

Dispersal of Limber Pine Seed By Clark's Nutcracker

A12

Ronald M. Lanner and Stephen B. Vander Wall

Reprinted from the JOURNAL OF FORESTRY
Vol. 78, No. 10, October, 1980

ABSTRACT—A 90+ year-old burn in the Raft River Mountains, Utah, is being restocked with limber pine (*Pinus flexilis* James) and other conifers. Limber pine's large wingless seeds are incapable of wind dispersal, and are being brought to the burn area by Clark's nutcracker, a bird that stores them in the soil for food. Unretrieved seeds germinate, often in clumps, and are reestablishing limber pine on this site. In some years nearly the entire seed crop may be harvested by nutcrackers. No other reliable dispersal agent of limber pine seed has been identified.

Most members of the Pinaceae have small winged seeds that are easily dispersed by wind. But a number of species, especially in the subgenus *Strobus*, the soft pines, have large wingless seeds. For two such pines of western North America, pinyon (*Pinus edulis* Engelm.) and whitebark pine (*P. albicaulis* Engelm.), recent research has shown that seeds are dispersed and buried in the soil by birds of the family Corvidae. Thus pinyon seeds are largely dispersed by the pinyon jay, *Gymnorhinus cyanocephalus* (Balda and Bateman 1971, Ligon 1978) and Clark's nutcracker, *Nucifraga columbiana* (fig. 1) (Vander Wall and Balda 1977); and whitebark pine seeds by Clark's nutcracker (Tomback 1978). Turcek and Kelso (1968) have summarized the voluminous literature dealing with similar corvid-pine interactions in Europe and Asia.

Limber pine is another western North American soft pine with wingless seeds. Its range (Critchfield and Little 1966) lies entirely within the breeding range of Clark's nutcracker (American Ornithologists' Union 1957). Vander Wall and Balda (1977), working in northern Arizona, reported the harvesting of limber pine seeds by Clark's nutcracker, and subsequent storing of those seeds in the soil. Since then we have made extensive observations on the harvesting and storing of limber pine seeds by nutcrackers in northern Utah and western Wyoming. This article documents the restocking of a burn, in part by limber pines established from seeds carried by nutcrackers.

The study was conducted in the Raft River Mountains (Sawtooth National Forest) of northwestern Utah, on the upper slope (2,500-2,550 m elev.) of a burned-over north-facing ridge overlooking Clear Creek (fig. 2). This windswept ridge is frequently used by nutcrackers as a seed storage area. The substrate is a highly metamorphosed micaceous schist forming occasional prominent outcrops on the ridgetop and a loose pavement of fragments on the upper slope.

Methods

A square sample plot of 0.64 hectare was established within the burn. The species and height class of all living trees were recorded. Increment cores were

taken from the largest trees of each species. The species of fire-killed snags and fallen trees were determined and diameters (at b.h.) of the largest individuals of each species were measured. During the autumns of 1977-1979 nutcracker activity was monitored for a total of 500 hours. Cone counts were made weekly during the late summer and fall on all cone-bearing limber pines on or adjacent to the sample plot.

Original and Present Stands

No later than 1886 an intense fire burned through a mixed conifer forest then occupying most of the study

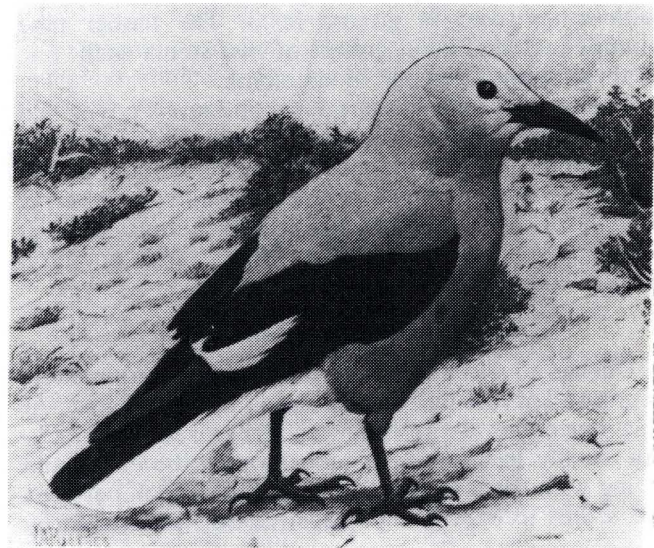


Figure 1. Clark's nutcracker (drawing by Louis Agassiz Fuertes).



Figure 2. A view in the sample plot. The standing snags are limber pines. The saplings in the center and extreme right are Douglas-firs; the others are limber pines.

area, including the sample plot. The forest consisted of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), and limber pine. Trees of these species had attained diameters of at least 50, 10, and 41 cm, respectively. The numerous snags and deposits of partially decayed fallen timber suggest a well-stocked stand. Lack of surviving fire-scarred trees around or within the study area prevented exact dating of the fire, but the oldest ring in the oldest tree of the new stand formed in 1886.

Since the fire, 436 trees have become established on the sample plot (681 stems per hectare). The present species composition (table 1) indicates that the new stand will eventually resemble the original one. Maximum tree ages are Douglas-fir, 93 years; subalpine fir, 68 years; and limber pine, 83 years. Clones of quaking aspen (*Populus tremuloides* Michx.) are found within 1 km of the sample plot, but this species has not been a pioneer on the burn. In addition to the trees listed in table 1, there were two seedlings of singleleaf pinyon, *P. monophylla* Torr. & Frém., on the sample plot.

All of the Douglas-firs and subalpine firs were single stemmed, but limber pines were often clumped. Thus 25 of the 109 limber pines (23 percent) were in contact with other trees at ground level. The limber pine clumps included eight groups of two stems each, one of three stems, and one of six stems.

The trees form a scattered discontinuous cover that is supplemented by a sparse to dense cover of herbs and shrubs. Among the more common woody shrubs are wild currant, *Ribes cereum* Dougl.; snowberry, *Symphoricarpos oreophilus* Gray; buffaloberry, *Shepherdia canadensis* (L.) Nutt.; and common juniper, *Juniperus communis* L.

Activities of Clark's Nutcracker

During all three years of observation, nutcrackers began to harvest limber pine seeds late in August. At this time cones are green and tightly closed. Nutcrackers usually harvest seeds by removing the cones and flying with them to perches where they peck between the scales to expose the seeds. Cones foraged on by

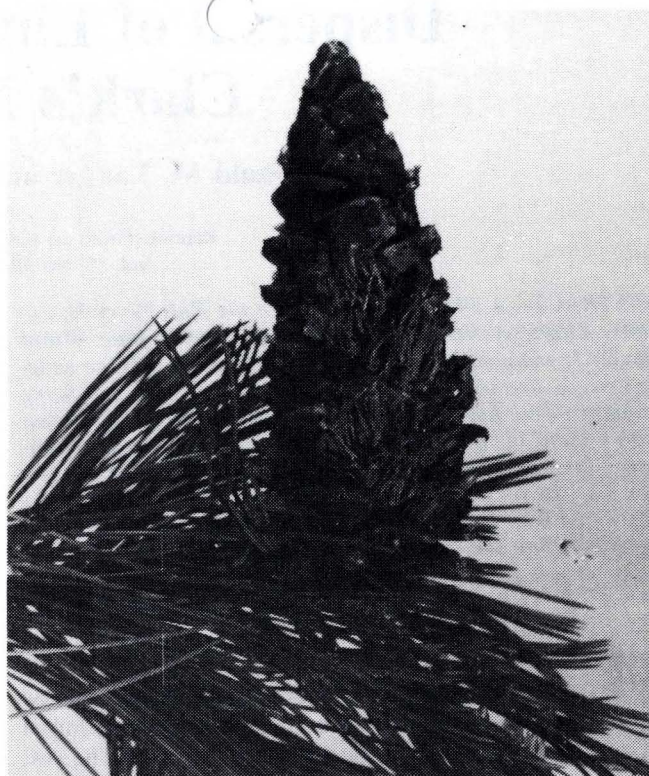


Figure 3. A limber pine cone that has been foraged on by Clark's nutcracker. Note the frayed appearance.

nutcrackers have a characteristic frayed appearance (fig. 3). The seeds are removed undamaged, and temporarily held in the nutcracker's sublingual pouch. This structure, located in the floor of the mouth, is capable of holding about 20 ml (Vander Wall and Balda 1977), a volume equivalent to about 125 limber pine seeds.

The bird then flies to a cache area where it makes numerous caches, usually containing 1-5 seeds each ($\bar{x} = 4.2 \pm 3.1$, $n = 52$), at a depth of 2-3 cm (Vander Wall, unpublished). These seeds are a major food source for both adult nutcrackers and their nestlings.

To determine the number of seeds cached by nutcrackers, we collected data on the number of caching birds observed per hour, number of seeds carried per bird, and length of the caching season. From these data we estimated that during the fall of 1979 about 30,000 seeds per hectare were cached in and adjacent to the sample plot. These seeds came from trees growing on the plot as well as from limber pines 1 km or more distant. Singleleaf pinyon seeds were brought from a dense woodland about 3 km away.

In 1979, a year of moderate cone production, 70 trees within or near the sample plot were monitored. Nutcrackers removed 90.5 percent of the 1,461 cones before they began to open. Of the remainder, 2.5 percent were destroyed by *Conophthorus* cone beetles. As the remaining 7.0 percent began to open on the trees, nutcrackers were immediately attracted and harvested the exposed seeds until the crop was depleted. Less detailed observations in 1978 indicated that, even in a bumper crop year, between 70 and 90 percent of the limber pine seeds were removed by nutcrackers.

The nutcrackers were the only seed harvesters active during this study. Red squirrels (*Tamiasciurus hudsonicus*), which commonly cut cones and eat the

Table 1. Height-class distribution of conifers on a 0.64 ha plot within a burned area in the Raft River Mountains, Utah.

Tree height class (m)	Limber pine	Subalpine fir	Douglas-fir
	Trees		
0-1	52	61	134
1-2	8	7	18
2-3	13	4	21
3-4	8	3	12
4-5	9	5	13
5-6	12	2	9
6-7	4	7	5
7-8	2	8	1
8-9	1	9	3
9-10	0	1	0
10-11	0	1	0
11-12	0	1	0
12-13	0	2	0
Total	109	111	216

seeds, were absent from the study area. Uinta chipmunks (*Eutamias umbrinus*) and golden-mantled ground squirrels (*Spermophilus lateralis*) were frequently seen, but were never observed cutting or carrying cones.

Discussion

Clark's nutcracker has played a major part in the reforestation of this burn. Two of the pioneering tree species, Douglas-fir and subalpine fir, have small, winged seeds easily carried by wind. The seeds restocking this burn probably came from scattered trees of those species within 0.5 km downslope or about 1 km to the west. But the heavy wingless seeds of limber pine were transported to the site and cached by nutcrackers. Initially, limber pine seeds were probably brought to the site from trees that were growing several kilometers away and were unaffected by the fire. As some of these seeds germinated and grew to trees of cone-bearing size, nutcrackers started to harvest and cache seeds of these trees as well. The heavy wingless seeds of singleleaf pinyon were also undoubtedly brought by nutcrackers from a woodland about 3 km away. Many nutcracker flights from this woodland were observed.

The long distance over which nutcrackers transport seeds greatly increases their effectiveness as dispersal agents. Vander Wall and Balda (1977) reported nutcrackers transporting pinyon seed up to 22 km in northern Arizona. Tomback (1978) observed nutcrackers transporting whitebark pine seeds up to 12.5 km in the Sierra Nevada. These capabilities make Clark's nutcracker an effective disseminator of conifer seeds on extensive burns as well as from peak to peak in mountainous areas.

The size-class distributions of all three tree species are heavily skewed towards the smallest class (table 1). The percentage of each species in that class is limber pine, 48; subalpine fir, 55; and Douglas-fir, 62. These size-class patterns are characteristic of invading species (Mueller-Dombois and Ellenberg 1974).

The high frequency of stem clumping in limber pine is due to the germination of more than one seed of a cache. Woodmansee (1977) described in some detail clumping of limber pine in Colorado, though he was unsure of its cause. Observations of mature limber pines in northeastern Utah show about two-thirds are members of multiple-stem clumps, and among whitebark pines in western Wyoming nearly half the trees were in clumps (Lanner, unpublished). Observations of clump frequency in trees beyond the seedling stage must be made with caution, because multiple stems may also arise from a tree damaged near the ground.

The disparity between the large number of seeds cached on the sample plot and the modest number of limber pines growing there is the result of four factors: rate of seed retrieval by nutcrackers, cache robbing by other animals, germination rate of surplus seeds, and survival rate of germinants. Our data do not measure the comparative significance of these factors.

Nutcrackers should not be considered strictly as seed predators, as are other seed harvesters like red squirrels (Finley 1969, Smith 1970). When squirrels stockpile cones in middens the seeds become unavailable for tree regeneration. Nutcrackers, however, re-

move seeds from cones and place them in the soil at a depth suitable for germination. It appears that having its seeds cached by nutcrackers is the most reliable means of regeneration for limber pine.

Importance to Forest Managers

Our findings are of some significance to forest managers in the Rocky Mountains. Although limber pine is not an economically important timber species, it does have other values. Its ability to grow on severe sites where other trees are absent helps protect watersheds by reducing erosion. It is relatively resistant to avalanches (Perla and Martinelli 1976), and, by forming stands on certain slopes, may reduce avalanche hazards. Limber pine is also an esthetically pleasing tree that adds variety to the subalpine landscape, and its seeds provide food for several bird and mammal species.

The importance of vertebrates in the dispersal of forest tree seed has become increasingly evident in recent years, both in tropical and temperate ecosystems. Some of the important temperate genera that depend on vertebrate seed dispersers are *Juglans* (Stapanian and Smith 1978), *Juniperus* (Salomonson 1978), *Quercus* (Bossema 1979), and *Prunus* (Thompson and Willson 1978). Foresters managing ecosystems containing these genera, and species of wingless-seeded pines, need to understand the relationship between regeneration of the trees and presence of the necessary animal dispersers. ■

Literature Cited

- AMERICAN ORNITHOLOGISTS' UNION. 1957. Check-list of North American Birds. Ed. 5., Baltimore, Md.
- BALDA, R. P., and G. C. BAILEMAN. 1971. Flocking and annual cycle of the piñon jay, *Gymnorhinus cyanocephalus*. Condor 73:287-302.
- BOSSEMA, I. 1979. Jays and oaks: an eco-ethological study of a symbiosis. Behaviour 70:1-117.
- CRITCHFIELD, W. B., and E. L. LITTLE, JR. 1966. Geographic distribution of the pines of the world. USDA Misc. Publ. 991.
- FINLEY, R. B., JR. 1969. Cone caches and middens of *Tamiasciurus* in the Rocky Mountain region. Contrib. in Mammal., Univ. Kansas Mus. Nat. Hist. Misc. Publ. 51:233-273.
- LIGON, J. D. 1978. Reproductive interdependence of piñon jays and piñon pines. Ecol. Monogr. 48:111-126.
- MUELLER-DOMBOIS, D., and H. ELLENBERG. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York. 547 p.
- PERLA, R. L., and M. MARTINELLI, JR. 1976. Avalanche Handbook. USDA Agric. Handb. 489, 238 p.
- SALOMONSON, M. G. 1978. Adaptations for animal dispersal of one-seed juniper seeds. Oecologia 32:333-339.
- SMITH, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecol. Monogr. 40:349-371.
- STAPANIAN, M. A., and C. C. SMITH. 1978. A model for seed scatterhoarding: coevolution of fox squirrels and black walnuts. Ecology 59:884-896.
- THOMPSON, J. N., and M. F. WILLSON. 1978. Disturbance and the dispersal of fleshy fruits. Science 200:1161-1163.
- TOMBACK, D. F. 1978. Foraging strategies of Clark's nutcracker. Living Bird 16:123-160.
- TURCEK, F. J., and L. KELSEY. 1968. Ecological aspects of food transportation and storage in the Corvidae. Commun. Behav. Biol. A. 1:277-297.
- VANDER WALL, S. B., and R. P. BALDA. 1977. Coadaptations of the Clark's nutcracker and the piñon pine for efficient seed harvest and dispersal. Ecol. Monogr. 47(1):89-111.
- WOODMANSEE, R. G. 1977. Clusters of limber pine trees: a hypothesis of plant-animal coaction. Southwest Nat. 21:511-517.

THE AUTHORS—Ronald M. Lanner is associate professor and Stephen B. Vander Wall is a postdoctoral associate in the Department of Forestry and Outdoor Recreation, Utah State University, Logan. Harry Hutchins and Susan Nelson assisted in data collection. The work was partially supported by grant DEB-78-02802 to the senior author from the National Science Foundation.