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Site and Tree Factors in Oregon White Oak Acorn Production in Western Washington and Oregon

Abstract

Acorn production in Oregon white oak is variable and not well understood. To determine tree, stand, and environmental characteristics influencing acorn production, we surveyed 284 trees in September and October 1999. Surveyed trees extended from Whidbey Island, Washington, to Roseburg, Oregon, and ranged in age from 11 to over 300 yr. Acorn production was ranked on a 1-4 scale (nonproducing to heavily producing), and tree size, condition, site, stand, and vegetation characteristics were recorded. All acorns were counted on 18 trees. Acorn production started around 20 yr and plateaued around 80 yr. Trees with inverted vase-shaped crowns typical of dense forest stands produced fewer acorns than those with columnar- or mushroom-shaped crowns typical of more open areas. Open-grown trees growing in well-drained, loamy soils had the highest productivity within natural settings. Trees in urban parks with fertilization or irrigation also produced well. Trees underburned 6-10 yr before the survey produced better than trees not underburned or trees underburned more recently. Trees growing in slough-sedge wetlands, steep south-facing rocky balds, or with unhealthy crowns produced the least. Understanding the factors that influence production of Oregon white oak acorns could help managers increase acorn crop size as many of the factors can be altered by management activities.

Introduction

Relatively little is known about the reproductive potential, silviculture, or ecology of Oregon white oak (*Quercus garryana*), a widely distributed western North American species (Stein 1990). Little is known about Oregon white oak reproduction in general, and acorn production in particular, even though acorns are a rich source of food for many mammals, birds, and insects (Barrett 1979, Ryan and Carey 1995a). The age when a tree first bears fruit, the age of maximum production, and the average quantity of acorns produced have not been determined (Stein 1990). Information is needed on the regularity of flowering and the variability within and between stands and locations (Stein 1990). It is not known if acorn crop variation is primarily controlled by variation in flower production, or success of flowering and fruit production.

The range of Oregon white oak extends from halfway up the eastern side of Vancouver Island, Canada, south through the Puget-Willamette Trough in Washington and Oregon, into northern California to the vicinity of San Francisco. A shrubby variety extends south along the western Sierra Nevada foothills to northern Los Angeles

County. The easternmost extension of the range occurs north and south of The Dalles, Oregon in Kootenai County, Washington, and Wasco County, Oregon. Data for this paper were collected from almost half the range of the tree form of the species (Figure 1).

Oregon white oak produces heavy seed crops on an irregular basis and acorns mature from September to November (Stein 1990). Anecdotal information for Oregon white oak suggests heavy seed-crop years are followed by one or more years of poor productivity, and that good and bad years are somewhat synchronized over broad geographic areas. Variation in production from year to year, species to species, and tree-to-tree can vary greatly for oak species (Koenig 1980).

Oregon white oak has been diminishing over its natural range since the beginning of Euro-American settlement (Reed and Sugihara 1987, Agee 1993, Bell and Papanikolas 1997). Conversion to agriculture, urban areas, and other forest types (intentionally or through natural succession) are the major reasons for loss of oak stands (Ewing 1997). Remaining oak stands are now changing rapidly due to introduction of exotic species, overtopping by conifers, and fire exclusion (Chappell and Crawford 1997, Tveten and Fonda 1999).

Western gray squirrels (*Sciurus griseus*) in Washington maintain populations only where

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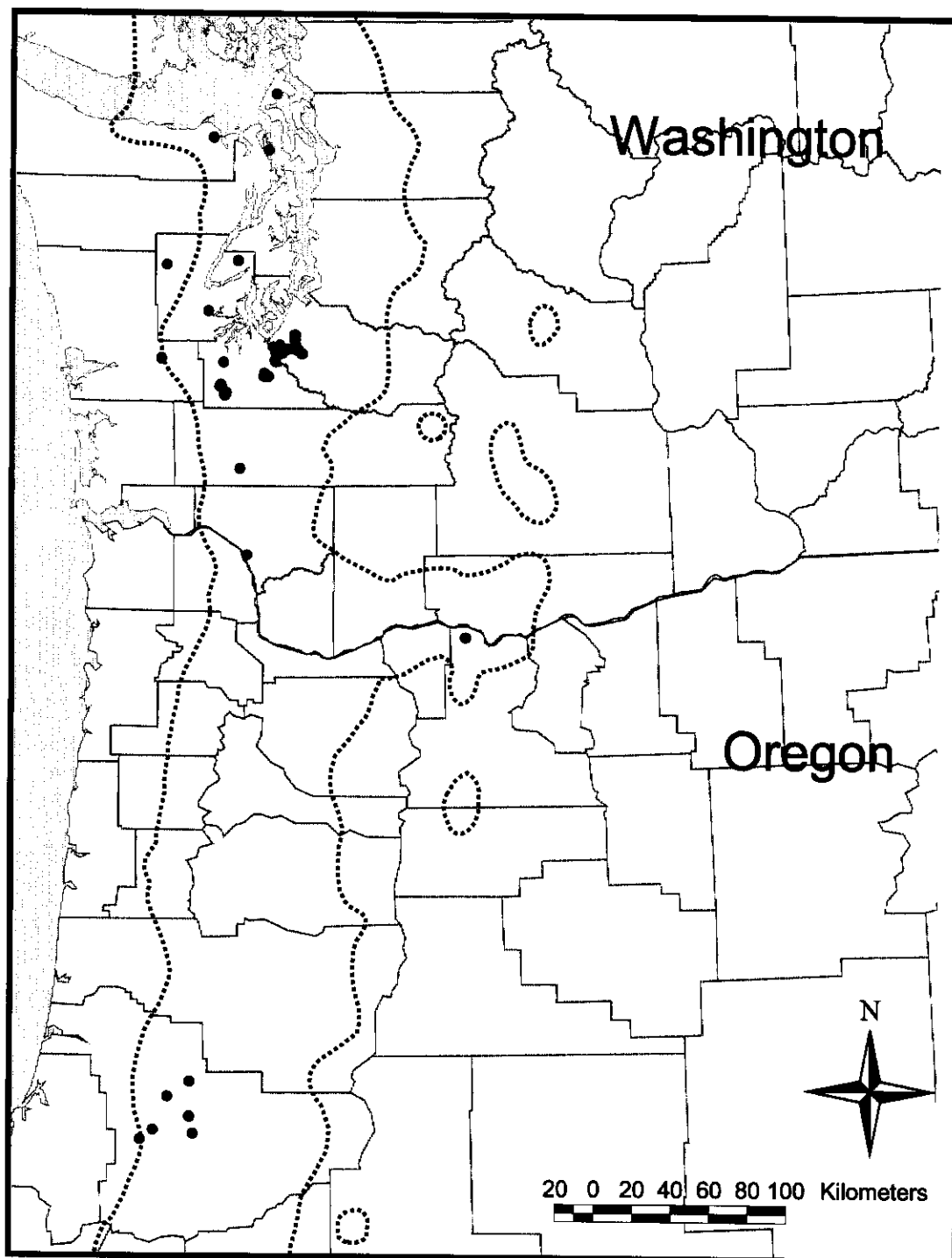


Figure 1. 1999 Oregon white oak acorn sampling sites in Washington and Oregon. Dashed line shows the range of Oregon white oak (Little 1971).

Oregon white oak communities exist (Roderick 1987). Acorns are critical fall and winter food for this squirrel (Steinecker and Browning 1970). One of the greatest threats to the western gray squirrel (threatened in Washington) at Fort Lewis, Washington, was Oregon white oak habitat loss due to succession and invasion of Douglas-fir (Ryan and Carey 1995b).

Recent public interest in Oregon white oak systems has focused new attention on how they can be managed and regenerated. We hope to provide new insights to aid managers in establishment of new oak stands, regeneration of existing oak stands and management of wildlife that utilize or depend on acorns. Specifically we asked how competition affects acorn productivity, how such competition can be recognized, what are the most important physical environmental variables for acorn production, and how past fire affects acorn production?

Methods

Surveys were conducted from 26 August to 14 October, 1999 before acorn drop. Data were collected by personnel from the United States Forest Service Pacific Northwest Research Station (PNW). Natural resource management professionals, amateur botanists from native plant society chapters, and forestry graduate students also volunteered to collect data. Volunteers obtained data forms and instructions by contacting the Olympia Forestry Sciences Lab or by downloading them from the project website. Oregon trees were sampled by volunteers who received only web-based instruction. Washington trees were sampled by PNW crew members or trained volunteers. Tree age, height, crown shape, and stand basal area were collected only on trees sampled by PNW personnel.

Acorn surveys were completed on 284 trees from 60 sites in 9 geographic areas. The PNW team sampled 153 Oregon white oak trees in Washington from Whidbey Island in the north to near Longview in the south. Volunteers contributed data for an additional 131 trees from the south Puget Sound area, a site near Mosier, Oregon, and from several sites near Roseburg, Oregon (Figure 1). Only acorns on the tree or healthy, ripe acorns that fell late in the survey period were considered (Table 1).

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

-
- Acorns should be mature—yellow-green to brown
 - If acorns are not readily observed, the tree is either a 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 a 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.
-

Characteristics of Sites

Sample sites were selected to represent the range of oak habitats, but a larger sample was obtained from more common habitats. Oak sites were selected across a continuum from slough-sedge wetlands to steep, dry, south-facing rock outcrops. Sites included agricultural, urban, and natural settings. Natural settings included savannas, forest edge, and oak or mixed oak-conifer forests. The largest sample (173) was from natural settings on relatively flat, extremely well-drained Spanaway soils in the south Puget Sound area, which is the most common oak habitat in western Washington. We deliberately selected several sites that had been prescribed burned in the last 10 yr to allow us to examine the effects of fire on acorn production.

Site data included percent of ground disturbance under the canopy, principal understory species, land use, water availability, and whether the tree had been fertilized in the past according to the landowner. The PNW team and some volunteers collected additional data on elevation, aspect, percent slope, years since last fire, soil series, understory species lists, and percent canopy coverage for grass, forbs, shrubs, trees, and bare ground. Missing elevation and aspect data were obtained from digital elevation models or USGS topographic maps.

For general descriptive purposes, data were averaged by nine geographic areas, chosen to represent specific populations or distinctive environments: Douglas County, Oregon; Wasco County, Oregon; Lower Columbia River, Washington; Lewis County, Washington; Lower Chehalis River,

TABLE 2. Sample size and mean site and stand characteristics by geographic area. The sites are in Washington unless otherwise noted.

Geographic area	n	Elevation (m)	Slope (%)	BH age ¹ (years)	Height (m)	Crown width (m)	Breast height diameter (cm)	Basal area m ² /ha	Crown contact (%)
Douglas Co., OR	30	228	8	-	17	8	68	-	32
Wasco Co., OR	5	416	28	-	8	7	34	-	27
Lower Columbia River	5	10	9	129	22	12	66	15	65
Lewis County	2	139	3	123	22	19	108	4	25
Lower Chehalis River	5	3	0	139	18	15	73	20	42
South Puget Sound	62	67	4	83	15	9	41	11	43
Fort Lewis	154	99	5	70	12	8	37	12	38
South Fork Skokomish	6	434	88	144	5	4	20	15	23
Northern Puget Sound	15	31	12	77	14	10	53	12	52

¹Breast-height age (1.3 m).

Washington; south Puget Sound, Washington; Fort Lewis, Washington; South Fork Skokomish River, Washington; and Northern Puget Sound, Washington. Fort Lewis is a subset of the south Puget Sound, Washington, area that we recognized as a separate unit because the sampling density in that area was much greater than elsewhere.

Mean elevation of all 60 sites in 9 geographic areas ranged from 3 m to 434 m above sea level (Table 2). The lowest elevation sampled was 2 m at Oak Bay in northern Puget Sound and the highest elevation was 463 m near the South Fork of the Skokomish River, which is a tributary to Hood Canal in western Washington. Most trees were on gentle topography. The sample was heavily weighted toward savanna and forest settings, although 19 trees were in urban settings and 15 in agricultural settings. Eight trees in city parks were irrigated, 18 were adjacent to wetlands, and 5 were in wetlands.

Moisture

To examine the relationship of moisture availability to acorn production we looked at available water content of the soil and precipitation. Soil series was assigned to tree locations using appropriate soil survey maps and field notes. This was done by overlaying field-mapped or GPS locations with soil series maps in ArcView®, or by locating mapped sites on USDA Soil Conservation Service county soil survey maps. Field notes were used to select the soil series from the list of possible soils in soil mapping unit descriptions, and

available water capacity (AWC) data were obtained for each soil series in the sample from the MUIR database (USDA, NRCS 1994). Total available water capacity (AWC = cm of water per cm of soil by soil layer) was calculated by summing the total available water in each layer in the top 150 cm of soil. Annual precipitation (cm) for each site was obtained from PRISM maps (USDA, NRCS, and OSU 1999). A simple moisture index was calculated by multiplying the AWC by the annual precipitation and dividing by 100. The scale at which these soil moisture and precipitation data are mapped make them inappropriate to use for analyses at the individual tree level, but we believe they are adequate for stand or regional averages as we have used them.

Characteristics of Trees

At each site 1-11 trees (mean = 4) at least 1.3 m tall were selected. Trees were selected without regard to numbers of acorns, shape, crown contact, health, age, or size. Data collected for all trees included diameter at 1.3 m above ground (breast height), acorn class, percent crown contact with other trees, and health class. Percent crown contact was defined as the percent of the sample tree's crown circumference that is merged with other tree crowns of similar or greater stature. Percent crown contact is a measure of the competitive environment around the sample tree.

Additional data collected by PNW personnel included tree height, crown width, crown class, height to live crown, crown shape, and basal area

around each tree. Basal area around the sample tree is a measure of competition. We used calibrated angle prisms on variable radius plots to determine basal area (Bell and Dillworth 1997). Basal area was taken at a point 1 m north of the base of the bole and did not include the sample tree. Crown width was measured at the long axis of the crown and an axis at right angles and averaged. Height to live crown was measured as the mean height from the ground to the lower tips of the foliage. Crowns were classed as mushroom, columnar, or vase shaped (Figure 2).

Acorn Abundance

All surveyors ranked acorn abundance on a 1-4 scale (nonproducing to heavily producing) (Graves 1980). Table 1 gives an abbreviated account of the method, but the full method was used to train surveyors. This method is a simple repeatable procedure that works well with minimally trained observers. Graves (1980) found that three observers gave the same classification to 74% of the trees, and that in the remaining 26% of the trees two of the three observers agreed. He showed a relationship between this method and the more quantitative seed trap method. There was a positive correlation between acorn abundance class and acorns collected per seed trap and significant differences between classes 2, 3, and 4 (light, medium, and heavy) for both trap sample weight and number of acorns per trap sample (Graves 1980). PNW crew members cross-checked during training were consistent in producing the correct class. Volun-

teers who received PNW instruction in the method have consistently been able to give the same results as the PNW trainer. Volunteers who first learned the method from the web site and were later checked by PNW crew members have also been consistently correct. This method works well with minimally trained volunteers because the classes are broad.

The PNW team also counted all the acorns in a subsample of trees. Eighteen trees were carefully inspected and acorns counted by one of two methods. Four trees were counted from a lift truck with a 15-m boom, which produced highly accurate counts. Fourteen trees were counted from the ground with binoculars. All counted trees were first classed using the abundance scale (Table 1). Trees were measured, photographed, and the shapes were sketched. External surface area of the crown shape was calculated to permit calculation of acorns/m² of external crown surface.

External crown surface area is the upper surface of a solid object of the size and shape of the tree crown, excluding non-foliar portions, such as the spreading area of limbs under the canopy. The number of acorns from each of 18 trees with total acorn counts was divided by the external surface area of the crown to give acorns/m² of external crown area. Calculations were made for the top half of the green crown, the bottom half of the green crown, and the total green crown. Acorns/m² for all 18 trees were averaged by top half, bottom half, and the entire canopy for each acorn class to quantify the acorn abundance classes.

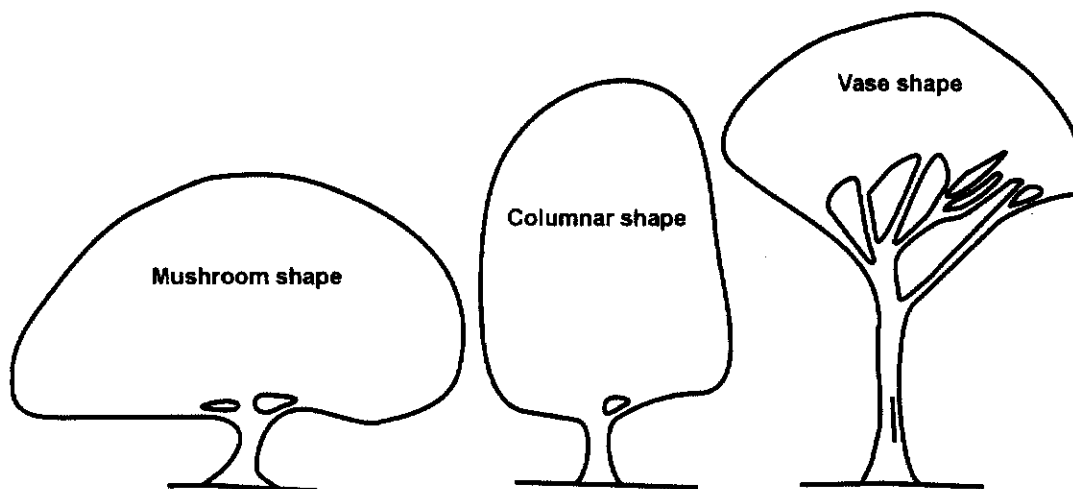


Figure 2. Canopy shapes assigned to oak trees in acorn survey. No relationship between shape and height is implied.

Health

We examined the broad effects of tree health on acorn productivity with a simple class system. Healthy trees had all bark and major limbs present and alive, no visible rot, and full crown of healthy leaves. Moderately healthy trees had some missing bark, broken major limbs, or visible rot, but otherwise appeared healthy. Unhealthy trees had much visible rot, sparse foliage, or major branches broken or dead.

Age

We extracted increment cores at 1.3 m above ground from 73 trees and counted rings to assess the effect of tree age on acorn productivity. Of these, 22 hit the pith, 36 were judged to be within 10 rings and an estimate was added to the ring count, and 15 missed the pith by more than 10 rings. An age-diameter relationship was calculated from complete cores for use in estimating total age at 1.3 m from cores judged to have missed the pith by more than 10 rings. A straight line was regressed through age/diameter data from 16 Puget Sound area trees < 50 yr old ($\text{age} = 16.23 + 1.14 \text{ dbh (cm.)}$; $r^2 = 0.56$). This relationship was used to estimate numbers of missing rings to pith from the inside of incomplete increment cores. Age at 1.3 m was used rather than total age because it is easier to obtain and the variation in the years between age at 0 m and age at 1.3 m is too great to allow extrapolation. The relationship of age to acorn abundance was examined by determining the percent of the sample in each abundance class by 20-yr age groups.

Underburning

The effect of prescribed burning on acorn productivity was examined by displaying the percent of trees in each acorn class by years since the last

prescribed underburn. Underburns are fires that do not ignite the canopy of the overstory and generally have flame lengths < 3 m. Underburning is prescribed for fuel reduction, to modify understory composition or to arrest succession toward conifer dominance. In most cases the severity of the underburn was not known, but fire-damaged boles and lower limbs were observed on many trees. Years since the last underburn was known for 55 trees. Most of these trees were on Fort Lewis, but eight were from Oak Patch Natural Area Preserve on the Kitsap Peninsula, Washington. Both locations are in the south Puget Sound area on similar Spanaway or Everett soils. An additional 119 trees on similar soils in the same general area, including trees from Oak Patch and Fort Lewis, were judged not to have been underburned in 20 yr or more and were compared with those with known burning history.

Statistical Analysis

We used ANOVA and logistic regression to examine relationships in the data. Since acorn production class is not normally distributed, standard statistical procedures were not appropriate in all instances, so that both non-parametric and parametric techniques were used. The level for statistical significance was set at $P = 0.05$.

We used Kruskal-Wallis nonparametric ANOVA (Zar 1999) to test for differences in acorn code distribution between categories of the independent moisture variables: precipitation, AWC, and moisture index. Data for the moisture variables were assigned to groups by dividing the range into thirds, so that there was a low, medium, and high group for each independent variable (Table 3). A fourth group was added to cover trees that received supplemental irrigation. The null hypothesis of no difference in acorn code distribution

TABLE 3. Characteristics of moisture analysis groups for Kruskal-Wallis ANOVA. P is the probability that there is a difference in distribution of acorn codes between the moisture classes.

Group	Available Water Capacity			Precipitation			Moisture Index		
	Mean	n	Acorn code rank mean	Mean (cm)	n	Acorn code rank mean	Mean index	n	Acorn code rank mean
Low	4.3	13	75	64	10	122	5.8	15	74
Medium	10.0	238	140	111	209	136	12.2	241	141
High	22.2	16	143	170	48	143	26.1	11	127
Irrigation	4.0	10	190	105	10	190	2.5	10	189
P	-	-	0.0022	-	-	0.1244	-	-	0.0007

among the four groups was tested for each independent variable. When the ANOVA indicated significance, we compared the groups with a Dunn test (Zar 1999).

We also used Kruskal-Wallis nonparametric ANOVA to analyze distribution differences in acorn abundance code between health class groups. When the ANOVA indicated significance, we compared health groups with a Dunn test.

We used parametric ANOVA to characterize the basal area and crown contact environments around sample trees in different acorn production classes. We determined which groups were different with Duncan's Multiple Range Test when the ANOVA indicated significant results.

To evaluate the effects of competition on acorn production of the sample trees, we used logistic regression with acorn code as the dependent variable (Allison 1999, SAS Institute Inc. 2000). Basal area of the surrounding stand, percent crown contact of the sample tree with surrounding trees, and crown shape were the independent variables. Logistic regression estimates the probability of a certain event occurring by calculating changes in the log probability of the dependent variable. For this analysis we reduced the acorn production data to two classes: nonproducing and producing (i.e. light and medium producing were combined into one class). There were 96 trees with basal area data, 124 trees with crown shape data, and 245 trees with percent crown contact data. Figure 3 was produced by plotting logistic regression output for the probability of acorn production at each 10% interval of crown contact.

Results

Site Characteristics

There were 68 sample trees growing on slopes > 3°; 45 were on south or west aspects, and 24 on north or east aspects. Due to wide variation in elevation and soil type of tree sites with slopes > 3°, it would not be meaningful to test for differences due to aspect.

Moisture

A wide variety of moisture conditions was represented on the survey sites (Table 4). In 1999, productivity was highest on well-drained irrigated soils and lowest on extremely dry or wet soils in our sample. There was a significant difference in

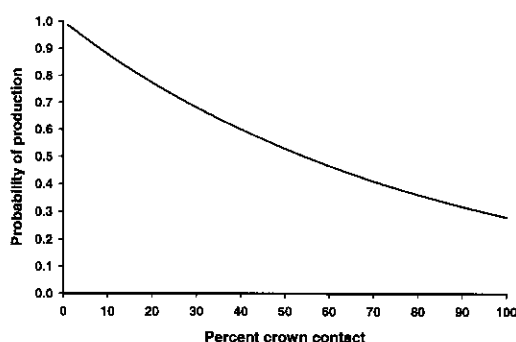


Figure 3. The probability of acorn production as a function of the percent crown contact.

acorn code distribution between soils with low, medium, or high available water capacity and irrigated soils ($P=0.002$) (Table 3). The low AWC group, which had the lowest overall productivity distribution had significantly lower acorn production than the irrigated group, which had the highest overall productivity distribution. Precipitation alone had no significant effect on acorn productivity, but when precipitation was combined with AWC into a moisture index there was a significant difference in acorn code distribution between low, medium, and high moisture index and irrigated groups ($P=0.0001$) (Table 3). All groups were significantly different from each other except the moderate and moist index groups. The lowest productivity distribution was in the low index group and the highest in the irrigated index group. Another group of five trees growing in a slough sedge (*Carex obnupta*) wetland was not included in this analysis but produced few acorns in 1999.

Tree Characteristics

Tree dimensions by geographic area ranged from 5-22 m tall, 4-19 m wide, and 20-108 cm diameter at 1.3m. Overall, there were 47% nonproducing trees, 34% light-producing trees, and 19% medium-producing trees in our sample. There were no heavily-producing trees in the 1999 sample. Most of the sample trees were dominant, codominant, or open grown but some were intermediate or suppressed. In 18 trees with complete counts, acorn density was greater in the top half of the canopy than the bottom half, and greater in medium-producing trees than non- or light-producing trees (Table 5). Mean tree surface area in-

TABLE 4. Percent of sample in each acorn class by soil series and soil moisture characteristics. Soil series are sorted by percent of nonproducing trees.

Soil Series (with treatments or amendments)	AWC ¹	Annual precipitation ² (cm)	Moisture index ³	Percent of trees in each acorn class			
				None	Light	Medium	n
Prather silty clay loam (fertilized)	21	119	26	0	0	100	2
Panther silty clay loam	24	114	27	0	0	100	1
Townsend sandy loam (fertilized, irrigated)	4	64	3	0	40	60	5
Nisqually loamy sand	12	117	14	14	43	43	7
Sequim very gravelly sandy loam (fertilized, irrigated)	4	48	2	20	80	0	5
Oakland silt loam	13	99	13	20	80	0	5
Carstairs very gravelly loam	8	168	14	22	44	33	9
Wamic loam	20	58	12	40	0	60	5
Pengra silt loam	20	114	23	40	20	40	5
Everett gravelly sandy loam and gravelly loam	9	142	13	41	18	41	17
Spanaway gravelly sandy loam	10	117	12	46	38	16	173
Atring gravelly loam	10	114	12	50	50	0	2
Spanaway stony sandy loam	10	130	13	67	33	0	3
Fitch gravelly sandy loam	10	104	10	70	30	0	10
Ritner gravelly silty clay loam	11	104	11	75	25	0	4
Wetlands	-	130	-	80	20	0	5
Nonpareil-Oakland complex	7	94	7	80	20	0	5
Fricaba extremely gravelly sandy loam	3	318	11	100	0	0	3
Waketick extremely gravelly sandy loam	1	318	4	100	0	0	3
San Juan gravelly sandy loam	9	69	6	100	0	0	5
Philomath-Edenbower complex	7	104	7	100	0	0	1
Veneta loam	27	94	25	100	0	0	5

¹AWC = available water capacity in the top 150 cm of soils (USDA, NRCS 1994).

²Average annual precipitation from PRISM data (USDA NRCS and OSU 1999).

³Moisture index = precipitation x AWC/100

TABLE 5. Mean number of acorns per square meter and external crown surface area ($\pm$ SE) by acorn class for the subsample of trees that had complete acorn counts. All trees were from the South Puget Sound or Fort Lewis areas.

Acorn class	n	Portion of crown			External crown surface area (m ²) ²
		Top	Bottom	Total ¹	
None	9	0.03	0.03	0.03	180
Light	5	0.30	0.08	0.19	233
Medium	4	2.64	0.72	1.60	368

¹Standard errors for total number of acorns were 0.03 for non-producers, 0.05 for light producers, and 0.6 for medium producers.

²Standard errors for crown surface area were 100, 46, 57.

creased with acorn class. Sample trees classed as medium producing not only produced a greater density of acorns but also had more crown surface area than the non or light producing trees.

Health

Most trees were rated as moderately healthy or healthy, but 16% were unhealthy. Differences in acorn class distribution between the three health classes were significant ($P=0.003$). The unhealthy tree group had a significantly lower acorn class distribution than the moderately healthy or healthy trees. Trees rated as healthy or moderately healthy were not significantly different.

Shape

Tree shapes were important indicators of productivity because they reflect the competitive environment around the tree. Overall, the sample had more vase-shaped trees (40%), than mushroom-shaped trees (35%), or columnar-shaped trees (25%), although proportions varied by site. Vase shaped trees comprised the highest percent of nonproducing trees and the lowest percent of

TABLE 6. Percent of sample trees by shape class and acorn class.

Acorn class	Tree shape		
	Vase	Columnar	Mushroom
Nonproducing	66	49	28
Light	30	41	41
Medium	5	11	31
Sample size	61	38	54

medium-producing trees (Table 6). The highest percent of producing trees were mushroom-shaped (72%). The effect of crown shape on probability of production in a binomial logistic regression was significant ($P=0.004$). Vase shaped trees were significantly greater than mushroom-shaped trees ($P=0.0001$).

Crown Contact

Percent crown contact ranged from 0 to 100% but averaged from 25% to 65% in different areas (Table 2). Percent crown contact and tree shape were related. Crown contact was 56% for vase, 33% for columnar, and 33% for mushroom shaped trees in our sample. Percent crown contact for vase-shaped trees was significantly greater than columnar- or mushroom-shaped trees ($P=0.0001$), which were not different from each other.

The effect of crown contact on probability of production in a binomial logistic regression was significant ($P=0.005$). As percent crown contact increased the probability of acorn production decreased in our sample (Figure 3). For example, a 20% increase in crown contact resulted in changing the odds of production by 0.73, so that if crown contact increases by 20%, the probability of acorn production decreases by 27%.

Basal Area

Mean stand basal area around the sample trees ranged from 4-20 m²/ha by geographic area (Table 2). Mean basal area surrounding the sample trees was 7 m²/ha in trees with medium production, 12 m²/ha in trees with light production and 16 m²/ha in trees with no acorn production (Table 7). The effect of basal area on the probability of acorn production was significant ($P=0.02$). A 10 m²/ha increase in basal area would be expected to change the odds of production by 0.64 (36% decrease in the likelihood that the tree would produce).

TABLE 7. Basal area (m²/ha) and number of sample trees by acorn class.

Acorn class	Mean	Standard error	n
Nonproducing	16	2.2	110
Light	12	1.6	86
Medium	7	1.6	49

Age

Ages clustered around 100 yr, but individual trees varied from 11 to > 300 yr at 1.3 m. No acorns were found in trees younger than 20 yr even though they were open grown (Figure 4). Between age 20 and 80 yr, the percent of nonproducing trees decreased and medium producing trees increased. In the 60-79-yr group, 41% of the trees were non-producing, 40% light producing, and 19% medium producing. There was no apparent trend in productivity after 80 yr. Trees older than 180 yr were mostly in the light- and nonproducing classes, and the oldest and largest tree (> 300 yr) in our sample produced no acorns despite its healthy appearance.

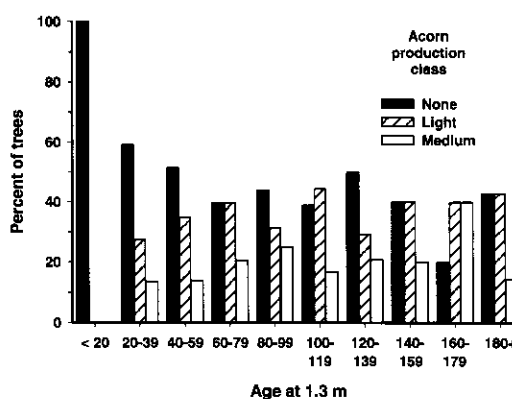


Figure 4. Percent of sample trees by acorn abundance class and age at 1.3 m.

Fire

There was an apparent relationship between acorn productivity and underburning history (Figure 5). Among sample trees underburned one year prior to survey, 71% were nonproducing. This compares to only 48% nonproducing trees in the unburned sample. Two to four years post-burning, sample trees averaged nearly the same percentage of nonproducing trees and medium-producing trees as unburned trees. Trees underburned

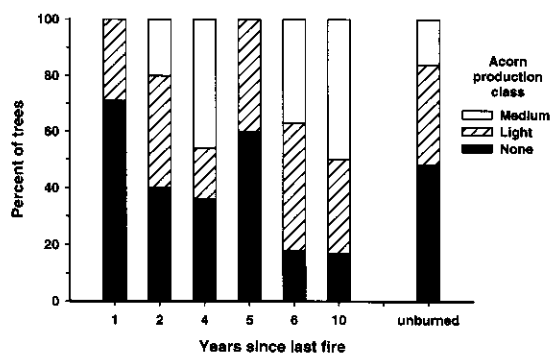


Figure 5. Percent of sample trees in each acorn productivity class by years since last fire.

6-10 yr ago produced much better acorn crops on average than non-burned trees. They had only 18% nonproducing trees compared to 48% in the non-burned group. They also had 41% medium-producing trees compared to 16% in the non-burned group.

Discussion

In general acorn production in our sample was influenced by competition (measured by basal area, tree shape, and crown contact), moisture (indicated by precipitation, AWC, and moisture index), age, and fire history. Productivity tended to be highest on well watered, well drained sites on trees at least 60-80 yr old that were growing under little competition from neighbors. The effect of fire history was more complex. Our data at least suggest that prescribed underburning may reduce acorn production in the year immediately following burning, but may also contribute to higher production 6-10 yr after underburning.

Annual variations in acorn crop size complicate the interpretation of acorn production. There is little published information on acorn crop sizes in Oregon white oak with which to compare these data. We believe that the 1999 acorn crop was moderate. In contrast the 1998 acorn crop was small at Fort Lewis (Andrew B. Carey, Pacific Northwest Research Station, Olympia, Washington, personal communication).

Large acorn crops occur every few years in Oregon white oak (Harlow and Harrar 1958). Coblenz (1980) followed acorn production on Oregon white oaks in the Willamette Valley for 3 yr and found one good crop, one moderate crop, and one crop failure. Good seed crops for blue

oak (*Quercus douglasii*) were observed every 2-3 yr, with larger crops every 5-8 yr (Olson 1974) or in 4 of 7 yr with one bumper crop (Carmen et al. 1987). Valley oak (*Quercus lobata*), another white oak species, had a similar pattern, with small crops in 5 of 7 yr and one bumper crop (Carmen et al. 1987). If acorn production varies widely in different years it remains to be seen if the patterns of acorn production found in this study change or simply shift in magnitude.

Oregon white oak has wide ecological amplitude, growing on sites that are seasonally flooded to excessively drained with low water-holding capacity. Presumably all sites are capable of acorn production in some years. In 1999, however, little production was observed in our sample where the moisture index was low or on poorly drained soils (Table 4). In addition, productivity was higher than would otherwise have been expected on droughty soils receiving supplemental irrigation suggesting that water was frequently limiting in 1999. Productivity was highest on moist, well-drained soils and generally declined as water availability declined or on poorly drained sites.

The sites that did not fit the pattern of declining acorn productivity with declining water availability are the Pengra silt loam, Veneta loam, and wetlands (Table 4). Based on soil texture and location we expect these soils to have abundant soil moisture through the growing season. Trees growing in wetlands may have a shallower distribution of roots than trees on better-drained sites, making it difficult to assess water availability during the time of acorn development using an index based on standard soil depth. Pengra silt loam is somewhat poorly drained with a high water table from November to May so that trees on this soil may also have a shallow root system. The Veneta loam is moderately well drained with a high AWC and moisture index, thus would be expected to have a deep root system and to produce well. Trees on this soil may produce well in other years.

In our sample there was an indication that tree age affects productivity with production starting around 20 yr increasing to around 60-80 yr, then leveling off (Figure 4). The oldest tree in the sample (> 300 yr) produced no acorns in 1999, but there was no clear decline in productivity associated with increasing age in the sample. A similar age related pattern was found in California black oak (*Quercus kelloggii*), which begins acorn production at 30 yr, but does not produce large quantities

on a regular basis until 80-100 yr. California black oak acorn production increases until at least 200 yr of age (McDonald 1990). We suspect that site quality characteristics and competitive conditions influence the onset of production. Our age data are not complete enough to show a difference in onset of acorn production between forest and open-grown trees, but the youngest producing trees in our sample were open grown.

Competition with other trees was an important factor in acorn production in our sample. As competition increased, crown contact and basal area increased and tree shape changed. Oregon white oak is not shade tolerant and will lose lower limbs under lateral shade, resulting in the vase shape typical of trees growing in dense stands (Stein 1990). Crown shape, although only measured on a subset of trees, was an easy variable to code and a good predictor of productivity (Table 6). High irradiances are associated with increased flowering in many plants (Halevy 1983, Krugman et al. 1974). It makes sense that in a species that produces acorns mostly on branch tips in full sun, a measure like crown shape, which provides an indication of light availability to the crown, would be effective. Our data set on crown shape was entirely composed of trees from stands that had not been thinned. Since acorns are an important food source for wildlife, maintaining acorn production is a management concern. The relationship of open-grown crown shapes, low crown contact, and low basal area to higher productivity suggests thinning is an option for increasing acorn production in forest stands, but we do not know how well Oregon white oak responds to thinning. If Oregon white oak responds to thinning, crown shape would be a simple criteria for selecting trees for release treatments, and for gauging recovery.

Basal area and crown contact were also significant predictors of acorn productivity in our sample (Table 7, Figure 3), but were somewhat less effective than crown shape (Table 6). We assume shape was important because it serves as an integrator of the competitive environment around the tree for an extended time period. In managed stands we suspect that both a shape variable (indicating past environment) and a measure of current competition (such as crown contact or basal area) would be important. In addition, it appears that young trees with good apical dominance and older trees receiving side light can both have co-

lumnar shapes. Adding age, or an age-surrogate such as height, may be useful in separating columnar trees into groups with less variation in acorn production.

In our sample open-grown trees are better acorn producers than crowded trees (Table 6, Figure 3), which is what Coblenz (1980) reported. Our measures of acorn productivity (the codes or the counts on a subsample of trees) were tree based. We do not know what level of stand density would result in the best productivity per unit area. A forest of vase shaped oak trees may have higher acorn production per unit of land than a savanna of mushroom shaped trees because every area in the forest is producing acorns. The relationships between tree- and stand-based measures of acorn productivity will need to be evaluated to provide managers with better tools to make decisions.

Underburning is a useful management tool for reducing shrub and tree competition around Oregon white oak, but it may affect acorn productivity. This is an important consideration when managing acorn-consuming species such as the threatened (in Washington) western gray squirrel. The data suggest that underburning at the intensities sampled for this study causes an initial loss of acorn productivity relative to unburned trees in the year after the burn (Figure 5). The mechanisms by which burning can impact acorn productivity have not been studied, but probably vary depending on site, tree characteristics, and intensity and duration of the fire. Following a recovery period of one to several years, productivity on burned areas may be enhanced relative to unburned trees. This relationship implies a reproductive benefit to trees following underburning and recovery, but the duration of the benefit is unknown. Most of the underburned trees in this study had a shrub understory component at the time of burning, which made fires more intense. Low intensity grass fires probably cause less tree damage and may not result in an initial loss of acorn production. This would have important implications for managers of oak stands using prescribed fire.

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