Life History and Biology

Western Juniper Varieties

Morphology of western juniper

Western juniper is submonoecious[9]. Trees are pyramidal to round in shape and typically reach 13–32 ft in height at maturity, but will occasionally reach 65 ft in height. Trunks are usually composed of a single erect stem 13.7–27.6 inches in diameter (maximum of 74.8 inches) (Vasek 1966, Cronquist et al. 1972). The largest reported western juniper, located in the Lost Forest in northern Lake County, Oregon, is 78 ft tall with a trunk circumference of 19 ft. Bark is typically gray but can turn reddish in some old trees (more than 300 years). Mature western juniper leaves are 0.039–0.118 inches in length, compressed to the stem and overlapping the next leaf (Fig. 7). Leaves occur as opposite pairs or in whorls of three. Each scale has a conspicuous resin gland on the dorsal side of the leaf (Fig. 7). In contrast, juvenile leaves are not compressed to the stem and are spiny tipped. Seed bearing can begin as early as 10–20 years of age, but significant fruit production usually starts at 50–70 years of age (Miller and Rose 1995). The yellowish-brown male cones are 0.12–0.16 inches long and occur at the end of a branchlet (Fig. 7). Male cones develop during the late summer and early fall and shed their pollen early the following spring (Vasek 1966). Female cones are bluish to bluish-black at maturity, covered with a resinous pulp, and contain two to three seeds (occasionally one seed). These cones begin development in early spring, attain full size the first summer and mature during the second summer. Female cones persist on trees for nearly 2 years. Morphological characteristics of western juniper and Utah juniper are usually distinct. Utah juniper lacks the resin gland on the back of the leaf scale and the female cones are brownish with a mealy to fibrous covering (Cronquist et al. 1972). However, in northwestern Nevada, where the distribution of the two species overlap, differences become less apparent due to hybridization (Vasek 1966, Terry et al. 2000).

Figure 7. Western juniper male cones and foliage showing white dried resin exuded from the resin gland located on the dorsal side of the leaf scale.

Morphology of Sierra juniper

Sierra juniper, a variety of western juniper, is located primarily south and southeast of the range of western juniper. Sierra juniper is distinguished from western juniper in that it is mostly dioecious[10], has reddish-brown bark rather than gray bark (Cronquist et al. 1972), can attain a larger size at maturity, and grows in different plant associations, higher elevations, and different climatic conditions. However, the bark on older western juniper trees also often attains a reddish color. Charlet (1996) reported that Sierra juniper material collected in Nevada was distinct from western juniper and suggested a taxonomic reevaluation of the variety. Further, the largest recorded Sierra juniper is 83 ft tall and 40 ft in trunk circumference, located in the Stanislaus National Forest, east-central California.

Seed Production, Dissemination, Germination, and Establishment

Although seed production occurs in most years (Sowder and Mowat 1958), western juniper seed-crop production is highly variable across sites and years. The environmental variables that trigger the initiation of male and female cones have not been identified. Research on factors influencing seed production and seedling establishment will be required to predict annual seed-crop production and better understand woodland dynamics (Chambers et al. 1999b).

[9] Submonoecious—male and female cones are borne on the same individual; however, some trees will produce predominantly male or female cones.

[10] Dioecious—male and female cones are borne on different individuals.

Seed dispersal of western juniper occurs through gravity, overland flow, and by animal transport. At least 12 species of birds feed on the fruits and as a group are the most important disseminator of western juniper seed (Fig. 8) (Gabrielson and Jewett 1940, Maser and Gashwiler 1978). American robins *(Turdus migratorius)* and Townsend's solitarie *(Myadestes townsendi)* often winter in woodlands and consume the female cones (Lederer 1977, Podder and Lederer 1982, Reinkensmeyer 2000). Townsend's solitarie can consume over 80 female cones/day. Mountain bluebirds *(Sialia currucoides)*, cedar waxwings *(Bombycilla cedrorum)*, and Steller's *(Cyanocitta stelleri)* and western scrub-jays *(Aphelocoma californica)* have been observed consuming female cones. Most birds have limited gut-retention times and fly short distances to perch and process the fruit, thus limiting the distance of most seed dispersal (Schupp 1993, Chambers et al. 1999b). After feeding on Ashe juniper *(Juniperus ashei)* fruits, American robins flew an average distance of 145 ft to a post-foraging perch, which could be another tree, shrub, or on the ground beneath a woody canopy (Chavez-Rameriz and Slack 1994). In Spain, Santos and Telleria (1994) reported birds feeding on juniper berries were more likely to visit large stands of trees and less likely to feed in small isolated juniper stands. Coyotes *(Canis latrans)*, cottontail rabbits *(Sylvilagus* sp.), and several rodent species also consume and scatter western juniper seeds (Chambers et al. 1999a). Mule deer *(Odocoileus hemionus)* have also been observed to eat western juniper fruits during winter months when preferred foods are unavailable (Leckenby 1968, Trout and Thiessen 1968). However, successful establishment of seed dispersed by mammals is probably limited, because seeds are deposited at high densities in microsites where establishment is poor (Schuppe 1993; Schuppe et al. 1997; Chambers et al. 1999a, b).

Western juniper seeds are initially dormant immediately following seed drop (Johnson and Alexander 1974). Germination potential is greatly enhanced by prolonged cool-moist stratification, which is cumulative from year to year (Young et al. 1988). This suggests germination of a particular seed crop may span several years. Seeds of several other juniper species are also long lived with an extended dormancy, resulting in highly persistent seed banks (Chambers et al. 1999a, b).

Little information is available on percent seedling survival or climatic conditions that influence seedling establishment. However, two studies indicate survival rates for western juniper seedlings are high (Burkhardt and Tisdale 1976, Soulé et al. 2004). In addition, Soulé et al. (2004) reported that wet cool summers may lower western juniper seedling mortality.

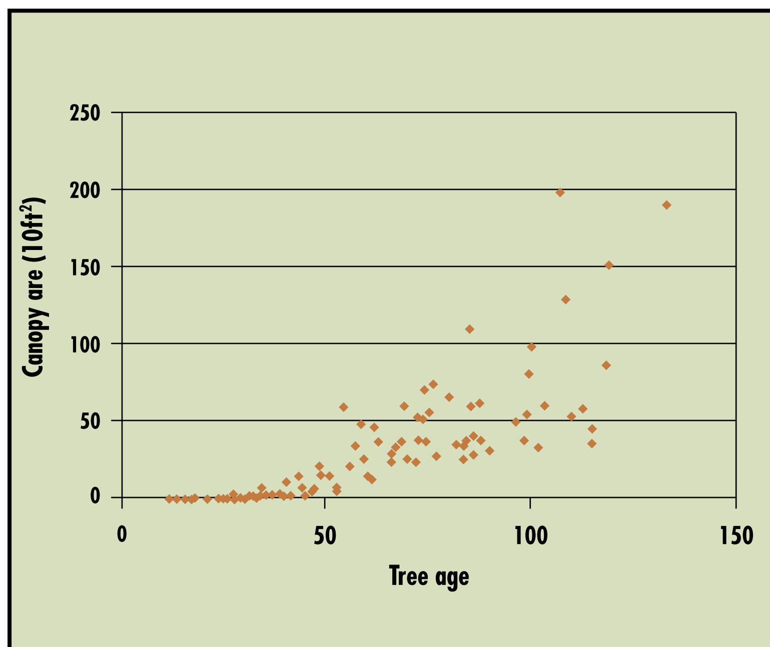
Much of successful western juniper seedling establishment occurs beneath shrubs (Burkhardt and Tisdale 1976, Eddleman 1987, Miller and Rose 1995, Soulé and Knapp 2000, Soulé et al. 2004). This may be attributed to a disproportionate amount of seed dropped by perching birds and/or more favorable growing conditions beneath the shrubs compared to the interspace. Growth rates of young trees beneath mountain big sagebrush canopies were greater (1.34 inches/year) than in the interspace (0.95 inches/year) (Miller and Rose 1995). Compared to bare soils in the interspace, soils beneath a sagebrush canopy can have nearly twice the moisture content and nitrification (Roberts and Jones 2000). Cooler temperatures and higher relative humidity beneath the sagebrush canopy also provide more favorable growing conditions for juvenile foliage, which has poorer stomatal control and lower water use efficiency than adult foliage (Miller et al. 1992). Safe microsites that modify the environment may be responsible for greater seedling survival rates under relatively dry conditions. Many seeds also germinate beneath the tree canopy; however, survival and growth rates are low because of high intraspecific competition from the overstory tree. No evidence suggests competition from associated shrubs or herbs limits the success of western juniper seedling establishment (Burkhardt and Tisdale 1976, Miller et al. 2000). However, an increase in bare ground and mature western juniper cover was negatively correlated with successful tree establishment across the mountain big sagebrush alliance in Oregon and California (Miller et al. 2000). This may be the result of intraspecific competition from overstory trees and limited safe sites for seedling establishment as woodlands approach late successional stages.

Figure 8. Mountain bluebirds consuming juniper berries early in the spring.

Photo by Rick Vetter.

Figure 9. Juniper roots in deep soils can have both large lateral and fine roots in the upper 24 inches, and a deep taproot. Taproots are often missing in shallow soils.

Figure 10. Canopy area and age for individual western juniper trees showing an increase in canopy expansion for trees over 45 years of age (from Miller and Tausch 2001).



Roots

During the first 10 years of growth, western juniper directs most of its effort into developing a taproot with only limited lateral root development (Kramer 1990). After 10 years, lateral root development increases, accounting for about 65 percent of the root biomass in trees 30–35 years old. Root: shoot ratios for young trees vary from 0.55 to 0.76 (Miller et al. 1990). Taproot development declines as trees begin to lose their juvenile foliage (Young et al. 1984) on shallow soils. However, taproots have been observed on some sapling and mature trees growing in deep soils (Fig. 9). Trees develop a massive fine root mat system with age. Young et al. (1984) reported most of tree roots were located in the upper 30 inches of the soil profile in a soil that is 40 inches deep. Large lateral roots commonly extend a distance that equals the height of the tree, but in some cases can extend as much as three times tree height.

Growth

Following germination, aboveground growth is relatively slow, averaging 1.18–1.58 inches/year in height for the first 10 years and increasing to 3.54–6.57 inches/year for older trees up to 100 years old (EOARC, unpublished data). Root development appears to far exceed aboveground growth during early development. Leaf canopy development remains relatively slow during the first 35–45 years. At the age of 45–50 years, the rate of tree canopy development increases (Fig. 10).

Current year's sapwood development begins during the spring and usually ends in early to late August, depending on the site and annual precipitation (Peter 1977). In wet years, ring growth can continue through August. Branchlet and leaf growth are greatest during June and July (Miller et al. 1992). Western juniper typically approaches its maximum height at 80–100 years of age across its geographic range (EOARC, unpublished data). Depending on site potential and competition from other trees, mean height of western juniper at 80 years of age will vary from 19.7 to 49.2 ft (Gedney et al. 1999). Site index curves that describe tree age and height relationships for western juniper varies widely across sites. Height for trees 80 years old at breast height (approximately 4.25 ft above the ground) ranged from 15 ft on scablands to 35 ft on sites associated with ponderosa pine (Sauerwein 1982). In central Oregon, mean height growth rate varied from 3.5 to 6.6 inches/year for dominant trees (Eddleman 1987). Several authors have developed regressions estimating western juniper leaf area, leaf biomass, and total standing crop using tree basal and sapwood areas (Gholz 1980, Miller et al. 1987). In a fully developed woodland in eastern Oregon,

Gohlz (1980) estimated foliage biomass of 4,550 lb/acre, total standing crop biomass of 23,300 lb/acre, and a leaf area index (LAI) of 2 (2 units of leaf area to 1 unit of ground area) for stands with a mean density of 608 trees/acre). Primary production was 1,200 lb/acre, about half that of adjacent ponderosa pine communities and 10 percent of Douglas-fir communities in the Cascades.

Leaf Morphology

Young western juniper trees (usually less than 25 years) have needle-like leaves, which are different than leaves on older trees (De Laubenfels 1953). Leaves on mature trees are triangular with minutely serrated margins and have a low surface-to-volume ratio (Fig. 11a) (Miller and Schultz 1987). Leaf margins are slightly cupped, which seals one leaf against the other and forms a chain-like cylinder. The leaf epidermis is heavily cuticularized (waxy covering on the leaf surface), which greatly reduces water loss through the leaf surface. Most of stomates are located on the protected side of the leaf surface facing the stem (Fig. 11c). Stomates on the outer surface are located at the base of the leaf and are covered by the adjacent subtending leaf (Fig. 11b). The leaf morphology of western juniper allows for maximum drought avoidance through low leaf area, low surface-volume ratios, thick cuticle layer, and protected stomata. Mean maximum leaf conductance (transpiration, measured as inches of water/second passing through the leaf surface to the atmosphere) per unit leaf area was lower (0.03–0.05 inches/second) than values reported for several other conifer species (0.05–0.16 inches/second) (Miller and Schultz 1987).

Water Use and CO_2 Assimilation

Ecophysiological (Moore et al. 1999) and morphological (Miller and Shultz 1987) adaptations allow western juniper to tolerate relatively large environmental changes. In addition, allocation of resources in young trees partially explains the species ability to compete successfully with other native species (Miller et al. 1990). By reducing allocation of resources to branches and trunks, juvenile and small adult western juniper allocate larger portions of dry mass to foliage and roots to optimize photosynthetic capacity and uptake of water and nutrients than mature trees.

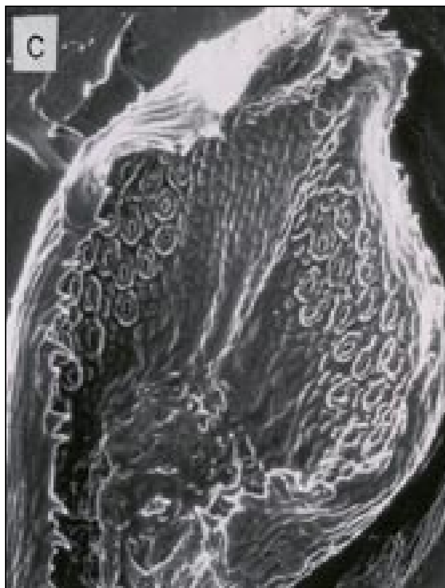
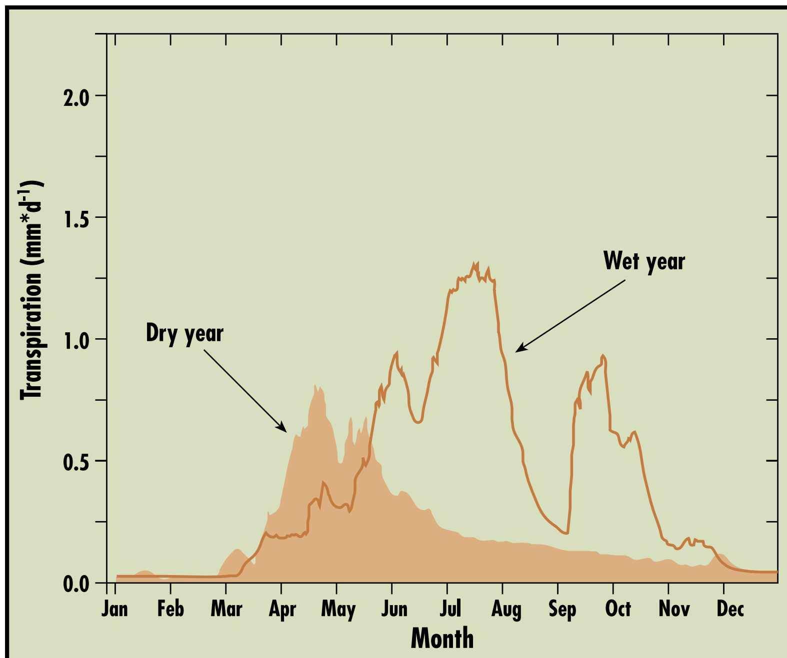


Figure 11. Leaf scales on the top (abaxial) [A and B at 150x] and lower (adaxial) [C at 250x] surfaces of western juniper. Most of the stomata are located on the adaxial leaf surface and a few are at the base of the abaxial surface, which is covered by the lower overlapping scale (Miller and Schultz 1987).

During winter, cold soil temperatures limit water use by western juniper (Miller and Schultz 1987). As soil temperatures drop below 40°F, water uptake at the root surface significantly decreases. As soil temperatures increase in March, trees begin to actively transpire and grow. In warmer climates, such as in the John Day or Mazama ecological provinces, more moderate soil temperatures may allow western juniper to transpire water during any month in the winter. In central Oregon, Jeppesen (1977) reported greater winter soil water loss at 20-inch soil depth in woodlands compared to thinned stands. Leaf conductance is strongly influenced by soil temperature and vapor pressure deficit during the spring. During the summer, soil water availability and vapor pressure gradient[11] are the primary factors influencing water use and CO_2 assimilation in western juniper (Miller et al. 1992, Angell and Miller 1994, Moore et al. 1999). Stomata closed when stem water potentials decreased to –2.0 MPa (mega pascals) (Miller and Schultz 1987). In a dry year, the greatest amounts of water were transpired during April and May, compared to June and July in a wetter-than-average year (Fig. 12) (Angell and Miller 1994). In a moderately stocked stand of 30 trees/acre and 1.6 LAI, the water-use model predicted western juniper would extract 2 inches of soil water in a dry year and 5.6 inches in a wet year. These predictions suggest soil water depletion rates will significantly shorten the growing season on the site, a point confirmed by Bates et al. (2000). They reported the growing season of the understory was shortened by as much as 6 weeks in uncut western juniper stands, compared to adjacent cut stands.

[11] The water vapor concentration gradient from inside the stomata to the open atmosphere.

Figure 12. Modeled daily transpiration for western juniper during a drought year (1990) and wet year (1984) (from Angell and Miller 1994).



Juveniles with the awl-shaped leaves have higher leaf conductance, transpiration, and greater total CO_2 assimilation per unit of leaf weight during the growing season than sapling and mature trees (Miller et al. 1992). The change from juvenile to mature foliage reduces the amount of carbon assimilated per unit leaf area but also reduces the amount of water lost to transpiration by 40 percent (Miller et al. 1993).

Insects

Artichoke-like galls located on the branchlets of western juniper (frequently misidentified as reproductive structures) are formed by midge larvae *Walshomyia* spp. (Purrington and Purrington 1995)(Fig. 13). Moth larvae *Heinrichiesa sanpetella* were found to inhabitat 40 percent of these galls, over-wintering and pupating there in early spring. Other moth caterpillars that feed on western juniper are the sequoia sphinx (*Semiothisa* spp., *Sphinx sequoiae*), cedar streak *(Lithophane logior)*, and *Mitoura grynes barryi* (Miller 1995). Other insects known to feed on western juniper include long-horned beetle *(Styloxus bicolor)*, juniper bark beetle *(Phloeosinus serratus)*, round-head borers *(Callidium califonrnicum* and *C. juniperi)*, wood-boring beetle *(Melonophila miranda)*, and grasshoppers *(Melanoplus* sp.).

The western juniper bark beetle is typically attracted to wounded or felled trees (personal communication, Jane L. Hayes, USDA US Forest Service Research Station, La Grande, OR). Insect attacks usually do not result in the killing of live trees, however in the 1920's and 1930's in addition to drought, areas of western juniper were killed by insects in central Oregon (Furniss and Carolin 1977). Current work has identified 25 species of bark and woodboring beetles feeding on western juniper (Hayes, unpublished work in progress).

During the grasshopper outbreaks near the John Day Fossil Beds in eastern Oregon in the late 1970's, the tops of some western juniper trees were nearly totally defoliated. On dead or dying juniper, round-

head borers or long-head beetles *(Creambydidae* spp.) deposit eggs in the bark (Swan 1996). Upon hatching, the larvae bore into the wood, deriving nourishment from the soluble carbohydrates in wood particles and/or fungal tissue.

Associated Nonvascular Plants

Mistletoe

Mistletoes that commonly infect western juniper are juniper mistletoe (*Phoradendron juniperinum*), and dense mistletoe *(P. densum)* (Geils et al. 2002). Juniper mistletoe is the primary species found on western juniper and is the most widespread mistletoe infecting juniper species throughout the West. Juniper mistletoe has leafless stems and pinkish-white colored berries about 0.16 inches in diameter. Dense mistletoe occurs in the southwestern range of western juniper. This species has white- to straw-colored berries 0.16 inches in diameter and is easily differentiated from juniper mistletoe in that it has leaves. Birds feed on the fleshy mistletoe berries and are the primary dispersers of the sticky seeds. Birds that commonly feed on the berries include American robins, Townsend's solitaires, cedar waxwings, flycatchers, mountain bluebirds, and thrushes (Sutton 1951). The mistletoe foliage is high in nutritional value (Urness 1969). Juniper mistletoe usually occurs in a patchy distribution with only a few heavily infected trees. Although it can stress the tree by absorbing relatively large amounts of water and nitrogen, the tree is rarely killed.

Mosses, fungi, and lichens

Limited information is available on the ecology and life histories of nonvascular plants associated with western juniper. We also know very little about the effects of western juniper expansion or removal on biological crusts. *Tortula ruralis* is commonly associated with mature western juniper trees where it grows beneath the tree canopies. Four species of wood-rotting fungi, *Antrodia juniperina, Pyrofomes demidoffii, Diplomitoporous rimosus,* and *Phellinus texanus,* may cause heart rot in western juniper (Knapp and Soulé 1999a). These fungi typically enter openings in the heartwood or in dead sapwood. Knapp and Soulé (1999a) reported a widespread occurrence of heart rot (suspected to be *Antrodia juniperina)* between 1730 and 1749 in western juniper across eastern Oregon and northeastern California. Heartwood rot is most commonly found in trees more than 150 years old (EOARC, unpublished data). Western juniper roots can be infected with symbiotic fungi mycorrhizae (Trappe 1981). Roberts and Jones (2000) reported higher levels of vesicular-arbuscular mycorrhiza fungi under western juniper canopies than under sagebrush or grass canopies.

Two species of foliose lichens commonly associated with western juniper are *Letharia columbiana* and *L. vulpina.* These lichens are brilliant fluorescent yellow-green or chartreuse in color, and highly branched. Both species are nearly identical in form except that *L. vulpina* lacks the small disk-like fruiting bodies (soredia). Both species can occur on a single tree and are often most abundandant on dead, barkless branches or snags.

Figure 13. Artichoke-like gall located on the branchlet of a western juniper (frequently misidentified as a reproductive structure) is formed by midge larvae Walshomyia species.