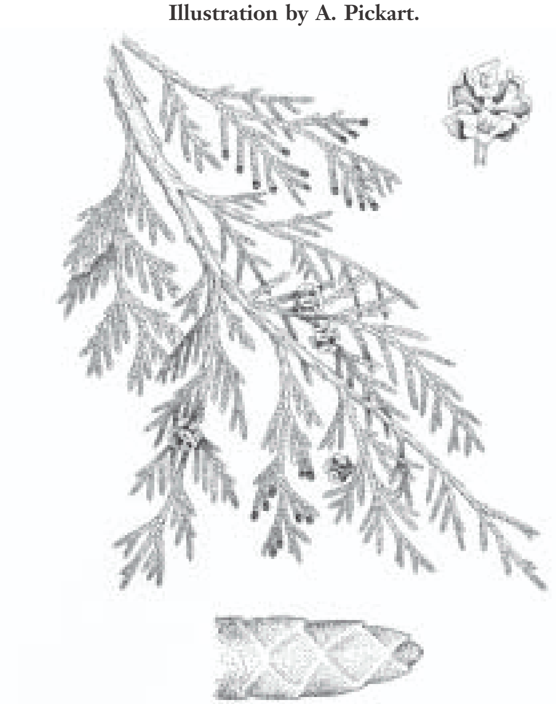
PORT ORFORD CEDAR AND THE NON-NATIVE PATHOGEN, *PHYTOPHTHORA LATERALIS*

by Cheryl A. Sinkiewicz and Erik S. Jules

For botanists traveling in northern California and southern Oregon, one of the greatest delights is spotting the large and elegant tree, Port Orford cedar (POC). While found across a relatively small region, this conifer plays a surprisingly important ecological role in many habitats, including riparian areas, serpentine soils, sand dunes, and coastal plains. Among the many characteristics of POC, its straight grain and extreme resistance to rot have made it equally valuable to builders and artisans, although working with old-growth POC lumber is becoming increasingly rare.

Unfortunately, both the ecological and economic services that POC provides are at great risk. Since 1952 the native range of POC has been steadily invaded by a fatal, non-native root pathogen, *Phytophthora lateralis*. This pathogen has gradually advanced into large portions of the cedar's range, spreading with the aid of human and animal activity into even remote watersheds. Many POC stands have been reduced to a fraction of their former abundance by *P. lateralis* infection, and longer-term impacts of this pathogen are a growing concern among land managers and conservationists alike.

Foliage and cones of Port Orford cedar. Illustration by A. Pickart.



TAXONOMY AND NATURAL HISTORY

Port Orford cedar (*Chamaecyparis lawsoniana*) is a member of the Cupressaceae and is the largest of eight taxa in its genus. These include Alaska cedar (*Chamaecyparis nootkatensis*) and eastern white cedar (*Thuja occidentalis*) from North America, and five additional species found in eastern Asia. Other common names used for POC are Lawson cypress, Oregon cedar, white cedar, ginger pine, and Port Orford white cedar. POC has reddish-brown bark, flattened branches, and scale-like leaves. It can sometimes be confused with Alaska cedar, incense cedar (*Calocedrus decurrens*), and western red cedar (*Thuja plicata*), but is generally easy to identify by the x-shaped stomatal bloom on the underside of the leaves. POC's spherical cones, comprised of 7–10 scales, are also useful to differentiate it from the latter two cedars.

POC is endemic to southwestern Oregon and northwestern California, with the greatest abundance of trees occurring in Oregon. Its range stretches from the Pacific coast to approximately 70 kilometers inland, and cedars can be found up to 1,500 meters in elevation. Old-growth POC trees often reach 30 to 60 meters in height and can be up to 2 to 3 meters in diameter. They can live up to 900 years of age. The largest known POC is found south of Powers, Oregon, at 69.8 meters in height and 3.65 meters in diameter.

Large POC trees exhibit an unusually high resistance to decay and insect damage due to high levels of volatile oil that give trees a strong, characteristic ginger-like odor. Because of these wood properties, individual trees are able to persist for many years after death. Amazingly, tree ring studies have shown that in some cases, dead specimens can remain standing for over 100 years. Field studies have revealed one cedar that is still standing after its death in 1738. Along with its thick, fire-resistant bark, POC's decay resistance provides for a stable, long-lived tree in many habitats.

POC is found in a wide variety of vegetation types. On the California side of its range alone, POC is an important member of at least 34 named associations. These range from mixed conifer stands—where POC can be found, for example, with western red cedar, Douglas fir (*Pseudotsuga menziesii*), sugar pine (*Pinus lambertiana*), and white fir (*Abies concolor*)—to California pitcher plant (*Darlingtonia californica*) fens, where POC is the only tree found within the fen. In part, POC's ability to grow with so many other trees is due to its wide tolerance of soils. POC is found on soils derived from numerous parent materials, including quartz diorites, metavolcanics, sedimentary materials, and ultramafics (including

serpentinite, dunite, and peridotite). Interestingly, POC can be found growing directly on sand dunes near Coos Bay, Oregon.

Although POC has a seemingly wide ecological amplitude within its range, it is quite limited to areas with high availability of water. Because of this limitation, POC is often found growing along streams where its roots are in direct contact with flowing water. Although POC's role in stream habitats has not been quantified in any comprehensive study, research and observations suggest that POC may play an important ecological role in these sensitive habitats.

Cedars in riparian areas help to shade the stream, reduce water temperatures, and stabilize streambanks, which are vulnerable to erosion during high winter flows. Large cedars can also act as an important stream channel-forming agent when their root systems become large enough to withstand channel movement. Once dead and fallen onto floodplain surfaces or into streams, POC's large trunk, decay-resistant wood, and exceptionally long residence time provides lasting and diverse habitat for salmonids and other aquatic life.

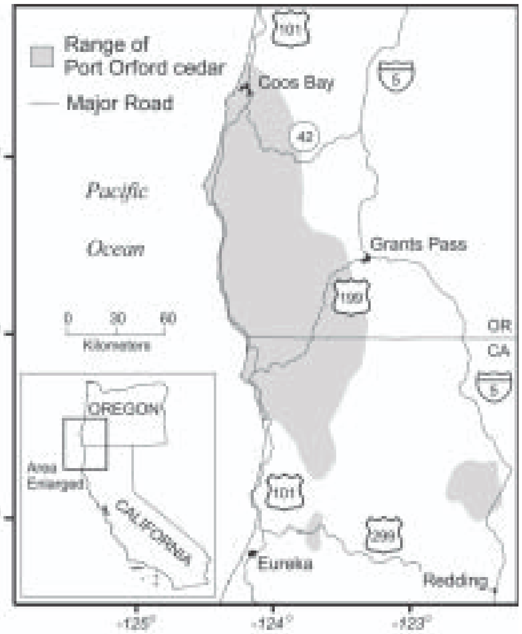
POC is particularly important to streams flowing through the Josephine ophiolite, an extensive, botanically unique area of ultramafic soils on the Oregon-California border. Ultramafic environments are nutrient poor, have low calcium to magnesium ratios, and contain levels of metals toxic to most plants (e.g., copper and zinc). On ultramafics the cedar is often the only large conifer in riparian areas and may help improve soil fertility by incorporating calcium into the soil.

The Josephine ophiolite is also home to most of the known *Darlingtonia* fens, unique wetlands that contain rare and endemic plants such as California pitcher plant (*Darlingtonia californica)*, Waldo gentian (*Gentiana setigera*), Oregon willow-herb (*Epilobium oreganum*), large-flowered rush-lily (*Hastingsia bracteosa*), purple-flowered rush-lily (*Hastingsia atropurpurea*), and western bog violet (*Viola primulifolia* ssp. *occidentalis*). POC is the dominant tree in these fens and is likely an important player influencing nutrient cycling, shade availability, fuel loads for fires, and erosion rates.

POC is also valuable to the timber and horticultural industries. There are approximately 220 cultivated varieties of POC used in landscaping applications, and they are readily available in North America as well as Europe. POC is easily propagated for landscaping since it is able to reproduce from seed at a very early age, and cuttings are easily induced to form new roots. In the best of nursery conditions, sexual reproduction (cone production) can begin within the first five to nine years of life.

In the timber trade, POC has historically been a valuable resource demanding a high market price. In the late 1800s, POC brought at least twice what redwood and Douglas fir sold for in San Francisco. Attributes that have made POC such a desirable wood to work with include its beautiful white sapwood (sometimes indistinguishable from its heartwood), its small knots, lack of splintering and tearing, and an ability to hold paint better than most other woods. Through the early 1900s it was utilized in the construction of ships and houses. At the peak of its production in the 1920s and 1930s, POC was used in the making of venetian blinds and electric storage battery separators, as well as in the construction of airplanes during World War I. An increased demand for storage battery separators during World War II led to POC's classification as a "critical material."

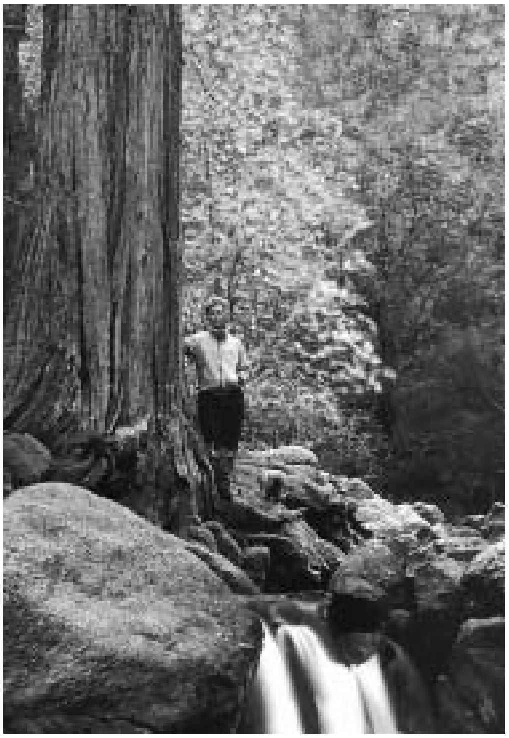
Besides small specialty uses, there has been little domestic production of POC for several decades. Starting in the 1960s, commercial production primarily served the export market to Japan. Due to its resemblance to the traditional Japanese hinoki cypress (*Cupressus obtusa*), which is no longer available in Japan, POC has been highly prized by the Japanese for use in the construction of temples and shrines. For a time, prices paid for large trees were exceptional, although this market has largely disappeared due to changes in the Japanese market and the restrictions on harvesting of POC in National Forests.



Range map of Port Orford cedar. Map by D. Ritts.

THE CULPRIT: *PHYTOPHTHORA LATERALIS*

The genus *Phytophthora* (meaning "plant destroyer") is commonly known as a fungus and was once thought to be a member of the fungi kingdom, Kingdom Myceteae. Currently however, *Phytophthora* is placed in the Kingdom Chromista, Phylum Oomycota. Once thought of as a "typical fungus," the Phylum Oomycota (or Oomycetes) is now known to vary at the molecular level



Old-growth Port Orford cedar along riparian area. Photograph by B. Ullian.

from the true fungi. For example, the cell walls of oomycetes contain cellulose and the amino acid hydroxyproline, unlike the cell walls of fungi, which are composed of chitin (a complex polysaccharide carbohydrate also found in animal exoskeletons and nematode egg shells) and glucans other than cellulose. The nuclei of oomycetes contain two sets of chromosomes, compared to fungi which only possess a single set of genetic information. Phylogenetic studies have shown the Oomycota to be a monophyletic group, having evolved from a common ancestor, the heterokont photosynthetic algae.

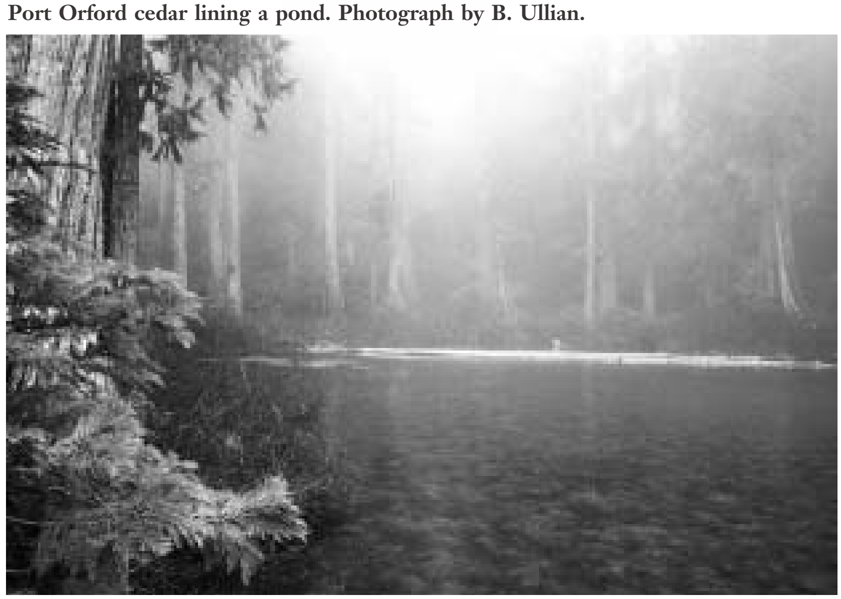
The family Pythiaceae contains the two closely related genera *Phytophthora* and *Pythium*. Both of these parasitic genera thrive in moist conditions on foliage and in soil. *Pythium* actually has the ability to act as a parasite on some *Phytophthora* species. For instance, *Pythium oligandrum* has been found to be an effective biological control for *Phytophthora infestans*. *Phytophthora infestans* is the pathogen responsible for the Irish potato blight and the first taxa to be named in the genus. Now a large genus of over 50 mostly rare species, *Phytophthora* has been found to affect an amazingly wide variety of cultivated and wild species with diseases such as sudden oak death, black pod of cacao, black shank of tobacco, and root rot of the avocado tree.

In 1923, *Phytophthora lateralis* was first reported affecting POC in the commercial nursery industry near Seattle, well outside the cedar's range. This resulted in the eventual collapse of the industry in less than 20 years after the initial discovery. The pathogen was finally named and fully described in 1942 by Tucker and Milbrath. Unfortunately, in 1952 *P. lateralis* had been carried south, almost assuredly by a vehicle, and was reported within the cedar's native range. Although the origin of *P. lateralis* remains unknown, its extreme virulence and episodic nature on POC clearly indicates that it is a non-native pathogen. Much later, in 1991, the Pacific yew (*Taxus brevifolia*) was reported to be a host for *P. lateralis*. Mortality is much lower for the Pacific yew, and is highest when present along streams with infected POC.

Infection of POC by *P. lateralis* initiates at the tree's roots, and symptoms of the host's impending mortality can occur after a few weeks or a few years, depending on the size of the tree. The first obvious symptom of infection is a change in foliage color from green to yellow, then to reddish brown, and eventually to brown. Symptoms of infection are most obvious after colonization of the entire root system, after which mycelial growth of *P. lateralis* (i.e., the asexually growing, or vegetative component of the pathogen) girdles the root collar and travels as much as 50 cm up the above-ground vascular cambium. Infected roots often appear dark brown and saturated with water and the above-ground cambium is also stained a diagnostic dark brown.

When POC becomes stressed during this process of infection, it is vulnerable to invasion by bark beetles and secondary fungi, which may further stress the infected trees. Death of the entire tree crown is most visible across the landscape in late spring and summer when moisture stress can become extreme. Importantly, the time between initial infection of the roots and death of the tree can be as short as a few weeks for small seedlings, and up

Port Orford cedar lining a pond. Photograph by B. Ullian.



Port Orford cedar root system along Silver Creek, Oregon. Photograph by B. Ullian.

to seven years or longer for old-growth trees. Large trees also differ from small trees in that they tend to have higher infection rates due to their larger root systems, which provide an easier target for incoming spores.

Spread of the root rot disease occurs in one of two main ways: either it is transported by vehicles, or spread from nearby infected trees. In the first instance, spores are transported long distances (e.g., many kilometers) from infected POC populations to uninfected populations by vehicles traveling the many roads within the cedar's range. While infecting a host tree, *P. lateralis* will produce chlamydospores (or, less commonly, oospores) which are relatively durable compared to the spores that actually infect roots (zoospores). Chlamydospores can be picked-up in mud or organic material on tire treads, the underside of a vehicle, or in goods being transported such as gravel or soil. If this material is released from the vehicle near uninfected cedar, a new infection may occur. Once spores are carried to an uninfected area, they can either be deposited near POC roots or washed into creeks and streams where the spores will be carried to vulnerable host sites. Because the spores of *P. lateralis* require moisture, exposure to sunny, dry conditions while in transit can kill the disease and reduce infection risk.

The deposition of chlamydospores near a potential POC host does not directly lead to infection. Rather, chlamydospores must germinate and produce a sporangium, from which flagellate, motile zoospores are released. Emerging from the sporangium, the zoospores have a tendency to move towards the water surface, possessing an ability to swim or move passively through water currents. Zoospores result in the development of the vegetative mycelium that infects POC roots. In unfavorable conditions, zoospores can encyst themselves in a thick cell wall, in which case germination and infection may occur later.

The second major way in which the pathogen is dispersed occurs at a more localized scale after infection begins on a host tree in a newly invaded population. Because the pathogen on newly infected hosts will be making additional spores while developing on the tree, the new host acts as a source of dispersing spores for downstream trees. Spores from this initial infection can move downstream or short-distances downhill in moving water. As such, once a body of water is infected, all POC trees downstream are at high risk. Studies have found a mortality rate greater than 90% in cedars whose roots are in direct contact with water.

A creek with Port Orford cedar infected with *Phytophthora lateralis*. Note the road crossing the creek as well as the culvert. Dead trees (without needles) and dying trees (with drying foliage) are shown, as well as a healthy tree (far left). Infections usually are transported to creeks by vehicles, and subsequent infection spreads through the population downstream. Illustration by C. Sinkiewicz.

Movement of infection down broad slopes is also observed most commonly near coastal sites where overland flow of water occurs at least seasonally. Also, wildlife and humans (collectively termed "foot traffic") can move *P. lateralis* over short distances. In the only study that has assessed the relative impact of foot and road traffic, foot traffic accounted for 28% of newly infected populations. Movement of disease by foot traffic, however, occurred over short distances compared with road traffic; the longest dispersal distance via foot traffic was 264 meters, while the longest dispersal by road traffic was 3.8 kilometers.

MANAGEMENT OF *PHYTOPHTHORA LATERALIS*

Because much of POC's range is heavily roaded and includes both publicly- and privately-owned land, slowing the spread of *P. lateralis* into uninfected areas has been challenging and, unfortunately, largely unsuccessful. While some efforts are definitely working, new infections continue to be found in remote areas. Almost always, however, long-distance movement occurs along roads.

For example, in the Kalmiopsis Wilderness of southwestern Oregon, activities facilitated by motorized access on an old existing mining road are thought to be responsible for the introduction of the pathogen deep into the heart of the wilderness. More than eight miles of river within the wilderness, including the National Wild and Scenic Chetco River, are now infected by the pathogen. *Phytophthora lateralis* was also recently introduced into a roadless area watershed and Forest Service Botanical Area, where the point of infection was an unused gravel pit at the top of the watershed. The introduction of the pathogen into the Klamath River Basin in 1995 was thought to be

Infected Port Orford cedar displaying characteristic staining of cambium by *Phytophthora lateralis*. Photograph by E. Jules.

from off-road vehicles in a headwater area. The second root disease introduction in the Klamath Basin (1996) occurred on a paved road, more than 30 kilometers from the nearest infection source.

Yet the fact that *Phytophthora lateralis* is dispersed primarily along roads is also a reason for optimism. Put simply, if the disease were dispersed aerially, as are other virulent diseases, we would have limited options for controlling the spread. Controlling the movement of chestnut blight, for instance, was impossible due to its aerial mode of transmission. That disease was able to completely alter the composition of forests of eastern North America in just a few decades.

Likewise, sudden oak death is caused by the closest relative of *P. lateralis*, *P. ramorum*, but the two diseases differ in two fundamental ways. First, *P. ramorum* appears capable of moving through the air, though the precise mechanism is still under study. And second, *P. ramorum* is known to infect over two dozen host species, a list that continues to grow. In comparison, the mode of *P. lateralis* spread on POC is severely limited to the movement of spores in moist organic material and water, and to only one primary host. Therefore, predicting areas of high risk and controlling the movement of the disease vectors should be much easier than for air-borne diseases.

Because vehicles traveling roads are the greatest threat to uninfected POC, efforts to slow the spread of *P. lateralis* focus primarily on regulating roads. These efforts have been coupled with a large suite of other strategies (see sidebar).

There is general agreement that permanent road closures offer the greatest chance of success in preventing further spread of the infection. Although miles of old logging roads have been closed, a related issue of access rights on public land has made this a difficult strategy to implement and enforce. Road closures during only the rainy season are easier to implement than permanent closures and are likely to reduce the spread of disease, although the risk reduction is difficult to quantify. The fact that some road surfaces can remain moist well into the summer within the cedar's range suggests that new infections may occur even in the dry season.

Public education efforts also face challenges, mainly because community opinion and support regarding the future of POC is highly variable. Even in light of the risk to such a valuable resource, resentment over road closures has led, for instance, to a large number of locked road-closure gates being vandalized. On the other hand, one place where efforts by federal agencies have not been contentious, and probably have been critical, is in the education of workers who frequently travel in remote areas, such as mushroom harvesters and bough cutting collectors (for floral arrangements). While there is strong agreement that these programs must continue and perhaps grow, unfortunately their success is difficult to monitor.

The washing of large equipment and vehicles traveling between infected and uninfected areas is a technique often employed that may be useful in preventing further spread of the infection. The ability to completely free a vehicle of mud and organic material using high pressure hoses has been questioned and we are unlikely to have a clear answer to this question anytime soon. However, vehicle washing can probably reduce somewhat the risk that logging vehicles pose to continued *P. lateralis* spread.

Another method employed to slow spread of *P. lateralis* is sanitation logging, which involves the removal of POC trees along roads. This technique has two different goals, depending on the site-specific situation. First, in areas that are not infected, the goal of sanitation is to reduce the number of host "targets" along the road, thereby reducing the probability that an infection will occur. Second, in areas that are already infected, the goal is

SLOWING DISEASE SPREAD

Strategies listed below are used to control the spread of *Phytophthora lateralis* to uninfected populations of Port Orford cedar (POC). The efficacy of some strategies remains untested.

- Permanent and seasonal road closure.
- Washing of vehicles after leaving infested areas and before entering uninfested areas.
- Using heavy equipment in the dry season only.
- Removing POC from road areas to lower infection risk (sanitation logging).
- Paving and elevating road surfaces.
- Directing water runoff away from POC areas.
- Utilizing pathogen-free water for road maintenance and fire fighting.
- Educating the public about the influences of human activity on disease transmission.
- Introducing POC to sites unfavorable to the spread of infection.
- Thinning of trees to create distance between potential hosts.
- Regulating harvesting of POC timber to reduce infection spread.

Port Orford cedar is often the only tree found within Darlingtonia (*Darlingtonia californica*) fens. Photograph by E. Jules.

to reduce inoculum (spores) along roads that may be transported elsewhere.

At this time it is unclear how successful this technique may be, but preliminary studies are underway. Due to its potentially destructive ecological impact, this is a controversial practice that is being debated by land managers, the scientific community, and concerned community members. Proponents of sanitation logging have been criticized for supporting the technique since so far there is little evidence for its efficacy.

Plant pathologists are actively seeking POC trees that are resistant to *P. lateralis*. This work has shown promise and may be one of the best options for reestablishing POC to areas already affected by *P. lateralis*. Some POC trees demonstrate heritable variation in susceptibility, which appears mainly to be expressed as an increase in time of death after exposure. Some individuals have lived while existing in infected areas for over 15 years. Although offering room for optimism, a fully resistant genotype has not yet been found. Resistant genotypes could be used to restore areas that once had healthy POC populations and aid the commercial production of POC timber. Of course, this would not provide ecological benefits for many years to come in areas where *P. lateralis* has decimated stands with centuries-old trees.

CONCLUSION

Although POC is in no danger of becoming extinct, its important ecological roles are certainly threatened. In infected areas, the loss of many of the larger, older trees due to *P. lateralis* infection has dramatically changed forest composition. In riparian areas, wetlands, and on ultramafic soils, its role appears to be unique and the effects of its loss poorly understood.

Fortunately, we already know enough about POC and *Phytophthora lateralis* to slow the spread of the root rot. There appears to be consensus among all groups that permanent road closures and a moratorium on new road construction are the most effective measures for excluding *P. lateralis*. That *P. lateralis* is spread primarily by way of the road system, then, should offer optimism to anyone working to conserve POC. Nonetheless, that optimism is met by stark reality—new infections along roads occur every year and the disease continues to spread across the cedar's range. Increased attention and more difficult decisions are needed from land managers and the public if POC is to retain its importance in our region's flora.

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