Pinus sabiniana Dougl.

Digger Pine

Pinaceae Pine family

Robert F. Powers

Digger pine (Pinus sabiniana), also called bull pine or gray pine, has limited commercial use today, but it once was important to California Indians, who used its seeds and parts of cones, bark, and buds as food supplements, and its twigs, needles, cones, and resin in basket and drum construction (23,30). Indians and early settlers used the resin of Digger pine for medicinal purposes. During California's gold rush period, from 1848 to 1860, all foothill timber, including Digger pine, was heavily used for fuel and structural materials. Despite these uses, Digger pine was viewed with contempt by many early settlers who placed slight value on a tree that provided little shade and poor lumber. In fact, the term "Digger" stems from a contemptuous name given by early settlers to the many small Indian tribes once occupying central California.

Habitat

Native Range

A California endemic, Digger pine (fig. 1) grows between latitude 34" 30' and 41" 15' N. Generally found between elevations of 300 to 900 m (1,000 to 3,000 ft) in dry foothill woodland communities of California's Central Valley, natural stands of Digger pine also grow from as low as 30 m (100 ft) at several locations on the floor of the Sacramento Valley to almost 2130 m (7,000 ft) near Sawtooth Peak in Invo County (10). Digger pine is found in the Coast and Cascade Ranges, Klamath Mountains, southwestern Modoc Plateau, western Sierra Nevada, and Tehachapi Mountains, and over a broad environmental sweep, from the westerly edge of the Mojave Desert, to the Santa Lucia Mountains in Monterey County within sight of the Pacific surf (6). Digger pine is absent in a conspicuous 89-km (55-mi) gap near its southern Sierra Nevada limit. The cause of the gap is unknown but was noted as early as 1865 (10).

Climate

Temperatures characterizing Digger pine's range span the gamut of coastal to Great Basin climates. Yearly means vary from 10" to 17" C (50° to 62" F),

with mean minima of -2" to 3" C (28° to 37" F), in the coolest months, and mean maxima of 31" to 36" C (88° to 97" F) in the warmest months (30). Individual summer days often exceed 38" C (100° F). Few tree species grow over as wide a range in precipitation as Digger pine, with annual averages varying from 250 mm (10 in) at the edge of the Mojave Desert to 1780 mm (70 in) at its upper limits in the Sierra Nevada (6). Sites receiving as little as 80 mm (3 in) of precipitation in a single season continue to support stable populations (30).

Despite the apparent diversity in climatic tolerance shown by Digger pine, four climatic conditions characterize most of its natural range: hot, dry summers; absence of summer fog; precipitation, mostly as rain; and generally mild winters. Digger pine's ability to withstand summer drought and to photosynthesize during mild periods of winter and spring give it a strong competitive advantage over many other species in the California foothills.

Soils and Topography

Digger pine grows on soils in five soil orders (Alfisol, Entisols, Inceptisols, Mollisols, and Ultisols) derived from a wide variety of geologic materials including granodiorite, dacite, andesite, basalt, peridotite, greenstone, schists of various types, limestone, river gravels, and sandstone. The striking feature in much of Digger pine's range is its association with ultramafic soils, particularly those formed from serpentinite. Inclusions of serpentinite or limestone in upland zonal soils produce nutritional imbalances that allow Digger pine to persist within the mixedconifer forest of the Sierra Nevada and the coniferhardwood forest of the north Coast Ranges (fig. 2) (6).

Soils supporting stable populations of Digger pine characteristically have low levels of available moisture. Even on sites where soil moisture is relatively high, Digger pine tends to dominate only the shallowest phases. Although found on deep, alluvial valley terraces, Digger pine has been eliminated systematically from many fertile sites by **stockmen** seeking to increase grass production (6,18,30). Today, many of the sites still supporting Digger pine consist of dry rolling hills, rocky slopes, and steep canyon walls (fig. 3). Few conifer species can match Digger pine's ability to persist under such **xeric**, sterile conditions.

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Figure 1-The native range of Digger pine.



Figure Z-Nutritionally imbalanced soils allow Digger pine to extend into other forest types. Here, exposed limestone supports a stand Of Digger pine in a forest of Pacific Ponderosa Pine-Douglas-Fir (SAF Type 244).



Figure 3—Digger pine is common to the foothills of the Sierras.

Associated Forest Cover

Digger pine forms a part of variants of seven forest cover types (3) and is a major component of an eighth, Blue Oak-Digger Pine (Society of American Foresters Type 250), where together with blue oak (*Quercus douglasii*) it forms a climax community in a nearly continuous band around California's Central Valley between valley grasslands and montane forest (21).

Associated trees in the cover type Blue Oak-Digger Pine include California buckeye (Aesculus californica), California scrub oak (Quercus dumosa), California black oak (Q. kelloggii), and interior live oak (Q. wislizeni) in the Sierra Nevada; and California buckeye, coast live oak (Q. agrifolia), California black oak, and valley oak (Q. lobata) in the Coast Ranges. Digger pine also grows with western juniper (Juniperus occidentalis) in the Pit River drainage of the Modoc Plateau, and Coulter pine (*Pinus coulteri*) in the southern Coast Range. Predominant shrubs include several manzanita (Arctostaphylos) species, primarily A. manzanita and A. viscida, buckbrush (Ceunothus cuneatus), redbud (Cercis occidentalis), birchleaf mountain-mahogany (Cercocurpus betuloides), silktassel (Garrya fremontii), toyon (Heteromeles arbutifolia), hollyleaf buckthorn (Rhumnus crocea), and western poison-oak (Toxicodendron diversilobum).

Digger pine also grows on ultramafic and calcareous soils within several forest types, including Redwood (Type 232) west of Healdsburg, and at the low elevational fringe of Douglas-Fir-Tanoak-Madrone (Type 234) and Pacific Ponderosa Pine-Douglas-Fir (Type 244). Within Pacific Ponderosa Pine (Type 245), Digger pine is found on westerly slopes of the southern Cascades and northern Sierra Nevada. The species also grows in low elevational fringes of California Black Oak (Type 246), Knobcone Pine (Type 248), and in portions of Canyon Live Oak (Type 249) and Western Juniper (Type 238) (3).

Life History

Reproduction and Early Growth

Flowering and Fruiting-Digger pine is monecious, and strobili appear on short stalks in early spring. Male strobili are 3 to 4 cm (1.2 to 1.6 in) long, green or yellow to reddish purple when immature and light brown when mature. Female strobili are initially small and green or red to purple. When mature they are heavy, ovoid to subglobose, light- to chocolate-brown woody cones. The cone is borne close to the branch on reflexed stalks 5 to 6 cm (2 to 2.5 in) long. Pollination occurs in March through April and archegonia are fertilized in the spring of the next year (16). Cones mature by September or October. Although cones have been noted on 2-year-old trees (30), 10 to 25 years usually must pass to attain full seed production (16). Seeds of Digger pine are large at maturity, averaging 19 to 25 mm (0.75 to 1.0 in) long (30), and weighing up to 1 g (0.04 oz) and more when air-dried (6). Embryos average 18 to 35 mg (0.3) to 0.5 gr) (9) and are surrounded by thick seedcoats.

Cleaned seeds average 1,280 per kilogram (580/lb) and range between 1,170 and 1,430 seeds per kilogram (530 and 650/lb). Among the American pines, only Torrey pine (*Pinus torreyuna*) rivals Digger pine in average seed weight (*16*).

One of Digger pine's most prominent features is its massive cones, among the largest produced by any pine species. Fresh cone weights average 0.3 to 0.7 kg (0.7 to 1.5 lb) and may exceed 1 kg (2.2 lb) (7). Lengths often reach 20 to 30 cm (8 to 12 in), although mature cones can be much smaller. Large elongated cones are frequently found in populations of the north Coast and Klamath Ranges. Smaller ovoid cones are more common in the Sierra Nevada (7). Prominent features of Digger pine cones are the conspicuous spurs that develop at the base of the cone. Formed from the combined umbo and apophysis of the scale, spurs tend to elongate and recurve, giving the cone a spiny appearance that is fairly constant within a tree, but quite variable within and between populations (7). Unlike most other conifers, Digger pine cones do not form an abscission layer of cells where the cone joins the branch. Thus, cones remain attached long after seeds are shed, unless broken from the tree crown by wind or cut from the tree by the western gray squirrel in quest of seed.

Seed Production and Dissemination-Compared with other species, Digger pine is a consistent seed producer, with large crops produced at 2- to 3year intervals. Cones may open slowly so that dispersal, beginning in October, sometimes extends into winter. Although open, cones may contain moderate numbers of seeds as late as February (*6,16,30*).

Digger pine seeds are disseminated in four ways. Wind, usually the primary distributor of seeds for most species, has less influence on Digger pine seeds because wings are poorly developed and seeds are heavy. Birds, primarily the acorn woodpecker and scrub jay, disseminate seed. Gravity also aids distribution of seeds. Digger pine cones, because of their shape and weight, may roll considerable distances on steep hillsides once severed from tree crowns. The large seeds of Digger pine also may roll when dropped from high in the crown. Finally, Digger pine cones are relatively buoyant, with specific gravities varying between 0.59 and 0.96 (7). Cones reaching running water may be transported considerable distances. In one instance, cones were found on a streambank within 13 km (8 mi) of the ocean, and 40 km (25 mi) downstream from the nearest known source (30).

Seedling Development-Seeds of Digger pine show both physiological and physical barriers to

early germination when field conditions may be unfavorable. Embryos require a moist, near-freezing chilling period of at least 30 days before germination is possible (9,13). Digger pine growing on sites where winter temperatures fluctuate greatly, such as the Modoc Plateau, may have adapted a longer requirement for chilling to prevent germination until spring. Seeds from populations growing on low-elevation sites with milder winters tend to require less chilling, thereby favoring early establishment before soil moisture becomes limiting (9).

Digger pine's thick seedcoat provides a formidable obstacle to water imbibition and gas exchange, and cracking it or reducing its thickness improves speed and completeness of germination if the chilling requirement is satisfied (9,13). A further physical barrier is the nucellar cap, and removing it improves germination more than seedcoat removal alone (9). No chemical inhibitors of germination in Digger pine seed are known.

Germination is epigeal (16). Seedlings are established best on bare mineral soil and under partial (but not deep) shade. Chaparral cover purportedly helps establishment (29). Cotyledons of Digger pine are unusually large, averaging 49 to 72 mm (1.9 to 2.8 in) in length, and seedlings with cotyledons spanning 20 cm (8 in) tip-to-tip have been noted (6,8). Cotyledon size and number in Digger pine (from 10 to 21 per seedling) help provide enough energy through photosynthesis so that, where soil depth permits, first-year seedlings may develop a deep taproot before soil moisture is depleted in late spring or early summer. Controlled studies show that most of the first season's growth is completed and bud differentiation begins within 5 months of germination. Firstyear foliage consists mainly of cotyledons and primary needles, although secondary needles (in fascicles of three) may be produced on better sites toward the end of the growing season. Although overall growth is depressed on poor sites, shoot-root ratios tend to be lower as well so that transpirationabsorption deficits may be balanced to some degree (8).

Vegetative Reproduction-Digger pine does not reproduce vegetatively in nature. No information is currently available on artificial reproduction.

Sapling and Pole Stages to Maturity

Growth and Yield-Early growth rates of Digger pine are among the highest of any conifer-an **amaz**ing fact, considering the droughty sites on which the species grows. Annual height growth of Digger pine in its native range may average as much as 70 cm (28 in) for the first 8 years after germination (*30*) and often exceeds 1 m (3 ft) during specific years. When introduced to Challenge Experimental Forest in northern California, a very productive Sierra Nevada mixed-conifer site at 790 m (2,590 ft) elevation, dominant and codominant Digger pine averaged 10.3 m (33.8 ft) in height and 19.3 cm (7.6 in) in d.b.h. 15 years after planting (25).

Growth can begin with the first fall rains and continue until soils become too dry in the spring or early summer (18). Within the natural range, high annual rates of growth probably reflect a long growing season that begins early, rather than rapid growth on a daily basis. Digger pine's sparse foliage suggests that daily rates of growth probably are low. On more productive timber sites, the growing season may begin later but extend further into the summer, producing growth rates similar to those on the best low-elevation sites within its natural range. In one study, height and diameter growth rates of Digger pine on a high quality site were comparable, but not superior, to those of native ponderosa pine (25).

The stem form of Digger pine seemingly disregards gravity. Even on steep slopes it may grow nearly perpendicular to the ground. Trees usually maintain a straight, conical form into the pole stage, but mature trees generally are twisted and have multiple forks (fig. 4). The poor form of mature trees probably is a genetic trait but may be traced partly to an open-grown nature that exposes the trees to the damaging effects of wind and to the tendency of lateral buds to elongate when the terminal bud remains static (6). Although Digger pine stands may approach stocking densities of 46 m^2 basal area per hectare (200 ft²/acre) (25), most stands are stocked much more lightly. Mature trees average 12 to 24 m (40 to 80 ft) in height and 30 to 90 cm (12 to 36 in) in d.b.h. The largest Digger pine officially recorded measured 48.8 m (160 ft) tall, 160 cm (63 in) in d.b.h., and had a crown spread averaging 20.7 m (68 ft) at the widest points (22). Size and age potentials are not determined easily from the trees existing today, because miners, wood cutters, and agriculturalists cleared Digger pine from its best sites more than a century ago. The maximum age reached by this species probably exceeds 200 years.

Rooting Habit-Digger pine produces a deep taproot where soil depth permits. However, hardpan soils are common along the margins of California's Great Valley, and this causes trees to have spreading but shallow root systems with weak taproots extending through duripans. Large trees growing on such sites are windthrown easily during the winter if



Figure 4-Digger pine typically has a conical and fairly straight form through the pole stage of development but becomes multibranched with maturity. The larger tree is 25 m (82 ft) tall and 110 years old; the smaller, 17 m (56 ft) tall and 75 years old. The site is a rocky phase of Blue Oak-Digger Pine (SAF Type 250). windstorms coincide with waterlogged sol conditions.

Reaction to Competition-Beyond the seedling stage, Digger pine is one of the least shade tolerant of all trees. It is classed as very intolerant of shade. The vigor of Digger pine declines rapidly when competing with such dense-crowned associates as ponderosa pine, blue oak, California black oak, and the live oaks. The wide spacing of Digger pine on xeric sites probably stems from root competition for soil moisture, rather than from mutual competition for light. On mesic sites with better soil development, the sparse crowns of even-aged Digger pine stands allow enough light penetration for needles to persist for 3 years, and stand densities may approach those of moderately-stocked ponderosa pine stands (25).

Digger pine's ability to persist and sometimes dominate on xeric sites on zonal soils probably results from its capacity to photosynthesize throughout the winter and early spring when soil moisture is abundant, and to minimize transpiration losses of water during dry seasons through low foliar biomass and good stomata1 action. On zonal soils of more mesic sites, Digger pine cannot compete with forest vegetation. Where they grow together in natural ecotones, ponderosa pine has more stomates per needle than Digger pine and maintains slightly lower leaf water potentials (33). This, coupled with its greater foliar density, gives ponderosa pine a growth advantage where soil moisture is adequate. However, Digger pine's sparse crown (and presumably lower absolute transpiration loss) gives it a sizable survival advantage where soil moisture is scarce.

Digger pine's ability to survive and grow slowly even under severe drought may not be helpful if it is introduced to more mesic sites. During 3 years of normal precipitation at Challenge Experimental Forest, height growth of planted Digger pine averaged 76 cm (30 in) per year-an average almost identical to the 74 cm (29 in) for native ponderosa pine (25). Annual height growth decreased 29 percent in Digger pine during 2 years of drought, however, compared with a decrease of only 12 percent for ponderosa pine.

Digger pine competes well on soils with calcium imbalances. On serpentinite soils, where calcium availability is low and magnesium availability high, Digger pine probably owes its success to low nutrient requirements and preferential absorption of calcium and exclusion of magnesium. These traits have been identified in some populations of ponderosa pine (14,24). On limestone soils, where calcium is abundant, calcium concentrations remain relatively low in Digger pine foliage (34). Results from such extreme soil conditions suggest that Digger pine is unusually effective in regulating its calcium supply.

Damaging Agents-Because of the species' ability to grow throughout the winter, succulent shoots of Digger pine are damaged easily by sudden frosts after periods of mild temperature. Digger pine also is particularly susceptible to damage by wind and hail (31). On sites where winter temperatures fluctuate greatly, stable populations may have evolved such adaptive strategies as delayed germination of seed (9). The thin bark of young trees, along with the species' high resin content and the presence of congealed flows that have dripped from wounds, make Digger pine susceptible to severe damage by fire.

Prominent diseases of Digger pine include western gall rust (*Peridermium harknessii*) and dwarf mistletoe (Arceuthobium occidentale). Western gall rust forms branch galls on Digger pine throughout its range but rarely causes appreciable damage or death. Dwarf mistletoe is a particularly damaging disease that is widely distributed in even the most open stands (12,26). Once infection is established, dwarf mistletoe spreads rapidly (11). Growth loss, deformity, and death often result with the buildup of the disease, and trees of all sizes are susceptible. Digger pine also is susceptible to **Heterobasidion** annosum root disease. This pathogen seldom is a problem in open stands, although the disease can spread rapidly in well stocked stands, such as plantations (1).

Digger pine is host to a wide variety of cone, twig, and foliage insects and is the specific host for **Ips spinifer**, an aggressive bark beetle that often kills trees weakened by fire or drought (5). Heavy production of resin by healthy trees provides a strong defense against many bark beetles, and vapors from its resins are toxic to some (28). Nevertheless, heavy production of resin favors a pitch nodule moth (**Petrova sabiniana**), which pupates within resin nodules (5). Thick seedcoats provide a protective barrier against damage from most seed insects, but much of the seed production is consumed by rodents and birds. However, predation does not seem to restrict Digger pine's range (32).

Special Uses

Seeds of Digger pine have considerable nutritional value. Their protein and fat contents are similar to those of *Pinus pinea* (a pine of the Mediterranean region whose seeds are harvested for the table), and are equal or superior to those of other commercial species (4). Although Digger pine seeds are not raised commercially, they once were an important supplement to the diet of California valley Indians (23,30).

Digger pine wood has many favorable properties that determine its special uses. Its 0.43 mean specific gravity almost matches that of Douglas-fir (*Pseudotsuga menziesii*), and its strength properties are comparable with those of ponderosa pine (27). Kraft pulps made from Digger pine rate high in bursting and tensile strength and compare favorably with pulps from most northern conifers (19). Poor form, high resin content, high proportions of compression wood, and low stand density, however, characterize a species commanding only minor commercial interest today

Currently, the tree's primary value is as a source of railroad tie material, with secondary values for box shook, pallet stock, and chips (17). Digger pine is expensive to log because of its low stand density, and to transport because of its heavy weight and often crooked form. Consequently, stumpage prices are low (17). One of Digger pine's few commercial advantages is that foothill stands can be logged during winter, when species at higher elevations often are inaccessible. Also, some potential exists as stock for shelterbelt plantings on arid sites (29).

Normal heptane, an alkane hydrocarbon of rare occurrence in woody tissues, is the principal constituent of Digger pine wood turpentine and constitutes about 3 percent of needle and twig oil (20).

Genetics

The most obvious variation between Digger pine populations is in cone shape and size (7). Stands in the north Coast Ranges and Klamath Mountains tend to bear large, elongated cones, while those in the Sierra Nevada produce cones that are smaller and ovoid. Variation within a population is great enough, however, that small or large cone races probably do not exist. Early claims of a variety *explicata* (15), based on strongly-hooked cone spurs and relatively long seed wings, are not supported by more recent sampling (7). One isolated Klamath Mountain population, however, tends to have blunt, straight spurs. Cones from the northern part of Digger pine's range tend to have lower specific gravities than those from the southern part.

Seeds collected from sites characterized by cold winters and short growing seasons show the slowest germination rates and require longer chilling periods to achieve full germination (6,9), presumably representing a survival advantage for a species whose seeds normally germinate during winter. Despite the ability of Digger pine to reproduce and grow on extremely infertile soils, such as those formed from serpentinite, no strong evidence has been found that edaphic ecotypes exist within the species (8). Digger pine is resistant to interspecific breeding, and no natural hybrids have been recognized although its range overlaps those of several species of pines. It has been successfully crossed artificially with Coulter and Torrey pines (2,7,10).

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