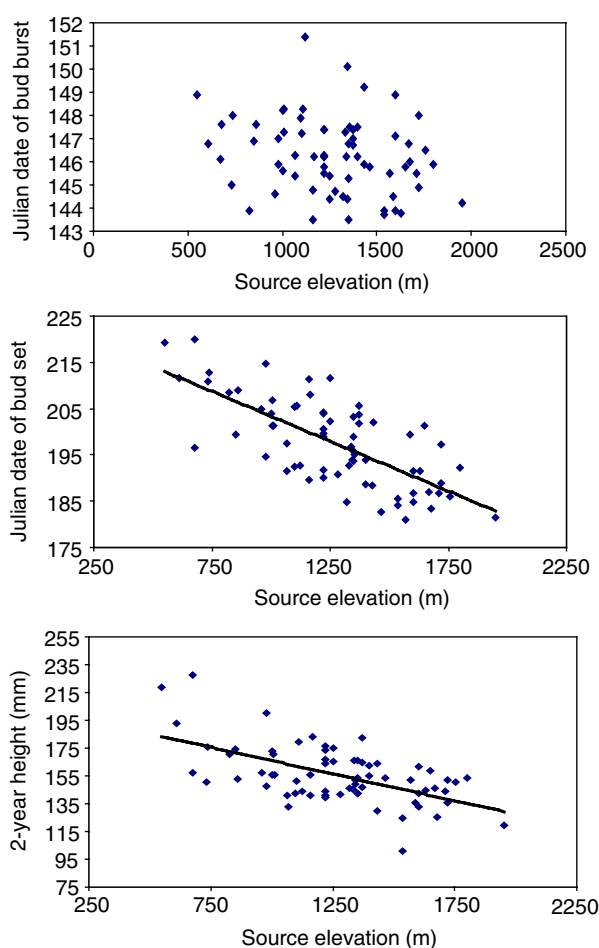
investigators use artificial freeze-testing of shoots or other tissue samples collected from genecological experiments or provenance trials to assess genetic clines in cold-hardiness. Shoot samples, or small pieces of leaves, buds, or stems, are placed in computer-controlled freeze chambers and the temperature is slowly reduced to a target freezing level. Damage is then assessed using one or more of several available methods, including visual scoring of damage following freezing, measuring the release of electrolytes from injured cells, measuring chlorophyll fluorescence of foliar samples following freezing.

Drought treatments can be created in seedling trials through the use of soils with low water-holding capacity in raised nursery beds with barriers to moisture entry, by withholding irrigation, and by using clear covers to block precipitation. The use of individual-seedling containers for the study of adaptation to drought is not recommended, as this approach usually confounds plant size with drought stress intensity owing to fixed soil volume and no competition.

### Data Analysis

The first step in analyzing provenance and genecological trials is usually analysis of variance (ANOVA) to test the significance of phenotypic variation among sites and provenances, as well as within-site environmental effects, including block effects. Provenance–progeny trial analysis also tests for the effects of families nested within provenances and their interactions with site, along with certain other effects. If provenances have been chosen randomly for inclusion in the experiment, unbiased estimates of variance components can be calculated for each effect and the proportion of variation due to provenances, and to families within provenances if applicable, can be estimated.

The next step in the analysis is to test for and characterize genetic clines. A cline is a geographic or environmental pattern of change in the mean of a trait associated with an underlying environmental gradient (Figure 2). Where specific environmental descriptors of provenances are lacking, geographic variables such as latitude, longitude, elevation, and distance inland from oceans are used as surrogates. Climatic records provide a better indication of source environments than these geographic variables but weather stations are typically underrepresented in extensively forested areas away from major human settlements. Some provenance trials have selected provenances with available weather records to address this problem, but this may result in a biased sample. More recently, climatic models have been available in some regions, or have been generated by



**Figure 2** Genetic clines associated with elevation in *Picea engelmannii* (with possible introgression from *P. glauca* at lower elevations) in southeastern British Columbia, Canada, for 2-year-old seedlings in a common-garden experiment established in nursery beds. Plotted against source elevation are the mean values of the open-pollinated progeny of individual seed parents. There is no pattern of variation in mean date of bud burst with elevation; however, date of bud set reveals a fairly strong, significant ( $P \leq 0.05$ ) elevational cline ( $r^2 = 0.45$ ) while height shows a weaker but significant cline ( $r^2 = 0.30$ ).

forest geneticists in partnership with meteorologists, to provide better descriptors of provenance environments. For example, predictions from the PRISM model are now available for much of North America.

To test for genetic clines, univariate or multiple regression analyses are conducted on each provenance trial or controlled environment separately, with geographic, environmental, or climatic descriptors as independent variables, and provenance means for assessed traits as dependent variables. A significant genetic cline, particularly if provenance means are significantly associated with a parallel environmental gradient in more than one geographic area, is considered evidence of varying natural selection pressures at different locations along that gradient.

Genetic clines associated with the elevation of parent origin observed in a short-term seedling genecological study of Engelmann spruce (*Picea engelmannii*) are illustrated in **Figure 2** for timing of bud burst, timing of bud set, and height. It is worth noting that, at any elevation, there is still substantial within-population variation for all traits, providing the raw material for adaptation to new conditions or for breeding programs. As traits vary in the strength of clines and spatial patterns of variation, and many traits are often assessed, statistical methods such as principal component analysis are often used to combine traits into multivariate indices.

### Genecological Trends

For widely distributed tree species in temperate and boreal regions, most species have broad genetic clines associated with gradients in mean annual temperature, growing-season length (i.e., frost-free period) and, to a lesser extent, total and growing-season precipitation. In mild test environments, overall growth is generally highest for populations with the mildest source environments, and lowest for those from particularly cold (or dry) locations. In harsher test environments, populations from warmer source environments often suffer higher mortality, while populations from similarly cold or dry environments have higher survival and good growth rates for those particular environments.

While local provenances in general are the safest to use for reforestation in the absence of good provenance data, as they have higher survival and productivity than provenances from afar, there are two common exceptions to this pattern. For a number of species, superior provenances have been identified, trees from which have higher than expected growth rates and perform well above the norm for the genetic cline over a wide range of test environments. The second trend is that for many western North American species, the most rapidly growing genotypes with comparable survival and health to local provenances are from slightly milder environments than the test site, e.g., 1–2°S, or 100–300 m lower in elevation. This may reflect adaptational lag, that is, the local adaptation of populations to past rather than current environments, given the long generation interval of trees, or it may reflect a lack of extreme climatic events as agents of natural selection since the provenance trials were planted.

The steepness of genetic clines varies with trait assessed (**Figure 2**). The steepest genetic clines often exist for phenological traits and cold-hardiness. The period of active primary growth from bud break (or growth initiation for indeterminate species) to bud set

(or growth cessation) varies with annual frost-free period of source environments. There is typically more variation within species for timing of growth cessation (or bud set) than for timing of growth initiation (or bud burst). Populations within species typically differ in the timing of growth cessation and initiation of cold acclimatization in autumn, or in the timing of dehardening in the spring, rather than in the level of maximum cold-hardiness achieved mid-winter. It should be noted that autumn and spring cold-hardiness are really different traits from a genetic standpoint, as variation in these traits is relatively uncorrelated. In Douglas fir, genetic mapping of quantitative trait loci (QTL) controlling cold-hardiness has revealed that autumn and spring cold-hardiness are controlled by largely independent sets of genes. These processes have different cues: acclimatization (hardening) in the autumn is triggered by photoperiod, while first sufficient chilling, then exposure to warm temperatures, initiates dehardening.

Areas with late summer drought generally have populations with earlier growth initiation and cessation, and greater allocation of biomass below ground (higher root/shoot ratios) than locations with more summer precipitation. The mean total growth of trees in populations tends to be correlated with length of the growing season (period between primary growth initiation and cessation), which explains at least part of the lower growth potential of populations from colder or drier source environments, even under favorable conditions. Populations adapted to dry environments are often phenotypically similar to those adapted to frost-prone locations.

Drought-avoidance mechanisms such as a shorter, earlier growing season, preemptive stomatal closure (resulting in cessation of photosynthesis at a higher water potential), and greater allocation of biomass to roots (as opposed to increasing photosynthetic leaf area) tend to decrease net growth; thus provenances from drier regions often have a lower inherent growth capability. Tolerance mechanisms include higher water-use efficiency (less water used per unit of photosynthesis) and a lower vulnerability to cavitation (the water potential at which xylem water columns embolize). Significant interprovenance variation has been observed for all of these drought-related traits in genecological studies of temperate forest trees, with changes in growth phenology and biomass allocation being the best documented.

### Phenotypic versus Genetic Estimates of Differentiation

Many studies rely on the use of selectively neutral DNA markers rather than genecological experiments



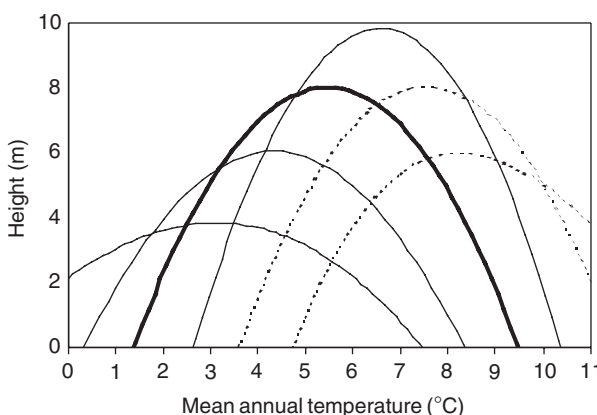
to determine population differentiation. The results of such studies provide an indication of historic population size based on levels of genetic diversity, as well as the strength of gene flow. Genetic marker variation is commonly partitioned among and within populations, and the amount of total genetic variation due to among-population differences estimated by  $F_{st}$ . The proportion of total genetic variation in a phenotypic trait due to differences among populations can also be estimated in a genecological test using a similar parameter,  $Q_{st}$ . If  $Q_{st}$  exceeds  $F_{st}$ , it is evidence of past differences in natural selection on different populations.  $F_{st}$  values in forest trees are usually between 5 and 10%, while  $Q_{st}$  values are usually higher and vary widely, with published values up to 80%. Thus, while useful for other purposes, selectively neutral genetic markers can greatly underestimate population differentiation and the potential for local adaptation.

While most genetic markers that are widely used for population genetic studies are not useful for studying variation in adaptive traits, as genomic methods develop and gene sequence databases grow, there will soon be new classes of markers available that reveal single nucleotide polymorphisms (SNP) in genes that affect adaptive traits. While most of the adaptive traits of interest are likely influenced by many genes, it will be possible to look for clines in allele frequencies for some of these genes, rather than just characterizing phenotypic variation, using methods of the emerging field of ecological genomics.

### Predicting Response to Climate Change

Local populations facing rapid environmental change have three possible fates. They can adapt *in situ* to new conditions. They can migrate, and track the environment to which they are adapted across the landscape. Or they can be extirpated due to maladaptation to new conditions. The pollen and macrofossil records indicate that tree species have migrated in response to past climate change, but the fossil record cannot reveal the extent to which adaptation has also played a role. It has been suggested that population structure and differentiation may have persisted during range expansions and contractions in the Pleistocene, and maintained adaptive structure within species during migration. With rates of anthropogenic climatic change predicted to be much higher than most of those in the past, combined with considerable range fragmentation by human development in some areas, it is likely that species migration will often be unable to keep pace with expected changes.

Established long-term provenance trials have been the focus of renewed interest in recent years; not only



**Figure 3** Norms of reaction of six *Pinus contorta* subsp. *contorta* populations to mean annual temperature (MAT) as derived by Rehfeldt GE, Ying CC, Spittlehouse DL and Hamilton DA (1999) Genetic responses to climate in *Pinus contorta*: niche breadth, climate change and reforestation. *Ecological Monographs* 69: 3375–3407, based on height at 20 years in a field provenance trial planted on 60 field test sites. Genotypes typical of each population will be found in geographic areas with an MAT for which that population has higher productivity than other populations. Each population has an optimum MAT at which its productivity is maximized; however, it may not occupy areas with that MAT due to displacement by more competitive genotypes. If climates warm 3–5°C, as predicted by models, productivity losses due to maladaptation will be substantial.

do they provide an opportunity to study differences among populations from different environments, but they also provide the ability to study the effects of a changing environment on these populations by substituting spatial for temporal environmental variation. As a result of moving seed from the point of origin to a series of new environments, the genetic and ecological response of these populations to these environments can be assessed.

This type of climate change analysis has been most thoroughly conducted by noted genecologist G.E. Rehfeldt, who analyzed provenance data for lodgepole pine in a provenance trial involving 140 populations and 60 field sites. **Figure 3** illustrates the derived responses, called norms of reaction, of height growth of just six of those populations to mean annual temperature of the planting environment. If mean annual temperature increases at the predicted rate of 3–5°C in the next century, it is clear that massive maladaptation will result in this species. It is predicted that it will take 4–12 generations of natural selection, or massive redeployment of genetic resources across the landscape for reforestation, for populations of lodgepole pine once again to be genetically matched to their environments.

**See also:** Genetics and Genetic Resources: Population, Conservation and Ecological Genetics. **Tree Breeding, Practices:** Breeding for Disease and Insect Resistance;

Genetic Improvement of Eucalypts; Tropical Hardwoods Breeding and Genetic Resources. **Tree Breeding, Principles:** Breeding Theory and Genetic Testing; Conifer Breeding Principles and Processes; Forest Genetics and Tree Breeding; Current and Future Signposts. **Tree Physiology:** A Whole Tree Perspective; Physiology and Silviculture. **Tropical Ecosystems:** Tropical Pine Ecosystems and Genetic Resources.

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## Cytogenetics of Forest Tree Species

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## Introduction

The discipline of cytogenetics was first defined by Sutton in 1903, as a field of investigation which

developed from the separate sciences of genetics and cytology. It is concerned with studies on the correlation of genetic and cytological (especially chromosomal) features characterizing a particular genetic system under investigation. With respect to forest trees, cytogenetic studies have generally been limited to chromosome studies, on the number, appearance, and behavior of chromosomes during mitosis and meiosis, chromosomal and karyotypic evolution, and the role of chromosomes in the transmission and recombination of genes.

Plant breeding can be traced to the ancient Babylonians, but a clear understanding of genetics has its beginning in the nineteenth century with Mendel's hybridization experiments and their subsequent rediscovery by de Vries, Correns, and von Tschermack in 1900. Cytology required the invention of the microscope, and began when Robert Hook observed cork cells in 1665. Early scientists studied cell structure, organelles, and division. Nageli first described chromosomes as visual bodies during cell division in 1844, and Fleming in 1882 described the complete process of mitotic nuclear division. However, it was not until the independent observations of Sutton and Boveri that chromosomes were first linked with the emerging field of genetics.

Cytogenetic investigations of forest tree species were first conducted in the early 1900s, after cytological investigations in most crop plants and animals were well established. Leading discoveries were made in the research of insect cytogenetics, and then followed by maize (*Zea mays*) cytogenetics, especially from the standpoint of the applied methods and materials. Thomas Hunt Morgan and his group of students and scientists made fundamental discoveries in the early decades of the twentieth century, investigating giant chromosomes of fruit fly, *Drosophila melanogaster*. The fly's short life cycle and variant phenotypes/genotypes allowed rapid progress in understanding cell differentiation, cell divisions, and breeding results. In contrast, the relatively long time to reproductive maturity of many forest tree species, and logistical problems in sampling, make trees less desirable for cytogenetic research. However, papers written at the turn of the twentieth century pointed to the suitability of conifer species for cytological research.

The main interest in forest tree cytogenetics in the early 1900s was in discovering and interpreting the process of fertilization in pines. Ferguson conducted very detailed observations on the development of the egg cells, fertilization, and microsporogenesis in various pine species (*Pinus strobus*, *P. nigra*, *P. rigida*, *P. resinosa*, and *P. uncinata*). She determined the precise number of chromosomes in the haploid