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Seeds, Seedlings, and Growth of Pacific Yew (*Taxus brevifolia*)

Abstract

Extensive logging damage and harvesting for taxol depleted many Pacific yew populations in western North America, and successful natural regeneration is needed to restore those populations. Field measurements of seed and seedling distribution, growth, and age indicate that yew seeds may remain dormant in the soil seed bank for more than three years. Seeds tend to be concentrated under the crowns of mature yew trees, and they can produce abundant seedlings on some clearcut-and-burned sites. Clearcutting, burning, or other major stand disturbances are not essential for seed germination and seedling survival, however; Pacific yew can also regenerate in the understory of undisturbed stands.

Introduction

Pacific yew (*Taxus brevifolia* Nutt.) occurs as an understory tree over a wide range of environments in western North America (Bolsinger and Jaramillo 1990). Many of those understory yew trees were killed during the extensive clearcutting of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) forests after World War II, and many more were destroyed when Pacific yew was harvested in large quantities from 1990 until 1993 for the anti-cancer drug taxol (USDA Forest Service and USDI Bureau of Land Management 1993a). Maintenance of the remaining yew population depends on the ability of Pacific yew to successfully reproduce and adapt to changes in its environment (USDA Forest Service and USDI Bureau of Land Management 1993b).

Unfortunately, the regeneration of Pacific yew is poorly understood. Yews often sprout from the stump, but our unpublished measurements of 900 unburned yew stumps indicate that stump-sprouting is variable and erratic. It does not occur where the stumps have been killed by broadcast burning. Seeds are borne almost every year on female yew trees (Rudolph 1974), however, and large seed crops sometimes occur. Little is known about seed-crop frequency, seed dispersal, or the soil seed bank.

Birds and rodents consume or carry off about 90% of the seeds of Japanese yew (*Taxus cuspidata* Sieb. and Zucc.) (Sakakibara 1989). The remaining 10% probably fall to the ground. The seeds of Pacific yew may be disseminated similarly. If they are, and if one assumes that seeds near a female tree were produced by that tree, the distribution of seeds that were not consumed or carried off can be determined by locating the seeds and seedlings that are present around isolated female yew trees. As the fate of local yew populations may depend on seeds and seedlings, their spatial and temporal distribution is critical. Growth rates of the resulting seedlings also will be important in the recovery of harvested populations. Measurements of large trees indicate that Pacific yew grows slowly under field conditions (Bolsinger and Jaramillo 1990, Busing and Spies 1995), and severe browsing often limits seedling growth. More growth data are needed for unbrowsed seedlings in the field.

Pacific yew successfully regenerates in old-growth forests (Busing et al. 1995), but it also may regenerate from seed soon after major disturbance. Indeed, some foresters believe that disturbance is essential to obtain yew regeneration. However, yew tends to be more abundant in northwestern old-growth than in younger stands (Spies 1991), and the species is very tolerant of shade (Minore 1979). Although tree size and age are not always correlated, all-sized diameter distributions suggest that uneven-aged, self-replacing age distributions may occur in Idaho (Crawford and Johnson 1985). It has been suggested that Pacific yew usually appears after canopy formation in the Bitterroot Canyons of Montana (McCune and Allen 1985). As it also has been suggested that population dynamics of *Taxus brevifolia* west of the Cascade crest in Oregon and Washington are similar to those of populations in Idaho and

[1] Retired

Montana (Busing et al. 1995), uneven-aged stands and seedling establishment after canopy formation may be common throughout the range of Pacific yew.

How are Pacific yew seeds and seedlings distributed with relation to mature yew trees? Do yew seeds remain viable in the soil for long periods? How fast do the seedlings grow when not browsed? Can yew seedlings survive and grow in the absence of major disturbance? We addressed these questions by counting and measuring yew seeds and seedlings in the field to test five null hypotheses:

1. Numbers of Pacific yew seeds in the soil do not differ with distance from mature female trees, direction from those trees, or by depth in litter and soil.

2. Yew seeds in the soil do not remain viable for more than one or two years.

3. Yew seedling abundance does not differ with distance or direction from mature yew trees.

4. Unbrowsed yew seedlings do not grow rapidly (i.e. they do not average more than 10 cm of height growth per year).

5. Seedlings of Pacific yew do not occur in the absence of major, stand-replacing disturbance.

We tested these hypotheses on Pacific yews growing in a relatively small portion of the Cascade Range of western Oregon. Therefore, rejecting or failing to reject a hypothesis does not necessarily imply rejection or failure throughout the range of Pacific yew. Rejected hypotheses provide information on local yew regeneration characteristics or species potentials, however, and they should be considered when managing or studying yew elsewhere.

Methods

Hypothesis #1 (uniform seed distribution) was tested by locating isolated, mature female yew trees in the central Cascade Range of western Oregon. After extensive searching in the Willamette National Forest (Lat. 43° 54' to 44° 24' N. and Long. 122° to 122° 15' E.), only five isolated female trees could be found. They were selected without regard to size or environment. Each bore fruit or female flower buds, and each was at least 33 m from another female tree. All were on level topography with little slash, brush, or debris at elevations between 700 and 1,100 m. Diameter, height, and crown dimensions of each isolated tree were recorded. We collected soil samples from the north, south, east, and west sides of each tree at distances of 0, 1, 2, 4, 8, 12, and 16 m from the bole. At each distance, the litter and soil in a 25 x 25 cm square was removed from three depths (0-5 cm, 6-10 cm, and 11-15 cm) and placed in plastic bags. We sifted each soil sample in the field through a series of progressively finer soil sieves. Intact yew seeds were trapped in No. 7 (2.80 mm) and No. 8 (2.36 mm) sieves, separated from debris of similar size, and saved in labelled plastic bags.

Beginning at the bole and working outward in each direction, we carefully sifted soil from all three depths at 0, 1, 2, and 4 m. If the two lowest depths were without seeds at 4 m from the bole, only the 0-5 cm sample was sifted at more distant sampling points. All depths were assumed to be without yew seeds when seeds were absent from the surface layer at these more distant points. Wherever seeds were found in the 0-5 cm depth, at any distance, soil samples from the other two depths also were sifted. Intact seeds obtained from each soil sample were taken to the laboratory, counted, and floated in water to separate hollow seeds (which floated) from sound seeds (which sank). Samples of both were cut to verify this test. Numbers of intact seeds at each location and depth were compared in a split-split plot analysis of variance in which directions were the main plots, distances were sub plots, and depths were sub-sub plots (Snedecor and Cochran 1967). Tree diameters, tree heights, and crown volumes were compared to total numbers of seeds in simple regression analyses.

Hypotheses #2, #3, and #4 (seed viability, seedling distribution, and seedling growth) were tested in a fenced Douglas-fir plantation established in a clearcut- and broadcast-burned area that supported many yew trees before it was logged. The clearcut area was located in the Cascade Range of western Oregon (Lat. 44° 02' N., Long. 122° 20' E., elevation 800 m). After it was broadcast-burned in June 1986, only dead yew stumps, seeds in the soil, and a few seedlings that escaped the fire remained. Abundant western redcedar (*Thuja plicata* Donn.) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) in nearby uncut stands indicated a moist, summer-wet, mesothermal environment (Klinka et al. 1989). Unusually abundant

Pacific yew stumps and seedlings in the clearcut area also suggested particularly favorable conditions for Pacific yew. We measured the abundance and distribution of yew seedlings that were present around six isolated yew stumps in August, 1993 by establishing six circular, 200 m^2 plots in the fenced plantation. Each plot had a radius of 7.98 m, and each was centered on a yew stump that was at least 16 m from other yew stumps. Only the most isolated yew stumps that were surrounded by seedlings were used as plot centers, but yew stump density in the clearcut unit precluded greater plot isolation. Each of the plot-center stumps was assumed to be the remnant of a female tree that produced the yew seedlings nearby. Because of the clumped manner in which seedlings surrounded the isolated stumps and the abundance of both stumps and seedlings elsewhere in the plantation, we also assumed that seedlings from off-site seed sources were absent. All of the yew seedlings in each plot were numbered, located by azimuth and distance from the central stump, and measured to determine total height. They were then cut at the soil surface, labelled, and aged by counting annual rings in the laboratory. We dug only a few seedlings, but none showed any evidence of sprouting, and age at the soil surface was recorded as total age.

Hypothesis #2 (seed viability limited to one or two years) was tested by counting the number of seedlings in each of the eight age classes that corresponded to the eight growing seasons between seed-source destruction and seedling harvest. Assuming that none of the seedlings came from off-site seed sources (a reasonable assumption because of the clumped distribution of seedlings around isolated stumps), seedlings less than five years old would provide support for rejecting this hypothesis.

Hypothesis #3 (uniform seedling distribution) was evaluated by dividing each of the circular 200 m^2 plots into halves. Three halving directions were tested in separate analyses: uphill versus downhill, north versus south, and east versus west. In each test, the semicircular halves were further divided into equal-area sub plots that occupied areas with inner and outer radii of 0 to 4.00, 4.00 to 5.64, 5.65 to 6.91, and 6.92 to 7.98 m. Seedling densities (the number of seedlings per square meter) were compared with split-plot analyses of variance in which directions (uphill versus downhill, north versus south, or east versus west) were the main plots and distances were the sub plots.

Hypothesis #4 (yew seedling growth) was assessed by determining mean seedling height by age class on the six plantation plots. To assure that all growth was protected by fencing and not influenced by browsing, only seedlings established during the eight growing seasons since June, 1986, were used.

Hypothesis #5 (relation of yew regeneration to major disturbance) was evaluated by sampling seven unfenced Douglas-fir stands with summer-wet, mesothermal environments in the Cascade Range of western Oregon. In selecting those stands we only sought to demonstrate the ability or inability of Pacific yew to regenerate between stand-replacing disturbances. Therefore, only stands that contained yew seedlings < 1 m tall in the understory were chosen, and a wide range of overstory stand ages was selected. The first ten understory yew seedlings were measured and cut at the soil surface as they were encountered in each stand. Overstory stand ages were estimated from Douglas-fir increment cores, and yew seedling ages were determined by ring counts in the laboratory. Large differences between Douglas-fir overstory and Pacific yew understory ages in one or more stands would provide grounds for rejecting hypothesis #5, because no major, stand-replacing disturbance occurred after the measured overstory trees became established.

Results and Discussion

Hypothesis #1 (seed distribution) was tested on female trees that varied in size and form. The smallest was 10 cm in diameter at breast height. It was 3.4 m tall with an average crown width of 2.9 m and a crown volume of 6 m^3. The largest tree was 41 cm in diameter, 9.9 m tall, 8.8 m wide, and had a crown volume of 174 m^3. The number of intact seeds found under and around the five mother trees varied among trees, but regression analyses indicated that seed abundance was not significantly ($P < 0.05$) related to the measured tree size and crown characteristics . Direction from the parent tree also was unrelated to seed abundance, because the average number of seeds per m^2 of soil did not differ significantly ($P < 0.05$) on the north, south, east, or west (Table 1). Significantly more yew seeds were found in the soil immediately next to the bole (0 distance) than

TABLE 1. Average number of yew seeds per square meter found in the soil around five female trees—by distance from the bole, depth, and direction.[1]

Distance (m) and Depth (cm)	North	South	East	West	All Directions[3]	All Depths and Directions[3]
0						169.9
0-5	441.6 ± 260.8[2]	441.6 ± 350.5	489.6 ± 359.6	284.8 ± 146.6	414.4 ± 135.3	
6-10	147.2 ± 100.5	60.8 ± 49.2	76.8 ± 65.5	28.8 ± 13.8	78.4 ± 31.5	
11-15	12.8 ± 9.3	12.8 ± 9.3	32.0 ± 24.8	9.6 ± 9.6	16.8 ± 7.1	
1						64.5
0-5	70.4 ± 23.5	294.4 ± 115.4	102.4 ± 38.7	153.6 ± 95.7	155.2 ± 41.0	
6-10	6.4 ± 6.4	60.8 ± 27.9	3.2 ± 3.2	35.2 ± 12.8	26.4 ± 9.0	
11-15	0	44.8 ± 23.4	0	3.2 ± 3.2	12.0 ± 7.0	
2						18.7
0-5	44.8 ± 19.8	51.2 ± 27.0	48.0 ± 16.0	51.2 ± 18.5	48.8 ± 9.5	
6-10	3.2 ± 3.2	16.0 ± 12.4	0	6.4 ± 6.4	6.4 ± 3.6	
11-15	0	3.2 ± 3.2	0	0	0.8 ± 0.8	
4						2.7
0-5	3.2 ± 3.2	3.2 ± 3.2	0	25.6 ± 21.8	8.0 ± 5.6	
6-10	0	0	0	0	0	
11-15	0	0	0	0	0	
8						0.8
0-5	0	9.6 ± 9.6	0	0	2.4 ± 2.4	
6-10	0	0	0	0	0	
11-15	0	0	0	0	0	
All distances[3]						
0-5	112.0 ± 58.8	160.0 ± 76.6	128.0 ± 76.1	103.0 ± 38.8	125.8	
6-10	31.4 ± 21.9	27.5 ± 12.0	16.0 ± 13.5	14.1 ± 4.7	22.2	
11-15	2.6 ± 2.0	12.2 ± 5.8	6.4 ± 5.2	2.6 ± 2.0	5.9	
All distances and depths	48.6	66.6	50.1	39.9		

[1]Based on 25 cm x 25 cm samples at each distance and depth in each direction. All seeds were intact and apparently undamaged, but cutting tests showed that only four percent were sound. None were found at 12 and 16 m.

[2]Standard error of the mean

[3]Differences among distances and differences among depths are significant (P<0.01). Differences among directions are not.

farther out, however, and there were more seeds at 1 m than at 4 or 8 m from the bole ($P < 0.01$). All seeds found at distances of 4 m or more from the bole occurred in the surface 0-5 cm. Only a few were found at the 8-m distance, and none occurred at 12 or 16 m from the bole. More than 80% of the seeds found were near the surface (0-5 cm) when all distances were considered (Table 1). There was a significant ($P < 0.01$) interaction between distance and depth, because seed numbers declined with increasing distance from the bole more rapidly at 0-5 cm than at the 6-10 or 11-15 cm depths. Floating and cutting tests showed only 4% of the intact yew seeds to be sound. Nevertheless, hypothesis #1 was rejected with respect to distance and depth, because almost all of the seeds present around the five isolated yew trees were under parent tree crowns and near the surface. It was not rejected with respect to direction, for our isolated trees showed no significant ($P < 0.05$) differences in seed distribution on the north, south, east, and west.

Hypothesis #2 (seed viability) seedling ages showed that yew seeds germinated over a 7-year period in the clearcut, broadcast-burned, and fenced Douglas-fir plantation. The age distribution of 613 yew seedlings resembled a normal curve (Fig. 1). A few older seedlings must have escaped the broadcast burning, but our data indicate that 59% of the seeds that germinated successfully after the broadcast burn did so during the following three growing seasons. The remaining 41% became established after more than three years. Indeed, 16% of the seedlings present in 1993 originated from seeds that did not germinate until at least the fifth growing season after logging and burning destroyed all local seed sources except the soil seed bank. Assuming that those late-germinating seeds were not transported to the site from non-local seed sources, we rejected hypothesis #2. Yew seeds probably remain viable for more than two years.

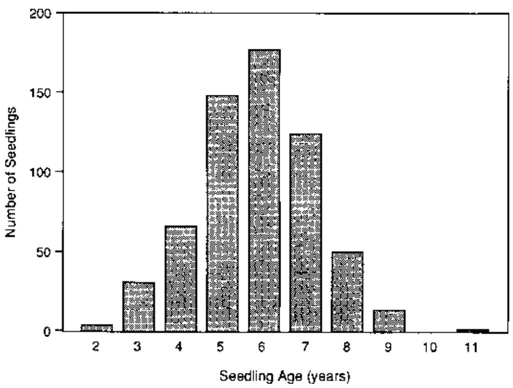

Figure 1. Age distribution of 613 yew seedlings measured during the eighth growing season after the broadcast-burning and fencing of a clearcut area.

Hypothesis #3 (seedling distribution) seedlings were not uniformly distributed among our sample plots. Numbers of seedlings around the six isolated yew stumps in the fenced Douglas-fir plantation ranged from 19 to 175 per 200 m^2 plot. Slopes varied from 45% to 66%, but there was no significant ($P < 0.05$) difference when seedling densities uphill and downhill from the parent stump were compared. There were significantly ($P < 0.05$) more seedlings west of the stumps (azimuths of 180° to 359°) than there were east of the stumps (azimuths of 0° to 179°), but the north-south difference was not significant. Seedling densities were highest near the stumps and lowest farther away (Table 2). Hypothesis #3 was rejected; seedling abundance differs with distance and direction from mature yew trees.

Hypothesis #4 (seedling growth) seedlings demonstrated a consistent growth trend with little

TABLE 2. Average number of yew seedlings per square meter, by distance and direction from six parent tree stumps.[1]

Distance (m)	----------Direction-------- West (180°-359°)	East (0°-179°)	All Directions[3]
< 4.00	1.0 ± 0.1[2]	0.5 ± 0.2	1.5 a
4.00 - 5.64	0.5 ± 0.2	0.4 ± 0.1	0.8 b
5.65 - 6.91	0.6 ± 0.2	0.5 ± 0.1	1.1 ab
6.92 - 7.98	0.3 ± 0.1	0.3 ± 0.2	0.6 b
All distances[3]	2.4 a	1.7 b	

[1]Each of the stumps was >16 m from any other yew stump in the clearcut-and-burned, fenced area surveyed. Equal-area, 25 m^2 plots were used.

[2]Standard error of the mean. n = 6.

[3]Means in the same row or column that are followed by different letters are significantly different ($P < 0.05$).

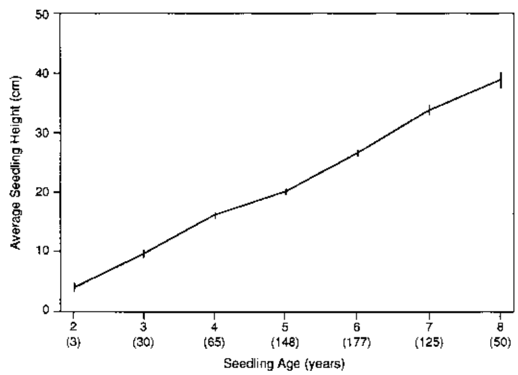

Figure 2. Average heights of unbrowsed yew seedlings, by age class. Numbers in parentheses indicate the number of seedlings measured in each age class. Vertical lines represent standard errors of the means.

variation when average height was plotted against average age for each age class (Fig. 2). All 598 seedlings were inside the fence and unbrowsed. They maintained a height-growth rate of about 6.5 cm per year during the six years from age 2 until age 8. That does not equal the arbitrary 10 cm threshold that we used to define rapid growth, and hypothesis #4 was not rejected.

Hypothesis #5 (regeneration and disturbance) stands had overstory Douglas-fir trees from 15 to more than 200 years old (Table 3). Average understory yew seedling ages ranged from 4 to 12 years in those stands, and none of the seedlings were more than 50 years old. Most were probably affected by browsing, and seedling height

TABLE 3. Overstory age, yew seedling ages, and yew seedling heights from seven Douglas-fir stands in western Oregon.[1]

Stand	Overstory Age (yrs.)[2]	Range in Seedling Age (yrs.)	Average Seedling Age (yrs.)	Range in Seedling Height (cm)	Average Seedling Height (cm)
A	15	2-6	4.1 ± 0.5[3]	7-30	14.1 ± 2.5
B	15	5-14	8.6 ± 1.0	21-88	35.8 ± 6.3
C	20	5-14	9.1 ± 1.0	20-46	36.0 ± 2.8
D	20	3-11	6.6 ± 0.9	16-37	22.7 ± 2.1
E	35	8-15	11.7 ± 0.9	25-115	62.6 ± 9.5
F	140	1-43	12.2 ± 4.1	4-70	30.6 ± 8.2
G	>200	2-14	6.9 ± 1.3	5-71	34.3 ± 6.7

[1]Ten yew seedlings were measured in each stand.

[2]From increment-borer cores

[3]Standard error of the mean. n = 10.

was not directly related to either seedling age or overstory age. The five stands with young (<50 years) Douglas-firs in their overstories had young yew seedlings in their understories that indicated seedling establishment during the stand replacement that occurred after major disturbance. Two stands with older (>100 years) Douglas-firs also had young yew seedlings in their understories, however, and those young seedlings did not require a stand-replacing disturbance to become established. Hypothesis #5 was rejected; seedlings of Pacific yew can become established in the absence of major, stand-replacing disturbance.

We did not study long-distance seed dispersal, but our data provide general, qualitative information about local yew seed and seedling distribution, and they illustrate characteristics of the species that probably are important in most yew environments under most stand history scenarios. For example, most yew seeds not consumed by birds or mammals tend to drop from the crown and remain nearby with little local dispersal. Many apparently fall straight to the ground and remain there. They are concentrated beneath the parent crown and are equally distributed on all sides of the bole. This may result in frequent regeneration within family clusters and could account for the high levels of yew inbreeding reported by El-Kassaby and Yanchuk (1994). Where abundant Pacific yew is the dominant forest species, however, yew seed dispersal is random (Crawford and Johnson 1985).

Yew seeds may be capable of surviving for more than three years in the soil seed bank, because some seeds germinated to provide a new crop of yew seedlings seven years after other local seed sources (live trees) had been destroyed. The seedlings around a mature yew tree tend to be most abundant near the bole or stump, but they may not be equally distributed on all sides of that tree. Differences in seed germination and seedling mortality associated with aspect, shading, and solar radiation may be responsible.

Clearcutting and broadcast burning do not always destroy yew seeds in the soil seed bank, and burned yew stumps may be surrounded by seedlings if conditions are favorable for seed germination and seedling survival. Those seed-bank seedlings may be critical in preserving local gene pools. They also enable Pacific yew to use the abundant light and favorable growing conditions created by major, stand-removing disturbances; thus maintaining local yew populations. Clearcutting, burning, or other major stand disturbances are not essential for seed germination and seedling survival, however; yew can also regenerate naturally in the understory of old stands, without major disturbance.

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