Reproductive Behavior of Port Orford Cedar from Different Provenances Grown in a Common Garden

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Study Design (2005)

A total of twenty-five accessions of Port-Orford-cedar were selected from three differing provenances at extremes of its range. These were (see map): Breeding Block 1 – Low Elevation (BB1-Low●), parent trees 0-450 m, SW Oregon; Breeding Block 1 – High Elevation (BB1-High, ●), parent trees 700-850 m, SW Oregon; and Breeding Block 6 (BB6, ●), parent trees 1100-1500 m, inland N. California. There were 10 genotypes from BB1-Low, 5 from BB1-High, and 10 from BB6. Higher elevations are shown in darker shades of green. The trees selected were from rooted cuttings of field trees and were grown in 9 gallon pots (photograph a). They were treated with gibberlin sprays (GA[3]) during early summer of 2004 and moved into the study greenhouse in late fall of 2004. Two replicates, each with one ramet of each parental genotype, were laid out side-by-side in an open greenhouse. Replicates were oriented N-S and had border trees surrounding them. Three branches on each tree were marked and rated on a regular basis (every 2nd or 3rd day) for proportions of various reproductive stages of female and male cones. (Pollen and seed cone study branches were not necessarily the same ones.)

Seed Orchard

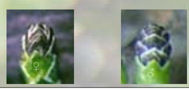
Introduction

Port-Orford cedar (POC) is very amenable to management in a Containerized Seed Orchard (CSO). However, maintaining genetic diversity in production seed orchards is difficult. The genetic contribution of a given tree in an open-pollinated orchard can vary greatly depending on the number of parents present, flower / cone abundance, and timing of pollination. Trees from geographical or physiographic extremes are likely to vary greatly in the timing of reproductive development. Even within a single geographic zone, there may be considerable variation in reproductive development. Variation due to these genetically-based factors is compounded by year-to-year environmental differences, and by interactions of genotype and environment.

Our objective was to examine variabilty in POC seed cone and pollen cone phenology in genotypes from extremes of its range. Of particular interest was the overlap between seed cone receptivity and pollen shed. Another behavior of interest was the degree of variation between ramets of the same genotype.

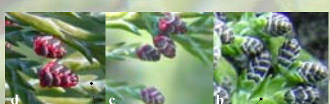
These behaviors have definite implications in the management and implementation of the Port-Orford-cedar CSO. Choice of parents, their placement in the CSO, and actions to avoid pollen contamination between trees from disparate backgrounds would be affected. The ability to preserve genetic diversity in seed crops from the seed orchard would also be affected by the management choices.

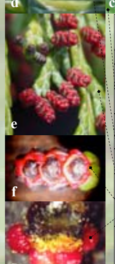
Reproductive Morphology



Male and female cones can be visually distinguished at early stages:
♀Female – cone scales long 'peaked' (tapered to tip), outer enclosing inner
♂Male – cone scales shorter, only slightly peaked, whitish margin, less overlapped, inner scales extended beyond outer, banded or striped appearance.
The earliest observable stages are early black scale / black tip – barely extending out from leaves at branch tips. These are often visible in late October but little further development occurs until the following January or February.

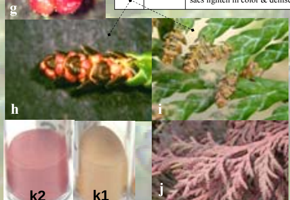
Male Cone Stages





Seven descriptive stages of **Pollen Cone Development** were defined. These correspond roughly to the stages defined by Hak and Russell (2004) for yellow-cedar.

Stage	Name	Description
0	Initiation	Not observable externally, covered by leaves at branchlet tip
1	Black Tip	Cones starting to emerge from leaves at branch tips
2	White Line	Cones elongating, exposing cone scales along entire length, whitish margins evident. Cones 2-3 mm long. (b)
3	Early-Redline	Cone scales starting to show red around the edges (c).
4	Mid-Redline	Pollen sacs emerging between cone scales (d).
5	Late-Redline	Pollen sacs fully emerged between scales, sacs full and round (e, f, g).
6	Pollen Shed	Cone internodes elongate, opening space between scales, cones 3-5 mm long, pollen sacs lighten in color & dehisce (h,i).



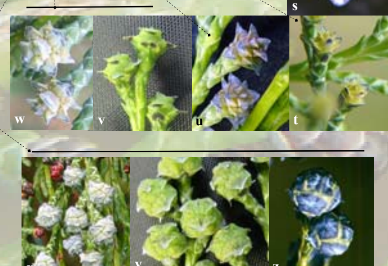
Unlike most conifers, pollen of *Chamaecyparis* species has a pinkish tint – from a light magenta to a yellowish-peach color. The photographs above (i, j, k1, k2) illustrate the extremes of the color range for *C. lawsoniana*.

Until its removal from the genus *Chamaecyparis* in 2004, the Alaskan yellow cedar (*Xanthocyparis nootkatensis*) had been the species to which Port-Orford-cedar was most often compared. Photograph l shows one difference between the two species, with each male cone scale (microsporophyll) having only two pollen sacs (microsporangia) per scale, as compared to the typical four per scale in Port-Orford-cedar (photo g). (Camus, 1914, and others noted only 3.) Also, *X. nootkatensis* has a pale yellow colored pollen. Meiosis occurs in the fall in *X. nootkatensis*(Owens & Molder, 1974) but, based on the corresponding stages in *C. lawsoniana*, apparently occurs in early spring in the latter species.

Female Cone Stages

Eleven descriptive stages of **Seed Cone Development** were defined. Degree of flare and expansion were the main characteristics defining them.

Stage	Name	Description
0	Initiation	Not observable externally, covered by leaves at branchlet tip
1	Black Scale	Cone scales projecting out & darkening (m)
2	Blue tip	Cone scales barely starting to flare, showing some blue color at tip (n)
3	Early Flare	Cone scales starting to flare only slightly, not enough for pollination drops, definitely bluish (o,p)
4	Early-Mid Flare	Cone scales flaring significantly, allowing space for pollination drops (q)
5	Mid-Mid Flare	Cone scales moderately flared, ~45° to axis (r,s)
6	Late-Mid Flare	Cone scales completely flared, outer not quite at right angles (t)
7	Early-Late Flare	Cones starting to expand between scales (u)
8	Mid-Late Flare	Cones expanding significantly between scales (v,w)
9	Late	Cones well expanded, ± globose, 3-10 mm dia. (x,y,z)
10	Mature	Dried, brown, ready to shed seed



Pollination drops are usually visible to the unaided eye, at least on cones in stages 6-8. Diameters range from less than 0.5 to over 1 mm. Drops were observed on females cones on various genotypes in all stages printed in blue in the table above. Pollination drops can be seen on cones in photographs p, s, and v above.
Photographs x, y, and z also illustrate the range in color of female cones.

Cone Distribution

Typical cone development patterns are shown in the photograph on the left (aa), with females clustered toward the end of branches and males scattered on older branchlets back toward the base of the branch. Male cone density varied greatly, as seen in the photos on the right (bb, cc, dd).
Female cone density showed a similar range of variation, from "extremely dense" (photographs ee and ff) to "very sparse" (scattered, single).

Phenology

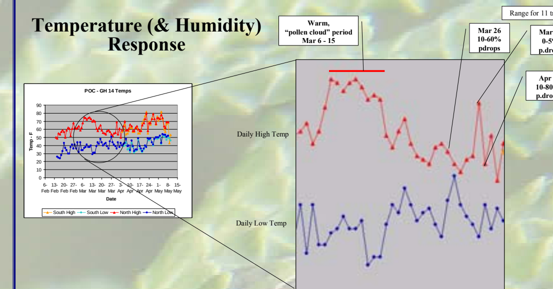
Most trees showed precocious male development, with pollen shed beginning before pollination drop production. In the phenology summary chart below, adjacent pairs of lines show the timing of male and female cone development for a given tree. Several study trees showed precocious female development (another greenhouse had a large percentage of trees in this category). This category included 1/3 of BB6 trees but no BB1-Low trees. One BB6 tree started pollen shed two weeks after the start of female receptivity. Photograph gg shows one non-study tree where the seed cones were already in the late stage while pollen cones were just barely starting into the whiteline stage. This condition would obviously favor outcrossing. A number of study trees had a small portion of female cones that were still receptive after their male cones had finished shedding.

Relative Timing

On the average, the BB1-Low trees started flowering earlier than the BB1-High and BB6 trees. However, there were exceptions to this rule and there was considerable variation within groups and between the ramets of a given genotype.

Pollen shed for a given tree was not uniform throughout the shedding period; most was shed with the first week and tapered off over two or three weeks after that. For the last dozen or so trees, the taper was pronounced – a very long, light tail of pollen shedding about a month long. During the last few weeks at the end of the observation period, there was relatively little pollen being shed – there was slow shed from a few trees, very light shed from several other trees, and isolated , tardy pollen cones developing among female cones near branch tips (photo hh). As mentioned elsewhere, this probably contributed to the very low maturation percentage in female cones that became receptive late in the study.

Temperature (& Humidity) Response



Temperature and humidity appeared to greatly influence the timing and extent of cone development. (The temperature effect is confounded with the humidity because of the inverse relationship of temperature and relative humidity, and since the cool days were also usually cloudy and rainy.)

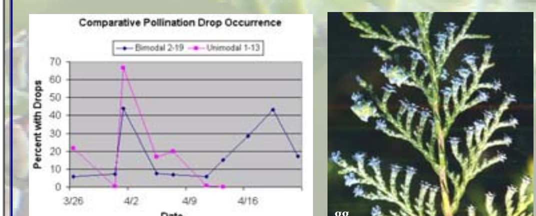
Male cone development progressed slowly in the late winter months as the weather slowly warmed. The earliest appearance of "red-line" cones was on January 28; that tree began shedding pollen on February 24 (see phenology chart to left) with peak shed a week later (1 March). A few other trees began showing red-line cones during the early February and shedding pollen in late February but the rest were at least two weeks later than that. Most BB1-Low trees were showing red-line cones by the end of February. On March 6th, an unusually warm, dry period began. During this time, pollen cones of many of the trees developed very rapidly and shed pollen profusely – a time we called the "pollen cloud". period. Most of these trees were from the BB1-Low provenance. Immediately after this, the weather turned cool and rainy. On the whole, pollen cone development and pollen shed slowed greatly. The weather gradually warmed up and heavier pollen shed resumed, but never to the extent that occurred during the "pollen cloud". The trees that still had male cones in the red-line stage at the end of April were mostly from BB6. The genetics of these trees and the frequent cool days combined to stretch the end of the pollen shedding into a long but very light tail.

Temperature effects on pollen development were probably evident in another behavior. Study trees were oriented so that the branches being studied were on the northern half of the tree. However, it was usually the case that branches on the south side of a tree started to shed pollen a day or two before the branches on the north side.

Female cone development also showed interesting development patterns relative to temperature and humidity. On warm, dry days, pollination drop abundance was greatly reduced. At the right side of the expanded portion of the temperature chart is an illustration of this effect. These were 11 trees that were well into female receptivity, as measured by pollination drop frequency. Pollination drop frequencies observed on three successive observation dates are summarized on the chart. With each tree, the pollination drop frequency dropped to zero (or nearly so) on the warm day in the middle and rebounded the next day when it was cool and rainy. The temperature / humidity change did not appear to affect pollination drop frequency on trees that were past their receptive period or that had not started it.

In *X. nootkatensis*, once pollen has been taken up by a given ovule, the pollination drop disappears permanently (Owens and Molder, 1974). This is probably also the case with *C. lawsoniana*. There were very few actual pollination drops observed during the "pollen cloud" period. Presumably, this is due to a combination of the temperature/humidity effect and the early take-up of pollen by the female cones that were receptive at that time.

Seed Cone Development Variation



Most trees had receptive female cones for about two weeks (e.g. Tree 1-13 in the comparative pollination drop graph). Several trees, though, showed a much longer period of receptivity for female cones. Six of these trees showed a bimodal pattern of seed cone development and pollination drop production (Tree 2-19 in the graph). They had an initial peak of female cone development but had a large portion of "reserve" cones that initially did not develop past the blue-tip or early flare stages (stages 2 and 3). About two weeks later, these "reserve" cones began to flare and produce pollination drops. However, very few of the second flush of female cones matured, as is evident in photo gg. This is probably due to the scarcity of pollen at the end of the observation period. The photograph (gg) is of a branch from one of these bi-modal trees. The two large cones are from the first flush of female development, the other blue small blue cones are from the second. The second group of cones were stationary in the early-late or mid-late flare stage (stage 7 or 8) and never progressed further.

There was one other tree that had a longer than usual receptive period but did not appear to be bi-modal. This was apparently due to a few cones that were tardy in their development, since the tree had no large concentrations of undeveloped cones remaining on the branches.

Summary

- This is the first detailed description of the stages and phenology of Port-Orford-cedar reproductive development.
- The period of female receptivity for a given genotype overlapped to some degree with the pollen shed period of over 80% of the other genotypes, across all groups.
- There was considerable variation in onset of pollen shed and female receptivity, both within groups and between groups.
- Both pollen and seed cone density were highly variable between genotypes.
- Ramets of a given genotype varied noticeably in phenology of reproductive growth.
- Pollen shed and pollination drop production was greatly affected by local temperature and humidity.
- Trees still having receptive female cones late in the season were less likely to be pollinated due to reduced pollen shed then.

Literature Cited

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