

A study of oak-pollen production and phenology in northern California: Prediction of annual variation in pollen counts based on geographic and meteorologic factors

David Fairley, Ph.D., and George L. Batchelder, Ph.D.

Columbus, Ohio, and Beverly, Mass.

To assess the characteristics of oak-pollen production and dispersal, 9 years of weekly volumetric air sampling, with modified swing-shield roto-slide pollen samplers, were obtained in San Francisco and San Jose, Calif. The Mediterranean climate of coastal California supports 9 million acres of oaks of nine different species. The major pollen contributors in the two sampling areas are coast live oak (Quercus agrifolia Neé) and valley oak (Quercus lobata neé). Sampling data indicate that grains may be wind transported at least 16 km (10 miles). A strong correlation exists between pollen capture and total rainfall a full year before pollen release. The correlation is statistically significant, based on a Spearman rank test. A positive regression line slope demonstrates that the greater the precipitation, the stronger the stimulus for pollen production. The median count can be predicted within a factor of two with high probability a full year before release. During most seasons, the peak pollen collection from coast live oak and valley oak occurs in early April. A second peak production period, in mid-May, represents the conglomerate of other oak-pollen types. However, there are major yearly differences in the relative amounts of pollen released during these two periods. Consequently, individual oak pollinosis may depend as much on variable production by the major species as on the total quantity of airborne oak pollen. These data will help clinicians predict and prepare for the intensity of the oak-pollen season and explain seasonal variations in clinical symptoms from year to year. The question of cross-reacting and specific allergens among oak species can be answered by RAST-inhibition studies. Although clinical and immunologic research on ragweed pollinosis has been invaluable as a model for other pollens, this study indicates that aerobiologic and immunologic investigation of other allergenic pollens is essential for proper diagnosis and treatment in practice. (J ALLERGY CLIN IMMUNOL 78:300-7, 1986.)

Until recently, relatively little attention has been directed to the immunology of angiosperm tree pollen, even though its biomass, especially from catkin producers, is greater than that of ragweed¹ and is produced by numerous species within more than a dozen genera during a longer release period.*

For a variety of valid reasons, there has been a

concentration on the allergy and immunology of ragweed (*Ambrosia* spp) and the grasses (Poaceae) in North America. However, the allergist needs accurate knowledge of the overlapping blooming periods, yearly fluctuations in productivity, and suspected cross-reactivity between related species of allergenic trees for skin testing and successful immunotherapy of tree pollinosis.

Studies presented here analyze the patterns of oak-pollen productivity from 9 years of air sampling in the San Francisco Bay area in an attempt to identify the possible relationships of oak-pollen production to meteorologic conditions and the distribution of local oak species.

A basic knowledge of oak-pollen production and its aerobiology is important for a logical interpretation of the data reported here. Throughout coastal California, the Mediterranean climate has fa-

From the Department of Statistics, Ohio State University, Columbus, Ohio, and Pollen Research Associates, Inc., Beverly, Mass. Supported in part by Allergy Foundation of Northern California; American Lung Association of San Francisco; American Lung Association of San Jose; Stanford University, Department of Statistics; and the Siam Institute for Mathematics and Society.

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Reprint requests: David Fairley, Ph.D., Dept. of Statistics, Ohio State University, Columbus, OH 43210.

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vored the development of more than 9 million acres of oak woodland.² Within the study area, nine oak species are distributed throughout their preferred natural habitats (Fig. 1).

In most temperate climates, the sequence of development of wind-transported, deciduous tree pollen embraces three phases. First, differentiation of flower buds and meiotic cell division within the anthers, later, exposure and dehiscence of the anthers, and finally, dispersal via wind currents or insect vectors. The total amount of pollen available for release during a pollen season is ultimately controlled by a preferential differentiation of flower buds from primordial tissue,³ since the greater the numbers of anthers produced, the higher the potential pollen release a year later. In temperate, non-Mediterranean climates, warm dry summers with light rain a year before pollen release have been found to stimulate pollen development.⁴⁻⁷ However, in the Mediterranean climate of coastal California, there is no appreciable summer rainfall, which greatly influences pollen maturation.

Local weather during the pollen season controls both its release and distribution. Initially, the accumulation of total heat units triggers the season.^{7, 8} The final tree anther dehiscence is stimulated by warm, dry days⁹ that shorten the season, whereas in-season rainfall, frost, and the wind strength and direction all influence the final distribution and capture of oak pollen.

Finally, it is important to emphasize that the dominant coast live oak and valley oak in the study area cease pollen release at the end of April but that all the other less common or more distant species continue to bloom through May or into June.^{10 *}

METHODS

Swing-shield roto-slide air samplers¹¹ were placed on the eighth-floor roof of a downtown office building in San Francisco and on the unobstructed roof of a one-story building in San Jose. Each sample was 144 minutes in duration accumulated in 30-second segments once every 10 minutes for 48 hours. One 48-hour sample was obtained per week for 12 months each year for 9 consecutive years. The roto-slide head speed was 1800 rpm. In place of the prescribed edge-set microscope slides, a pair of clear lucite rods, 1.6 mm square and 60 mm long were used for the sampling surfaces. The silicone-coated edges of the rods were set flush with the leading edges of the slide holders for unobstructed exposure to the atmosphere.

In the laboratory, dilute Calberla's stain¹² was applied to the rod surfaces. The impacted aeroallergens were identified

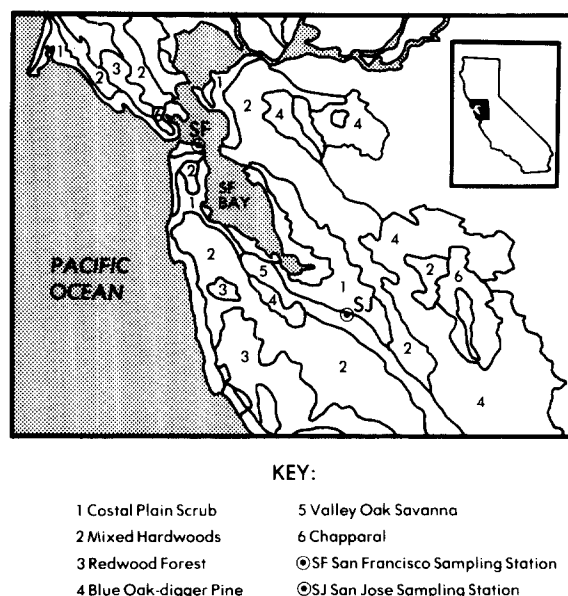


FIG. 1. Potential natural vegetation in the study area from Küchler.¹⁴

and counted at x400 magnification with the bright field-and-phase contrast lighting systems of an Olympus (Olympus Corp. of America, New Hyde Park, N. Y.) model BH microscope. Twenty-two millimeter segments of each rod surface were studied in order that 70.4 mm² were observed for most samples. The pollen counts on each rod were tallied separately for comparative purposes.

The natural distribution and blooming periods of the oak species in the study area were determined, in part, through field studies, but primarily from published distribution maps,^{13, 14} California floras,^{10, 15-17} herbarium records from the California Academy of Sciences, and personal communications.*

Although there are five major taxonomic groups of oaks in the United States that may represent "allergenic classes,"¹⁸ neither pollen from the various species nor members of the major groups can be readily differentiated with transmitted light microscopy. However, pollen from tanbark oak (*Lithocarpus densiflora*) (Hook. & Arn.) Rehd., and chinquapin (*Castanopsis* spp) is quite distinctive from the true oak species. Because of their particular distribution in the study area, these grains helped evaluate the suspected long-distance wind transport of oak pollen from at least one source area.

The following statistical techniques were used to analyze the data: a chi-square test to check data accuracy, a Spearman rank test and linear regression to investigate the effect of winter rainfall on yearly pollen concentrations, multiple linear regression to identify daily meteorologic factors and seasonal factors affecting pollen release, and nonlinear

*Tucker J, Bartholomew B: Personal correspondence.

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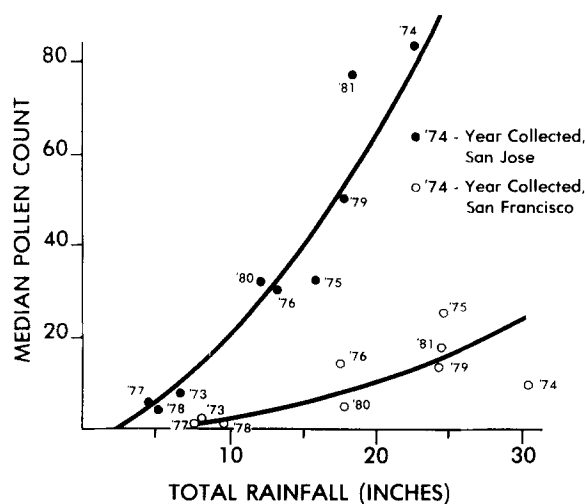


FIG. 2. Median pollen count versus total winter rainfall 1 year previous for San Francisco and San Jose. The curves are the fitted regression lines. The counts are for a 48-hour collection period.

regression, including a simulation, to study the bimodal year-to-year variation in the seasonal oak-pollen concentration curve.¹⁹

RESULTS

Our results are presented in four parts: (1) the identification of pollen source areas, (2) the meteorologic influences of rainfall a full year before pollen release that affect potential pollen production, (3) the daily meteorologic and seasonal influences on pollen release, and (4) an analysis of the yearly variation in shape of the plots of weekly oak-pollen concentrations.

Pollen source areas

Potential source areas for oak pollen in San Francisco (Fig. 1) include the Presidio military reservation, 4.8 km (3 miles) to the west of the sampling station, Golden Gate Park, 8.0 km (5 miles) southwest, the Marin County hardwood forest, 16 km (10 miles) northwest, the redwood forest of Mt. Tamalpais, 16 to 24 km (10 to 15 miles) northwest, and isolated specimens remaining in the urban landscape. Winds from San Bruno Mountain, 12.8 km (8 miles) due south are uncommon, and the natural forest has been mostly destroyed or replaced by *Eucalyptus* species.

Oak-tree density and species diversity around San Jose is greater than near San Francisco. The city itself lies in the remnants of the valley oak savanna (Table I). Mixed hardwood types survive 3.2 km (2 miles) to the north and northwest and 12.8 km (8 miles) west

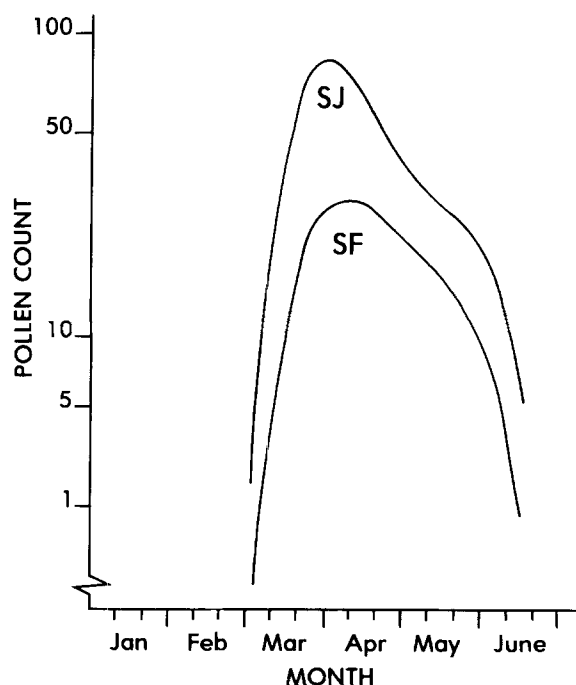


FIG. 3. Composite seasonal curves of oak-pollen concentrations for San Jose and San Francisco. The vertical scale is the count for a 48-hour collection.

and continue to the base of the Santa Cruz Mountains, whereas 29.0 km (18 miles) west is the redwood forest of the Santa Cruz Mountains. Infrequent east winds might carry pollen from the slopes of Mt. Hamilton 22.5 km (14 miles) away.

Table I summarizes the locations of various source areas for both stations. Evidence for a carrying distance of 16 to 24 km (10 to 15 miles) is offered in the 9-year pollen collections from San Francisco that contain pollen from tanbark oak (*Lithocarpus densiflora*) or chinquapin (*Castanopsis* sp) and redwood (*Sequoia sempervirens*) grains. Tanbark oak and chinquapin are commonly associated with mixed hardwood and redwood forest, the closest occurrence of which is Marin County, 16 km (10 miles) upwind (northwest) of the San Francisco sampling station. Redwood pollen, which was collected at both San Francisco and San Jose, is a less definitive indicator of long-distance transport, since it might have originated from relict specimens or fast-growing recent ornamental plantings in city parks, whereas tanbark oak and chinquapin are seldom used in urban landscaping.

There are several published references to long-distance transport of pollen similar in size and specific gravity to oak (≈ 28 to $32 \mu\text{m} \times 34$ to $40 \mu\text{m}$; specific gravity $1.04^{20, 21, 22}$).

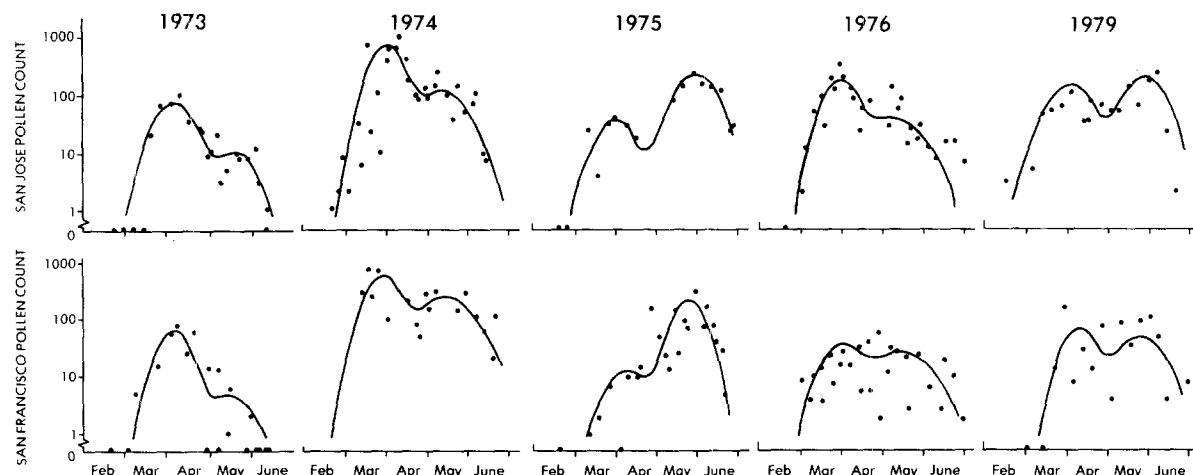


FIG. 4. Weekly 48-hour oak-pollen counts for representative years at San Jose and San Francisco. Bimodal curves indicate the two groups of species, I and II, releasing pollen around April 1 and May 15, respectively (see also Table II).

Relationship between rainfall and yearly median pollen concentrations

The correlation between the median pollen concentrations during nine pollen seasons and total rainfall during the rainy season (October to April) immediately before pollen release was not statistically significant, based on a Spearman rank test. However, a strong positive correlation was found between median pollen concentrations and the total rainfall during the previous rainy season, a full year before final pollen release. (Two-sided p values were 0.0002 for San Jose and 0.06 for San Francisco.)

Fig. 2 illustrates this generally increasing relationship at both sites.

Regression lines presented in Fig. 2 predict the median pollen counts from total winter rainfall a whole year before release.* Ninety percent of the year-to-year and between site variation in the median pollen counts is explained by the regression. In other words, most of the year and site differences in the median counts can be attributed to the difference in average pollen concentrations at the two sites and the effect of the rainfall of the previous year. The San Jose mean concentration was significantly larger than that for San Francisco, indicating a greater density of oaks in the source areas for San Jose than for San Francisco. The positive slope of the regression line indicates that higher median pollen levels are associated with greater total rainfall.

The estimated slope is significantly larger than

unity, which transforms into regression lines with positive curvature on the original scale. In addition, this curvature indicates that the influence of rainfall levels on oak-pollen concentrations is more pronounced at higher rainfall levels than at lower levels in the observed range 5 to 25 inches. For example, a 1-inch increase in rainfall from 20 to 21 inches causes a larger increase in the predicted median pollen count than a 1-inch increase from 10 to 11 inches.

This analysis yields reasonably accurate predictions of the median pollen count for a season based on the total winter rainfall in the previous year. Roughly speaking, the median pollen count can be predicted within a factor of 2 with high probability. (See the Discussion section for a numerical example and application.)

Analysis of daily and seasonal factors affecting pollen release

A multiple regression was performed for each site to predict the individual weekly pollen counts from (1) yearly rainfall, (2) daily temperature and humidity, (3) an average "seasonal curve" reflecting the varying average amount of pollen ready to be released at different times during the pollen season, and (4) terms representing yearly changes in the shape of this curve.

The results for San Jose and San Francisco were quite similar. Both regressions were highly significant and explained a high proportion of the variability in the daily concentrations ($R^2 = 0.85$ for San Jose and 0.82 for San Francisco). The root mean squared errors were 0.74 and 0.71 respectively; therefore the log pollen counts were estimated with a standard deviation of a factor of $e^{0.74}$, which is a factor of about 2. As

*The regression is linear on the log scale. Separate slopes were tried and found not statistically different; therefore Fig. 2 uses the combined slope.

TABLE I. Natural plant communities and distance from sampling stations

Plant community	Distance from sampling station				Species	Common name
	San Francisco		San Jose			
	km	mi	km	mi		
Coastal plain scrub	8.1	5	—	—	<i>Baccharis pilularis</i> DC	Coyote bush
Mixed hardwood forest	16.2	10	3.2 to 12.9	2 to 8	<i>Quercus agrifolia</i> Neé	Coast live oak
					<i>Q. chrysolepis</i> Liebm.	Canyon oak
					<i>Q. kelloggii</i> Newb.	Black oak
					<i>Q. wislizenii</i> A. DC.	Interior live oak
					<i>Lithocarpus densiflora</i> (H.&A.) Rehd.	Tanbark oak
Redwood forest	16.2 to 24.2	10 to 15	29.0 to 32.2	18 to 20	<i>Sequoia sempervirens</i> (D.Don)Endl.	Redwood
					<i>Q. garryana</i> Dougl.	Oregon oak
					<i>L. densiflora</i>	Tanbark oak
Blue oak-digger pine forest	—	—	12.9 to 22.5	8 to 14	<i>Q. douglasii</i> , H.&A.	Blue oak
					<i>Q. lobata</i> Née	Valley oak
Valley oak savanna	—	—	0.5	0.3	<i>Q. wislizenii</i> A.DC.	Interior live oak
					<i>Q. lobata</i> Née	Valley oak
					<i>Q. agrifolia</i> Née	Coast live oak

Source modified from Küchler.¹⁴

expected, the constant term for San Jose was significantly larger than for San Francisco.

The temperature and humidity coefficients for both sites were significantly nonzero. The temperature coefficients were positive, and the humidity coefficients were negative. Thus, warm, dry days were associated with higher pollen concentrations, as observed by Sharp and Chisman.⁹

The curves in Fig. 3 demonstrate a composite of the daily oak-pollen concentrations of San Francisco and San Jose during the pollen seasons under study. Since the pattern of pollen concentrations vary widely from year to year (Fig. 4), these curves may not be typical of a particular season but instead represent an average over many seasons. The curves are fourth degree polynomials fit with linear regression techniques.¹⁹

In Fig. 3, the San Jose curve is consistently higher than the San Francisco curve, indicating that San Jose tends to have higher concentrations throughout the season. The secondary hump around May 15 in the San Jose curve is due to pollen release by species different from those responsible for the main April 1 peak.

Seasonal variation in pollen concentrations

The seasonal pattern of daily oak-pollen concentrations varies in general shape from year to year. Fig.

4 demonstrates early April peaks in 1973, 1974, and 1976 for San Jose, but not in 1975 or 1979.

Live oak and valley oak are probably the major contributors to these April peaks. Neither of these species release much, if any, pollen after May 1. Thus, in all likelihood, most of the pollen after the May 1 peak is derived from one or more of the other species (Table I). Therefore, the year-to-year variation in the general shapes of the plots is due to different relative amounts of pollen collected from two groups of species: group I, which reaches maximum pollen output around April 1, and group II, peaking about 6 weeks later (Table II). Bimodal curves have been drawn on Fig. 4 to highlight the presence of these two groups of species.

To assess the amount of year-to-year variation in the shapes of these seasonal plots and also the amount of yearly variation in the initiation of the oak-pollen season, these yearly seasonal curves were modeled as mixtures of two unimodal curves.¹⁹ The changes in the relative heights of the modes and the timing of the peaks during the pollen season accounted for about 30% of the total variation of the log pollen counts. Much of this seasonal variability can be attributed to changes in the relative heights of the two modes rather than changes in the dates for each peak. Therefore, there were major differences in the relative amounts of pollen collected from different species in different

TABLE II. Oak distribution* and blooming period in the San Francisco Bay area

Pollen groups	Species	Common name	Blooming period	San Francisco	Southern Marin County	Mt. Tamalpais	San Jose valley	Santa Cruz Mts.
Group I	<i>Quercus agrifolia</i>	Coast live oak	February	±	±	±	±	±
			March					
			April					
Group II	<i>Quercus lobata</i>	Valley oak	March	—	±	—	±	—
			April					
	<i>Quercus wislizenii</i>	Interior live oak	March	—	±	—	—	±
			April					
			May					
	<i>Quercus dumosa</i>	Scrub oak	March	—	—	±	—	—
			April					
			May					
	<i>Quercus kelloggii</i>	Black oak	April	—	±	—	—	±
			May					
	<i>Quercus chrysolepis</i>	Canyon oak	April	±	±	±	—	±
			May					
	<i>Quercus douglasii</i>	Blue oak	April	—	—	±	±	±
			May					
	<i>Quercus durata</i>	Leather oak	April	—	—	±	—	—
			May					
	<i>Quercus garryana</i>	Oregon oak	April	—	±	±	—	—
			May					
	<i>Lithocarpus densiflora</i>	Tanbark oak	June to November	—	±	±	±	±

± = Present; + = common; — = absent.

*Relict natural distribution of oak species.

TABLE III. Estimated proportions of pollen from group I species (the species releasing pollen around April 1)

	1973	1974	1975	1976	1977	1979	1980
San Jose	0.87 (0.06)	0.83 (0.06)	0.18 (0.13)	0.70 (0.11)	0.40 (0.16)	0.49 (0.17)	0.80 (0.12)
San Francisco	0.86 (0.06)	0.57 (0.13)	0.11 (0.09)	0.56 (0.13)	—	0.48 (0.14)	0.89 (0.05)

The numbers in parentheses are standard errors estimated through simulation.

TABLE IV. Estimated times of peak pollen potential in the group I species

	1973	1974	1975	1976	1977	1979	1980
San Jose	4/5	4/9	3/31	3/27	4/5	4/2	3/22
San Francisco	4/7	3/28	4/3	3/29	—	4/8	4/4

Estimated standard errors for these peaks range from 4 to 6 days.

years. Table III demonstrates the estimated relative proportions of pollen collected from Group I species (mainly live oak and valley oak).

As expected from Fig. 4, these proportions are high in 1973, 1974, and 1976, but not in 1975 or 1979. A similar pattern of changes in relative heights of the

modes occurred at both San Jose and San Francisco. For example, Table III demonstrates that both were high in 1973, both low in 1975, and both about 50% in 1979. A simulation of the model demonstrates that the differences in proportions between San Francisco and San Jose for the same year were not statistically

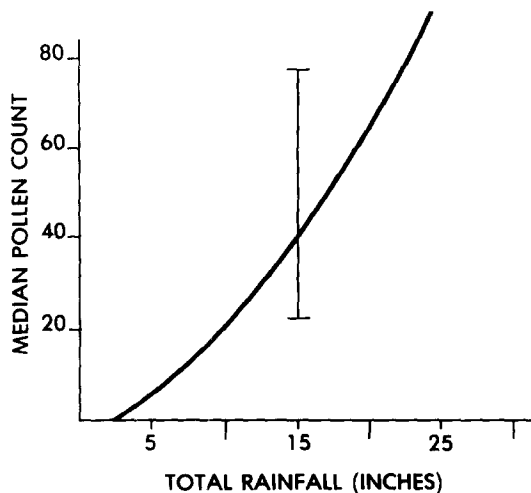


FIG. 5. Prediction of median oak-pollen production for San Jose based on total winter rainfall during the previous year. There is about an 80% chance that when the rainfall is 15 inches, the pollen count a year later will lie within the bounds of the vertical bar, 23 to 77.

significant, whereas the year-to-year changes were highly significant.

Once the variation in the relative heights of the modes is accounted for, the timing of the peaks of the pollen season is only marginally significant. Table IV presents estimates of the timing of the peak of the pollen season for the Group I species.

The peak times demonstrate no consistent region-wide pattern. In particular, there are large discrepancies in estimated first peak times between San Jose and San Francisco of 12 days in 1974 and 13 days in 1980.

DISCUSSION

The peak blooming time for San Jose oaks is typically around April 1 with the major contributors being coast live oak and valley oak. Our analysis demonstrates that the date of the peak for these species changes little from year to year.* However, in some years, such as 1975, the pollen productivity of these species is small relative to the total oak pollen released. Another group of species, releasing pollen after May 1, was responsible for most of the pollen released that year (Fig. 4). Thus, the late releasing group acts somewhat independently of the early releasing group. Hence, mild allergic symptoms to oak around April 1 may not guarantee continued mild symptoms through the end of May, since severity of reactions to different oak species may vary. In addition, mild reactions during the first peak could prime

patients to react more strongly to the second peak, even if the second peak pollen counts are lower than those of the first peak.

The San Francisco results were quite similar to San Jose results. The peaks occurred at similar times, and even their relative heights were close (Table III; Figs. 3 and 4). The fact that the peaks varied together indicates a region-wide cause, perhaps differential drought resistance between species or heavy rainfall in late March, knocking anthers off the trees. Because the cause is unknown, we cannot predict in which years the pollen will peak early (around April 1) and which years, late (around May 15).

The similarity in shape of the San Jose and San Francisco curves (Figs. 3 and 4) was surprising. In particular, the April 1 peak for San Francisco in some years was unexpectedly large and implies that there can be considerable pollen from coast live oaks and/or valley oaks in downtown San Francisco. The pollen origin is probably within San Francisco and as far away as Marin County, as implied by evidence cited above.

As mentioned previously, in non-Mediterranean climates, warm summers with low precipitation stimulate pollen production. In contrast, the Mediterranean climate of the San Francisco Bay area lacks summer rainfall. Therefore, some water-dependent physiologic activities of plants, such as pollen production, become winter-precipitation dependent. This may explain why the study demonstrates that heavy oak-pollen release occurs 12 to 14 months after a winter with heavy precipitation. For example, heavy rains during the winter of 1972 to 1973 apparently stimulated flower-bud differentiation during the summer of 1973 that, in turn, resulted in very high pollen counts for San Jose during the spring of 1974. This pattern of high pollen productivity a year after heavy winter rains is repeated in all instances except San Francisco in 1974.

Predictions of median oak-pollen concentrations can be made a whole year ahead by use of the results described above. For example, if the total San Jose rainfall is 15 inches, the regression curve predicts a median pollen count of 42 in the spring a year later, and the probability is about 80% that the median will lie between 23 and 77 (Fig. 5).

Finally, the validity of our results can be tested by use of future winter-precipitation totals to predict subsequent northern California oak-pollen production. Other important related investigations have already been completed. First, the allergenicity of coast live oak has been recently demonstrated by Abba I. Terr* who found that 62% of 100 patients, sensitive enough

*The 17-day range of the estimated peak concentrations (Table IV) is small relative to the range found for other tree genera.⁸

*Terr AI: Unpublished data.

to spring-blooming trees to require immunotherapy, developed 2+ or greater prick test reactions to that species, ranking it fourth of the 15 spring-blooming trees routinely tested. In addition, Zenger and Wedner²³ have demonstrated multiple antigenic protein-banding patterns, different between species, in aqueous extracts of pollen from eight eastern oaks.

Further interdisciplinary study of the phenology and immunology of all oak species will lead to improved clinical evaluation and treatment of oak-sensitive patients.

SUMMARY AND CONCLUSIONS

1. The major peak in the oak-pollen season generally occurred around April 1 and was due mainly to pollen production of coast live oak and valley oak. The timing of this peak varied only slightly during the 9-year study period. A secondary peak around May 15 was sometimes apparent and was due to a different group of species.
2. In the San Francisco Bay area, the amount of winter rainfall, a year before each pollen season, influences oak productivity. The greater the rainfall, the higher the oak-pollen production 12 to 14 months later. Thus, the intensity of oak-pollen production can be predicted long before the season occurs.
3. There was considerable year-to-year variation in the relative amounts of pollen collected from the two groups of species, and this variation was region wide. Thus, the pollen season might be unusually heavy for some species but not for others; therefore, the effect on an allergy patient might depend more on the patient's sensitivity to certain species rather than the total oak pollen in the air. The causes of this yearly variation are unknown. Two possibilities are heavy rainfall around April 1 in some years and differential drought resistance between oak species.
4. Recovery of *Lithocarpus* (tanbark oak) pollen at the San Francisco sampling station implies that small nonvesiculate grains, probably including *Quercus* sp (oak), were transported at times of northwest winds for at least 16 km (10 miles).

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