

**INCIDENCE, SIZE AND SPATIAL STRUCTURE OF CLONES  
IN SECOND-GROWTH STANDS OF COAST REDWOOD,  
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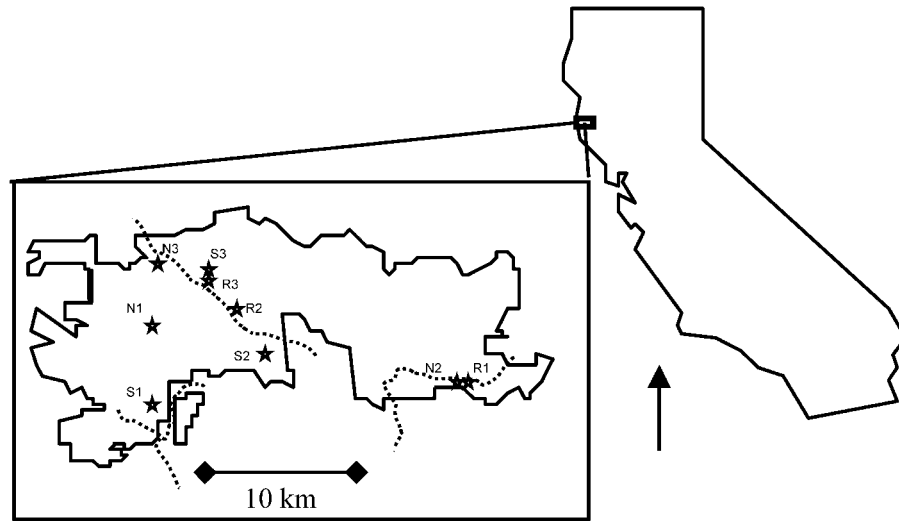


Fig. 1. Sample sites of *Sequoia sempervirens*

Sampling included clumped and forked stems that met the size requirement at forking point. With a target of up to 45 trees sampled per site, different stand densities resulted in a variation in total site areas (Table 1). In a few instances we were unable to collect leaf material due to the extreme height or canopy structure of a tree. Mean stem diameters were measured for comparison in parallel plots of the same size outside the sampled stands and no significant differences were found.



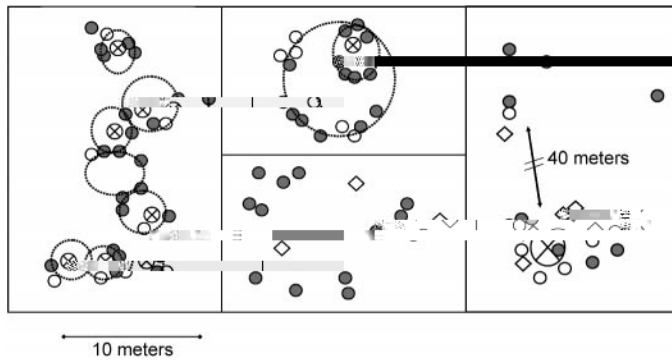


Fig. 3. A selection of four genets that demonstrate the range of *Sequoia sempervirens* clonal structures found in the Jackson Demonstration State Forest, north coast of California, including (a) chains of overlapping rings on site S2, (b) concentric rings on site S1, (c) disjunct stems on site R1, and (d) distantly disjunct stems on site N2. Solid circles represent ramets from a single clone. Open circles represent trees not sampled, open diamonds represent single stem genets, crossed circles represent stumps, and dotted circles outline perceived fairy-rings.

cantly greater on the north-facing slopes ( $P = 0.014$ ). This was not due to a small-scale density difference, but appeared to be due to a more common occurrence of disjunct ramets. Ramet clusters were found to be as far as 40 m from each other on these north-facing slopes. Maximum between ramet distances were positively correlated with the number of stems in a clone ( $R^2 = 0.290$ ,  $P = 0.002$ ) so that clones with larger numbers of ramets tended to have a greater overall footprint.

A weak but suggestive negative correlation was found between mean stem diameters at a site and Mantel  $R$  correlations ( $R^2 = 0.389$ ,  $P = 0.072$ ), implying that increased clustering of clonal ramets was associated with larger mean stem diameters at the site. Accordingly, a weak negative correlation between site PD value and mean stem diameter at a site was also detected ( $R^2 = 0.347$ ,  $P = 0.095$ ), suggesting that as the importance of cloning at a site increased, mean stem diameters at the site also increased. In summary, clonal importance, stem clustering, and stem diameters appear to be positively correlated.

## DISCUSSION

**Importance of clonal spread and clone structure**—Our

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(3) *Greater genetic representation*—Large redwood genets have greater genetic representation on a site with more stems, pollen, and seeds—all important factors driving evolutionary potential. When regeneration by seed is possible, larger clones have a greater likelihood of being a genetic contributor to the cohort.

“Although clonal plants generally sprout, only a small fraction of woody sprouters are clonal and capable of vegetative spread” (Bond and Midgley, 2001, p. 45). The important distinction here is that sprouting on a local scale emphasizes stem replacement, whereas clonal spread emphasizes lateral ramet multiplication in addition to stem replacement. Our results show that redwoods are an example of the latter. We identified many distinct clonal structures, demonstrating great variability in how redwood clones spread. The well-recognized fairy rings were a standard unit of clonal structure typical of the local sprouter type, but at a larger scale, clones showed a wide range of shapes with large numbers of ramets that were unlikely to thin to a single replacement stem over time. For example, ramets from the same clone were found to be up to 40 m apart from each other and, without the limitations of our sample size, may prove to be even more widely dispersed.

Little is known about how redwood clonal spread occurs beyond local basal sprouting. While fairy rings, concentric circles, and figure eights or longer chains can be explained by repeated basal sprouting of new ramets, it is still unclear how disjunct structures come about. Rogers (2000) suggests that this may be the result of trees falling, branches being buried by the impact, and finally resprouting at distances equivalent in some cases to the average height of these trees. Olsen et al. (1990) point out that redwoods are able to sprout anywhere along the stem and that this could also result in the establishment of distant sprouts along fallen trees. Another possibility is that ramets may be produced from disturbed existing root systems (Weber, 1990; Lavertu et al., 1994). In our second-growth stands, more complex patterns of clonal structure may have resulted from site disturbance during harvesting and the movement of soil and slash. An example of this may be the disjunct and somewhat chaotic pattern found on site R1 (Fig. 3c). This is an important area for further research.

We were unable, from our data, to determine if redwood clonal spread is of a phalanx or guerilla type. While Mantel test results suggested a phalanx structure with well-clustered ramets, mapping revealed instances of well-spread ramets more typical of a guerilla structure. It is most likely that redwoods combine phalanx and guerilla types of clonal spread. This emphasizes the need to complement tests of association, such as Mantel tests used here, with direct mapping of clonal structure.

*Old growth vs. second growth and site variability*—Comparison of our results with clonal structure of old-growth stands (Rogers, 1994, 2000) provides insight into how clonal structure may change as stands develop through time. These comparisons need to be treated with some caution as isozymes were used for the identification of ramets in old-growth stands. These markers are less efficient for this purpose than the AFLPs used in our second-growth work (Smulders et al., 2002).

In general, the results from old-growth sites were very similar to those from second-growth sites, both having similar structures, such as multiple genets in a fairy ring, disjunct ramets, and complex clone configurations. In a clonal forest,

a harvest appears to be a one-time clearing of ramets, leaving potential sprouting sites (stumps, root systems, etc.) that are the result of site history that predates this event. As a result, the long-term development of large-scale clonal structure may be more important than the short-term effects of harvesting. In fact, a harvest may simply resemble another in a long series of disturbances (fire, flood, etc.) that the genets have survived over time.

The most significant difference between second-growth redwood forests and old growth forests was the greater number of ramets per genet found in the former. Second growth stands had a maximum of 20 ramets per clone and the site with the greatest mean number of ramets per genet (5.29, including single stem ramets), whereas the old growth stands had a maximum of six ramets per clone, and site mean values of less than two. Presumably, gradual self-thinning has occurred within the denser clumps of ramets, resulting in fewer ramets per genet surviving through time. In the absence of disturbance and new resource availability over time, there is a decrease in the number of ramets per genet on a local scale. This is similar to dynamics in stands of *Populus tremuloides* Michx. through time (Peterson and Squires, 1995).

In this study few significant differences in clonal size or structure were found by site type. This may have been a result of limited clone sample size, with many sample stems being identified as clonal ramets. Rogers (2000) also found only “modest” differences between upland and lowland. To more accurately assess site type differences, a more extensive sampling scheme would be necessary that can both identify the extent of clones on a local scale, but also cover a large area and capture a more significant number of clones. The fact that redwood genets can be very large and that there are no good surrogates for clone identification makes it difficult to economize on the sampling intensity.

*Conclusions*—In clonally spreading species many classical assumptions of how stands should be managed for biological diversity, maintenance of viable population size, regeneration,

