

GENETIC VARIATION IN CALIFORNIA OAKS

by Constance I. Millar, Diane L. Delany and Lawrence A. Riggs

In forestry the importance of genetic variation for successful reproduction, survival and growth has been widely documented for commercial conifers; until recently, little genetic work has been done on the California oaks. Even before the nature of genetic variation was scientifically investigated, its importance was suspected in operational forestry. Many failures of commercial plantations were traced to the use of seedlings that, although of native species, were derived from populations distant from the planting site. Similarly, in areas that were regenerated with planted seedlings following catastrophic fires, trees of non-local origin grew poorly, if at all.

Subsequently, many studies have shown that wind-pollinated tree species are highly variable, that variation is often patterned geographically, and that much of this variation is adaptive. Within species, trees from geographically distant regions (such as Sierra Nevada vs. Rocky Mountains) have genetic traits that relate to the unique aspects of the regional environment in which they evolved. Similarly, populations of trees from different habitats within a region (such as different elevations within the Sierra Nevada) evolve adaptations to local environments. The raw source of variation that natural selection works on is the genetic variability among trees within populations. Recognizing that this genetic architecture is important to survival and growth of commercial species, forest geneticists draw seed zone maps and establish transfer rules that limit the distance between seed collection and plantation sites.

Unfortunately, little genetic information is available to hardwood managers despite its importance to reforestation and restoration. Genetic variation has been much less studied in angiosperm trees, and oaks are no exception. Although there have been some studies of oaks from central and eastern North America, information on our California species is only now being generated. In the wild, California oaks appear highly variable, leading specialists to conclude that oaks, like conifers, contain high amounts of genetic variation. The presence of intermediate forms between many oaks further suggests that species boundaries are not strong and that species are not sharply differentiated. With little direct genetic information, however, these ideas have been untested and other questions about the implications of genetic variation for natural regeneration and for restoration have remained unanswered.

As a first approach to analyzing genetic structure in oaks, we studied allozyme variation in valley oak

(*Quercus lobata*, a white oak), blue oak (*Q. douglasii*, a white oak) and coast live oak (*Q. agrifolia*, a black oak). Allozymes are alternative forms of commonly occurring enzymes that are detectable by the laboratory process called electrophoresis. They are useful genetic markers that allow genetic variation among and within natural populations to be directly measured. Allozymes are also useful for genetic detective work; for example, in evaluating putative hybrids, and in detecting genetic contaminants, that is, plants that contain non-local genes introduced through human activities. Because allozyme techniques are widely used, geneticists are familiar with the results from studies of many organisms, and the results can be meaningfully compared across taxa.

We studied populations that span the California range of the three species, including fifteen populations of coast live oak, and seven populations each of valley oak and blue oak, for a total of 860 individual trees. Because hybridization (detected from morphology) is commonly assumed to occur between blue and valley oaks, we expected to find relatively small amounts of allozyme variation among the species and relatively large amounts of variation within these species. This is the expectation for conifers that have similar life history and hybridization patterns. What we found was quite surprising: large genetic differences between all pairs of the species including blue and valley oaks, with many unique genes distinguishing each species. This result suggests that, at least among the species and populations we studied, relatively little hybridization has occurred in either the distant or recent past.

Another interesting result is the pattern of genetic relationships among the species. Blue oak has been classed in both subgenera of *Quercus*, in the white oaks for its leaf shape and acorn physiology, and in the red oaks for its wood characteristics. Our results indicate that, despite major differences among the species, blue oak and valley oak are much more closely related to each other than either is to coast live oak. This points to the correct classification of blue oak as a white oak.

There were surprises about genetic variation within the species as well. Both coast live oak and valley oak had little variation within populations. Blue oak was about twice as variable as the other two species, and it compared to a conifer with low-moderate levels of variation. Most interestingly, within each of the species, all populations were very similar to each other. We detected no geographic pattern in allozyme variation in



The California black oak (*Quercus kelloggii*) in Yosemite Valley in autumn. Photograph by David Cavagnaro.

any of the species, and no indication of racial or subspecific variation. The low amounts of variation within individual trees of coast live oak and valley oak (i.e., low heterozygosity) further suggest that the populations we studied of these species have not been involved in hybridization with any other oaks. Even blue oak, which had a fair amount of variation, had little indication of hybridization because the pattern of variation was uniformly distributed throughout the range of the species.

Allozymes are useful markers of genetic variation, especially in their ability to quantify species differences, and to detect evolutionary events such as hybridization, and migration or fragmentation of populations. But implications to management must not be made hastily. Allozymes do not necessarily tell the whole story of genetic variation, as they are not often directly related to adaptive traits that are important to survival of trees. Other kinds of studies need to be done

to understand the evolution of adaptive differences, and to build the base of information needed to make seed zone maps and infer transfer rules. These include common-garden studies, where physiological and morphological traits can be observed among trees from many sources growing in one environment. For long-lived species these studies often require years before useful results can be obtained. Analysis of DNA-level variation, where even finer resolution than allozymes is possible, may also prove useful for detecting patterns of genetic variation in oaks. Larry Riggs is currently undertaking such a project in the hope of further unraveling the mysteries of oak genetics.

Constance I. Millar, Diane L. Delany, USDA Forest Service, Pacific Southwest Forest & Range Experiment Station, Berkeley, CA 94701; Lawrence A. Riggs, Genetic Resource Consulting, Berkeley, CA 94709