Spatial Genetic Patterns in Four Old-Growth Populations of Coast Redwood[1]

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Key words: canonical surface analyses, demographic structure, spatial autocorrelation

Introduction

The mating systems of plant species and their patterns of pollen flow and seed dispersal create a pattern in the distribution of genetic diversity which is referred to as spatial genetic structure (Wright 1946). Over time, that pattern may be modified by other influences such as natural selection. In studying the spatial genetic structures of plant species directly, we can infer the past events of gene flow that contributed to those structures. Elucidating the dynamics of gene flow within a species improves our understanding of the nature of local populations—the units within which the majority of gene sharing occurs, and the units that are often the focus of conservation or management.

The capacity of coast redwood (*Sequoia sempervirens* D. Don) to reproduce sexually to produce genetically distinct seedlings or by sprouting to produce clonal replicates provides for many possibilities for its spatial genetic structure. Results of previous common-garden studies of morphological and physiological traits (Anekonda and Criddle 1993, Anekonda and others 1994, Millar and others 1985) and of allozyme diversity (Rogers 2000) have revealed high levels of genetic diversity in coast redwood. This diversity provides the potential for detecting local spatial genetic structure. Furthermore, results from the first genetic study of clonal structure in the species showed that clone sizes were generally small (in other words, few ramets per clone), indicating that many of the studied redwoods were genetically distinct (Rogers 2000). In addition, the increasing array of available genetic markers and statistical methods provide more opportunities and analytical power for illuminating genetic structure. For example, whereas estimates of gene flow based on Wright's *F*-statistics represent evolutionary averages (for example, Bossart and Prowell 1998), recently developed statistical methods performed on hypervariable markers such as microsatellites allow the potential to detect contemporary patterns of dispersal (Smouse and Peakall 1999). Multivariate statistical methods commonly employed to study spatial genetic structure include principal components analysis, canonical variate analysis, canonical correlation analysis and spatial autocorrelation methods. Most recently, multilocus spatial autocorrelation methods have been

developed and applied to studies of spatial genetic structure. This multiallelic approach (as opposed to a locus-by-locus, allele-by-allele analysis) may be particular appropriate for fine-scale spatial genetic structure studies, strengthening the spatial signal by reducing stochastic noise (Peakall and others 2003, Smouse and Peakall 1999).

Methods

In this study, we employ multilocus spatial autocorrelation procedures and canonical correlation analysis to describe fine-scale spatial genetic structure in old-growth populations of coast redwood. We compare two geographically proximate but contrasting redwood habitats to illustrate that microgeographic selection and population history, not just gene flow, may play a role in spatial genetic patterns for this species.

Four sites were selected from old-growth populations of coast redwood in Humboldt Redwoods State Park in northern California. Two were located in upland areas with (relatively) dry microclimates, mixed species canopy conditions, and with historically frequent fire disturbance. Veirs (1980a, 1980b) studied fire disturbance patterns in the general vicinity and determined that fire frequency was sometimes ten times greater on the xeric sites (comparable to the upland sites of this study) than on the more mesic sites (lowland sites). Fire influences a variety of reproductive and early growth conditions relevant to coast redwood including soil sterilization and mineralization (McBride and Jacobs 1977), vegetative sprouting, and removal of overstory (Jacobs 1987). Two sites were selected from another typical old-growth condition—that of lowland, flood-influenced areas where redwood was dominant.

Foliage was collected from 121 to 160 contiguous trees from each of the four sites, mapping the location of each tree. Diameter (at breast height) was measured on each sampled tree. See Rogers (2000) for additional detail on site conditions and sampling methods. Foliar tissue was assayed for allozyme loci. According to previously established methods, we resolved four alleles at each of seven loci (Rogers 1997, 1999). Because coast redwood is a hexaploid and staining intensities from the protocols used in this study do not accurately or consistently reflect allele frequencies (Rogers 1997), individual isozyme phenotypes were scored for the presence or absence of each allele. Consequently, multilocus allozyme phenotypes rather than allele frequencies were analyzed.

To examine within-site spatial patterns of individual phenotypes, we regressed a second-order model of the x and y coordinates of each individual against its multilocus phenotype by canonical trend surface analysis. In the lowland and upland sites, the dominant pattern was in the x-direction, which was roughly coincident along the Eel river in the former and with elevation in the latter. In all sites, the direction of least change was in southeast to southwest sector. To further examine spatial relationships we generated directional spatial correlograms at each site. Though some differences are apparent, the general pattern of highest correlations was in a similar direction on all sites, consistent with the trend surface results, possibly reflecting the dominant wind pattern within the region. Spatial autocorrelations were positive and significant within the first 100-foot distance interval (in other words, in pairwise comparisons of all trees included in the study) on all four sites. However, the values were generally larger on the two upland sites, and continued to be positive

at greater distances (relative to the two lowland sites). Inclusion of putative clones greatly increases autocorrelation in the first two distance intervals, especially on the upland sites.

Discussion

Some features of coast redwood are traditional indicators of long-distance gene flow and absence of fine-scale spatial genetic structure. The tall stature of mature trees, wind dispersal of pollen and seed, high rates of outcrossing, and high levels of inbreeding depression are traits that are generally correlated with low expectations of genetic structure (Hamrick and Godt 1990). Yet we found considerable fine-scale genetic structure. Some of this is related to clonal replicates, although even when this effect is removed, significant and positive spatial autocorrelations remain within one hundred feet on all sites, and at greater distances and higher values on the upland sites.

Differences in elevation and disturbance events between the upland and lowland sites would seem to provide different selection regimes that could be expected to result in some degree of genetic differentiation between site types. The higher and more widespread autocorrelations on upland sites might be related to several factors. The redwoods that persist on these fire-influenced sites compete with other tree species such as Douglas-fir *(Pseudotsuga menziesii)*, tanoak *(Lithocarpus densiflora)*, madrone *(Arbutus menziesii)*, and Pacific yew *(Taxus brevifolia)*. Consequently, following a fire disturbance, microsites would quickly become colonized and are more likely to reflect recruits from the dominant seed source at a specific time, rather than gradual recruitment of redwoods from multiple parents. The age structure, too, may differ between the upland and lowland sites. Coast redwood is a very difficult species from which to infer age based on diameter—because of factors including false rings and missing rings (Brown and Swetnam 1994). However, the size distributions for the four sites showed a much higher proportion of very large trees (for example, above 60 inches diameter) on the two lowland sites (20 to 25 percent) relative to the two upland sites (five to 15 percent). Generalizing that very large trees are older than much smaller trees, it seems probable that a disturbance that was sufficiently severe and comprehensive to be considered 'stand replacing' probably has occurred more recently (and more frequently, in the long term) on the upland sites relative to the lowland sites. Also, the upland sites contained some younger (seedling and sapling) trees of nonclonal origin. The lowland sites, with much higher densities of coast redwood, contained almost no young trees that weren't sprouts from pre-existing trees. Studies of genetic structure in other plant species have suggested that spatial structure may also vary with life stage and age class (for example, Kalisz and others 2001).

Although the study is limited to old-growth conditions in one particular region of the species' range, and covers only a modest geographic distance, the results suggest that the majority of gene flow in coast redwood may be more local than might be expected on the basis of generalizations concerning open-pollinated conifers. The seeds of redwood—although light, small, and borne at often-great heights in the canopy—are, nevertheless, wingless, and may settle relatively close to the parent trees. However, in communities that have persisted for long periods, as is likely in the lowland sites, gene flow will diminish spatial structuring across the site.

Conclusion

In conclusion, coast redwood in old-growth context can have considerable fine-scale spatial genetic structure. This is a reflection of both (albeit limited) clonal reproduction and patterns of seed and pollen dispersal, possibly reinforced by local natural selection. The local structure is stronger on upland (relative to lowland) sites and consistent with low effective population size and low dispersal distance conditions simulated in Epperson and others (1999), reflecting younger and sparser redwood populations that colonize quickly, and in competition with other species, following a fire disturbance. Although upland and lowland sites are distinguished in their autocorrelation values and distances, the direction of correlation is similar on all sites. This may reflect a common direction for the predominant winds in this region during the months of most abundant pollen and seed dispersal, generally December through January (Boe 1961, Metcalf 1924). The generally small clone size previously reported for coast redwood (Rogers 2000), coupled with the fine-scale genetic structure reported in this study, suggest that in areas that are managed to conserve natural genetic structure and ecosystem processes of coast redwood, attention should be paid to maintaining local populations that are probably smaller than suggested by the tree's stature. In particular, any restoration activities that involve seeding or planting of coast redwoods in natural or conserved areas, should consider using genetic material from the immediate vicinity unless there are higher-priority concerns that would over-ride genetic considerations, or additional information that indicates that the local populations for the target area are different from those in this study.

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