DEMOGRAPHIC STRUCTURE OF CALIFORNIA BLACK WALNUT (*JUGLANS CALIFORNICA*; JUGLANDACEAE) WOODLANDS IN SOUTHERN CALIFORNIA

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ABSTRACT

Three woodlands dominated by California black walnut were studied. At one site, *Quercus agrifolia* was a co-dominant whereas at the other two sites *Juglans californica* dominated >90% of the relative areal coverage. *Heteromeles arbutifolia* was a significant component of all three woodlands. At two of the sites most of the walnuts were single-stemmed and some of them exceeded 15 m in height. Another site was a more open savanna type woodland and many trees had multiple stems; 40% had 4 or more stems per plant and one had 16 stems. The age structure of the three *Juglans* populations is presented. At all sites there were stems at least 70 years of age. All populations had substantial seedling recruitment and densities ranged from 275 to 1975 seedlings (defined as stems ≤5 years of age and not attached to a mature tree) per hectare. It is hypothesized that irregularities in annual seedling establishment and seedling mortality play an important role in structuring these populations.

California black walnut (*Juglans californica,* nomenclature according to Munz 1974) is a low growing hardwood tree endemic to southern California. Woodlands dominated by this walnut occur in the southern Santa Inez and Santa Susana Mountains of Ventura Co. and the eastern-most portion of the Santa Monica Mountains and foothills of eastern Los Angeles Co. Most of these woodlands occur below 500 m although well-developed walnut woodlands may extend up to 1000 m (e.g., the north side of Oat Mt. in the Santa Susana Mts.). Outside of this range, *J. californica* occurs more often as scattered individuals amongst other hardwoods which form the Southern Oak Woodland Community. *Juglans californica* extends eastward to the western flanks of the San Bernardino Mts. and south to northern San Diego Co. (Beauchamp 1986). The northern limit of distribution appears to be central Santa Barbara Co.; reports of the species in San Luis Obispo Co. are considered to be either ascribable to *J. hindsii* (Jeps.) Jeps. (Hoover 1970) or plantings (Griffin and Critchfield 1972). The tree has been used in southern California as a rootstock for commercial walnut crops, and it has been widely planted in urban forestry projects, e.g., in the western Santa Monica Mountains (Radtke 1978).

Despite widespread current interest in California hardwoods, *Ju-*

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glans californica woodlands have not received much attention. Apart from a few papers on the systematic affinities (Jepson 1908, 1917; Thomsen 1963) the only studies are two unpublished master's theses (Swanson 1967; Leskinen 1972). Throughout its range this species tends to be best developed on N-facing slopes with deep, well developed soils with high water-holding capacity derived from Tertiary marine shales. On many sites it is closely associated with two other tree species, *Quercus agrifolia* and *Heteromeles arbutifolia* (the latter is often associated with adjacent chaparral communities where, due to frequent fires, it is a shrub). Swanson (1967) reported that *Juglans* seedling reproduction was absent in the Los Angeles Co. population he studied and suggested this was due to low precipitation.

Due to urban sprawl much of the California black walnut woodland has been destroyed or is threatened, and it is considered to be one of California's rare and imperiled natural communities (Jones & Stokes Associates 1987). An understanding of the age structure of such woodlands is an important first step towards evaluating the reproductive status and, thus, the future health of the remaining remant woodland stands. The focus of this study was to assess the age structure of three *Juglans californica* stands.

Study Sites and Methods

Study sites. Three sites of one to several hectares of walnut woodland were located as follows. 1, N-facing slope of Sulphur Mt. (350 m elev.) W of Hwy 150, 10 km N of Santa Paula, Ventura Co.; 2, N-facing slope of Mt. Washington (250 m), 3 km NE of Elysisan Park, city of Los Angeles, Los Angeles Co.; 3, E-facing slope (225 m) in Montecito Park, 5 km SW of South Pasadena, city of Los Angeles, Los Angeles Co.

Methods. At each site, 18 10 × 10 m plots were randomly located and the basal diameter of stems of all tree and large shrub species within the plots was recorded. Stems connected to the same root-crown were indicated and the height and diameter of the canopy of each individual was recorded. Heights of trees beyond the reach of a 4 m pole were determined by calculation from the geometric relationship between angle to the top of the tree (measured with an inclinometer) and distance to the tree along the same contour. At each site nine to 10 *Juglans* trees were cored at 25 cm above the ground with an increment borer and the basal diameter, areal diameter and height were recorded. Also, 18 seedlings and saplings, too small to be cored, were cut and a section of the stem near the base was removed. The increment cores and stem sections were returned to the lab for ring counts.

The quadrat data were analyzed for community indices of density and coverage for all woody species. Basal coverage and areal cov-

TABLE 1. RELATIVE AREAL COVERAGE, BASAL AREA COVERAGE, AND DENSITY FOR *JUGLANS CALIFORNICA* DOMINATED WOODLAND ON THE NORTH-FACING SLOPE OF SULPHUR MT., VENTURA COUNTY, CALIFORNIA.

Species	Relative areal coverage (%)	Basal area coverage (m^2/ha)	Density (no./ha)	
			Stems	Individuals
Juglans californica				
Alive	49	11.4	3925	3500
Dead	<1	<0.1	50	50
Quercus agrifolia	39	38.2	1390	1240
Heteromeles arbutifolia	12	1.6	1450	1140
Sambucus mexicana	<1	<0.1	90	80
Rhamnus crocea	<1	<0.1	30	30

erage were calculated by assuming the trunks and canopies approximated a circle. Densities of stems (ramets) as well as individuals (genets) were calculated. The *Juglans* cores and stem sections were sanded and the number of rings determined. On older stems the coloration of the heartwood made ring counts impossible without first bleaching with a 5% solution of sodium hypochlorite. It was assumed that rings were laid down annually, a reasonable assumption for a temperate climate deciduous tree, and true for other trees in southern California (Schulman 1947). A regression analysis of age and basal diameter was done using a linear regression and polynomial regression program available on BMDP (Brown 1977). The equation giving the best fit was used to predict the ages of all *Juglans* stems recorded in the quadrats.

RESULTS

There were marked differences in the community characteristics of the three walnut woodlands. At the Sulphur Mt. Site (Table 1) *Quercus agrifolia* (coast live oak) was a co-dominant whereas at the other two sites (Tables 2 and 3) *Juglans californica* was the only dominant. At Sulphur Mt. areal coverage was estimated to be greater for walnut but due to the massive trunks of several of the live oaks, basal area coverage was substantially greater for that species. At this site the *J. californica* were nearly all single stemmed and thus the number of individual genets was similar to the number of stems (ramets) (Table 1). Although *Juglans* was the only dominant at the other two sites (Tables 2 and 3) there were marked differences between these two stands. At the Mt. Washington Site *J. californica* basal area coverage was double that recorded at Montecito Park whereas the latter site had more than double the number of stems as the Mt. Washington Site. In other words the Mt. Washington Site

TABLE 2. RELATIVE AREAL COVERAGE, BASAL AREA COVERAGE, AND DENSITY FOR *JUGLANS CALIFORNICA* DOMINATED WOODLAND ON THE NORTH-FACING SLOPE OF MT. WASHINGTON, LOS ANGELES COUNTY, CALIFORNIA.

Species	Relative areal coverage (%)	Basal area coverage (m^2/ha)	Density (no./ha)	
			Stems	Individuals
Juglans californica				
Alive	90	38.4	1360	1130
Dead	<1	0.1	50	50
Heteromeles arbutifolia	8	3.4	410	150
Prunus ilicifolia	2	0.6	220	200

was a woodland of large, mostly single-stemmed, trees whereas the Montecito Park Site was a more open woodland with many smaller, multiple-stemmed trees and a greater number of dead *Juglans* trunks. At all sites *Heteromeles arbutifolia* was a significant component of these woodlands. *Sambucus mexicana, Rhamnus ilicifolia, Prunus ilicifolia,* and *Toxicodendron diversilobum* were present at all three sites, although they were not always recorded from the plots. Swanson (1967) reported putative hybrids between *J. californica* × *J. regia* from an area on Sulphur Mt.; however, I did not observe any at the Sulphur Mt. Site.

The distribution of stem diameters of the three co-dominants at Sulphur Mt. showed marked differences. For *J. californica* (Fig. 1) there was more continuous distribution of size classes (up to 85 mm) compared to that for *Q. agrifolia* (Fig. 1). This coast live oak population had 90% of the stems in the smallest size class and very few greater than 25 mm. The maximum stem diameter was 1000 mm for *Q. agrifolia* which was nearly three times greater than the largest *J. californica* and six times greater than the largest *H. arbutifolia* (Fig. 1).

The tallest *J. californica* trees were 11 m although only 10% of the population was greater than 5 m. *Quercus agrifolia* reached 18 m and 10% were taller than 10 m. Several of the *Heteromeles arbutifolia* were 10 m in height.

At the Sulphur Mt. Site, 27 *Juglans* stems were aged and the oldest was 98 years. Age was significantly correlated with all of the parameters measured: basal diameter (Fig. 2), areal diameter (Fig. 2) and height (Fig. 2). The relationship between age and areal canopy diameter was best described by a linear equation whereas the relationship between age and basal diameter or age and height best fit a higher order polynomial equation. The regression equation relating age and basal diameter was used to estimate the ages of the

TABLE 3. RELATIVE AREAL COVERAGE, BASAL AREA COVERAGE, AND DENSITY FOR *JUGLANS CALIFORNICA* DOMINATED WOODLAND ON AN EAST-FACING SLOPE IN MONTECITO HEIGHTS, LOS ANGELES COUNTY, CALIFORNIA.

Species	Relative areal coverage (%)	Basal area coverage (m²/ha)	Density (no./ha)	
			Stems	Individuals
Juglans californica				
Alive	95	19.6	2790	1710
Dead	3	4.2	478	100
Heteromeles arbutifolia	1	0.1	78	20
Prunus ilicifolia	1	<0.1	20	10

Juglans stems recorded from the quadrats and these are shown in Fig. 3. The oldest trees encountered in the sampling were estimated to be about 73 years of age. Fifty percent of the population, or 1975/ha, were estimated to be seedlings (defined as stems ≤5 years of age and not attached to a matured tree). This seedling pool had an areal canopy diameter of ≤0.5 m and 20% of this cohort exceeded 1.0 m in height. There were gaps in some age classes but most were represented and the decrease in density with age best fit a negative third order polynomial relationship ($p < 0.001$, $r = 0.95$).

At the Mt. Washington Site stem diameters of *Juglans* were significantly larger than those observed at Sulphur Mt. with the largest being 900 mm. Heights of these trees were also greater; one tree was 15.5 m and 10% of the population exceeded 8 m. The same pattern of larger trees at this site was observed for *H. arbutifolia.* One stem had a basal diameter of 575 mm and a height of 11 m. The only other woody species recorded was *Prunus ilicifolia* although many of the specimens appeared to be hybrids with *P. lyonii* (a Channel Island endemic) which grew at the site and may have escaped from cultivation or been planted by aerial spraying (Radtke 1978). At this site the largest *Juglans* stem cored was rotted in the middle so the exact age was unknown. From the intact cores, a linear model was the best fit between age and basal diameter. Using this equation the largest *Juglans* stem encountered in the quadrat sampling was estimated to be 132 years of age (Fig. 3). Only 25% of the stems (275/ha) were 1–5 year old seedlings and the decrease in density of older age classes approximated a second order polynomial curve ($p < 0.01$, $r = 0.94$).

At the Montecito Park Site the largest *Juglans* stem had a diameter of 675 mm and was 10 m tall. The largest *Heteromeles* stem had a basal diameter of only 71 mm. The oldest *Juglans* stem aged was 81 years of age and a linear model was the best fit for the age/

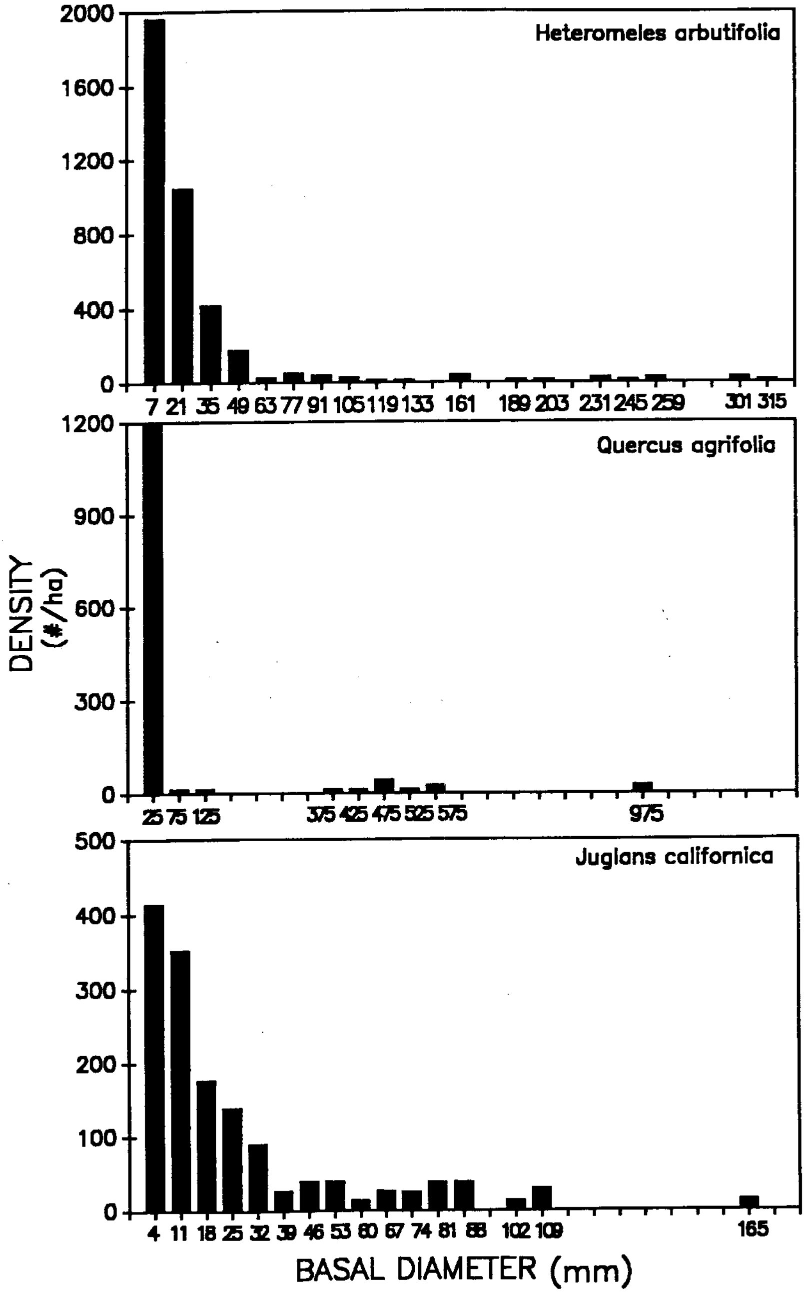

FIG. 1. Frequency distribution of stem diameters for *Juglans californica, Quercus agrifolia,* and *Heteromeles arbutifolia* at the Sulphur Mt. Site.

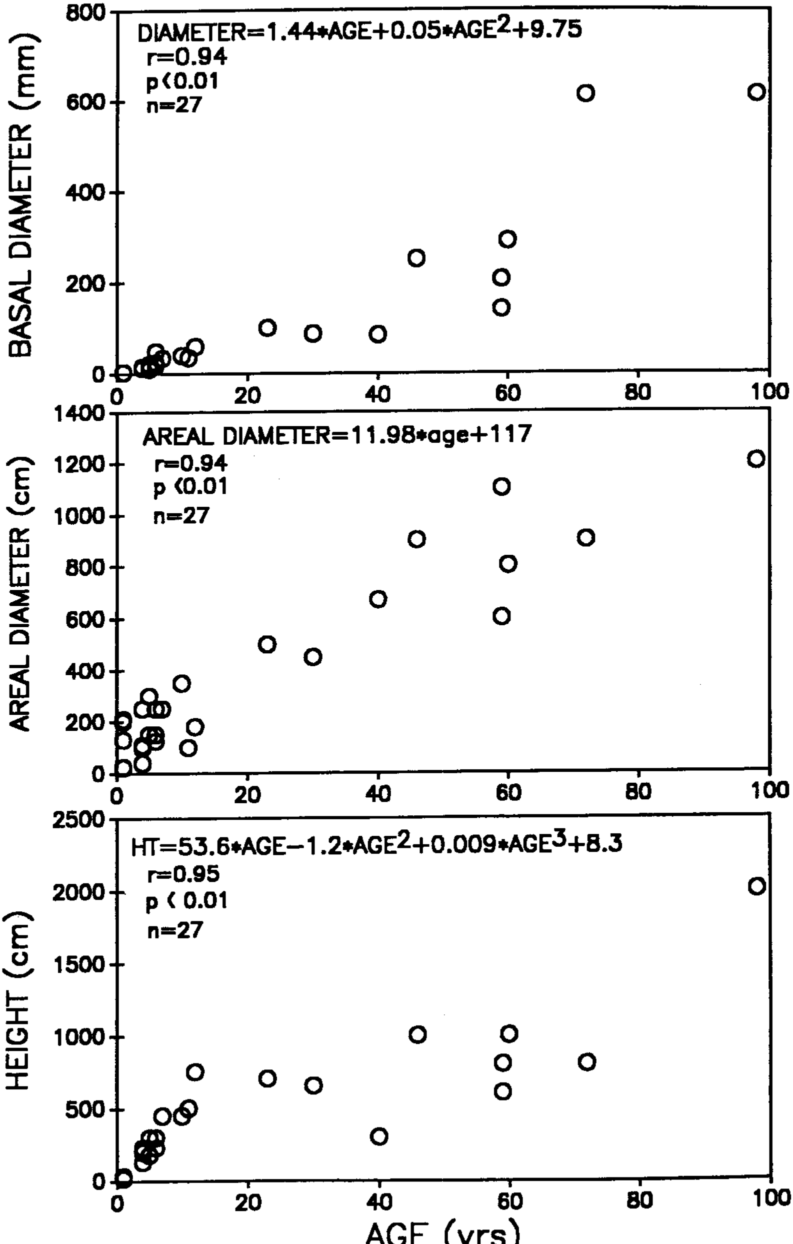

FIG. 2. Relationship between age and height, areal diameter, and basal diameter, for *Juglans californica* at the Sulphur Mt. Site.

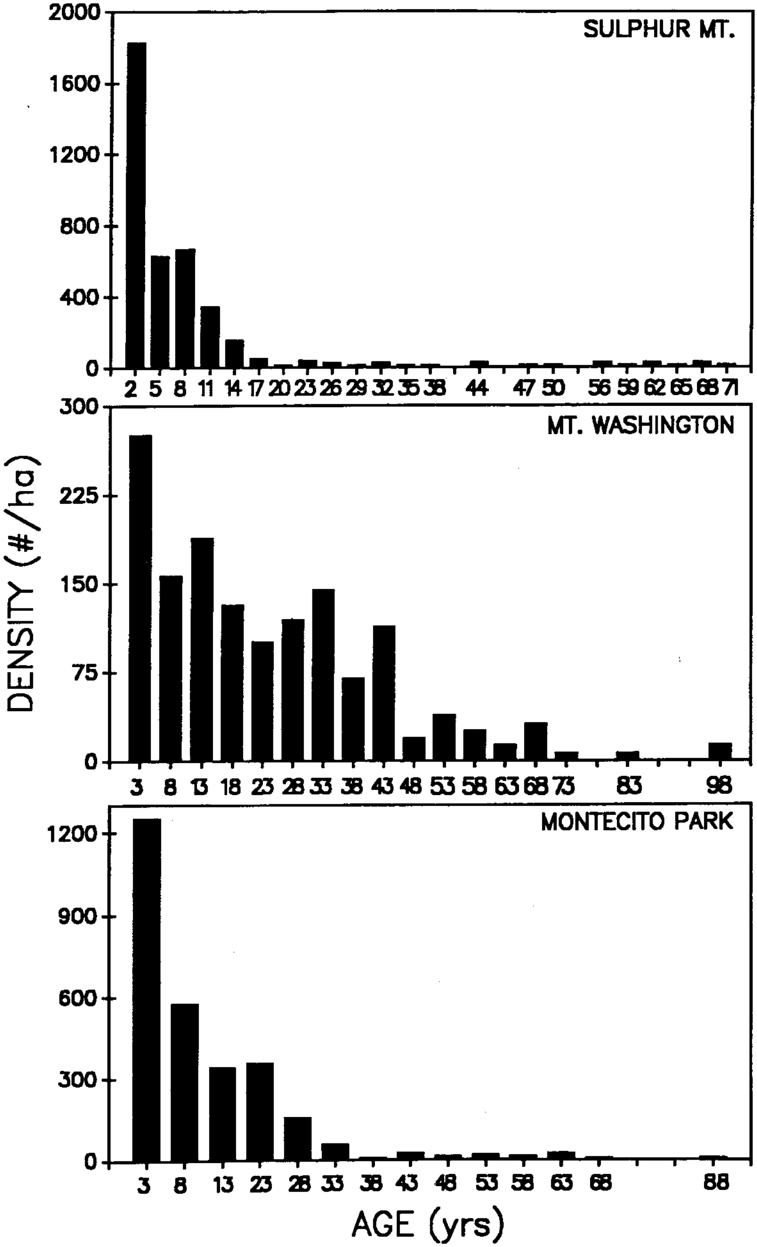

FIG. 3. Estimated age structure of *Juglans californica* stems at the three study sites (live = solid bar, dead = open bar). Age of stems recorded in the random quadrat sampling was predicted from the equations: Sulphur Mt. Site: Age = 0.313•Diameter

diameter relationship. This equation predicted the oldest tree sampled in the quadrats was 77 years (Fig. 3) and that 45% of the population of *Juglans* stems (1250/ha) were ≤ 5 years of age. There was a very rapid drop in density of older age classes which approximated a third order polynomial curve ($p < 0.001$, $r = 0.97$). As can be seen in Table 3, there were many more stems than individual genets at this site. Seedlings and saplings were seldom multiple-stemmed, rather these were generally the larger trees. Of these, 40% had four or more stems and one tree had 16 stems. The age-structure of individual genets, as reflected in a histogram of the oldest stem on each genet (not shown), was compared with the histogram for all stems (Fig. 3). The shape of these histograms was remarkably similar and the number of individual genets ≤5 years (i.e., seedlings) was 51% of the population or 860/ha.

Discussion

Black walnut woodlands in southern California may be dominated by *Juglans californica* alone or walnuts associated with sclerophyllous evergreen trees. The most common ones reported in this study, *Quercus agrifolia* and *Heteromeles arbutifolia,* have also been reported from other studies (Swanson 1967; Leskinen 1972; Campbell 1980). Axelrod (1977) contends that this *Juglans* dominated woodland is quite ancient, dating back to at least the Miocene when it was associated with an even greater array of evergreen broadleaf trees.

A number of the evergreen trees and shrubs currently associated with *Juglans* woodlands, e.g., *Heteromeles arbutifolia, Prunus ilicifolia,* and *Rhamnus ilicifolia,* are common elements in the widespread chaparral community which is often juxtaposed with walnut woodlands. These evergreens persist in the fire-prone chaparral due to their proclivity to resprout after fire. The reproductive biology of these evergreens, however, is poorly adapted to this community in that the seeds have no imposed dormancy and thus germinate readily after dispersal. These seedlings do not survive in most chaparral stands; consequently, seedling reproduction by these species is seldom observed in chaparral. Reports of reproduction are usually restricted to extremely old chaparral (Keeley and Keeley 1988) or woodlands, as observed in this study. These taxa persist in walnut woodlands, as well as other broadleaf woodlands (Campbell 1980), as "gap-phase" species, which is consistent with the fact that these

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$- 0.00029 \cdot \text{Diameter}^2 + 0.08$ ($p < 0.001$, $r = 0.96$, $n = 27$); Mt. Washington Site: $\text{Age} = 0.141 \cdot \text{Diameter} + 4.77$ ($p < 0.001$, $r = 0.91$, $n = 25$); Montecito Park Site: $\text{Age} = 0.126 \cdot \text{Diameter} + 3.59$ ($p < 0.001$, $r = 0.93$, $n = 23$).

species produce bright, red, bird-dispersed berries unlike most other chaparral taxa. These evergreen taxa have been part of oak woodlands and the mixed evergreen forest since at least Miocene (Axelrod 1977) and today are still considered to be "characteristic components" of four different woodland communities in California (Barbour and Major 1977).

The three sites studied here describe woodlands of quite different structure. The Montecito Park Site was the most open savanna-like woodland of the three sites. Total dominance of all woody species (as measured by basal area coverage) was less than half that observed at the other two sites. Records of prior disturbance in this area are non-existent. Observations of the surrounding hills, which are dominated by *Brassica nigra* and other non-native annuals with remnants of a few resprouting chaparral shrubs, suggests this area has burned frequently in the past; a characteristic of much of the Los Angeles Basin (Freudenberger et al. 1987). The savanna-like aspect of the Montecito Park Site may be due to such disturbance. The multiple-stem character of most of the walnut trees at that site would be consistent with that hypothesis since this species resprouts readily after burning. In addition, the significant number of sizeable dead *Juglans* at this site (Table 3) compared to very few at the older Mt. Washington Site (Table 2) also supports the idea that fires have been a part of the Montecito Site's history.

The Mt. Washington Site is an example of a more closed-canopy type woodland with a much greater dominance of *Juglans*. The structure of this woodland suggests it has been free from disturbance for an extended period of time. Most of the walnuts are single-stemmed and there are many large specimen trees, both *J. californica* and *H. arbutifolia,* of extraordinary size. There was no obvious evidence of fire at this site in recent decades as was true of the Sulphur Mt. Site, which likewise had mostly single-stemmed walnut trees.

Seedling regeneration of *Juglans* was evident at all three sites. The density of seedlings at Sulphur Mt. was similar to that observed by Swanson (1967) for a site near our Sulphur Mt. site. Neither of the Los Angeles Co. sites described here lacked seedling reproduction as Swanson (1967) reported for his Brea Canyon site in eastern Los Angeles Co. He hypothesized that this lack of *Juglans* seedling establishment was due to the lower precipitation in the southern part of its range. His hypothesis seems unlikely in light of the continuous seedling establishment apparent over the past several decades in the two Los Angeles Co. sites described here (Fig. 3). Intensive cattle grazing present at Swanson's (1967) Brea Canyon Site may account for lack of seedling recruitment there; grazing in recent decades has not been a factor at any of the sites described here. The large seedling population observed at the Montecito Park Site suggests that, if protected from fire, eventually this savanna-like woodland may develop into a denser woodland.

Interpretation of the age structures reported here requires careful analysis. If we assume that all three populations have constant rates of annual recruitment, and mortality is constant with age, we could conclude that these populations are relatively stable. That is, barring disturbance, recruitment and survival of seedlings and saplings is sufficient to maintain these populations in the future. If these assumptions were true one could account for gaps in certain age classes by a low intensity disturbance such as a ground fire which selectively eliminated seedlings during those years but failed to kill older age classes. Such a hypothesis seems unlikely since, due to the low canopies and lack of self-pruning in these walnuts, fires generally are much more intense and consume the entire canopy of the forest.

In general, a model of constant recruitment and constant mortality is probably a poor one for interpreting age structure of walnut populations. The shape of age-structures (Fig. 3) could be explained by an increase in fruit production as the trees in the forest age. This is an unlikely explanation since abundant fruit production is observed on trees after about 20 years (pers. obs.) plus the Mt. Washington stand with the largest and oldest trees did not have greater seedling production than the other two younger stands.

I suggest reproduction and mortality are not constants in these walnut populations and that they vary in a stochastic rather than a deterministic manner. Although no quantitative data exist on *Juglans californica* reproduction, one can readily observe years of little or no fruit production, commonly in drought years, in contrast to mast years of very heavy walnut production during wetter years. Since the seeds of this species have no imposed dormancy and germinate readily after dispersal (Keeley 1987), it follows that seedling establishment would not be constant from year to year. Due to the potentially lethal effect of occasional severe droughts, it seems likely that mortality is also not constant for all age cohorts. Thus, I hypothesize that gaps in certain age classes in some of the age structures presented here are due to annual variations in recruitment and mortality, resulting from annual differences in climate, especially precipitation.

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