Modernizing a Garden Classic

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Cultivated evergreen rhododendrons are in need of a makeover. Since the mid-20th century they have been broadly popular in the United States and a mainstay of garden landscapes, but this exalted position is eroding. Rhododendrons have lost some of their luster in the marketplace. Recently, I listened to a trade conference talk on recommended woody plants given by a nursery owner in Lake County, Ohio (my locale), and rhododendrons were not mentioned.

What's going on? The main problem is a static inventory. The same cultivars that helped popularize rhododendrons decades ago—the so-called 'ironclads' with white, rose, or purple flowers—continue to make up the bulk of commerce today. Newer introductions with better flower colors and foliage, such as the cold-hardy varieties developed by David Leach and breeders in Finland and Germany, are sold to a much smaller specialty market comprised of knowledgeable and discerning gardeners with the skills to grow them. Rhododendrons are finicky plants to grow under less-than-ideal (most) conditions and this is where the "old-timer" hybrids developed over a century ago outperform the newer breeds. Their vigor and adaptability to a wide range of conditions results in more success for homeowners and fewer replacements by landscapers.

These are the main considerations guiding my breeding work at the David G. Leach Research Station. My goal is to increase the popular appeal of new introductions by adding disease resistance and heat tolerance to them, traits that can improve their performance under challenging conditions and broaden their marketability to include the deep South (USDA hardiness zone 8), regions where rhododendrons currently have a limited presence. These traits are not independent. My working hypothesis is that evergreen rhododendrons do not grow well in warmer regions because they are more susceptible to a soil disease under those conditions, not because of direct temperature stress on plants. If I am correct, breeding for disease resistance should confer greater adaptability to southern climates.

A Pervasive and Persistent Pathogen

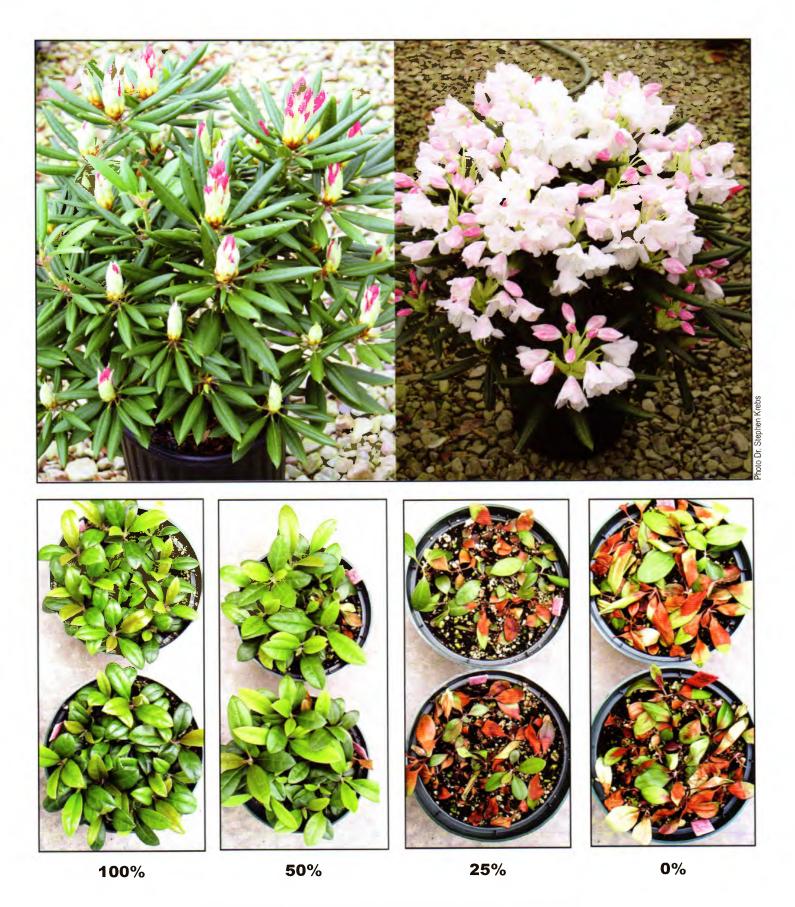
The disease problem I'm working on is called rhodo-dendron root rot, caused primarily by the soil fungus *Phytophthora cinnamomi* (Figure 1), an invasive pathogen that affects more than 1,000 plant species globally. Root rot is the most common cause of rhododendron mortality in commercial nurseries and home landscapes. The pathogen enters the root system of susceptible host plants and destroys cells during its acquisition of carbohydrate nutrients, including the root vascular (water-conducting) structures. By the time above-ground wilting symptoms are observed, the plant is nearly dead.

A majority of evergreen rhododendrons are susceptible to the disease, but can be grown in infested soils if they are well-drained. This is a disease avoidance strategy, because free groundwater facilitates infection by 'swimming' fungal spores. Adding composted pine bark to the soil mix improves performance by increasing porosity and actively suppressing the disease. These cultural techniques are used, for example, in Holden's Helen S. Layer Rhododendron Garden for growing plants on heavy soils with a high water table. Soil drenches with fungicides can also provide a prophylactic protection against the disease, and are used in container production nurseries, but this approach is neither effective nor advisable in home gardens.

None of these strategies is fail-safe, and rhododendrons would benefit greatly from an additional layer of defense. This could be achieved by adding genetically-conferred resistance to *P. cinnamomi* to cultivated rhododendrons. Should the cultural methods of disease control fail, the host plant would then have genes and physiological mechanisms

▼ Figure 1—Typical field wilting symptoms due to root rot disease (right). A chlamydospore of *P. cinnamomi* that is capable of long-term survival in soils (left). It germinates and eventually releases zoospores that "swim" toward and infect roots.





▲ Figure 2—Vegetative and flowering forms of *R. hyperythrum* (top). Seedlings with different levels (%) of *R. hyperythrum* in their genetic constitution vary in root rot resistance (bottom). At the 50% level (a resistant x susceptible F₁ cross) the progeny are nearly as resistant as 100% *R. hyperythrum* seedlings two months after inoculation. In this example, *R. hyperythrum* was crossed with the susceptible cultivar *R.* 'Calsap'.

for minimizing fungal damage to its root system. Transfer of host resistance genes can be achieved by finding a good source of resistance (rhododendron species or cultivar) and breeding it by cross-pollination to non-resistant plants that are ornamentally superior. Success in this venture requires a controlled and reliable method of screening plants for resistance, a bit of luck in finding rare, high-level resistance, and time to grow out generations of rhododendrons from seed to flower.

A Species for the Future

In the search for resistance, a genetically diverse group of about 350 evergreen rhododendron cultivars and species have been screened by hand-inoculating greenhouse-grown plants with *P. cinnamomi*. Much of this groundwork was done in the 1970s by researchers at Ohio State University, and we completed a screen of more contemporary cultivars at Holden in 2002. Fewer than five percent of these plants proved to be resistant, and an even smaller number were both resistant and cold-hardy, another key requirement for our breeding program.

These disease screens provided important information about the nature of resistance. The responses of different cultivars and species to inoculation were not discrete, either resistant or susceptible, but continuous, ranging in increasing severity from genotypes with healthy roots, fine root damage, necrosis of coarse roots, crown rot, or complete plant death. These varying levels of resistance among test plants are an indication that the resistance genes do not confer complete immunity to the disease, and that resistance is controlled by multiple rather than single genes. Also called 'partial' resistance, it is often adequate for field-level plant protection, and has an advantage over single-gene 'complete' resistance in being more durable, harder to overcome by any genetic changes in pathogen virulence.

Our initial decision was to use resistant cultivars rather than species for breeding, since they had already been selected for ornamental value and had more color than the available resistant species—all white-flowered. However, this approach turned out to be mostly a dead end, since many of the hybrid cultivars were either sterile or had poor breeding value—although they were themselves resistant, they were not able to transmit this trait effectively to their progeny.

In 2004, our attention shifted to a somewhat obscure species from Taiwan, *R. hyperythrum* (Figure 2). Because it grows at a high elevation, it is also reasonably cold hardy (flower bud hardy to USDA zone 6). This species is resistant to root rot and was being used by hobby nurseryman John Thornton, D.V.M., to hybridize rhododendrons for his zone 8 location in southern Louisiana. It was during a visit to his nursery, after seeing vigorous *R. hyperythrum* hybrids growing in red clay soil under a hot sun, that the connection between root rot resistance and high temperature tolerance became evident to me. John gave me some of his hybrids. I acquired *R. hyperythrum* accessions from the Rhododéndron Species Botanical Garden, and began making crosses with them on a large scale.





▲ Figure 3—Examples of selections from F₁ hybrids between cold-hardy rhododendron cultivars and R. hyperythrum.







Promising Results

Breeding involves reshuffling parental traits via genetic recombination, with the goal of creating a hybrid which combines the best features of both parents and none of their shortcomings. In addition to root rot resistance, R. hyperythrum has many ornamental attributes—excellent foliage, a dense, mounded habit, and a very floriferous nature. It transmits these traits readily to progeny, and tests of its breeding value for resistance in greenhouse experiments suggest that first generation (F₁) hybrids between R. hyperythrum and non-resistant throwing out most of what he grows. His e-mail address is cultivars will have high level, if not full, resistance (Figure 2). skrebs@holdenarb.org.

What R. hyperythrum lacks for commercial purposes and is provided by careful selection of the other parent in a cross—is flower color, USDA zone 5 cold hardiness (our northern Ohio winter climate), and a compact 'truss' or inflorescence that is the preferred commercial standard. There are plenty of rhododendrons that meet these criteria at the Leach Research Station and in the Helen S. Layer Rhododendron Garden at Holden, and we have crossed them with R. hyperythrum in flower color groups of pink, red, yellow, purple and white.

In spring 2009 and 2010, 40 of these F₁ crosses totaling 2,500 progeny bloomed in the field at Madison, Ohio. While 2010 was a mild winter, plants in winter 2009 were subjected to deep frosts of -10° to -13°F (-23° to -25°C). Selections were made for individuals combining cold hardiness with ornamental value. On hand to assist with evaluation were representatives of two commercial enterprises interested in our plants-Briggs Nursery Inc. in Washington State, and Plant Development Services Inc. (PDSI) in Loxley, Alabama. More than two dozen high quality plants were identified (Figure 3), and the top six of these were chosen for tissue culture propagation at Briggs and subsequent evaluation at multiple sites ranging from hardiness zones 5 to 8. PDSI will trial the propagated plants under their production and field conditions, and good performers will be entered into their Southern Living Plant CollectionTM.

Within four years, the first wave of these "modernized" rhododendrons may be available to the nursery trade. During the interim, more selections will be made from the F₁plants and second-generation F₂ populations will be created to identify plants that have higher resistance and more flower color saturation than the F₁s. I think of this as an R&D pipeline for "Leach Plus" plants, because we're adding landscape value to the fine cultivars Leach created. This doesn't mean we've abandoned the "Leach Classics"—we will continue to select, evaluate, and introduce fancy, new plants for the specialty market. The real prize, however, will be improved rhododendrons that are easier to grow; have a broader, including Southern, market; and are better positioned for a future of climate change due to a disease resistance that confers increased adaptation to warmer growing conditions.

Stephen Krebs received a doctorate degree in plant breeding and genetics from Michigan State University. He has worked on trait improvements in various crop plants such as celery (disease resistance), blueberry (fruit size and quality), and meadowfoam, a wildflower valued for its seed oil. The switch to ornamental plants started in 1992, when he joined The Holden Arboretum to work with Dr. David G. Leach on rhododendron and azalea breeding. In addition to the core emphasis on cold-hardiness, the selection criteria have been expanded to include disease resistance (to root rot in rhododendron and powdery mildew in azaleas), vigor under openfield (high light) conditions, and heat tolerance, all combined in plants with attractive foliage and flowers. That means