

Synchronicity and Geographic Variation in Oregon White Oak Acorn Production in the Pacific Northwest

Abstract

We explored geographic patterns and synchrony of Oregon white oak (*Quercus garryana*) acorn production over 8 years from Vancouver Island, British Columbia to Medford, Oregon. We divided our data into geographic areas: Puget-Willamette Trough, Columbia Gorge-East Cascades (Eastside) xeric, Eastside mesic, Cascade Mountain foothills, Roseburg, and Medford to compare annual acorn production among areas. We observed high within-area synchrony, but synchrony across areas was only apparent in 2004 and 2006 (high production), and 2005 (low production). Correlogram analysis indicated significant acorn crop correlation throughout the Puget-Willamette Trough, but synchrony was higher over greater distances among stands than among trees. Relationships between acorn production and mean monthly temperature or precipitation were examined with correlation analyses for each month between floral initiation and acorn maturation over 8 years of observations. Acorn production in the Puget-Willamette Trough was negatively correlated with spring precipitation, possibly due to an effect on floral processes, and winter temperature, which might relate to bud chilling requirements. In Eastside uplands, June precipitation positively correlated with current acorn production, but negatively correlated with the following year's production suggesting a climatically mediated depression by one year's production on that in the following year. Eastside production negatively correlated with precipitation in March suggesting precipitation interferes with floral processes at that time. We developed predictive linear regression models for the two analysis areas with largest sample sizes. Oregon white oak masting is similar to that in other white oaks in terms of periodicity and the effects of spring weather, but is also influenced by other weather related factors following floral induction.

Introduction

Oregon white oak (*Quercus garryana* Douglas ex Hook.), a widely distributed western North American species of oak, produces heavy seed crops on an irregular basis (Stein 1990). Little is known of the factors that affect its acorn production (Stein 1990), but Peter and Harrington (2002) suggested that tree, stand and environmental conditions including age, competition, and water availability are important. A better understanding of the factors affecting acorn production would aid wildlife management, since Oregon white oak acorns are an important source of food for many wildlife species (Silen 1958, Barrett 1980, Ryan and Carey 1995).

In general, acorn production varies greatly between trees and across years, but tends to synchronize over large populations (Koenig 1980, Sork et al. 1993, Healy et al. 1999). Synchronous production of large seed crops by a population of trees is known as masting (Janzen 1969, 1971; Silvertown 1980). Masting has been studied in a number of oak species (Downs and McQuilken 1944, Christisen and Korschgen 1955, Goodrum

and Reid 1971, Sork et al. 1993, Koenig et al. 1994, Koenig and Knops 1995, Koenig et al. 1996), but little attention has been paid to acorn production in Oregon white oak.

The causes of masting have been much debated (Ims 1990, Kelly 1994). It is presumed to be an evolved means of maximizing seedling survival through a variety of mechanisms (Kelly 1994) including predator satiation (Silvertown 1980), increased pollination efficiency (Nilsson and Wastljung 1987, Norton and Kelly 1988, Smith et al. 1990) or resource matching where seed production tracks availability of one or more resources (Norton and Kelly 1988). Weather parameters, including temperature and moisture, are usually considered exogenous cues that influence masting periodicity by affecting access to resources. Weather conditions influence many plant processes including pollination (Sharp and Chisman 1961, Sharp and Sprague 1967) through frost damage (Goodrum and Reid 1971, Neilson and Wullstein 1980), drought or temperature stress (Sweet 1973, Sork et al. 1993), and photosynthetic efficiency (Norton and Kelly 1988). Weather also influences the buildup of photosynthetic reserves for reproduction which, in turn, determines acorn crop size (Koenig and Knops 2002). In addition, the degree

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of resource depletion following a large crop might determine the interval size between large crops within limitations imposed by weather (Sork et al. 1993, Piovesan and Adams 2001, Greene and Johnson 2004). Greene and Johnson (2004) suggested that no “true” mast cycle has been demonstrated. In their view, climatic cues are more important than resource depletion in determining crop size and periodic tendencies.

White oak floral primordia are initiated in June (Turkel and Rebeck 1955, Merkle et al. 1980) 15 months prior to fruit maturation. Development proceeds through the summer and resumes in late winter or early spring with flowering and pollination occurring in March to June and acorn maturation from late August to October. We examined the effects of temperature and precipitation on Oregon white oak acorn production over eight 15-month floral initiation to acorn maturation periods. Our goal was to determine the extent of synchrony in acorn production in the Pacific Northwest, whether acorn production differed geographically and whether differences in temperature and precipitation were involved. We examined whether temperature and precipitation had greater effects in some months than in others and if major habitat differences, such as riparian vs. uplands, modify the way weather affected acorn production.

Study Areas

We sampled 873 trees in 115 local populations (one or more stands growing on a similar soil and landform) from Courtenay on Vancouver Island, British Columbia near the northern limit of the species distribution to Medford, Oregon in the south. Because of large differences in topography and climate, we divided our data into five more uniform geographic analysis areas for analysis (Figure 1). In the highly maritime Puget-Willamette Trough, trees grew mostly on flat to rolling topography from near sea-level to around 200 m elevation mostly in the Western Hemlock Zone (*Tsuga heterophylla*) (Franklin and Dyrness 1988). Trees from the Columbia Gorge and east of the Cascade Mountains (hereafter referred to as “Eastside” trees) grew in a topographically complex area on a variety of aspects, slopes and elevations (56–680 m). We refer to lower elevation areas (including the Ponderosa Pine Zone [*Pinus ponderosa*] [Topik et al. 1988]) where Eastside

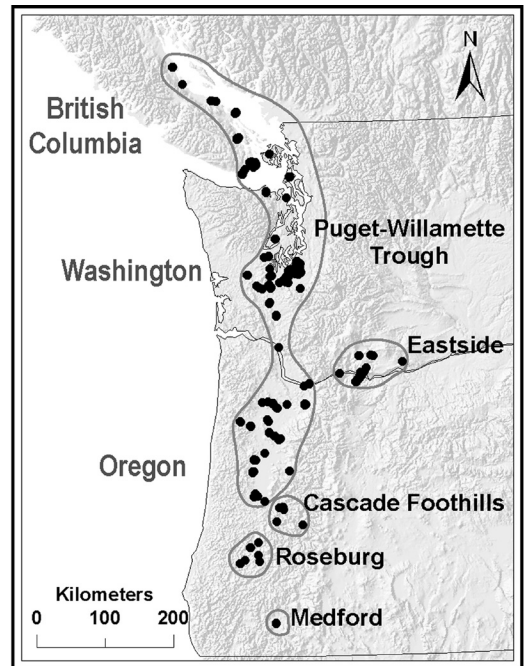


Figure 1. Map of the study location showing locations of trees and the geographical analysis areas.

oak trees grew as the Eastside xeric area and the cooler, moister sites (including the Douglas-fir [*Pseudotsuga menziesii*] [Topik et al. 1988] or higher Zones) where Eastside oaks grew as the Eastside mesic area. Eastside xeric areas tend to be dryer as well as warmer in the summer and cooler in the winter than the other areas. In the Cascade foothills area south and east of Eugene, OR, sample trees grew on relatively flat topography in narrow river valleys ranging in elevation from 200 to 400 m. Trees sampled in the Umpqua River area near Roseburg, OR grew in a topographically complex area on a variety of slopes and aspects from 150 m to 440 m in elevation. The southernmost trees came from a flat, riparian site near Medford, OR (elevation = 384 m). Roseburg and Medford had the warmest mean annual temperature of all the areas during the acorn survey (13 °C).

Methods

Acorn Surveys

We conducted acorn surveys in August and September from 1999 through 2006. Data were collected by personnel from the U.S. Dept. of Agriculture, Forest Service, Pacific Northwest Research Station

and other natural resource management professionals and volunteers. Sampling began in the Puget-Willamette Trough (mostly in the South Puget Sound area) and in the Roseburg areas in 1999 and in all other areas in 2000. Generally, several sample trees were randomly selected within each stand. Our sample includes healthy trees (little or no interior rot visible, few large broken limbs, full crown of healthy leaves, not overtopped by other trees) larger than 10-cm in diameter at breast height (dbh; 1.3 m) from a range of forest to open grown situations. None of the stands selected for this analysis had been thinned, underburned, fertilized or irrigated during the survey period, so our sample represents mature, healthy, relatively undisturbed, naturally growing trees. Surveyors ranked acorn abundance on a 1-4 scale (non-producing to heavily producing) (Graves 1980). Table 1 gives an abbreviated account of the survey method. All trees were surveyed at least 3 and up to 8 yrs during the study period.

Floral Surveys

Since weather strongly influences flowering success and thus pollination effectiveness (Norton and Kelly 1988, Koenig and Knopps 2002), it is important to know when flowering occurs. To determine this, we surveyed 290 trees at Fort Lewis, WA from March 8 to May 14 in 2003 until signs of budbreak were observed. Thereafter we visually estimated the percentage of branch tips bearing staminate flowers for each tree on each observation date. Pistillate flowers, which emerge after the staminate flowers are too small to be easily seen, so were not surveyed.

Sensitive and Insensitive Trees

Surveyed trees were classified into those in which the acorn production class did not change during the survey period (87 “insensitive” trees) and those

which changed class at least once (786 “sensitive” trees) (Table 2). We used sensitive trees to evaluate the effects of monthly precipitation and temperature on annual acorn crop size. To examine acorn production over time, and across geographic analysis areas or habitats (see below), we combined sensitive and insensitive trees. We also pooled sensitive and insensitive trees to calculate the percent of non-producing trees which had been observed in 5, 6, 7 or 8 years (133 to 235 trees/yr). The number of trees sampled in just 3 or 4 years was small (≤ 31 trees/yr) so these trees were not included in this analysis of non-producing trees.

Geographic Analysis Areas

Our study focused most strongly on the South Puget Sound area of Washington (especially the Fort Lewis Military Reservation), but oaks were also sampled from Vancouver Island to Medford Oregon. Of the entire sample, 78 % came from the Puget-Willamette Trough, and 76% of those trees came from the South Puget Sound area. Individual tree acorn abundance classes were averaged into local population means for each year (71 local population means in the Puget-Willamette Trough and 23 elsewhere) (Table 2). The sample size averaged 8 trees per local population (although two local populations were represented by single trees). These means were then averaged into geographic analysis area means including: Puget-Willamette Trough, Eastside xeric, Eastside mesic, Cascade foothills, Roseburg, and Medford analysis areas. Thus, we emphasize comparisons of acorn production between the Puget-Willamette Trough and several adjacent areas differing in climate or topography. Trees were further stratified into upland and riparian habitat groups (Table 2). Riparian trees grew on wetland soils or within two canopy widths of open water. Other trees were considered upland trees.

TABLE 1. Abbreviated method for classification of acorn abundance (Graves, 1980).

<ul style="list-style-type: none"> • Acorns should be mature—yellow-green • If acorns are not readily observed, the tree is either Class 1 (nonproducing) or 2 (light producing). No acorns = Class 1. One or more acorns = Class 2. • If acorns are readily observed, the tree is either Class 3 (medium producing) or 4 (high producing). The tree is Class 3 if acorns are readily visible all around the tree and borne predominantly singly. The tree is also Class 3 if the acorns are only on one side, but are numerous or borne in multiples. A Class 4 tree is characterized by clusters of two or more acorns, all around the tree. The limbs often bend from the weight of acorns.

TABLE 2. Sample sizes of trees and local populations and the weather stations used in the correlation analysis. The data are arranged by the geographic area used to stratify acorn production data, habitat and sensitivity. Analysis area totals are for sensitive trees only.

Analysis Area	Trees			Local Populations			Weather Stations ¹
	upland	riparian	total	upland	riparian	total	
Puget-Willamette Trough (BC, Canada; WA, OR, USA)	621	57	678	60	11	71	Victoria Intl. Airport, Coupeville, Centralia, Olympia, Tacoma, Toledo, Longview, McMinnville, Portland Port Townsend, Sequim, Bremerton, Oregon City, Corvallis, Eugene, Salem
Eastside Xeric (WA, OR)	33	4	37	6	1	7	Bickelton, Dalles ² , Dufur, Goldendale, Hood River
Eastside Mesic (WA, OR)	29	0	29	3	0	3	Bickelton, Dalles ² , Dufur, Goldendale Hood River
Cascade Foothills (OR)	13	0	13	5	0	5	Dorena, Lookout, Oakridge
Roseburg (OR)	13	6	19	6	1	7	Roseburg
Medford (OR)	0	10	10	0	1	1	Medford
Total Sensitive	709	77	786	80	14	94	
Total Insensitive	86	1	87	20	1	21	
Grand Total³	795	78	873	81	15	96	

¹Where multiple weather stations are indicated, data from all stations were averaged.

²Average of The Dalles and Dallesport weather stations.

³Insensitive trees occur in many of the same stands as sensitive trees so totals do not add arithmetically.

Weather Data

We obtained mean monthly temperature and total monthly precipitation data from the Western Regional Climate Center (2006) (<http://www.wrcc.dri.edu/>) and Environment Canada (2006) (<http://www.climate.weatheroffice.ec.gc.ca>) (Table 2). Most weather stations did not have complete data sets for the survey period. Stations missing entire years of data were rejected. Stations with gaps up to a few months were used if other nearby stations existed with complementary data such that averaging the two would produce a complete record. To represent the analysis areas, multiple stations from the entire area were averaged.

Statistical Analysis

Most statistical analyses were conducted using SAS 9.1 for Windows (2002-2003), with significance of $P = 0.1$. We assessed normality with Q-Q plots and used a combination of parametric and non-parametric methods depending on the shape of the data distribution. While mean acorn classes were normally distributed at the level of local or analysis areas, acorn classes at the tree level were not normally distributed. Thus, parametric

ANOVA was used to compare acorn class means, while Kruskal-Wallis ANOVA (KW ANOVA) was used to compare distributions of acorn classes at the tree level.

We compared acorn production in geographic areas differing markedly in topography or climate by comparing upland analysis area means (all trees over all 8 yrs combined) with ANOVA. To characterize variability within geographic analysis areas, we compared acorn production means of local populations with ANOVA. Where significant differences were indicated by ANOVA, we used Tukey's HSD tests to determine which geographic areas or local populations were different. However, we used Kruskal-Wallis ANOVA to compare acorn classes of riparian and upland trees within, and in some cases between, analysis areas.

We used a repeated measures ANOVA (RM ANOVA), with year as a within-subjects factor and acorn production as a between-subject factor over all analysis areas combined, for the Puget-Willamette Trough, (separately for upland and riparian) and for the upland Eastside xeric analysis area. Where significant differences were indicated, we used Tukey's HSD tests to determine which years were different.

Our largest sample came from Puget-Willamette Trough upland trees, so in this area we used the NCF package (Bjornstad 2008) in the R programming environment (R Development Core Team 2008) for a modified correlogram analysis to test for spatial autocorrelation of acorn production and distance between trees and between local populations with a 95% bootstrap confidence envelope (Koenig and Knops 1998, Koenig 1999). This nonparametric covariance function shows how correlation of acorn production between trees or local populations changes with distance and differs from Mantel correlograms by using the 0 level of correlation, not the mean regional level of correlation as the reference point (Bjornstad et al 1999). We analyzed acorn classes in each year for individual trees (621) and local populations (60).

To identify when precipitation and/or temperature influenced acorn development, we conducted a correlation analysis of mean annual acorn production in sensitive trees in the analysis areas with mean monthly precipitation or temperature for each of 15 months prior to acorn production in the 8 years of the study. The mean acorn data sets were normally distributed but most of the monthly precipitation data sets and some of the monthly temperature data sets were not, so non-parametric Spearman's correlation analysis was used (Zar 1999). Sufficient data for a meaningful correlation analysis was only available in the Puget-Willamette Trough and Eastside areas.

We used simple and multiple linear regression analysis to explore the predictive capacity of the precipitation and temperature data in the months suggested as important by the correlation analyses for acorn production in sensitive trees. The mean acorn class by year for each geographic area was the dependant variable. Independent variables were monthly mean temperature or total precipitation averaged over the stations within the geographic area.

Results

Variation and Synchrony in Acorn Production

Average upland acorn production over all 8 years was similar in the five geographic analysis areas. There were no significant

differences in mean upland acorn class among the five geographic analysis areas, but there were differences at the level of local populations in the upland Puget-Willamette Trough (ANOVA, $df=59$, $F = 3.67$, $P < 0.01$), Eastside Xeric (ANOVA, $df=5$, $F=2.31$, $P =0.07$), and Roseburg analysis areas (ANOVA, $df=5$, $F = 3.22$, $P = 0.08$), but not among upland populations in the Eastside mesic, or Cascade foothills analysis areas.

While overall production was similar in the geographic analysis areas, synchrony was only present in some years (Figure 2). Acorn production in most areas peaked in 2004 and 2006, with 2005 a consistently poor year. Over all geographic analysis areas, acorn production in 2004 was significantly higher than in any other year (RM ANOVA, $df \text{ years} = 7$, $df \text{ acorn prod.} = 505$, $F = 28.6$, $P < 0.01$). Also, acorn production in 1999, 2001 and 2006 was higher than 2003 or 2005. Production in the Puget-Willamette Trough and the Eastside was asynchronous in 2002 and 2003, but synchronous in 2004 and 2005 (Figure 2). There was significant variation from year to year in upland Puget-Willamette Trough (RM ANOVA, $df \text{ years} = 7$, $df \text{ acorn prod.} = 385$, $F = 31.6$, $P < 0.01$) and Eastside xeric acorn production (RM ANOVA, $df \text{ years} = 6$, $df \text{ acorn prod.} = 34$, $F = 4.1$, $P < 0.01$). There were no significant differences among years in the Eastside mesic, Cascade foothills or Roseburg areas, although like other areas, they tended to be high in 2006 and low in 2005.

Synchrony in upland Puget-Willamette Trough local populations is reflected in the peak years,

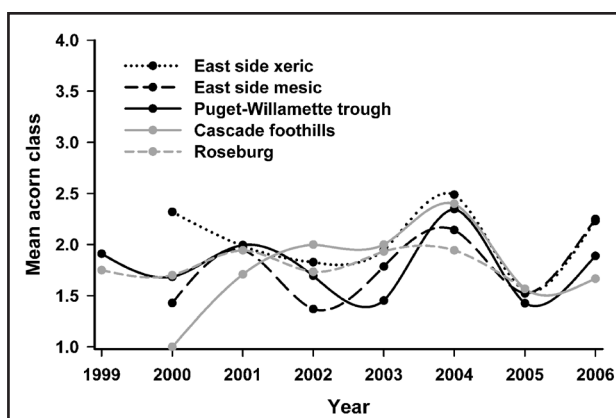


Figure 2. Patterns of upland mean analysis group acorn production over the 8 years of the survey. Note that almost all areas peaked in 2004.

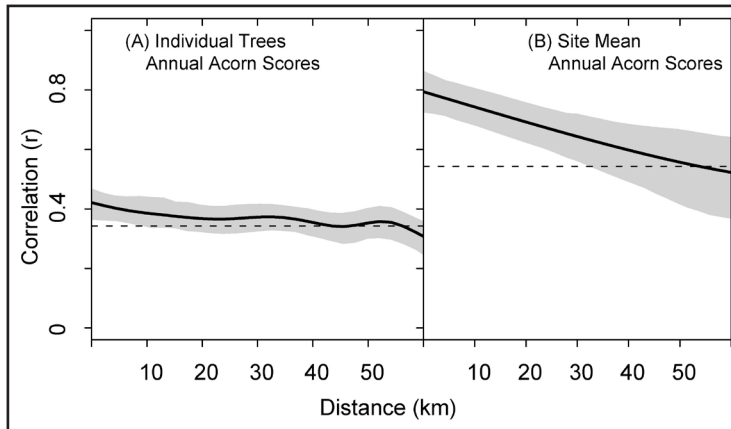


Figure 3. Spatial autocorrelation correlogram of annual acorn production from upland Puget-Willamette Trough trees (A) and local populations (B) over 8 years by distance in km with 95% confidence envelopes.

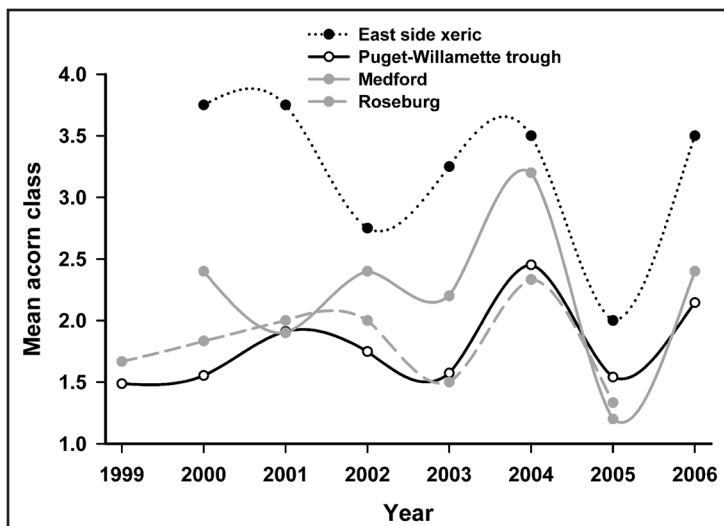


Figure 4. Patterns of riparian mean analysis group acorn production over the 8 years of the survey. Note that all areas exhibited a relative peak in 2004.

which were 2001, 2004, and 2006 for 98% of all Puget-Willamette local populations (Figure 2). These three years were significantly (RMANOVA, $df\ years = 7, df\ acorn\ prod. = 385, F = 31.6, P < 0.01$) more productive than the low-production years of 2003 and 2005 (lowest in 93% of local populations). The highest acorn production year was 2004 for 85% of these local populations.

The correlogram analysis showed that upland Puget-Willamette Trough acorn production synchrony between individual trees varied little with distance (Figure 3). Adjacent trees were only slightly more synchronized ($r = 0.42$) than

trees at distances greater than about 11 km ($r = 0.35$). However, correlations were higher for local populations where r went from 0.80 for adjacent populations to the regional average of 0.55 at a distance of 33 km.

Acorn productivity and annual variation were generally high in riparian areas (Figure 4). Riparian Eastside xeric (Rock Creek) and Puget-Willamette Trough trees had a significantly higher overall class distribution (KW ANOVA, $P < 0.01$) than upland trees from their respective areas indicating the important effect of habitat. Overall, riparian eastside xeric trees were significantly (KW

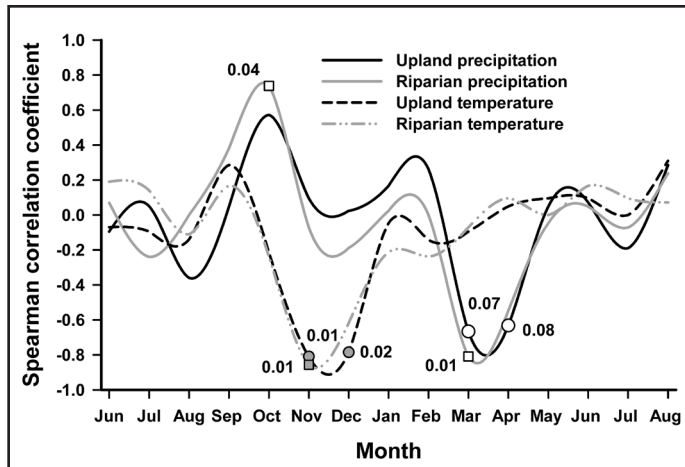


Figure 5. Monthly correlations of precipitation and temperature with annual acorn production for upland and riparian sites in the Puget-Willamette Trough. Significant correlations (P values shown) are indicated with open symbols for precipitation and closed symbols for temperature. Circles indicate upland sites and squares, riparian sites.

ANOVA $P < 0.01$) more productive than trees from any other riparian or upland area and Medford riparian trees were more productive than trees from upland Puget-Willamette Trough or Eastside mesic areas. The Rock Creek riparian stand in the Eastside xeric area is an exceptional example of consistently high production where 3 of 4 trees were coded as acorn class 3 or 4 for 5 out of 6 years and as class 2 in one year. There were no significant differences in mean acorn class among years in the riparian analysis areas.

Ten percent (87 trees) of the pool of trees that otherwise met the selection criteria were insensitive, but not all were surveyed in all 8 yrs. Seventy-five were consistently acorn class 1 (never produced acorns), 11 produced at the level of acorn class 2 and one at acorn class 3. The proportion of insensitive trees in the sample decreased with the number of years each tree was observed. The percentage of all sampled trees that did not produce acorns was 18% for trees sampled for 5 yrs, 8% for trees sampled for 6 yrs and 3% for trees sampled either 7 or 8 yrs. Thus, the incidence of non-production in apparently healthy trees leveled out at 3% as the length of the sample period increased from 5 to 8 yrs. However, sensitive and insensitive trees were not distributed equally across habitats. Riparian trees produced acorn crops more consistently than upland trees; only one riparian tree failed to produce acorns in

any yr (1% insensitive), but 86 upland trees were insensitive (10%).

Correlation of Temperature and Precipitation with Acorn Production

Precipitation and temperature were seasonally correlated with acorn production. The strongest correlations with precipitation in the Puget-Willamette Trough were positive in the fall-winter and negative in the spring (Figure 5). Riparian and upland correlations were similar, but a positive correlation of precipitation with mean acorn class in October was significant in riparian, but not in upland habitats (Figure 5).

Temperature in the Puget-Willamette Trough was negatively correlated with acorn production in November and December (Figure 5), but was otherwise only weakly related to annual acorn production. This pattern was also observed in the Eastside mesic, but not in the Eastside xeric analysis area (Figure 6). In the Puget-Willamette Trough, temperature was correlated with acorn production when there was no correlation with precipitation and vice-versa (Figure 5), so these effects appear to be independent.

Correlations of annual acorn production with precipitation in the Eastside xeric area followed a similar trend as in the Puget-Willamette Trough (Figure 6). In the Eastside xeric area, however,

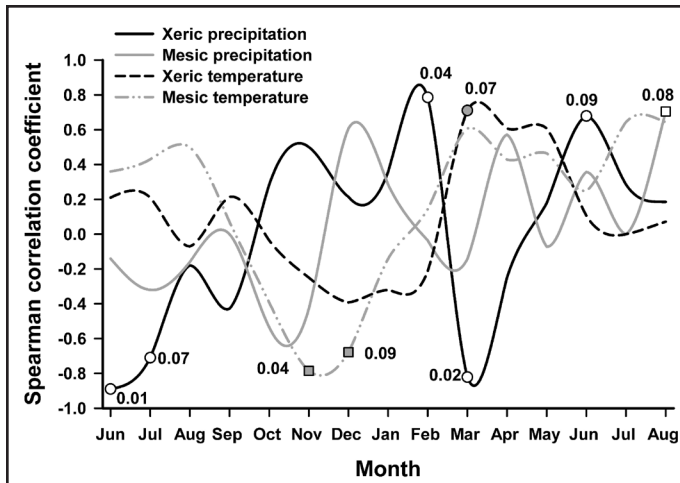


Figure 6. Columbia Gorge/East Cascades (Eastside) upland group correlations between mean acorn class and either monthly temperature or precipitation. Significant correlations (P values shown) are indicated with open symbols for precipitation and closed symbols for temperature. Circles indicate xeric sites and squares, mesic sites.

there was also a strong positive correlation with precipitation in February and again in June, and a strong negative correlation with precipitation during the floral initiation period in June and July of the year prior to acorn production. Correlations between acorn production and monthly temperature were generally low, with the exception of a positive correlation in March (Figure 6).

There were no significant correlations with precipitation in the Eastside mesic Area, (Figure 6). However, similar to the relationship observed in the Puget-Willamette Trough there was a strong negative correlation with temperature in November and December which appeared independent of precipitation.

Correlations of monthly precipitation and temperature with acorn production in the Roseburg area were erratic and non-significant with the exception of January temperature, which was negative ($r = -0.74$, $P = 0.06$). Correlations of acorn production with temperature and precipitation in the Cascade foothills area were also non-significant with the exception of August precipitation which was positive ($r = 0.90$, $P = 0.01$).

The correlation analyses suggested that acorn production might be predictable with a combination of key monthly temperatures and precipitation totals. For the Puget-Willamette Trough, all combinations of mean temperature in November and December, and total precipitation in March

and April were tried singly and together in linear regression models with acorn production as the dependent variable. Performance was as follows for single variable models (AIC/ R^2 / P): November temperature (-21.7/0.54/0.04), December temperature (-21.2/0.51/0.05), March precipitation (-23.3/0.62/0.02) and April precipitation (-22.9/0.61/0.02). Better models resulted from averaging the temperatures for November and December and by summing the precipitation over March and April (Table 3 models a, b). However, the best model combined mean temperature in November and total precipitation in April to explain mean acorn class over the 8 yrs of the survey period (Table 3, model c). Interactions among variables were investigated in all multiple regression models and found to be non-significant.

Two models predicted Eastside acorn production (Table 3, models d, e). Precipitation in June from the year prior to acorn maturation (closely corresponding to the time of flower primordia initiation) was the single variable with the highest predictive value.

Flowering

In 2003, flowering commenced in mid-late April at Fort Lewis, WA. Sixty-one percent of branch tips were bearing staminate inflorescences on May 1, tapering to 38% by May 15. No flowering was observed in June.

TABLE 3. Linear regression models for mean acorn class (MAC) in the Puget-Willamette Trough (models a-c) and the Eastside analysis areas (models d-e) based on mean monthly temperature and total monthly precipitation for months in which the temperature or precipitation parameter had a significant correlation with mean acorn class. In model d, “Jun” refers to June during the year of maturation while in model e, Jun lag 1 is the June in the year prior to acorn maturation (during flower primordia initiation).

Model	n	AIC	Model r ²	Model P	P int.	P var. 1	P var. 2
a MAC = 4.367 – 0.433 * Temp ^{Nov&Dec}	8	-26.40	0.75	< 0.01	< 0.01	< 0.01	
b MAC = 2.671 – 0.006 * Precip ^{Mar&Apr}	8	-25.95	0.73	< 0.01	< 0.01	< 0.01	
c MAC = 3.584 – 0.199 * Temp ^{Nov} – 0.009 * Precip ^{Apr}	8	-29.62	0.87	< 0.01	< 0.01	0.03	0.02
d MAC = 1.204 + 0.0105 * Precip ^{Feb} + 0.0222 * Precip ^{Jun}	7	-19.22	0.82	0.03	< 0.01	0.03	0.05
e MAC = 2.502 - 0.036 * Precip ^{Jun lag1}	7	-21.79	0.84	< 0.01	< 0.01	< 0.01	

Discussion

Acorn production is probably affected by many tree, stand and environmental factors including competition with other vegetation, tree health and genetics. Our work, which focuses on production controls operating at a regional scale, including climate and a division of the landscape into riparian and upland areas, indicates that climate-driven synchronous temporal variation in acorn production or “normal masting” (Kelly 1994) occurs in Oregon white oak. Although a longer record is needed, it appears that large, synchronous crops occur about 2 to 3 years apart within our analysis areas. Similarly, Coblenz (1980) found that Willamette Valley oaks produced one large crop and one crop failure in 3 years of observation. Masting periods of 2-3 years have also been suggested for blue oak (*Q. douglasii*) and valley oak (*Q. lobata*) (Olson 1974, Carmen et al. 1987, Koenig et al. 1994). Koenig et al. (1994) suggest that oaks with similar acorn maturation periods share similar masting periodicity. Thus, based on our results and those previously published, white oaks in the western U.S. and Vancouver Island BC appear to mast at intervals of 2 to 3 years.

Our data show that synchrony can occur over large and diverse areas. Prior to 2004 there was little synchrony in our data between geographic areas, but we found that 2004 was a good year and 2005 a poor year for acorn production from Vancouver Island to southern Oregon on both sides of the Cascade Mountains, and in both riparian and upland areas. However, synchrony was not perfect over 8 yrs, with differences between some analysis areas and between riparian and upland groups in years other than 2004 and 2005. This suggests that there are both widespread triggers for acorn production as well as local determinants.

The correlogram analysis showed a significant level of acorn production synchrony between trees and especially between local populations; this synchrony was also reflected in our repeated measures ANOVA analysis which showed that some years were significantly more productive than others. However, synchrony between local populations was higher over a wider radius (33 km) than between individual trees (11 km). Thus, local populations probably respond mostly to large scale patterns of precipitation and temperature, while individual trees respond to these factors, but are more strongly affected by localized factors, such as genetics, tree vigor, local soil conditions, and competition from surrounding vegetation. Similarly, blue oak trees from the Hastings Reserve in California showed little spatial variation in acorn production (Koenig and Knops 1998). Also, site-level synchrony in acorn production for 3 species of California oaks closely matched the geographical synchrony in spring temperature and rainfall, but individual trees had higher variation (Koenig 1999). Understanding the factors that affect synchrony and production at the tree level might interest wildlife managers as some of these factors might be manipulated to increase or make acorn production more dependable.

Not all trees showed temporal variation. Productive trees showing no variation were rare, but approximately 3% of mature, apparently healthy trees failed to produce a detectable quantity of acorns in a period of 8 years. There did not appear to be a geographic difference in the way insensitive trees were distributed, but, since most insensitive trees grew in upland, not riparian habitats, moisture stress may play a role in determining sensitivity. Soil moisture limitation of acorn production is also supported by the higher

productivity of riparian trees than upland trees. Piovesan and Adams (2001) observed that beech (*Fagus* spp.) of low vigor were characterized by low seed production and the absence of endogenous cycles. Thus, trees may require access to some minimum level of resources before becoming sensitive to masting cues.

We suggest that masting in Oregon white oak is strongly influenced by weather, which was also found by Koenig et al. (1996) in 4 species of California oaks including two white oak species. They found that variation in weather explained 38% to 78% of crop variation. In the Puget-Willamette Trough, negative correlations between acorn production and precipitation in March and April suggest that precipitation in these months may hinder floral processes including pollination and thus reduce future crop size. Negative correlations of acorn production and temperature in November and December suggest acorn production may be linked to bud chilling requirements. Our strongest predictive model used a combination of November temperature and April precipitation to predict acorn production. Thus, multiple climatic determinants of acorn production operating “downstream” from floral induction collectively influence crop size and periodicity.

Some climatic determinants of acorn production were different in the Eastside xeric area than in the Puget-Willamette Trough, although the smaller sample size in the Eastside area limited our ability to draw inference. In March, both precipitation (negatively) and temperature (positively) were strongly correlated with acorn production. Also, there were strong positive correlations between acorn production and precipitation in February and June during the year of acorn production and a strongly negative correlation with precipitation in June during floral initiation the year prior to acorn maturation. June precipitation might encourage acorn production by providing the soil moisture necessary to carry the developing crop to maturity in this dry summer climate. But, this in turn might discourage acorn production in the following year due to consequences of resource depletion. These correlations, including the one with apparently opposite effects in succeeding years, suggest the factors influencing acorn production on the Eastside are different from and possibly more complex than those in other areas.

Our data showed that weather may have a greater affect on acorn production at some times

of the year than others, but does not reveal the underlying physiological mechanisms. However, some plausible interpretations emerge by comparing some of these correlations with bud dormancy release mechanisms as currently understood. In species with chilling requirements for bud burst, temperature, not photoperiod is the major controlling factor (Smith and Kefferd 1964). Thus, the date of bud burst is dependent on chilling (the accumulation of time between about 0°C and 10°C), and forcing (the accumulation of time above about 10°C once chilling is satisfied) (Perry 1971, Chuine and Cour 1999, Cesaraccio et al. 2004). Prior to release of bud dormancy, temperatures above 10°C can negate previous chilling (Perry 1971), and temperatures below 0°C are usually not effective (Perry 1971, but see Rinne et al. 1997 for exceptions). Forcing cannot begin until dormancy is released by chilling, but, forcing requirements often decrease as chilling increases (Murray et al. 1989, Chuine and Cour 1999). The correlation of acorn production with low winter temperatures in the Puget-Willamette Trough and the Eastside mesic area suggests that Oregon white oak has a bud chilling requirement. It is not uncommon in the Pacific Northwest for rainy tropical air masses to arrive in the winter with temperatures above 10°C for several days at a time. These warm fronts could delay release from dormancy, delay when forcing begins or increase the amount of forcing required. Thus these warm fronts could delay bud burst, with consequences for acorn production. The positive correlation between Eastside xeric acorn production and March temperature may reflect when forcing or bud burst is usually most conducive to acorn production in that area. Further studies of bud physiology and timing of bud activity in relation to chilling and forcing in this species would help in understanding the basic mechanisms responsible for the observed relationships and help us predict how future changes in weather might affect acorn production.

The importance of warm spring temperatures in promoting acorn production has been noted by others (Sharp and Sprague 1967, Sork et al. 1993, Koenig et al. 1996). Koenig and Knops (1995) concluded that weather during the pollination period was important for acorn production in several species of California white oaks where acorn production increased with April temperature; this was consistent with what we observed in our Eastside analysis area. Warmer spring temperatures might

contribute to lower humidity conducive to pollination, but our floral survey at Fort Lewis, WA and a survey of University of Washington herbarium records (2007) indicated that most flowering occurs in April and May: (flowering/fruitlet records): March—2/0, April—8/3, May—9/6, June—1/5 (<http://biology.burke.washington.edu/herbarium/collections/list.php>). Thus, the significance of warmer temperatures in March on the Eastside may be the accumulation of thermal forcing units or the acceleration of the final stages of pistillate primordial development prior to flowering rather than pollination.

If flowering occurs too early, frost may destroy the flowers (Neilson and Wullstein 1980) and if it occurs too late, there is less time to mature a crop, especially if summer drought reduces acorn development time (Sork et al. 1993). Although flowering in our study area occurs mostly in April and May, it appears to begin earlier farther south (e.g., from late March through April in northern California [Tucker 1953]) suggesting that chilling and forcing is satisfied earlier there. Further studies are needed to determine the relative roles of chilling, forcing and genetic variability in these processes.

Precipitation in March and April may interfere with pollination. This relationship has been observed for other species of oaks (Sork et al. 1993, Cecich 1997, Cecich and Sullivan 1999). But, our flowering observations and University of Washington herbarium records suggest that most flowering occurs after March, so although the effect of precipitation on pollination may be important, the March correlation suggests a more complex relationship. It may be that early flowering (March) when precipitation is low benefits acorn production, but we do not have the necessary data to evaluate this hypothesis. Thus, we cannot make a definitive statement concerning pollination—only that our findings are consistent with the importance of weather during pollination on acorn production.

Internal bud temperatures are probably affected by both air temperature and solar insolation. Low rainfall, and thus higher insolation in March and April might result in higher internal bud temperatures than indicated by air temperature alone. This might affect development and phenology since most pistillate flower development occurs shortly before bud burst (Turkel et al. 1955). Solar insolation during the period of flowering was related to

acorn crop size in Blue oak in California (Koenig et al. 1996). Although spring weather appears to be important, physiological data are needed to tie events taking place in the spring to acorn production in the fall.

In the Eastside xeric area, there were strong positive correlations between acorn production and precipitation in February and June suggesting soil moisture availability may limit production. But, a strong negative correlation of production with precipitation in March suggests an important reproductive requirement that may be at odds with the summer moisture requirement. Although a droughty March might enhance floral processes, the trees ability to carry an acorn crop to maturity and its vegetative growth might otherwise benefit from higher soil moisture resulting from March precipitation. However, measurements of growth taken with acorn assessments and a longer record of acorn production will be needed to resolve these questions.

Large seed crops tend to depress the size of subsequent crops (Sork et al. 1993, Greene and Johnson 2004). The degree of resource depletion due to large crop production is likely a contributing factor to the size of the interval between large crops since “depleted” trees may not respond to exogenous floral triggers as they would when “primed” with sufficient reserves (Piovesan and Adams 2001). The two largest crops in our survey data occurred 2 years apart suggesting that, on an average site, resource recovery can occur in 2 years after heavy masting in the Pacific Northwest. Also, some trees with abundant sunshine and moisture (most notably at Rock Creek) have produced comparatively large crops in multiple consecutive years, so a rest period is not always obligatory. But on more stressful sites, local environmental conditions may determine how soon stored reproductive reserves can recover, influencing the length of the intermasting interval (Silvertown 1980). The preponderance of our insensitive trees in upland areas may be a reflection of this. This suggests that vigorous trees growing in productive environments recover and are “primed” for masting sooner than trees of lower vigor growing in harsher environments.

We were hampered in our ability to draw conclusions in some areas because of small sample sizes in relation to the diversity of habitats. Nevertheless, we found similar responses to climatic cues in the large, relatively uniform Puget-Willamette

Trough. The topographically diverse areas in the more mountainous terrain to the east and south exhibited either no marked patterns (the Roseburg sample) or multiple masting patterns (the Eastside sample). Thus there was a tendency for masting patterns to match spatial environmental heterogeneity at multiple scales as suggested by Ims (1990).

In conclusion, we believe that there are multiple climatic and habitat factors that affect acorn production in Oregon white oak during and downstream from floral induction. Some are important to bud development and dormancy, others to flowering processes, the ability of the tree to carry a crop once it is set, and/or the ability of a tree to rebuild resources after producing a large crop. Thus, masting is strongly affected by weather and habitat. Factors that reduce summer drought tend to promote more acorn production as do cool winters and dry early springs. Climatic effects operating in similar fashion over large areas can synchronize masting at larger scales, but local

environmental conditions and tree vigor vary the masting response at the tree and local population levels. Our work also provides a preliminary basis for identification of productive acorn producing sites, which will aid managers in prioritizing habitat for restoration or preservation to benefit acorn dependent wildlife species.

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Literature Cited

- Barrett, R. H. 1980. Mammals of California oak habitats - Management Implications. In T. R. Plumb (editor), Proceedings of the Symposium on the Ecology, Management, and Utilization of California oaks. USDA Forest Service General Technical Report PSW-44. Pacific Southwest Forest and Range Experiment Station, Berkeley, CA. Pp. 275-291
- Bjornstad, O. N., R. A. Ims, and X. Lambin. 1999. Spatial population dynamics: analyzing patterns and processes of population synchrony. Trends in Ecology and Evolution 14:427-432.
- Bjornstad, O. N. NCF: 2008. NCF: Spatial Nonparametric Covariance Functions. R package version 1.1-1. Available on line at <http://onb.ent.psu.edu/onb1/R> (accessed 12 November 2008).
- Carmen, W. J., W. D. Koenig, and R. L. Mumme. 1987. Acorn production by five species of oaks over a seven year period at the Hastings Reservation, Carmel Valley, California. In T. R. Plumb and N. H. Pillsbury (editors), Proceedings of the Symposium on Multiple-use Management of California's Hardwood Resources. USDA Forest Service General Technical Report PSW-100. Pacific Southwest Forest and Range Experiment Station, Berkeley, CA. Pp. 429-434.
- Cecich, R. A. 1997. Influence of weather on pollination and acorn production in two species of Missouri oaks. In S. G. Pallardy, R. A. Cecich, H. G. Garrett, and P. S. Johnson (editors), Proceedings of the 11th Central Hardwood Forest Conference. USDA Forest Service General Technical Report NC-188. North Central Forest Experiment Station, Columbia, MO. Pp. 252-261.
- Cecich, R. A., and N. H. Sullivan. 1999. Influence of weather at time of pollination on acorn production of *Quercus alba* and *Quercus velutina*. Canadian Journal of Forest Research 29:1817-1823.
- Cesaraccio, C., D. Spano, R. L. Snyder, and P. Duce. 2004. Chilling and forcing model to predict bud-burst of crop and forest species. Agricultural and Forest Meteorology 126: 1-13.
- Christisen, D. M., and L. J. Korschgen. 1955. Acorn yields and wildlife usage in Missouri. Transactions of the North American Wildlife Conference 20:337-357.
- Chuine, I., and P. Cour. 1999. Climatic determinants of bud-burst seasonality in four temperate-zone tree species. New Phytologist 143:339-349.
- Coblentz, B. E. 1980. Production of Oregon white oak acorns in the Willamette Valley, Oregon. Wildlife Society Bulletin 8:348-350.
- Downs, A. A., and W. E. McQuilkin. 1944. Seed production of southern Appalachian oaks. Journal of Forestry 42:913-920.
- Environment Canada. 2006. National Climate Archive. Available on line at <http://www.climate.weatheroffice.ec.gc.ca> (accessed 15 October 2007).
- Franklin, J. F., and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis.
- Goodrum, P. D., and V. H. Reid. 1971. Acorn yields, characteristics, and management criteria of oaks for wildlife. Journal of Wildlife Management 35:520-532.
- Graves, W. C. 1980. Annual oak mast yields from visual estimates. In T. R. Plumb (editor), Proceedings of the Symposium on the Ecology, Management, and Utilization of California Oaks. USDA Forest Service

- General Technical Report PSW-44. Pacific Southwest Forest and Range Experiment Station, Berkeley, CA. Pp. 270-274
- Greene, D. F., and E. A. Johnson. 2004. Modelling the temporal variation in the seed production of North American trees. *Canadian Journal of Forest Research* 34:65-75.
- Healy, W. M., A. M. Lewis, and E. F. Boose. 1999. Variation of red oak acorn production. *Forest Ecology and Management* 116:1-11.
- Ims, R. A. 1990. The ecology and evolution of reproductive synchrony. *Trends in Ecology and Evolution* 5:135-140.
- Janzen, D. H. 1969. Seed-eaters versus seed size, number, dispersal, and toxicity. *Evolution* 23:1-27.
- Janzen, D. H. 1971. Seed predation by animals. *Annual Review of Ecology and Systematics* 2:465-492.
- Kelly, D. 1994. The evolutionary ecology of mast seeding. *Trends in Ecology and Evolution* 9:465-470.
- Koenig, W. D. 1980. Acorn storage by acorn woodpeckers in an oak woodland: an energetics analysis. *In* T. R. Plumb (editor), *Proceedings of the Symposium on the Ecology, Management, and Utilization of California Oaks*, USDA Forest Service General Technical Report PSW-44. Southwest Forest and Range Experiment Station, Berkeley, CA. Pp. 265-269
- Koenig, W. D. 1999. Spatial autocorrelation of ecological phenomena. *Trends in Ecology and Evolution* 14:22-26.
- Koenig, W. D., and J. Knops. 1995. Why do oaks produce boom-and-bust seed crops? *California Agriculture* 49:7-12.
- Koenig, W. B., and J. M. H. Knopps. 2002. The behavioral ecology of masting in oaks. *In* W. J. McShea and W. M. Healy (editors), *Oak Forest Ecosystems, Ecology and Management for Wildlife*. The Johns Hopkins University Press, Baltimore, MA. Pp. 129-148.
- Koenig, W. D., J. M. H. Knops, W. J. Carmen, M. T. Stanback, and R. L. Mumme. 1996. Acorn production by oaks in central coastal California: influence of weather at three levels. *Canadian Journal of Forest Research* 26:1677-1683.
- Koenig, W. D., and J. M. H. Knops. 1998. Testing for spatial autocorrelation in ecological studies. *Ecography* 21:423-429.
- Koenig, W. D., R. L. Mumme, W. J. Carmen, and M. T. Stanback. 1994. Acorn production by oaks in central coastal California: variation within and among years. *Ecology* 75:99-109.
- Merkle, S. A., P. P. Feret, J. G. Croxdale, and T. L. Sharik. 1980. Development of floral primordia in white oak. *Forest Science* 26:238-250.
- Murray, M. D., M. G. R. Cannell, and R. I. Smith. 1989. Date of budburst of fifteen tree species in Britain following climatic warming. *Journal of Applied Ecology* 26:693-700.
- Neilson, R. P., and L. H. Wullstein. 1980. Catkin freezing and acorn production in gambel oak in Utah, 1978. *American Journal of Botany* 67:426-428.
- Nilsson, S. G., and U. Wastljung. 1987. Seed predation and cross-pollination in mast-seeding beech (*Fagus sylvatica*) patches. *Ecology* 68:260-265.
- Norton, D. A., and D. Kelly. 1988. Mast seeding over 33 years by *Dacrydium cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: the importance of the economies of scale. *Functional Ecology* 2:399-408.
- Olson, D. F., Jr. 1974. *Quercus* L., Oak. *In* C. S. Schopmeyer (editor), *Seeds of Woody Plants in the United States*. USDA Forest Service Agricultural Handbook No. 450. Washington, D.C. Pp. 692-703
- Perry, T. O. 1971. Dormancy of trees in winter. *Science* 171:29-36.
- Peter, D., and C. A. Harrington. 2002. Site and tree factors in Oregon white oak acorn production in Western Washington and Oregon. *Northwest Science* 76:189-201.
- Piovesan, G., and J. M. Adams. 2001. Masting behaviour in beech: linking reproduction and climatic variation. *Canadian Journal of Botany* 79:1039-1047.
- R Development Core Team (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, Available on line at <http://www.R-project.org> (accessed 12 November 2008).
- Rinne, P., H. Hanninen, P. Kaikuranta, J. E. Jalonen, and T. Repo. 1997. Freezing exposure releases bud dormancy in *Betula pubescens* and *B. pendula*. *Plant, Cell and Environment* 20:1199-1204.
- Ryan, L. A., and A. B. Carey. 1995. Biology and management of the western gray squirrel and Oregon white oak woodlands: with emphasis on the Puget Trough. USDA Forest Service General Technical Report PNW-348, Pacific Northwest Research Station, Portland, OR.
- SAS Institute Inc. 2002-2003. SAS System for Windows, v 9.1. Cary, North Carolina.
- Sharp, W. M., and H. H. Chisman. 1961. Flowering and fruiting in the white oaks. I. Staminate flowering through pollen dispersal. *Ecology* 42:365-372.
- Sharp, W. M., and V. G. Sprague. 1967. Flowering and fruiting in the white oaks. Pistillate flowering, acorn development, weather, and yields. *Ecology* 48:243-251.
- Silen, R. R. 1958. Silvical characteristics of Oregon white oak. USDA, Forest Service, Silvical Series 10, Pacific Northwest Forest and Range Experiment Station, Portland, OR.
- Silvertown, J. W. 1980. The evolutionary ecology of mast seeding in trees. *Biological Journal of the Linnean Society* 14:235-250.
- Smith, C. C., J. L. Hamrick, and C. L. Kramer. 1990. The advantage of mast years for wind pollination. *The American Naturalist* 136:154-166.
- Smith, H., and N. P. Kefferd. 1964. The chemical regulation of the dormancy phases of bud development. *American Journal of Botany* 51:1002-1012.
- Sork, V. L., J. Bramble, and O. Sexton. 1993. Ecology of mast-fruiting in three species of North American deciduous oaks. *Ecology* 74:528-541.
- Stein, W. I. 1990. *Quercus garryana* Dougl. ex Hook. Oregon white oak. *In* R. M. Burns and B. H. Honkala (editors), *Silvics of North America*. Volume 2. Hardwoods. USDA Forest Service Agricultural Handbook No. 654. Washington, D.C. Pp. 650-660

- Sweet, G. B. 1973. Shedding of reproductive structures in forest trees. *In* T. T. Kozlowski (editor), *Shedding of plant parts*. Academic Press, New York, NY. Pp. 341-382
- Topik, C., N. M. Halverson, and T. High. 1988. Plant association and management guide for the ponderosa pine, Douglas-fir and grand fir zones. USDA Forest Service, Region 6 R6-ECOL-TP-004-88, Portland, OR.
- Tucker, J. M. 1953. Two new oak hybrids from California. *Madroño* 12:119-127.
- Turkel, H. S., A. L. Rebeck, and A. R. Grove. 1955. Floral morphology of white oak. *Pennsylvania State University Agriculture Experiment Station Bull.* 593, University Park, PA.
- University of Washington Herbarium. 2007. Herbarium online collections. Available on line at <http://biology.burke.washington.edu/herbarium/collections/list.php> (accessed 10 November 2007).
- Western Regional Climate Center. 2006. Western U.S. climate historical summaries. Available on line at <http://www.wrcc.dri.edu/> (accessed 20 September 2007).
- Zar, J. H. 1999. *Biostatistical Analysis*, Fourth edition. Prentice Hall, Upper Saddle River, New Jersey.

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