Stuck Between a Squirrel and a Hot Place

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Lodgepole pine (*Pinus contorta*) is an impressive plant. I say this in spite of the fact that lodgepole forests are among our least diverse plant communities and provide a less than emotionally moving backcountry experience. The trees are most often small and grow close together, resulting in “doghair” stands. These are surpassed in their impenetrable nature only by stands that have self-thinned leaving two-thirds of the poles stacked at all angles. As the Lewis and Clark diaries attest, these forests are generally not welcoming and majestic. What is impressive is the fact that lodgepole has one of the largest ranges of any tree in North America, dominating more than 50 million acres (50 times bigger than Glacier National Park), from the Yukon south to Mexico and from the Pacific Ocean to South Dakota and Colorado. Three common geographic races are recognized in this large geographic range: var. *contorta*, the shore pine, occurs in sandy soil along the coast; var. *murrayana*, Sierra lodgepole, is found in California’s Sierra Nevada Range; and var. *latifolia*, the Rocky Mountain lodgepole, with the largest distribution, is centered in the Rocky Mountains. How does such a scrawny little tree with a spindly crown come to be so abundant?

Several traits contribute to lodgepole pine’s dominance across western North America. Lodgepole pine grows well in infertile soils. It tends to be most abundant in coarse, sandy soils such as those found along the coast or those derived from sterile granite such as in the Sierra Nevada or Idaho Batholith of the Bitterroot Range. Other trees, such as Douglas-fir, gain a competitive advantage in more fertile soils. Lodgepole pine also grows fast. For that reason it has been planted extensively in Scandinavian countries, the British Isles, and New Zealand; over one million acres have been planted in Sweden alone. Probably the single most important reason lodgepole is so abundant is its ability to colonize after fire. It germinates explosively following fire, forming the dense, even-age stands we are so familiar with. Lodgepole accomplishes this feat thanks to a trait unique among western pines: serotiny.

Serotiny refers to the production of cones that remain sealed shut by resin until opened by extreme heat, usually by fire. Trees without serotinous cones must recruit seed from outside the burned area, but trees with serotinous cones have a source on site and ready to go. Lodgepole pine trees in the Rocky Mountains can be either serotinous or non-serotinous. Both kinds have open cones when young, but after 50-70 years serotinous trees begin to produce closed cones, while non-serotinous trees never do. Producing open cones early in life may allow lodgepole trees to produce seed that can disperse to areas that remained uncolonized immediately after the fire. To be effective, this open-cone period must end and serotinous cones come on-line before the next fire. So the 50- to 70-year open-cone period usually corresponds to the average time between fires.

Although individual trees are either serotinous or not, nearly all stands of Rocky Mountain lodgepole are composed of a mixture of the two types (unexplainably, Sierra Nevada var. *murrayana* does not have serotiny). Why? Studies in Yellowstone National Park and Montana's Bitterroot Range suggest that lodgepole stands with a higher proportion of serotinous trees experience more frequent fires because of climate or topography, or those stands were initiated by a fire. Stands exposed to other types of disturbance, such as wind throw or insects, had higher proportions of open-cone trees. The existence of both types of trees in most stands suggests that most stands experience variability in disturbance types. But this expectation is at odds with the fact that fire is the dominant disturbance throughout most of the Rocky Mountains. Does some other factor bear on the proportion of serotinous trees in the Rockies? Researchers from New Mexico came to Montana to answer that question.

Red squirrels are the predominant cone predator and occur throughout the range of lodgepole pine. Craig Benkman knew that red squirrels feed on serotinous cones as well as open cones. When squirrel predation is high, serotinous cones never get a chance to shed their seeds, but some open cones disperse seeds before they are taken by squirrels. Serotinous trees can be at a disadvantage with squirrels around. Benkman wondered whether squirrel predation might be responsible for maintaining the presence of open-cone lodgepole trees even when fire dominates the disturbance regime. If this were true Benkman reasoned, then lodgepole stands in areas where squirrels don't occur should have fewer open-cone trees than stands where they do. It turns out that there are a handful of isolated mountain ranges where there are lodgepole pines but red squirrels have not been present since before the last ice age. These include the South Hills of Idaho, the Cypress Hills of Alberta, and the Sweetgrass Hills, Little Rocky Mountains, and Bear's Paw Mountains in north-central Montana. Benkman found that these squirrel-free lodgepole pine stands all had more than 85% serotinous trees. On the other hand, Jim Lotan, from the Forestry Science Lab in Missoula, reported that 341 different stands with pine squirrels all had less than 85% serotiny, with the average around 34%. These researchers showed that it was not just the frequency of crown fires but also the occurrence of squirrel predation that determined the frequency of serotinous and open-cone trees in Rocky Mountain lodgepole pine forests. You can think about all of this and maybe count serotinous trees next time you're bored to tears hiking through a lodgepole forest.

Further reading:

Muir, P. S. and J. E. Lotan. 1985. Disturbance history and serotiny of Pinus contorta in western Montana. Ecology 66: 1658-1668.

Benkman, C. W. and A. M. Siepielski. 2004. A keystone selective agent? Pine squirrels and the frequency of serotiny in lodgepole pine. Ecology 85: 2082-2087.