

Seed Dispersal in Limber and Southwestern White Pine: Comparing Core and Peripheral Populations

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Introduction

According to the geographic mosaic theory of coevolution (Thompson 2005), the potential for coevolutionary relationships between interacting species varies with the presence of other species within a community. This implies that the strength of coevolution between two species may vary geographically. In this study, we ask whether there is a shift in vertebrate seed dispersers between core range and peripheral populations in two related five-needle white pines, limber (*Pinus flexilis*) and southwestern white (*P. strobiformis*). In the Rocky Mountains, limber pine ranges from southern British Columbia and Alberta south to New Mexico. Southwestern white pine ranges through the higher mountains of northern Mexico north to southern Colorado and Utah, and northern Arizona. The pines overlap in southern Colorado, southern Utah, northern New Mexico, and northern Arizona (Fig. 2a in Tomback and Achuff 2010).

The seeds of both limber and southwestern white pine are essentially wingless, lacking all or most of the thin, woody seed wing that enables dispersal by wind for species in Family Pinaceae. The seeds are also moderately large to large: the average masses of limber and southwestern white pine seeds are 0.093 mg and 0.168 mg, respectively (Tomback and Linhart 1990). The syndrome of large, wingless seeds typically corresponds to seed dissemination by vertebrates—either birds of the family Corvidae or rodents (Tomback and Achuff 2010).

Limber Pine in a Peripheral Population

Throughout the core range of limber pine, Clark's nutcracker (*Nucifraga columbiana*) is the primary seed disperser, influencing growth form and population structure (Lanner and Vander Wall 1980; Schuster and others 1989; Carsey and Tomback 1994). On the eastern plains in northern Colorado and southern Wyoming, limber pine forms isolated, peripheral populations on rocky escarpments, 100 km east of the core Rocky Mountain populations. We (DFT, AWS) studied limber pine seed dispersal at Dave's Draw, Pawnee National Grasslands, Colorado, between 1600 and 1690 m elevation (Tomback and others 2005). Nutcrackers are rare visitors to this region, and none were observed by researchers over several years. Previous studies indicated that the limber pine population at Dave's Draw is highly genetically

substructured, unlike limber pine within core populations, suggesting differences in seed dispersal distances despite long-distance pollen flow (Schuster and Mitton 2000). We hypothesized that seed-caching rodents were the primary seed dispersers at Dave's Draw. Chipmunks and squirrels, however, are absent in this region, so nocturnal rodents were the candidate dispersers.

Methods

Research methods included fluorescent pigment tracking of seed dispersers for 6 nights to determine dispersal distances, cache type, and cache location. This entailed setting out 1 to 4 seed stations each night, each station comprising a glass dish containing limber pine seeds on a sandpaper tray. Both the seeds and sandpaper were covered with a different fluorescent pigment color at each seed station, and seed stations were placed under limber pine canopies, 30 to 40 m apart. Each night beginning at 03:00, we used a powerful UV light to follow the fluorescent tracks created by small mammals after they had removed seeds from seed stations, dispersed, and cached them. Small mammal trapping was also conducted for 3 nights, using 106 Sherman traps in two traplines to determine the identity of potential seed cachers. Furthermore, we constructed an experiment using replicated simulated seed caches based on observed rodent cache types in order to test for seed germination. We had observed rodents store two-seed caches on substrate surfaces, and bury larger numbers of seeds under plants and soil. Each replicate of simulated seed caches consisted of 5 five-seed caches buried under plants and 5 two-seed caches placed on the soil surface, for a total of 5 replicates; and three additional replicates of 5 two-seed caches placed on duff and protected by hardware cloth. Simulated caches were examined for germination during the following summer.

Results

The results are summarized from Tomback and others (2005). Using fluorescent pigment tracking, we found a total of 36 seed caches: 20 buried, with a mean of 4.4 seeds per cache, dispersed a mean of 8.2 m from a seed station; and 16 surface caches, with a mean of 1.6 seeds, dispersed a mean of 5.5 m from a seed station. We left caches in place and revisited them over several weeks. Our traplines caught 73 animals consisting mostly of deer mice, but also western

harvest mice (which do not store seeds), and Ord's kangaroo rats. Simulated caches buried under plants and soil had higher germination success than caches on the soil or litter surface.

Conclusions

These results indicated that nocturnal rodents, especially deer mice and kangaroo rats, may be the major dispersers of limber pine seeds in the Dave's Draw population, and potentially in other peripheral populations (Tomback and others 2005). Repeated visits to natural caches revealed that not all seeds were removed over time, and thus seeds could potentially germinate. Rodents moved seeds relatively short distances from seed stations to cache sites, thus potentially creating much greater population substructure than observed for core populations.

Southwestern White Pine in Core and Peripheral Populations

We (DFT, SS, EP) studied southwestern white pine seed dispersal within a peripheral population, the San Juan Mountains, Colorado, and within a core population, the Chiricahua Mountains, Arizona (Samano and Tomback 2003; Pruett 2007; Tomback and Samano, unpublished data). The latter population is part of the "sky island" forests of southwest desert ranges, which are typical habitat of southwestern white pine. We asked whether there were differences in seed dispersers or seed predators between the two populations. We also looked for differences in cones and seeds that might correspond to differences in seed dispersers and seed predators.

Methods

In both study areas during September, we monitored cone opening phenology and quantified differences in cone orientation on tree branches. We identified potential diurnal seed dispersers and seed predators by observing diurnal birds and mammals foraging for seeds; we used fluorescent pigment tracking in both study areas during good cone years to determine if nocturnal rodents were dispersing seeds, and if so, how far seeds were dispersed and where they were cached. In the Chiricahua Mountains, we set up two traplines consisting of 100 Sherman traps for three nights in order to identify potential nocturnal seed cachers.

Results

Cone opening among southwestern white pine in the San Juan Mountains occurred from late August through late September, and in the Chiricahua Mountains from early September through early October (Samano and Tomback 2003; Pruett 2007). Cone opening in both areas

was asynchronous both within and among trees, a trait associated with seed dispersal by vertebrates. In the San Juan Mountains in September, we routinely observed nutcrackers disperse southwestern white pine seeds, but never observed nutcrackers in the Chiricahuas: their dependable range ended farther north. Nocturnal rodents were not attracted to our seed stations in the San Juan Mountains, but we documented rodents making 28 caches over 6 nights of fluorescent pigment tracking in the Chiricahua Mountains (Pruett 2007). The 11 buried caches contained a mean of 2.5 seeds per cache and were on average 8.7 m from a seed station; and, the 17 surface caches contained a mean of 1.7 seeds and were on average 7.2 m from a seed station. Only deer mice were trapped in the Chiricahua Mountains. The red squirrels in the San Juan Mountains were highly efficient seed predators that cut down cones for winter stores; the Chiricahua fox squirrels were less efficient at pine seed removal and did not store cones (Samano and Tomback 2003; Tomback and Samano, unpublished data).

Southwestern white pine differed morphologically between the two study areas: the cones on southwestern white pine in the San Juan Mountains were most frequently horizontally-directed, whereas the cones in the Chiricahua Mountains were most frequently pendulous, a morphology avoided by nutcrackers in the San Juan Mountains (Samano and Tomback 2003; Pruett 2007). Seed dimensions (length, width, and depth) and mass from the Chiricahua Mountains were significantly greater than those of seeds from the San Juan Mountains. In fact, seed dimensions taken from the Santa Catalina and Huachuca Mountains, neighboring ranges to the Chiricahua Mountains, had similarly larger seed dimensions (Tomback and Samano, unpublished data).

Conclusions

Primary seed dispersers differed between core and peripheral populations of southwestern white pine, with Clark's nutcrackers dispersing seeds in the San Juan Mountains, and nocturnal rodents dispersing seeds in the Chiricahua Mountains. Seed predators, cone orientation, and seed morphology also differed between these populations. The predominantly horizontal cone orientation in the San Juan Mountains was also the orientation preferred by Clark's nutcrackers.

Questions raised by our results: Are the morphological differences between southwestern white pine in the San Juan Mountains (peripheral population) compared to the Chiricahua Mountains (core range) the result of selection by nutcrackers or by red squirrels, or both? Or, alternatively, could morphological differences result from gene flow from limber pine to southwestern white pine in the San Juan Mountains (an area of overlap), reducing seed size and altering cone orientation? Are nocturnal rodents the primary seed dispersers for southwestern white pine throughout its core range?

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