

Development of Oregon White Oak Seedlings

Abstract

Seedlings of Oregon white oak (*Quercus garryana* Dougl. ex Hook.) growing in western Oregon developed a multi-stemmed morphology that persisted for many years before shifting to a form dominated by a single stem (a sapling). These multi-stemmed seedlings were up to 56 cm tall and had one to six stems ranging in age from 1-9 years; several ages of stems usually were present on one plant. Height growth per seedling averaged 4.6 cm per year; taproot growth averaged 7.3 cm per year. Stem death averaged 8 percent per year; new stems were produced at a rate of 0.2 stems per plant per year and were closely associated in time with stem death on the same plant. The change from seedling to sapling morphology appeared to be rapid; sapling height growth averaged 15.7 cm per year for the single dominant stems. Root systems of saplings averaged 13 years older than the dominant stem; in one plant the difference was 42 years.

The causes of the prolonged seedling phase and subsequent shift in morphology and growth rate are not clear. Browsing by sheep and deer did not contribute to the prolonged multi-stemmed phase; little evidence of browsing was found. The shift to the sapling phase did not appear to be related to moisture availability; we could find no difference in predawn plant water potential between seedlings and saplings.

Introduction

Oregon white oak (*Quercus garryana* Dougl. ex Hook.) is found on dry sites from southwest coastal British Columbia to northern California. Today, this species occurs in forest stands and in woodlands where the trees are scattered throughout a grass matrix (Morris 1934, Habeck 1961, Thilenius 1968). Regeneration is rare (Sprague and Hansen 1946, Habeck 1961, Thilenius 1968, Johannesen *et al.* 1971), as has been found generally for oaks in Mediterranean climates (Griffin 1976). The largest populations of Oregon white oak are found in western Oregon, particularly in the valleys drained by the Willamette River and its tributaries.

Very little is known about the regeneration of Oregon white oak and, in particular, about seedling survival and growth. *Silvics of North America* (U.S. Forest Service 1990) describes initial shoot growth as slow and root growth as rapid. Cole (1977) reported what he described as stunted seedlings on ridges and upper slopes at the south end of the Willamette Valley. Our early observations did reveal many small oaks with multiple stems and a shrubby appearance; these may be equivalent to Cole's (1977) stunted seedlings.

Other oak species and close relatives commonly pass through a seedling stage characterized by multiple stems, frequent stem death, and the development of a root system older than the aboveground parts (Merz and Boyce 1956, Hibbs 1983, Tappeiner and McDonald 1984, Tryon and Powell 1984). Such observations led to the formal definition of a seedling sprout as a seedling that has a

root collar diameter less than 5 cm and a root system that is older than the aboveground growth (Society of American Foresters 1950).

The causes for such a developmental process have not been explored. Tryon and Powell (1984) described a dieback of oak seedling sprouts in West Virginia as resulting from "suppression," although they did not elaborate further. The eastern oaks, however, differ from Oregon white oak in that they regularly occur in light-limited environments. Under these conditions, dieback of stems can result from the respiratory requirements of larger (older) stems exceeding photosynthesis. Most of the Oregon white oak seedlings we have seen grow in open grasslands where light is not limiting.

Given the scarcity of information on Oregon white oak seedling survival and development, or even of good species for comparison, we undertook an initial investigation of this process and its underlying causes. We began with a characterization of the seedlings and, for comparison, small saplings. If Oregon oak seedlings could be characterized as seedling sprouts, then we wanted to know, first, how long they continued to die back and resprout; second, what characterized the transition from this stage to saplings; and, finally, what caused the transition. Research on California oaks (Griffin 1971, 1973, 1976) led us to expect that herbivory and drought could affect early growth.

Study Area

The study area, which included two adjacent sites (A and B), was in the west-central portion of the

Willamette River Valley, near Corvallis, Oregon. Soils were a clay loam in the Jory series. Depth to the highly fractured basalt bedrock was 100 to 200 cm. Precipitation averaged 1004 mm, with only 47 mm falling during June through August (Franklin and Dyrness 1973). The study area was representative of the *Quercus garryana*/*Rhus diversiloba* community type (Thilenius 1968).

Site A was on a west-facing hillside (10 to 40% slope) and consisted of open grasslands, oak woodlands and forests, and patches up to 0.5 ha of apparently even-aged oak seedlings. These seedlings were growing in open areas, usually where mature oaks had been harvested 15 to 25 years previously and where one to ten large trees per ha still remained. In our experience, this hillside was unusual because of the large amount of oak regeneration present there. We believe the soil disturbance caused by removal of mature oaks contributed to the high density of oak seedlings and saplings. Sheep have grazed the site annually for at least the past 15 years, and the area also contains a large deer herd. There was no evidence of a recent fire history.

Site B was used to provide an estimate of the duration of the seedling stage under a different disturbance regime. It was immediately west of Site A, but no history of logging activity was apparent at this site. Slope was slight (<5%). Soil type, grazing, and fire history were similar to those of Site A. Regeneration was scattered sparsely among widely spaced oak trees.

Methods

Characterization of Seedlings and Saplings

We began with the casual (non-quantitative) observation that the site contained a large number of oak plants of a shrubby form and a lesser number of plants with a more upright or tree-like form. In this paper we have defined seedlings as multiple-stemmed plants with no single dominant stem (plus single-stemmed recent germinants) and saplings as plants with a dominant stem. Sample plants were chosen to include the range of sizes present, but were restricted to plants with a minimum of aboveground competition. We did place an artificial upper limit of 2 m on height.

Twenty-three oak seedlings and 27 saplings were excavated from the study area. All 23 seedlings came from Site A. Nine of the saplings came from Site B. The root systems of oak seedlings and

saplings were excavated with shovels and trowels. Seedlings were excavated to a depth of 30 to 120 cm (wherever the taproot diameter diminished to 1 mm). Saplings were excavated to about 30 cm depth.

The number of live stems on all seedling samples was counted, heights and diameters of live stems were measured, and incidence of browsing was noted. Height and diameter (measured just above the root collar) were recorded for the dominant stem of each sapling. Taproot lengths and diameters were measured just below the root collar, and diameters were measured at 30-cm intervals along the root.

Stem and root ages were determined for all samples. We used ring counts to obtain aboveground ages. Seedling ring counts were cross-checked against counts of bud-scale scars from a subsample of 10 stems, and counts agreed to within 1 year. Stem ring counts were made at the base of live stems, just above the enlarged portion of the plant at the root-stem juncture (Figure 1). Belowground age was determined by counting rings in the taproot 2 cm below the ground and at 30-cm intervals along the taproot. Partial rings were observed, so we suspect missing rings; ring counts probably underestimate true belowground age.

Growth rates were calculated by dividing length (stem, total root, or root section) by the years required to grow the length. Root volume was calculated as the sum of the product of the length times the average of the cross-sectional area at the two ends of each 30-cm section.

Remeasured Seedlings

In the spring of 1987, 23 additional seedlings on Site A were permanently marked, and each stem was tagged and measured. Every spring (before leaf emergence) and fall (after leaf senescence) through spring of 1990, seedlings were relocated and stems remeasured. Stem length and basal diameter were measured, and incidence of damage (browse, dieback) was recorded. New stems were tagged and measured as they arose.

Water Potential

Predawn twig water potential (Ψ_{twig}) was measured from 20 pairs of seedlings and saplings at Site A. The members of each pair grew within 2 m of each other. Twig Ψ was also measured on large trees distributed throughout the study area. Measurements

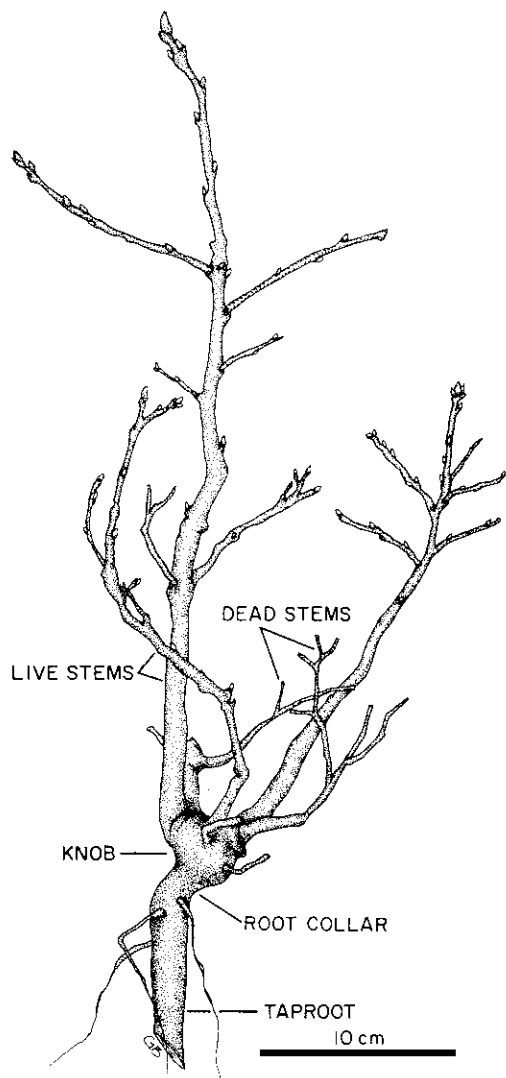


Figure 1. Drawing of the features common to older, multi-stemmed seedlings of Oregon white oak: a taproot, a knob at the top of the root, and live and dead stems.

were taken with a portable pressure chamber between 3 and 5 a.m. on August 22, 1985, and July 3 and 29, 1986. The summers of 1985 and 1986 were similar in precipitation and water demand (Oregon State University Hyslop Farm record, unpub. data).

Results

Excavated Seedlings

Each sample had one to six stems 2-56 cm tall; we found no plants more than 56 cm tall that met our morphological definition of a seedling. Most stems originated from the enlarged knob above the root collar area at or near the soil surface, not from existing stems (Figure 1). Although some seedlings had belowground ages of up to 21 years, individual stem ages averaged 4.6 years and never exceeded 9 years (Table 1). The maximum age span for the stems on any one plant was 7 years. All seedlings had stems more than 1 year old. Stem height growth averaged 4.6 cm/year.

Browsing is usually indicated by a missing distal end of a stem. This symptom was not seen on the excavated oaks, although other plant species at the site exhibited it; poison oak (*Rhus diversiloba* T. & G.), for example, was heavily browsed. However, apical meristems of white oak occasionally failed to grow, resulting in the growth of several lateral buds, producing a branchy appearance.

Each seedling had a single taproot with small laterals (diameter < 0.5 mm) along its length. Taproot lengths averaged 56.3 cm, and diameters averaged 1.2 cm at a depth of 2 cm (Table 1). The taproots grew slowly, averaging 7.3 cm/year. The growth rate increased distally. Growth averaged 4.9 cm/year for the first 30 cm and increased to 7.7, 15.8, and 12.5 cm/year for the three subsequent 30-cm depth intervals.

Age of the seedling taproot ranged from 7 to 21 years, averaging 13.8 years (Table 1). Taproot diameter was strongly correlated with age (Pearson correlation, $r = 0.62$, $P < 0.05$) (Figure 2a); root volume was also strongly correlated with age ($r = 0.71$, $P < 0.01$).

Excavated Saplings

The average height of the dominant stem of each sapling was almost 1.2 m at Site A (Table 1); none was found to be less than 65 cm tall. Mean height growth was 15.7 cm/year. Sapling stem ages ranged from 3 to 17 years, averaging 7.5 years.

Whole root systems were not excavated for the saplings, but the taproot was still distinct at a depth of 30 cm. The average diameter of sapling taproots was 4.0 cm at a depth of 2 cm (Table 1). Lateral roots, which had diameters less than 1 cm, were commonly observed to depths of 30 cm. Taproot

TABLE 1. Characteristics of excavated Oregon white oak seedlings and saplings grown in western Oregon (Site A). Except for maximum ages, mean values are given. Standard deviations are shown in parentheses.

Sample	No. per plant	Length (cm)	Diameter* (cm)	Age (years)	Maximum age (years)	Height/depth growth (cm/yr)
Stems						
Seedlings <i>n</i> = 23	2.4 (1.4)	21.2 (13.3)	0.7 (1.2)	4.6 (2.0)	9	4.6
Saplings‡ <i>n</i> = 18	1	117.6 (32.5)	2.5 (1.0)	7.5 (3.9)	17	15.7
Taproots						
Seedlings <i>n</i> = 23	1	56.3‡ (30.7)	1.2 (0.5)	13.8 (4.4)	21	7.3‡
Saplings <i>n</i> = 18	1	—	4.0 (1.3)	20.2 (5.0)	28	—

*Just above (for stems) or below (roots) the root collar.

‡For tallest stem only.

†*n* = 16 (not all seedling root systems were excavated to their distal end).

age of the saplings varied from 12 to 28 years, averaging 20.2 years. For saplings alone, taproot age and diameter were not correlated ($P > 0.05$). However, for combined seedling and sapling data, root age and diameter were correlated ($r = 0.69$, $P < 0.01$) (Figure 2a). The maximum difference between above- and belowground ages at Site A was 21 years.

The saplings from Site B had an average stem age of 42.0 years, with a maximum of 60 years. Taproot age ranged from 55 to 72 years and averaged 64.8 years. Regeneration at this site is clearly older than that at Site A. The maximum difference between above- and belowground ages at Site B was 42 years.

Seedling/Sapling Comparisons

Reconstructing the growth history of saplings showed that oak seedlings undergo a prolonged period of dieback and resprouting before producing a stem that grows into a sapling. Figure 2 further characterizes these two morphological stages in a form that facilitates comparison of the stages and an examination of the transition. Note that we sampled all sizes of both seedlings and saplings.

Figure 2a portrays a developmental continuum between the two stages. There is no jump in size between seedling and sapling stages; the transition is smooth. Although all saplings were taller than all seedlings (Figure 2b), seedlings and saplings overlapped widely in height growth rate. Among

the seedlings there are many slow-growing stems; none of the sapling stems grew as slowly as the slowest seedling stems. Some seedling stems had high growth rates, similar to those of the fastest saplings, but these plants were short and still had the morphology of the seedling stage.

Figure 2c, showing plant age vs. stem growth, elaborates these points. Here, only the tallest stem of each plant is included. Seedlings and saplings overlapped widely in age (Figure 2c). Except for the two fast-growing seedlings, there was a clear delineation between seedlings and saplings. The two aberrant plants are seedlings morphologically; functionally, they are behaving like saplings and may soon have the appearance of a sapling.

Seedling Population Dynamics

In 3.5 years, three of the 23 remeasured seedlings died; each had had its tap root severed by pocket gophers. A total of 78 stems on 23 seedlings (average = 3.4 stems/plant) were censused during this period. Of these, 22 died—15 during the winter and 7 during the summer. During any one measurement period, no more than one stem on a plant died. Stems that died tended to be among the smaller on a plant. During the census period, 16 new stems were produced. Plants on which stems died and plants that produced new stems had similar numbers of stems per plant (4.6 and 5.0), but had significantly more stems than other plants ($P \leq 0.05$). Only two incidences of stem production

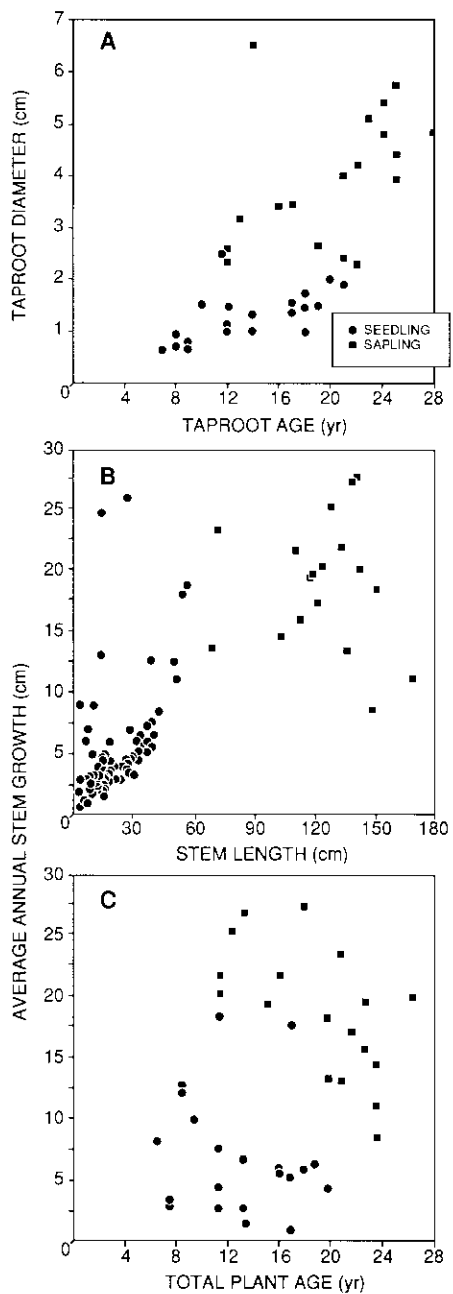


Figure 2. Seedling and sapling size and growth. A. Taproot age and diameter (taken just below the soil surface). Note that there is little overlap in diameter between the two morphological classes. B. Stem length and growth, showing large overlap in stem growth rate between the two morphological groups (includes all seedling stems). C. Plant age and stem growth, showing separation between seedlings and saplings in growth and age characteristics (includes only the tallest seedling stem).

occurred on plants not experiencing stem death, and four stems died on plants that were not producing new stems.

Nine incidences of browsing were found during 3.5 years. In addition, four stems exhibited partial dieback from the top at some point during the study period. Browsing was more common during the winter; dieback was more common during the summer. Most of the summer stem mortality occurred during only one of the three summers (1988).

Stem diameter increased through the three growing seasons (Table 2). Average height of live stems varied, although height growth appeared to increase with time.

TABLE 2. Stem diameter and height growth of 23 white oak seedlings.

Year	Size of stems alive at beginning of growing season		Growth of stems alive at beginning and end of growing season			
	N	Diameter (mm)	Height (cm)	N	Diameter growth (mm/yr)	Height growth (cm/yr)
1986*	64	5.4	33.8	—	—	—
1987	61	6.0	34.7	60	0.46	0.1
1988	60	6.3	31.5	47	1.08	1.4
1989	56	7.4	38.1	55	0.85	4.7

*Based on measurements taken in spring 1987.

Twig water potential (Ψ_{twig})

Water potential did not differ between seedlings and saplings at any date (paired t-test, $P < 0.01$) (Table 3). Tree water potential was significantly ($P \leq 0.05$) greater at the late-season date (August 22) than were seedling and sapling water potentials.

TABLE 3. Predawn twig water potential for seedling, sapling, and tree samples of Oregon white oak.

Date	Seedlings (-mPa)	Saplings (-mPa)	Trees (-mPa)
August 22, 1985	1.86 <i>a</i>	1.87 <i>a</i>	0.69 <i>bc</i>
July 3, 1986	0.40 <i>c</i>	0.37 <i>c</i>	0.38 <i>c</i>
July 29, 1986	1.05 <i>b</i>	0.95 <i>bc</i>	0.74 <i>bc</i>

NOTE: Values followed by the same letter are not significantly different ($P < 0.05$, Scheffé's range test). N = 20 except Trees, where N = 10 for August 22, 4 for July 3, and 6 for July 29.

Discussion

The initial morphological distinctions that we made between seedlings and saplings have been supported and augmented by measurements of size and growth (Figure 2). While the age ranges of seedlings and saplings overlapped greatly, seedlings were generally smaller and grew more slowly; saplings were taller and grew faster. The few seedlings with high growth rates appear to be in the transition between the two classes; with such high rates of growth, they are unlikely to retain the appearance of seedlings for long.

After germination, Oregon white oak seedlings develop a multi-stemmed morphology that can persist for more than 20 years as stems repeatedly die back to the ground and new stems sprout. These plants fit the definition of seedling sprouts (Society of American Foresters 1950), although they support an unusually large number of stems. The root system, especially the taproot, expands throughout this stage.

New stems are continually produced, averaging 0.2 stems per plant per year, but browsing does not appear to be an important factor regulating their growth. In spite of the regular presence of sheep and deer, little browsing was observed. Partial dieback of stems also appears unimportant; its incidence was low. The cause of this partial dieback is not clear but may include insects and water stress.

Stem death is common; 22 of 78 stems died in 3.5 years, a death rate of 8 percent per year. The causes of death are not clear. Only one of the several stems on a plant died in any given measurement period. Because the stems that died were among the smallest stems on the plants, self-shading is a possible cause. However, these seedlings are growing in a high light environment and have shallow crowns. It seems unlikely that self-shading would be sufficiently intense to cause mortality; perhaps carbohydrate shortages induced by moisture stress are a more likely cause.

All recorded seedling death was caused by pocket gophers. We have not been successful at putting this in an historical context; we could find no reports of early gopher population densities. Populations of gopher predators are low today, so gopher populations may be higher now than in the past.

While Figures 2a and 2b suggest a continuum of some characteristics between plants with seed-

ling and sapling morphologies, Figure 2c shows a distinction in terms of age and growth. The scarcity of plants falling into a transitional condition indicates that the transition was probably fairly rapid. The more vigorous growth of stems of saplings than seedlings (15.7 vs. 4.6 cm/yr) shows how the multiple-stemmed seedlings can change into single-stemmed trees; one stem dominates and outgrows the rest. For several years, the remnants of the other stems can be seen at the base of new saplings.

The cause of this transition is still unclear. Browsing was found to be too uncommon to maintain seedlings in a multi-stemmed form. The primary alternative external factor regulating growth is moisture availability (Griffin 1971, 1973, 1976). As the root system of a seedling develops, its ability to capture moisture improves; if it survives, the seedling eventually taps deep water reserves that ultimately change its growth rate. However, we could document no differences in predawn twig water potential between seedlings and saplings and so could not support the hypothesis that water availability regulated the shift in growth pattern. Larger trees, however, apparently can utilize moisture reserves not available to seedlings or saplings. The patterns and ranges we found for predawn Ψ_{twig} are similar to those found for young California oaks (Griffin 1973, Baker *et al.* 1981), which grow in a region with a similar though drier climate pattern.

The pattern of early development of Oregon white oak has much in common with other oak species. However, an unusual feature of this species is its utilization of a multi-stemmed (seedling sprout) phase even though light is not a limiting environmental factor. We were not able to show that browsing or moisture availability was associated with the shift in morphology from multi-stemmed to single-stemmed sapling form. This shift might be regulated by an internal factor such as carbon storage. Such a mechanism would be an adaptation for building fire resistance quickly, once large investments in aboveground biomass begin. The levels of moisture availability observed in this study indicate that seedling growth is probably moisture limited, and moisture also may be important to individual stem mortality.

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