



Silvical Characteristics of Monterey Pine

(*Pinus radiata* D. Don)

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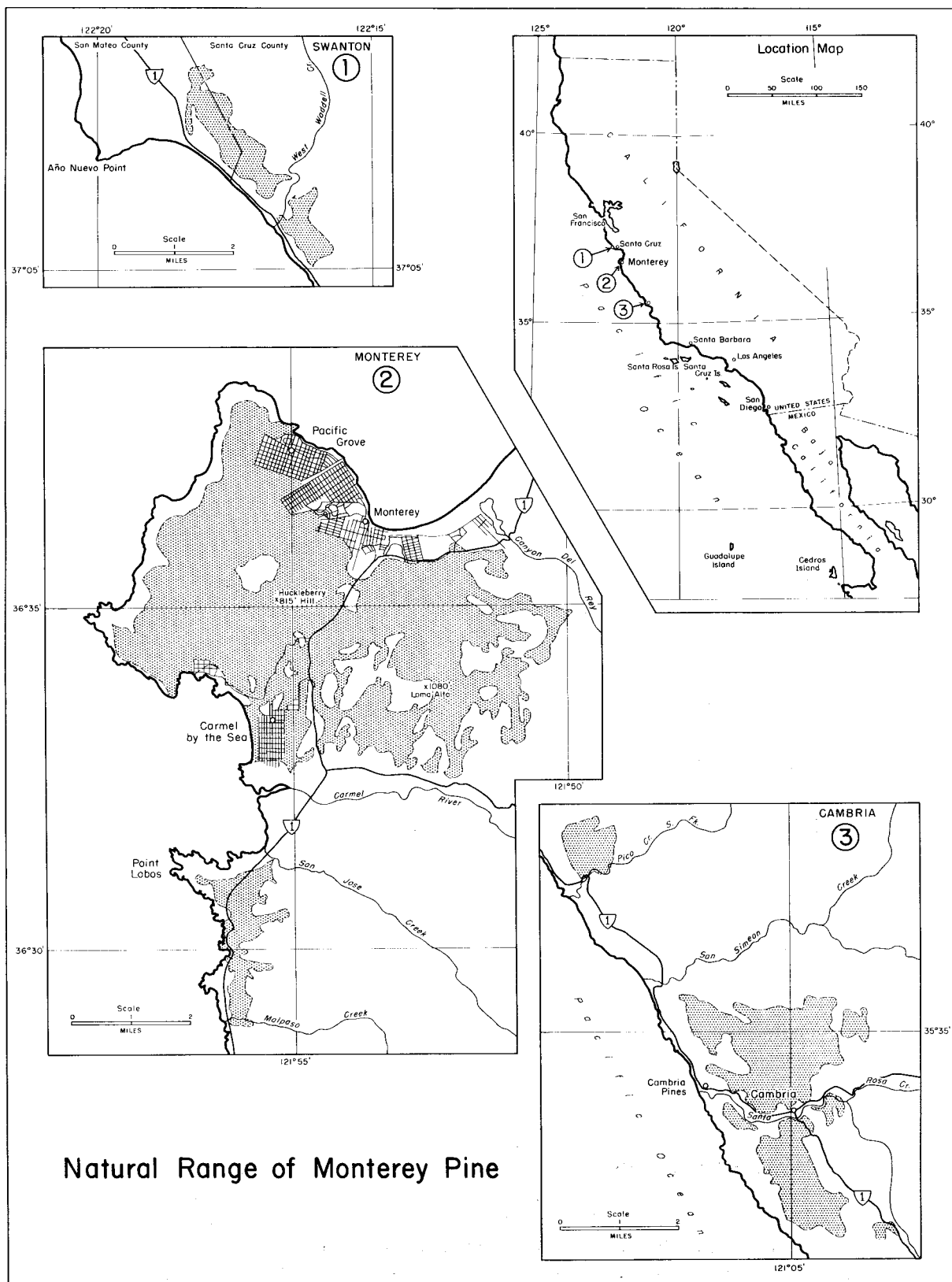


Figure 1.—The natural range of Monterey pine.

Monterey pine (*Pinus radiata* D. Don) is paradoxical. This tree, which now has little economic importance in its native stands, has been planted more abundantly throughout the world than any other American tree. Its introduction as a forest tree into the Southern Hemisphere has been particularly successful. Extensive stands of Monterey pine now grow in New Zealand, Australia, Chile, and South Africa. Plantings also have been successful in Spain, Argentina, and Uruguay.

The natural range of Monterey pine is extremely limited. On the United States mainland it is confined to three localities on the central California

coast (fig. 1). The largest stand is 8,000 to 12,000 acres¹ on and adjacent to the Monterey Peninsula. The second largest is about 2,500 acres surrounding the town of Cambria, which lies about 85 miles southeast of Monterey. Another isolated stand of about 500 acres is at Pico Creek, about 6 miles north of the main Cambria forest. The northernmost grove probably is less than 1,000 acres,² and only a part of this area is clothed by pure stands of pine. It is in the Swanton area, 40 miles northwest of Monterey and about 14 miles from Santa Cruz.

Another natural stand is found on Guadalupe Island situated about 200 miles off the coast of Lower California (fig. 1).³

Habitat Conditions

Climatic

Monterey pine grows in a humid climate. The annual precipitation is seasonal, however, and varies from 15 to 35 inches. The minimum rainfall in one year has varied from 5.68 inches at Del Monte to 12.37 inches at Santa Cruz. And maximum annual rainfall has ranged from 28.98 inches at Monterey to 50.41 inches at Santa Cruz. About 70 to 75 percent of this moderate amount falls in the rainy season that extends from December through March. Three-fourths of the 50 to 55 rainy days in each year occur during these four months. Each of the other eight months have, on the average, less than 2 inches of rain. In fact, rainy days in July and August are rare (Lindsay [1932]; Martin and Kincer 1934).

Although Monterey pine grows in a humid climate throughout the year, humidity is higher in summer and winter than in spring and autumn. For example, the average minimum relative humidity at Monterey for July is between 60 and 70 percent (Lindsay [1932]). This high humidity is maintained by summer fogs. The characteristic patterns of fog movement inland seem to explain the distribution of the Monterey pine forest where other factors are not limiting.⁴

Forests on the Monterey Peninsula are shrouded by clouds or fogs at least one-third of the time. Consequently summer fogs contribute significant amounts of available moisture. As much as 0.57 inch of fog-drip per week was measured at higher elevations of the peninsula.⁵

Average mean daily temperatures range from 48° F. to 52° F. during January and 60° F. to 64° F. in July. Winters are relatively mild although frosts occur occasionally. The last killing frosts in the spring generally come between February 5 and February 28; the first killing frosts in the fall are expected between November 30 and December 10. The days free of killing frosts each year number 300 or more. The greatest seasonal range of temperature recorded near Monterey pine stands is 24° F. to 98° F. (Sprague 1941).

¹ McDonald, John Bruce. *An ecological study of Monterey pine in Monterey County, California*. 1959. (M.S. thesis on file at Univ. Calif., Berkeley.)

² Forde, Margot Bernice. *Variation in the natural populations of Monterey pine (Pinus radiata [D.] Don) in California*. 1962. (Ph.D. thesis on file at Univ. Calif., Berkeley.)

³ Howell 1941; Jepson 1910, 1923, 1925; Newcomb 1959; Sargent 1922.

⁴ Forde, M. B. *Op. cit.* See footnote 2.

⁵ McDonald, J. B. *Op. cit.* See footnote 1.

Edaphic

Monterey pine grows on a variety of soils developed from different parent materials. The soil series represented characteristically are coarse-textured sandy loams, strongly to very strongly acid in reaction, and extremely to moderately permeable. Sometimes they are leached in an A-2 horizon. The best sites have soils that are sandy barns to fine sandy loams in texture, well drained and moderately deep. McDonald⁶ reported that he could not find trees growing on soils less than 9 inches deep. Near rock outcroppings, Monterey pine generally does not grow taller than 70 feet, and soils at least 3 to 4 feet deep appear necessary for trees to reach 100 to 120 feet (Lindsay [1932]).

Most of the Monterey Peninsula is formed by granitic rocks, but basalts, sandstones, shales, and schists also occur. The soils, however, are derived mainly from an overlying shallow marine deposit. The most extensive soil series is the shallow phase of Elkor, which sustains a uniform forest with trees occasionally more than 100 feet tall and 36 inches in diameter. Most of this soil is 3 to 4 feet deep. It is a calcareous sandy loam that is well drained and often is high in organic matter.⁷ The shallow phase of McClusky sandy loam also supports a large forested area, but is less productive. This soil is 20 inches to 5 feet deep, averaging 40 inches. Bedrock outcrops in a few places. The relatively heavy subsoil causes imperfect drainage. Other poorer soils in the Monterey area are Santa Lucia clay loam derived from slow weathering of silicious shales, and Chamise sandy loam. Monterey pine also grows on these soils and on coastal dune sand, which is fine, high in silica content, and poor at retaining moisture (Carpenter and Cosby 1929).

The rocks in the Cambria area are early Jurassic slates, cherts, sandstones, and limestones, but the Monterey pine forest grows almost entirely on Arnold sandy loam (Carpenter and Storie 1933). Derived from softly consolidated sandstone, this soil is low in organic matter and erodes easily. An edge of the Cambria forest extends onto Los Osos fine sandy loam.

At Swanton the rocks are shales and marine sandstones of the Miocene age. The pine forest grows mainly on the steep and shallow phases of

Santa Lucia clay loam, which is high in organic matter, acid in reaction, permeable, well drained, and easily eroded. Colma loam also is represented. This soil, formed from weakly consolidated marine sediments, is slightly acid and well drained. Small areas of Tierra loam, Lockwood loam, and Watsonville loam also are within the forest.

Humus development generally is good on sites where mature pines reach heights of 80 feet or more. Here pole stands, 50 to 60 feet tall, and stands of larger trees have litter 3 to 6 inches deep with active disintegration on the bottom to form a definite humus layer. Beneath this layer, considerable organic matter darkens the soil several inches deep. On poor sites humus does not develop (Lindsay [1932]).

Physiographic

In general, Monterey pine is found on gentle to moderate slopes, from sea level to a maximum elevation near 1,000 feet, and from the sea to about 6 miles inland. At Swanton, where rainfall is more abundant, this species grows on all aspects. But at both Monterey and Cambria, which are significantly drier, the hot and dry south aspects are not favorable sites. All areas where Monterey pine is established naturally are well drained.

Swanton, at latitude 37° north, is the most northerly area of natural Monterey pine stands. Here patches of Monterey pine are scattered on the narrow coastal stretch of rolling terrain between the sea and the steep slopes of Ben Lomond Mountain. Most of the pines grow at elevations between sea level and about 500 feet, but a few are found on the steep slopes up to 800 feet. The best sites are on the hilly country a few hundred yards to a mile and a half from the coast (Lindsay [1932]).

The main pine stand in the Monterey area is located on the Monterey Peninsula, latitude 36½° N. The highest elevation here is 815 feet. The forest continues southeasterly beyond the neck of the peninsula, mainly on the northern side of the ridge, to elevations of almost 900 feet, for about 4 miles. Here it is broken by grassland and chaparral and disappears. Trees on the peninsula grow best on the gently sloping and flat land between the ridge and the sea. Inland, the best growth is on the sheltered northern slopes. Growth is fair on some slopes and gully bottoms on the south side of the ridge, but tree sizes there do not compare with those attained on the northern slopes. South

⁶ McDonald, J. B. *Op. cit.* See footnote 1.

⁷ Forde, M. B. *Op. cit.* See footnote 2.

of the Monterey Peninsula, patches of Monterey pine are found on Point Lobos and up to 1,000 feet elevation on the adjoining seaward slopes of the Santa Lucia Mountains.⁸

At Cambria the latitude is 35½ ° N. Here Monterey pine grows on gentle and moderate slopes, which are not more than 2 miles inland nor higher than 300 feet. Growth is poor on south slopes.

The latitude of Guadalupe Island is 29° N.

Biotic

Monterey pine occurs within the life zone classified as Austral Transition (Merriam 1898). Along the coast near Monterey it occasionally grows with Monterey cypress⁹ and Gowen cypress. Further inland in this area the forest overstory is pure Monterey pine (Sudworth 1908), except near the top of Huckleberry Hill, where groups of bishop pine grow. The most common tree found with Monterey pine is California live oak, which generally is an understory tree under 30 feet high (Lindsay [1932]).

The plant associations of Monterey pine in the Monterey area vary considerably with different soils and aspects. Changes in these associations are both gradual and abrupt.

One typical association is the mesophytic pine forest found in canyons throughout the peninsula. Another, found on favorable sites on the gentle lower slopes, particularly on northern aspects, is composed of well-developed pines that form a closed canopy. The understory is fairly open with scattered California live oaks and shrubs, and the ground cover is grass, ferns, brambles, poison-oak, and other soft-leaved species. On steeper parts of the peninsula where the soils are shallow, the pines are poorly formed and widely spaced, and have a dense undergrowth of manzanitas, California huckleberry, blueblossom, and coyote brush. Inland, California live oak becomes increasingly prominent until Monterey pine disappears and a grass-woodland type dominates.¹⁰

The Monterey pine forest at Cambria is surrounded by grassland. Parts of the forest have been logged repeatedly for timber, and parts have been burned to improve grazing for cattle. These areas generally are open and lack undergrowth other than grasses. The stands which are relatively

undisturbed resemble those growing on the better sites at Monterey where the understory is dominated by California live oak.

The drier forest sites at Cambria are covered by an open stand of pines with a dense understory of California live oak and shrubs. On shady areas California live oaks are infrequent and the ground under the forest is covered mainly by ferns, grasses, and soft-leaved shrubs.

The forest types at Swanton are not as clearly delineated as those at Monterey and Cambria. Where Monterey pine grows in pure stands the trees are widely spaced and heavily branched. This type is restricted, however. Generally, it is confined to drier, south-facing sites along the exposed seaward margin of the forest. More often, Monterey pine at Swanton is not the dominant conifer, but is associated with other trees—with redwood on lower slopes, with Douglas-fir on middle slopes, and with knobcone pine on the drier upper slopes where the soil is shallow and stony.

The redwood association is mesophytic with tall and dense tree and shrub layers, and with abundant ferns and herbaceous vegetation on the ground. Conspicuous codominant or understory species are California live oak, wax-myrtle, and California-laurel; and manzanita and ceanothus are prominent in the shrub layer.

The best individual Monterey pines grow with Douglas-fir on north-facing slopes with deep soil.

The vegetation growing with Monterey pine has been described in detail (Lindsay [1932]; Mason 1934).^{11 12 13} Shrubs, forbs, and grasses are numerous, and the Monterey region is especially rich in endemic species. Floristic lists follow:

Trees—Conifers

Cupressus goveniana Gord. (Gowen cypress)
C. macrocarpa Hartw. (Monterey cypress)
Pinus attenuata Lemm. (Knobcone pine)
P. muricata D. Don (Bishop pine)
Pseudotsuga menziesii [Mirb.] Franco (Douglas-fir)
Sequoia sempervirens [D. Don] Endl. (Redwood)

Trees—Hardwoods

Aesculus californica [Spach] Nutt. (California buckeye)

¹¹ Coleman, George A. *Report upon Monterey pine, made for the Pacific Improvement Company*. 1905. (Unpublished report on file at Pacific SW. Forest and Range Exp. Sta., U.S. Forest Serv., Berkeley, Calif.)

¹² Dunning, Duncan. *A working plan for the Del Monte Forest of the Pacific Improvement Company*. 1916. (M.S. thesis on file at Univ. Calif., Berkeley.)

¹³ Forde, M. B. *Op. cit.* See footnote 2.

⁸ Forde, M. B. *Op. cit.* See footnote 2.

⁹ See floristic lists in this paper for scientific names.

¹⁰ Forde, M. B. *Op. cit.* See footnote 2.

Alnus rhombifolia Nutt. (White alder)
A. rubra Bong. (Red alder)
Arbutus menziesii Pursh (Pacific madrone)
Lithocarpus densiflorus [H. & A.] Rehd. (Tanoak)
Quercus agrifolia Nee (California live oak)
Q. chrysolepis Liebm. (Canyon live oak)
Umbellularia californica [H. & A.] Nutt. (California-laurel)

Shrubs

Adenostoma fasciculatum H. & A. (Chamise)
Arctostaphylos canescens Eastw. (Hoary manzanita)
A. glandulosa Eastw. (Eastwood manzanita)
A. hookeri G. Don (Monterey manzanita)
A. nummularia Gray var. *sensitiva* [Jeps.] Mc-Minn (Littleberry manzanita)
A. pumila Nutt. (Dune manzanita)
A. tomentosa [Pursh] Lindl. (Shaggy-barked manzanita)
A. tomentosa [Pursh] Lindl. var. *tomentosiformis* [Adams] Munz (Woolly manzanita)
Artemisia californica Less. (California sagebrush)
A. douglasiana Bess. in Hook. (Douglas sagebrush)
A. pycnocephala DC. (Sandhill sagebrush)
Baccharis pilularis DC. var. *consanguinea* [DC.] C. B. Wolf (Coyote brush)
Castanopsis chrysophylla [Doug.] A. DC. var. *minor* [Benth.] A. DC. (Golden chinkapin)
Ceanothus thyrsiflorus Eschs. (Blueblossom)
Cornus x californica C. A. Meyer (Western red dogwood)
Corylus cornuta Marsh. var. *californica* [A. DC.] Sharp (California hazel)
Cytisus monspessulanus L. (French broom)
Dendromecon rigida Benth. (Bush poppy)
Eriodictyon californicum [H. & A.] Torr. (Yerba Santa)
Eriogonum latifolium Sm. (Coast wild buckwheat)
E. parvifolium Sm. (Seacliff eriogonum)
Eriophyllum confertiflorum [DC.] Gray (Golden-yarrow eriophyllum)
E. staechadifolium Lag. (Lizard tail)
Garrya elliptica Dougl. (Silk-tassel bush)
Gaultheria shallon Pursh (Salal)
Haplopappus ericoides [Less.] H. & A. (Heather goldenweed)
H. squarrosus H. & A. (Sawtooth goldenweed)
Helianthemum scoparium Nutt. (Rush-rose)
Heteromeles arbutifolia M. Roem. (Toyon)
Holodiscus discolor [Pursh] Maxim. (Cream bush)
Lepechinia calycina [Benth.] Epl. in Munz (Pitcher sage)
Lonicera hispidula Dougl. var. *vacillans* Gray (California honeysuckle)
L. involucrata [Richards.] Banks (Twinberry)
Lupinus albifrons Benth. (Whiteface lupine)
L. arboreus Sims (Tree lupine)
Mimulus aurantiacus Curt. (Bush monkey-flower)
Myrica californica Chain. & Schlecht. (Wax-myrtle)
Osmaronia cerasiformis [T. & G.] Greene (Oso berry)
Pickeringia montana Nutt. (Pea chaparral)
Polygala californica Nutt. (California polygala)

Prunus virginiana L. var. *demissa* [Nutt.] Sarg. (Western choke cherry)
Rhamnus californica Eschs. (Coffeeberry)
R. crocea Nutt. in T. & G. ssp. *ilicifolia* [Kell.] B. Wolf (Buckthorn)
Rhododendron macrophyllum D. Don (Pacific rhododendron)
Rhus diversiloba T. & G. (Poison-oak)
Ribes divaricatum Dougl. (Straggly gooseberry)
R. malvaceum Sm. (Chaparral currant)
R. menziesii Pursh (Canyon gooseberry)
R. sanguineum Pursh var. *glutinosum* [Benth.] Loud. (Red flowering currant)
R. speciosum Pursh (Fuchsia-flowered gooseberry)
Rosa californica Cham. & Schlecht. (California wild rose)
R. gymnocarpa Nutt. ex T. & G. (Wood rose)
R. nutkana Presl (Nootka rose)
Rubus parviflorus Nutt. (Thimble-berry)
R. spectabilis Pursh (Salmon-berry)
R. ursinus Chain. & Schlecht. (California blackberry)
Salix lasiolepis Benth. (Arroyo willow)
R. scouleriana Barratt (Scouler willow)
Salvia mellifera Greene (Black sage)
Sambucus callicarpa Greene (Pacific red elder)
Solanum umbelliferum Eschs. (Blue witch)
Symphoricarpos mollis Nutt. in T. & G. (Spreading snowberry)
S. rivularis Suksd. (Snowberry)
Vaccinium ovatum Pursh (California huckleberry)

Ferns

Adiantum jordanii C. Muell. (California maidenhair)
Dryopteris arguta [Kaulf.] Watt (Coast woodfern)
Pityrogramma triangularis [Kaulf.] Maxon (Gold-
 enback fern)
Polypodium californicum Kaulf. (California polypody)
Polystichum munitum [Kaulf.] Presl (Sword fern)
Pteridium aquilinum [L.] Kuhn var. *lanuginosum* [Bong.] Fern. (Bracken fern)

Forbs

Achillea borealis Bong. ssp. *arenicola* [Heller] Keck (Yarrow)
A. borealis Bong. ssp. *californica* [Pollard] Keck (Yarrow)
Arnica discoidea Benth. (Coast arnica)
Astragalus nuttallii [T. & G.] J. T. Howell (Milk-vetch)
Brodiaea Sm. sp. (Brodiaea)
A. crocea [Wood] Wats. (Golden brodiaea)
B. pulchella [Salisb.] Greene (Blue dicks)
Calochortus albus Dougl. ex Benth. (Fairy lantern)
Castilleja affinis H. & A. (Scarlet cup)
Chenopodium californicum [Wats.] Wats. (California goosefoot)
Chlorogalum pomeridianum [DC.] Kunth (Amole soapplant)
Chrysanthemum segetum L. (Corn chrysanthemum)
Cirsium occidentale [Nutt.] Jeps. (Western thistle)
Convolvulus cyclostegius House (Morning-glory)
Corethrogyne DC. sp. (Cottonaster)

Cynoglossum grande Dougl. ex Lehm. (Western hound's tongue)
Daucus pusillus Michx. (Rattlesnake weed)
Dentaria californica Nutt. (Toothwort)
Dudleya farinosa [Lindl.] Britt. & Rose (Bluff lettuce)
Erechtites arguta [A. Rich.] (New Zealand fireweed)
E. prenanthoides [A. Rich.] DC. (Australian fireweed)
Erigeron glaucus Ker. (Seaside daisy)
Eschscholtzia californica Cham. (California poppy)
Fragaria californica Cham. & Schlecht. (Wood strawberry)
Franseria chamissonis Less. spp. *bipinnatisecta* [Less.] Wiggins & Stockw. (Bursage)
Galium aparine L. (Goose grass)
G. californicum H. & A. (California bedstraw)
G. nuttallii Gray (Nuttall bedstraw)
Gnaphalium chilense Spreng. (Cotton-batting plant)
G. purpureum L. (Purple cudweed)
G. ramosissimum Nutt. (Pink everlasting)
Grindelia robusta Nutt. (Gum-plant)
Heracleum lanatum Michx. (Cow-parsnip)
Hesperocnide tenella Torr. (Hesperocnide)
Hieracium albiflorum Hook. (White hawkweed)
Horkelia Chain. & Schlecht. sp. (Horkelia)
Iris douglasiana Herb. (Mountain iris)
Lathyrus torreyi Gray (Torrey peavine)
L. vestitus Nutt. ex T. & G. ssp. *bolanderi* [Wats.] C. L. Hitchc. (Bolander peavine)
Lomatium parvifolium [H. & A.] Jeps. (Hog-fennel)
Lotus heermanii [Dur. & Hilg.] Greene (Bird's-foot trefoil)
L. scoparius [Nutt. in T. & G.] Ottley (Deer-weed)
Madia capitata Nutt. (Tarweed)
L. elegans D. Don (Common madia)
Marah fabaceus [Naud.] Greene (California big-root)
Mesembryanthemum L. sp. (Ice plant)
Montia perfoliata [Donn] Howell (Miner's-lettuce)
Pedicularis semibarbata Gray (Lousewort)
Phacelia malvifolia Chain. (Stinging phacelia)
Ranunculus californicus Benth. (California buttercup)
Sanicula crassicaulis Poepp. ex DC. (Gamble weed)
S. laciniata H. & A. (Coast sanicle)
Satureja douglasii (Benth.) Briq. (Yerba Santa)
Scrophularia californica Cham. & Schlecht. (Figwort)
Sidalcea malvaeflora [DC.] Gray ex Benth. (Checker bloom)
Silene laciniata Cay. ssp. *major* Hitchc. & Maguire (Mexican silene)
Sisyrinchium bellum Wats. (Blue-eyed grass)
Smilacina stellata [L.] Desf. var. *sessilifolia* [Baker] Henders. (Star-flower)
Solidago californica Nutt. (California goldenrod)
S. spathulata DC. (Coast goldenrod)
Stachys bullata Benth. (Puffnettle betony)
Trientalis latifolia Hook. (Star-flower)
Trillium sessile L. var. *chloropetalum* Torr. (Rock lily)

Vicia americana Muhl. (American vetch)
V. benghalensis L. (Vetch)
Viola quercetorum Baker & Clausen (Violet)
Xerophyllum tenax [Pursh] Nutt. (Bear-grass)
Zigadenus fremontii Torr. (Star-lily)

Sedges

Carex L. sp. (Sedge)
C. globosa Boott (Sedge)

Grasses

Agrostis diegoensis Vasey (Thingrass)
A. semiverticillata [Forsk.] C. Chr. (Water bent)
Aira caryophyllea L. (Silver hairgrass)
Avena fatua L. (Wild oat)
Briza maxima L. (Big quaking grass)
A. media L. (Perennial quaking grass)
B. minor L. (Little quaking grass)
Bromus carinatus H. & A. (California brome)
B. laevipes Shear. (Chinook brome)
B. orcuttianus Vasey (Orcutt brome)
B. rigidus Roth (Ripgut grass)
B. rubens L. (Foxtail chess)
Calamagrostis nutkaensis [Presl] Steud. (Pacific reedgrass)
A. rubescens Buckl. (Pinegrass)
Danthonia californica Bol. (California oatgrass)
Deschampsia caespitosa [L.] Beauv. (Tufted hairgrass)
A. danthonioides [Trip.] Munro ex Benth. (Annual hairgrass)
D. elongata [Hook.] Munro ex Benth. (Slender hairgrass)
Distichlis spicata [L.] Greene *stricta* [Tory.] Beetle (Desert saltgrass)
Elymus condensatus Presl (Giant wild-rye)
E. glaucus Buckl. (Blue wild-rye)
Festuca californica Vasey (California fescue)
F. dertonensis [All.] Asch. & Graebn. (Brome fescue)
F. microstachys Nutt. (Small fescue)
F. myuros L. (Rattail fescue)
Hierochloa occidentalis Buckl. (California sweetgrass)
Holcus lanatus L. (Velvet grass)
Hordeum californicum Covas & Steb. (California barley)
H. jubatum L. (Foxtail barley)
H. murinum L. (Mouse barley)
Koeleria cristata [L.] Pers. (Junegrass)
Lolium perenne L. (Perennial ryegrass)
L. temulentum L. Darnel (Darnel ryegrass)
Melica imperfecta Trin. (California melic)
Monerma cylindrica [Willd.] Coss. & Dur. (Thintail)
Phalaris californica H. & A. (California canarygrass)
Poa annua L. (Annual bluegrass)
P. douglasii Nees (Douglas bluegrass)
P. stenantha Trin. (Trinius bluegrass)
Polypogon interruptus HBK. (Ditch polypogon)
P. monspeliensis [L.] Desf. (Rabbitfoot grass)
Stipa lepida Hitchc. (Foothill needlegrass)
S. pulchra Hitchc. (Purple needlegrass)

Animals, birds, insects, and fungi also are parts of the biotic habitat conditions under which Mon-

terey pine reproduces, grows, and dies. Each plays some role in the life history of the tree.

Life History

Seeding Habits

Flowering and Fruiting

Monterey pine flowers in late winter or early spring. Female flowers are borne in whorls, or nodal clusters, of three to seven on both the main stem and branches where they may be either subterminal or lateral (Lindsay [1932]). This pine is multinodal, usually producing one to three nodes each year. Consequently one to three clusters of cones also are produced.¹⁴

Male flowers usually are produced on side branches. Pollination seems to be most effective during the first week after the female flowers are fully open, and continues to be reasonably effective through the second week. Viable seed has been produced by both intraspecific crossings and in selfings (Pawsey 1961).

Cones seem to develop only after receiving viable pollen, even though that pollen may be incapable of producing seed (Pawsey 1961). Non-pollinated conelets wither and die in 3 months or less. Some normal-appearing mature cones have been found to contain only empty seeds or wings.

Cones mature in the autumn of the second season. They often open during the first warm days in the following spring.

Seed Production

Monterey pine is a prolific, and sometimes precocious, annual seeder. Female conelets occasionally are produced by 4-year-old seedlings, but trees raised vegetatively commonly begin to produce cones when 3 years old (Pawsey 1950). Generally, however, trees of good vigor do not produce abundant cones until they are 15 to 20 years old, or considerably older if the timber stand is dense (Goudie 1925; MacDonald *et al.* 1957).

The number of cones accumulated over several years on one tree about 55 feet tall was estimated as not less than 6,100 (Jepson 1910). Each cone produces from 120 (Adams 1950) to 200 (Fielding 1964; Scott 1960) seeds.

The size of cones and seeds varies considerably. Young trees bear cones substantially larger than those on older trees (Fielding 1953). Cone size also is related to heredity, position in the crown, and tree vigor (Fielding 1964). Larger cones produce larger and heavier seeds (Healy 1940).¹⁵ The number of seeds per pound ranges from 12,000 to 23,000, averaging 16,000 (Goudie 1925; U.S. Forest Service 1948). Commercial seed should be 98 percent pure and 95 percent sound (U.S. Forest Service 1948).

Seed viability is high and persistent (Sudworth 1908), and is about the same regardless of seed size (Healy 1940), averaging between 70 and 80 percent. Viability as high as 94 percent has been reported (Mirov 1946). Badran¹⁶ reported germination of seeds from current year's cones to be 78 percent, dropping in a straight-line relationship with increasing age to 53 percent for seeds from cones remaining on trees for 11 years.

Extracted seeds can be stored under a wide range of conditions for 10 or 11 years with little loss in viability (Allsop 1953). Seed in cold storage for 14 years was 81 percent viable (Mirov 1946), and seed lots stored 16 and 21 years retained viabilities of 66 and 86 percent, respectively (Schubert 1952).

Not all Monterey pine cones survive to maturity. Adults of the Monterey pine cone beetle (*Conophthorus radiatae* Hopk.) attack the green second-year cones in spring by girdling the axis of the cone near its base, and then extending a gallery distally along the cone axis. This injury prevents further cone development. Insect damage to cones in natural stands has been limited so far to the Monterey area, where it has varied by location from light to 100 percent (Ruckes 1958; Schaefer 1962).

Unusual climatic conditions, especially where Monterey pine grows as an exotic, can also affect seed production. In Australia, for example, a loss in the number of cones bearing viable seed has

¹⁴ Badran, Osman Adly. *Maintenance of seed viability in closed cone pines*. 1949. (M.S. thesis on file at Univ. Calif., Berkeley.)

¹⁶ Forde, M. B. *Op. cit.* See footnote 2.

been attributed to summer drought (Pawsey 1960a).

Seed Dissemination

Monterey pine cones may be opened by fire (Sudworth 1908), but lacking this agent, generally remain attached to trees for many years, and usually do not release all their seeds during the first year after maturing. Cones open when their moisture content is reduced to less than 20 percent (Fielding 1947). Cone opening without fire generally requires blocking of the water supply. This blockage occurs naturally by secretion of resin in the vascular tracheids of the peduncle (Allen and Wardrop 1964).

Cones sometimes remain closed several years. In exposed, sunny positions, however, they may open a year or two after ripening (Dallimore and Jackson 1923). Cones also open sooner when they are unsheltered from the hot, dry winds which occasionally blow from the interior valleys. Few cones remain closed longer than 6 years.¹⁷

After their initial opening, cones close and open repeatedly, depending upon air temperatures and relative humidities. Weather conditions which dry the cones occur most often in September and October or in the spring. Some seeds usually are shed each time the cones open. Consequently the oldest cones contain few seeds.

Seeds are dispersed by wind and gravity (U.S. Forest Service 1948) for distances of 130 to 200 feet (Jolliffe 1940-41). Other factors, such as rodents and birds, do not help significantly in seed distribution.

Several birds and mammals have been reported as ravenous consumers of Monterey pine seed. In fall, large flocks of common crows (*Corvus brachynchos*)¹⁸ and numerous Steller's jays (*Cyanocitta stelleri*) and California jays (*Aphelocoma coerulescens*) as well as smaller seed-eating birds, feast on the fallen seeds. The California mouse (*Peromyscus californicus californicus* [Gambel]), deer mouse (*P. maniculatus gambelii* [Baird]), dusky-footed wood rat (*Neotoma fucipes luciana* Hooper), California ground squirrel (*Spermophilus beecheyi beecheyi* [Richardson]), western gray squirrel (*Sciurus griseus nigripes* Bryant), western spotted skunk (*Spilogale gracilis phenax* Merriam), striped skunk (*Mephitis mephitis holzneri* Mearns), raccoon (*Procyon lotor psora* Gray), and gray fox

(*Urocyon cinereoargenteus townsendi* Merriam) are listed as Monterey pine seed eaters,¹⁹ although some of these animals seem unlikely.

Vegetative Reproduction

Monterey pine generally does not reproduce naturally by sprouts, but some instances of this happening in New Zealand have been reported (Lindsay [1932]). Sprouting in natural stands has not been recorded.

Cuttings of Monterey pine root easily if selected with care. Those rooting best are cut from first order branchlets (Sherry 1942) and from young trees. Cuttings from trees under 12 years old have rooted well (Thulin 1957), but slips from trees 2 to 7 years old seem preferred.²⁰ However, 60 percent of the cuttings from 20-year-old trees rooted when the basal cuts were in wood not more than 1 year old (Allsop 1953). In one study, branches with terminal buds bearing male cone primordia failed to root (Jacobs 1939).

The best time for collecting cuttings from 5- to 7-year-old trees is after the overwintering terminal buds are formed. And cuttings from the sunny side of the trees, where growth is most vigorous, are desirable. The best slips from 2- to 4-year-old trees are cut in spring from the first laterals after they have developed woody tissue (Allsop 1950).

Rooting success of Monterey pine cuttings has been as high as 95 percent. In this case slips were taken by pulling the branchlets from the top whorl of 2-year-old seedlings. When the stock was planted out after 14 months the root systems produced were as good as those of seedlings. Field survival (88 percent) and rate of growth (20 feet in five seasons) also compared favorably to the performance of seedlings (Field 1934).

Other experience indicates that planting stock raised from cuttings is not as hardy as seedling stock and requires more care in handling. Nevertheless, survival in plantations of bare-rooted plants propagated from cuttings was more than 90 percent (Pawsey 1950).

Single leaf-fascicles also can be set and raised successfully for planting stock (Pawsey 1950).

Limited observations suggest that trees vary in their ability to produce cuttings which root and that this variation is inherent (Duffield and Liddicoet 1949).

¹⁷ Badran, O. A. *Op. cit.* See footnote 14.

¹⁸ Scientific names of birds from Peterson (1961).

¹⁹ Coleman, George A: *Op. cit.* See footnote 11.

²⁰ Allsop 1950; Cutten 1946; Jacobs 1939; Mirov 1944; Sherry 1942.

Grafting Monterey pine by the single cleft method has been successful. Healthy unions are produced regularly by 80 to 90 percent of the grafts attempted (Thulin 1957).

Seedling Development

Establishment

Monterey pine seed germination is epigeous and relatively fast and complete without stratification (Bibby 1953). Germinative capacity averages about 60 percent, but may be higher than 89 percent (U.S. Forest Service 1948).

Although not necessary for good performance of seed, stratification increases the amount and rate of germination (Bibby 1953). In one case the germination for seeds stratified at 40° F. for 2 months was 89 percent after 15 days compared to 41 percent for unstratified seed (Grose 1958). The same treatment for half the time also hastened germination (Allsop 1952). In another instance stratification at 38° F. for varying periods of 3 to 28 days, or soaking at room temperature for 3 days, significantly increased the germination rate. Soaking for 7 to 14 days increased the speed of seed germination even more (Rodger 1957).

Temperature is another agent that influences germination of Monterey pine seed. The day-night temperature combinations cited as best for germination are, respectively: 80° F. and 60° F. (U.S. Forest Service 1948), 77° F. and 68° F. (Allsop 1952), and 72° F. and 64° F. (Allsop 1953). Germination capacity at a constant 68° F. was 25 percent greater than at 77° F. (Jacobs [1961]).

Natural reproduction generally is obtained easily after clear-cutting (Ure 1949), but several factors can play significant roles. For example, the density of reproduction can be reduced greatly by dense slash (Fielding 1947). The distribution of natural reproduction can be improved sometimes by scattering the slash (Chapman 1949a), and light slash has improved seedling survival and early growth. Another important factor in obtaining natural reproduction in Australia is the season of felling. Regeneration cuttings are most successful when timber is felled immediately after seed fall, and least successful when cuttings are completed just before seed fall (Fielding 1947). Microtopography also has influenced the number and growth of young trees (Thomson and Prior 1958). The requisites for abundant reproduction under exotic stands include mineral soil, negligible competition from other plants, and no serious drought (Chap-

man 1949b), although Monterey pine seedlings have been called drought-hardy (Adams 1951). Where conditions are favorable 1,000 to 10,000 seedlings per acre are not uncommon 2 years after logging (Hinds 1951; Kennedy 1957; Lindsay [1932]). On one area 10 feet square, more than 600 4-year-old seedlings were counted (Jepson 1910).

Clearcutting in exotic Monterey pine stands in areas of high rainfall may result in reproduction that is too dense. When this condition is likely, regeneration can be regulated by partial cutting that controls the amount of sunlight reaching the ground. When logging leaves 70 or more stems per acre, regeneration is sparse. If only 50 stems are reserved, regeneration is prolific (Anon. 1956a).

Some natural reproduction grows under the canopy of mature Monterey pines. In most stands this consists of spindly, isolated seedlings or saplings, but a dense understory of young pines can be found occasionally (Lindsay [1932]). Seedlings can get a start because the desirable seedbed and light conditions are not necessary for germination and early growth. For example, the best seedbed is a moist mineral soil, but many seedlings begin growth where pine litter is several inches deep (Lindsay [1932]). Maximum development of seedlings seems to require full sunlight, but the amount of light under the canopy of a fully stocked mature stand is not reduced enough to inhibit early growth. The critical factor in survival of reproduction under existing stands is soil moisture (Moulds 1955).

Monterey pine often becomes established under the canopy of California live oak. Successful penetration of the oak canopy by pine poles is evidence that the oaks act as nurse trees (Lindsay [1932]). Pine seedlings also invade grasslands. They can compete with annuals, but have difficulty becoming established in perennial grasses (Pryor 1941).

Dense reproduction almost always becomes established after Monterey pine stands are burned (King 1925; Lindsay [1932]; Sudworth 1908). Fires open the cones so that all available seed are shed on ideal, weed-free seedbeds, and standing dead trees provide a changing shade pattern like a lath house. Seedlings under exotic fire-killed stands number 500,000 (Entrican 1960; Hinds 1951; Kennedy 1957) to more than 1,000,000 per acre (Fenton 1951; MacArthur 1952).

New seedlings bear 5 to 10 cotyledons with 7 prevalent. First growth produces a shoot with

primary needles, but secondary needles in fascicles of three appear when the plant is a few months old. Both primary and secondary needles are produced until the plant is about 3 years old (Lindsay [1932]).

No information on mycorrhizal symbionts in natural stands of Monterey pine has been published (Offord 1964). Several mycorrhizal fungi are native to California, however. Fungi proved or suspected of forming mycorrhizae in exotic Monterey pine stands have been listed by several authors.²¹ The mycorrhizal fungi associated with Monterey pine have been compiled (Trappe 1962). They are:

Amanita muscaria (Fr.) Hooker
Cenococcum graniforme (Sow.) Ferd. & Winge
Gomphidius rutilus (Fr.) Lund. & Nanf.
G. vinicolor Peck
Inocybe lacera (Fr.) Kumm.
Laccaria laccata (Fr.) Berk. & Br.
Lactarius deliciosus (Fr.) S. F. Gray
Rhizopogon luteolus Fr. & Nordh.
R. roseolus (Corda) Hollos
R. rubescens Tul.
Scleroderma aurantium (Vaill.) Pers.
R. bovista Fr.
Suillus granulatus (Fr.) O. Kuntze
S. luteus (Fr.) S. F. Gray
S. piperatus (Fr.) O. Kuntze
S. subaureus (Peck) Snell

Cantharellus cibarius Fr. and *Marasmius oreades* Fr. are two additional mycorrhizal symbionts of Monterey pine which have been reported from Spain.²²

The Monterey pine seedling grows a tap root. On poor sites this is almost the only root produced. In coarse-textured, rich soils, however, the tap root may produce as many as a dozen side roots per inch. Mycorrhizal associations with the roots in the top 4 inches of soil appear necessary for rapid growth (Adams 1951; Kessell 1943).

Early Growth

Monterey pine seedlings are fairly large when they emerge from the ground and growth is rapid. Both tops and roots develop best when seedlings get full light (Baker 1945). Root systems of new seedlings are small compared to tops. Although

seedlings are supported at first by tap roots, this form of root system usually disappears as extensive lateral roots expand.

Nutrient requirements of seedlings are not high. A solution containing 100 p.p.m. of nitrogen, 1 p.p.m. of phosphorous, 10 p.p.m. of potassium, and 10 p.p.m. of magnesium provided enough minerals to maintain good growth. Adequate supplies of nutrients are available when foliar analyses show contents of 1.6 percent nitrogen, 0.1 percent phosphorous, 1.1 percent potassium, and 0.11 percent magnesium (Will 1961).

Trees one year old may be over 12 inches tall. Three-year-old trees generally measure 3 to 6 feet in height (Goudie 1925; Fenton 1951). Some individuals this age are 9 to 10 feet, however, and 10 inches in diameter 6 years after planting (Anon. 1957a).

Many examples of fast growth have been reported. One 6-year-old tree grew 8 feet in height; another grew 13 feet (Jepson 1910). A tree in an Australian plantation grew 20 feet in its fifth year to reach 30 feet (Stoate 1920-22).

Although plants established from cuttings are smaller in diameter than seedlings of the same height during the first 3 or 4 years (Pawsey 1950), their growth catches up. For example, mean annual growth for 7-year-old cuttings planted in light, well-drained sand in New Zealand were 0.97 inches in diameter and 4.4 feet in height (Field 1934).

Young stands can modify sites in short periods. In Chile a plantation of Monterey pines spaced 2 x 2 meters had produced a litter cover sufficiently deep to prevent erosion and to create favorable infiltration characteristics within 5 to 6 years (Roberts 1957).

Seasonal Growth

Monterey pine in its natural range generally begins height growth in February or March when the mean temperature reaches 51 to 53° F. Other conifers in the same area begin growth later. The pines grow fastest between February and June when mean temperatures vary from 51 to 61° F., and the mean maximums range from 62 to 75° F. Growth stops in September or October when available soil moisture is depleted (Lindsay [1932]). This level of soil moisture seems to be near 5.7 to 6.1 percent (Anon. 1929; Lindsay [1932]). When winter rains begin the temperatures are too low for trees to resume rapid growth. Although

²¹ Birch 1937; Clements 1938; Cromer 1935; Dos Santos de Azevedo 1959; Morrison 1957; Rawlings 1951, 1960; Walker 1931.

²² Martinez, Jose Benito. *Third annual report of progress of research sponsored by P. L. 480*. 1963. (Unpublished report to Inst. Forest. Invest. Expt., Madrid.)

double growth rings are common in Australia, they are rare in California (Lindsay [1932]).

The annual height growth pattern of Monterey pine as an exotic varies from place to place and depends upon seasonal variations of climate and inherited characteristics (Fielding 1955). Seasonal growth begins in Australia when solar radiation reaches 400 gram-calories per square centimeter per month. Thereafter, growth is intimately related to the amount of rainfall (Anon. 1929). Growth is least in winter and summer, greatest in spring, and relatively uniform in the fall. The growing season lasts, on the average, 10 months. The dormant periods do not correspond to either the coldest or warmest periods (Jacobs [1961]).

In New Zealand little or no snow falls in the plantation areas and Monterey pine does not decrease growth appreciably during the winter (Baigent 1956). The growth of summer wood continues for at least 10 months in the North Island, but not quite as long in the South Island (Chapman 1949a).

The most detailed growth observations of Monterey pine originate from Canberra, Australia. Here shoot elongation begins in late winter and increases in rate until grading into a burst of spring growth. Spring growth of most shoots stops more abruptly than it begins, but growth slows in a short transition period. Shoots can be called dormant only for a few weeks immediately following spring growth. Although most shoots are relatively dormant during late summer, fall, and winter, they elongate appreciably and some grow actively during this period (Fielding 1955).

Sapling Stage to Maturity

Growth and Yield

In native stands Monterey pine is a moderately large tree; it varies in height from 32 to 124 feet, but generally is 70 to 110 feet tall, and from 2 to 3 feet in diameter at maturity. Occasionally it may exceed 5 feet in diameter (Dallimore and Jackson 1923; Lindsay [1932]; U.S. Forest Service 1908). Heights of 100 to 120 feet are regarded as good in Australia. Exceptional growth of 145 to 155 feet at 40 to 50 years has been measured in New Zealand and South Africa (Lindsay [1932]), and of 185 feet for mature trees in New Zealand (Chapman 1949a).

Trees vary widely in many characteristics. Some of these are growth rate, wood density, trunk form, branching habit, and abundance of cones (Ban-

nister 1962; Fielding 1953, 1960). In dense stands, however, boles tend to be reasonably straight with little taper; and crowns are narrow and remain pointed for 35 to 45 years before rounding off and becoming flat. For example, trees 90 to 110 feet high may have crowns only 15 to 30 feet wide and clear boles of 25 to 50 feet. Open grown trees develop wide, irregularly and excessively branched crowns (Lindsay [1932]).

Stand density also determines the length of green crowns. Trees 36 to 40 years old and 70 to 100 feet high may have green crowns on one-sixth to one-fifth of the total tree heights when in dense stands, compared to one-third or one-half the total height when open grown (Lindsay [1932]).

Boles may have many irregularities, especially in understocked stands. They may be elliptical or irregular in cross-section, with sweep, crooked, or leaning. And trees may have double leaders or bayonet tops, (Lindsay [1932]). Studies of Monterey pine stands developed from different initial spacings ranging from 6 to 11 feet found that bole crookedness and lean were not influenced by spacing (Rodger 1957).

Roots of mature trees are superficial (Wendelken 1955). They generally do not penetrate deeper than 2 feet, and are usually found in the top 12 inches of soil, but this lateral system is widespreading and strong (Lindsay [1932]). The large roots extend 30 to 40 feet from the tree²³ and interlock with roots of other trees in the stand (Wendelken 1955). Root grafting is common (Adams 1940; Rawlings and Wilson 1949; Pawsey 1962). Another feature of the Monterey pine root system is the reinforcing development of wood between horizontal roots and stems. These developments appear as swellings at ground level. They act as brackets and, with the rest of the root system, create windfirm trees. Growth of both brackets and lateral roots is stimulated by wind movement (Pryor 1937).

Young Monterey pine grow quickly; internodes 3 to 6 feet long are common on trees 5 to 15 years old (Lindsay [1932]). Height growth culminates on poorer sites as early as 15 years (Larsen 1915), but on better sites usually remains fast for the first 30 to 40 years. It slows considerably at 50 to 60 years.

²³ Larsen, Louis T. *Monterey pine*. 14 pp. 1914. (Unpublished report on file at Pacific SW. Forest and Range Exp. Sta., U.S. Forest Serv., Berkeley, Calif.)

Native stands on average to good soil conditions will be 30 to 40 feet high at 10 years, 60 to 65 feet at 20 years, 70 to 90 feet at 30 years, and 90 to 110 feet at 40 years (Lindsay [1932]). Examples of faster height growth are common. In the redwood belt of California many Monterey pines were 30 to 50 feet tall, and 6 to 11 inches in diameter 12 years after planting. The largest tree was over 74 feet tall and 11.3 inches in diameter (Sindel 1963). Annual height growth of 6 to 8 feet over a number of years has been reported for individual trees in an area where height growth averaged 4 feet a year for 22 years (Goudie 1925). In New Zealand the mean heights of trees at 20 years are 98 to 116 feet for site I, 81 to 98 feet for site II, and 63 to 81 feet for site III (Ure 1950).

Monterey pine is short-lived. Its average life is not more than 80 or 90 years, and a tree rarely lives beyond 150 years (Lindsay [1932]). Its ultimate height may be reached in 35 to 40 years (Lindsay [1932]). Full size is attained in 80 to 100 years (Sudworth 1908), but the tree may be mature on poor sites at 40 years.

Generally understocked mature native stands average less than 20,000 board feet per acre. Better stocking produces significantly higher yields. One 50-year-old stand considered better than average had 165 trees and 35,000 board feet per acre. These trees averaged 15.5 inches in diameter and 84 feet high (Larsen 1915). Another stand on a good site had 43,000 board feet per acre at 25 years. The trees were 77 feet tall, 14.1 inches in diameter, and numbered 270 per acre.²⁴ The heaviest stand measured near Monterey contained 195 trees and 120,000 board feet per acre. The average tree was 20.3 inches in diameter and 94 feet tall (Larsen 1915).

Data from New Zealand show that Monterey pine can produce yields higher than those measured in native stands. For example, stands 35 to 40 years old yield 50,000 to 60,000 board feet per acre (Chapman 1949a). At 40 years a fully stocked stand on good soil had 10,000 to 12,000 cubic feet of timber per acre (Wilson 1923). Another New Zealand stand that had not been thinned produced 10,000 cubic feet per acre at 26 years. The trees averaged 120 feet high and 200 to 250 per acre (Ure 1949). Finally, a volume of 21,730 cubic feet per acre was produced

by a 58-year-old stand that was originally planted at a 9 foot spacing, and unthinned. Each acre had 103 crop trees and 557 square feet of basal area. The average tree height was 135 feet (Blithe 1953).

Reaction to Competition

The tolerance of Monterey pine probably depends upon site factors and age. Although ratings have ranged from "very tolerant" to "intolerant," Monterey pine appears more tolerant than any other pine in western America. Foresters in California judged the tree "intermediate," the middle class in a scale of five broad divisions (Baker 1949, 1950). Reasons cited for judging Monterey pine tolerant are the occasional ability of reproduction to become established and to grow under a mature stand to form a two-storied forest (Lindsay [1932]), good growth in dense stands (Sudworth 1908), and the persistence of limbs and foliage in dense stands.²⁵

Monterey pine has been recognized as less tolerant in Australia (Lindsay [1932]). And its intolerance to shade in New Zealand, resulting in absence of advance reproduction under either closed or partially closed canopies, has been described as a conspicuous feature (Baigent 1956).

Even where tolerant in youth, trees become less tolerant as they grow older. The crowns of mature Monterey pines require full light.²⁶

Under some conditions Monterey pine seedlings can not compete against a dense ground cover (Kennedy 1957). Generally, however, they dominate and suppress weeds or scrubby growth (Crutwell [Crutwell] 1953; Goudie 1925).

Monterey pine's ability to differentiate well-spaced dominant trees in dense stands is well known. Some trees emerge above the general canopy level early in life and quickly suppress competitors, eliminating any possibility of stagnation.^{27 28} Trees that remain dominant grow with little set-back (Crutwell [Crutwell] 1953). Many plantations in New Zealand thin themselves so effectively that their final yield is almost equal to that from stands thinned repeatedly (Chapman 1949a; Ure 1949).

Monterey pine is not self-pruning. Its branches remain tough indefinitely, although stubs left on

²⁴ Larsen, Louis T. *Op. cit.* See footnote 23.

²⁵ Larsen, Louis T. *Op. cit.* See footnote 23.

²⁶ Larsen, Louis T. *Op. cit.* See footnote 23.

²⁷ Harrison-Smith 1956; Hinds 1951; Kennedy 1957; Lewis 1957; MacArthur 1952.

²⁸ Coleman, George A. *Op. cit.* See footnote 11.

trees after thinning may rot and sometimes brush off readily from trees 35 to 45 years old in thinned stands (Bednall 1957).

Some young stands of Monterey pine, especially those regenerated after fire, have excessive stocking of more than 500,000 trees per acre and require early thinning (Chapman 1951). The first thinning may be best when the trees are 3 or 4 years old and about 5 feet tall (Anon. 1957b; Fenton 1951; Ure 1949). Response to early thinning sometimes is slow (Adams 1940), but thinning generally produces quick and impressive results (Rankin 1936).

Older stands will respond to thinning either from above or from below (Lewis 1957). Opportune thinning can reduce cutting cycles, produce higher quality timber, and reduce danger from fires, insects, fungi, and windfall (New Zealand Forest Service 1955; Robertson 1951). Response in diameter growth appears the first year. Thinning at 17 years, for example, increased annual diameter growth almost immediately from ¼ to 1 inch (Harrison-Smith 1957). All trees respond more to severe thinning than to light thinning, and larger trees respond more than smaller trees (Jacobs 1962). Periodic thinning can maintain vigorous growth in some stands until the 60th or 70th year (Anon. 1956b).

Proposed thinning schedules for Monterey pine are as follows:

Levels of stocking recommended for: Kenya, ¹ South Africa, ² and New Zealand ^{3,4} Chile ⁵		
Age (years):	(number of trees)	
2-3	1,000	
5-10	240-350	810
12-13	200	
14-15	150	610
18-20	80-125	
25	80-100	280-365

¹ Pudden 1957.

² King 1951.

³ Anon. 19576.

⁴ Ure 1949.

⁵ Robertson 1951.

The natural Monterey pine forests seem to be a stable vegetational type at Monterey and Cambria. The marked control of pines by soil types at both Monterey and Cambria also indicate Monterey pine is an edaphic climax, although the effects of fog and sea must not be overlooked (Lindsay [1932]).

Principal Enemies

Monterey pine has many enemies, both as a native tree and as an exotic. One survey at Monterey showed more than 10 percent of the trees

and 20 percent of the seedlings and saplings were diseased (Lindsay [1932]). Some other native stands are worse.

Over 70 pathogens recently have been listed as occurring in native stands and plantations of Monterey pine in western North America. Of these, about 49 percent are saprophytes, 35 percent wound parasites, and 16 percent obligate parasites. Of the 86 other pathogens found on exotic Monterey pines, nearly 44 percent are classed as saprophytes, 31 percent as wound parasites, and 10 percent as obligate parasites; and pathogenicity was not classified for 15 percent (Offord 1964).

The most important pathogens in native stands and West Coast plantations are (Offord 1964):

Stem Diseases

Western dwarfmistletoe (*Arceuthobium campylopodum* f. *typicum* [Engelm.] Gill).—Trees of all sizes, including seedlings, are damaged, deformed, or killed. Not found at Swanton.

Coastal gall rust (*Peridermium cerebroides*²⁹ Meinecke).—Damaging at Cambria, Monterey, and Swanton, and in plantations throughout central coastal California.

Western gall rust (*P. harknessii* J. P. Moore).—Found in Oregon, Washington, and British Columbia, and in some plantations in California. Both gall rusts retard the growth of infected stems and kill some trees.

Root Diseases

Fomes root rot (*Fomes annosus* [Fr.] Cke.).—This most important root disease is especially damaging to trees of low vigor growing on thin, poorly drained, and heavy soils.

Shoestring fungus rot (*Armillaria mellea* [Vahl.] Quél.).—Widely distributed where oaks are present, but causes small losses only.

Velvet top fungus (*Polyporus schweinitzii* Fr.). Occurrence is widespread. Often associated with vigorous young trees.

Foliage Diseases

Needle rust (*Coleosporium madae* [Syd.] Arth.).—A heteroecious rust whose alternate hosts, the tarweeds (*Madia* spp.), are suppressed with increased age and density of pine regeneration.

Twig blight (*Diplodia pinea* [Desm.] Kickx).—Rarely found on native trees but a major twig blight on injured exotic Monterey pines, especially those wounded by hailstones.

²⁹ A nomen nudum as described by Meinecke (1929); has not yet been described validly as a species.

Needle cast (*Hypoderma pedatum* Darker).

Needle cast (*Hypodermella limitata* Darker).

Needle cast (*Lophodermium pinastri* [Fr.] Chev.).—Usually a mild parasite but can become damaging when winters are mild and summers hot.

Needle cast (*Naemacylus niveus* [Fr.] Sacc.).—The most widespread and damaging needle cast in the areas of native Monterey pine.

A needle blight, *Dothistroma pini* Hulbary, has been destructive in Monterey pine plantations of East Africa (Offord 1964). Although this disease has not yet been reported on Monterey pine in California, it has been identified recently on several other conifers in the Western United States.

As an exotic, Monterey pine often is relatively free of diseases. Incidence of tree diseases is light, for example, in an extensive region in New Zealand, where more than 30 inches of rain fall each year (Crutwell [Crutwell] 1953). When introduced, Monterey pine thrives best in climates similar to coastal central California. Pathological troubles become increasingly important as the climate diverges from the dry summers and wet winters of the native range (Rawlings 1957).

Pathogens reported most often for exotic Monterey pine are:

Shoestring fungus rot (*Armillaria mellea*).—Reported from Chile, Great Britain, Kenya, New Zealand, and Spain.^{30 31}

Twig blight (*Diplodia pinea*).—Attacks favored by overmature trees, overcrowded forests and poor tree vigor resulting from excessive competition for soil moisture, warm humid weather, and tree injury by leaf-sucking insects, frosts, or hail. Found in Argentina, Australia, Chile, New Zealand, Union of South Africa, Southern Rhodesia, and Spain.³²

Needle cast (*Lophodermium pinastri*).—Attacks are favored by cool wet summers and mild wet winters. Identified in New Zealand, Union of South Africa, and Spain.³³

Needle cast (*Naemacylus niveus*).—Found in

Kenya, New Zealand and Spain (Gibson 1962; New Zealand Forest Service 1960; Scott 1960).

Twig canker (*Phomopsis strobil* Syd.).—Important only where unseasonable frosts occur. Reported in Australia and New Zealand.³⁴

Seedling blight (*Phytophthora cactorum* [Leb. & Cohn] Schroet.).—Found in New Zealand (Newhook 1957, 1959).

Root rot (*P. cinnamomi* Rands).—*Phytophthora* spp. epidemics require abnormally early rewetting of soil in the autumn, with wet conditions continuing until spring (Newhook 1959). Poor soil drainage also enhances attacks (Sutherland, Newhook and Levy 1959). The pathogens kill the fine rootlets. Observed in Argentina and New Zealand (Newhook 1957; Scott 1960; Spaulding 1956).

Almost 90 insects found on native Monterey pine have been recorded³⁵ (Burke 1937; Essig 1926; Keen 1952). These pests include a variety of defoliators, sap suckers, needle and twig miners, cambium miners, and wood borers. Although several insects are destructive and often weaken infested trees, only five can be classed as tree killers. They are:

Red turpentine beetle (*Dendroctonus valens* Lee.).—Sometimes confined to fire-injured trees or to trees more than 80 years old,³⁶ but often becomes primary in attacking and killing trees (U.S. Department of Agriculture 1927; Keen 1952), even healthy ones (Essig 1926). Infests stems from near the ground to 20 feet high (Essig 1926).

California five-spined ips (*Ips confusus* [Lee.]).—Is destructive to saplings, poles, young trees up to 30 inches in diameter, and to the tops of mature trees (Keen 1952; Struble 1961).

California four-spined ips (*I. plastographus* [Lec.]).—Often destructive to small and large trees (Essig 1926), and associated with attacks by the Monterey pine ips and the red turpentine beetle (Keen 1952; Struble 1961). Larvae mine the cambium layer.³⁷

Monterey pine ips (*I. radiatae* Hopk.).—Usually attacks weakened trees and works downward from the crown (Essig 1926). Is generally a secondary enemy associated with other bark

³⁰ Birch 1937; Gilmour 1954; Green 1957; Kennedy 1957; New Zeal. Forest Serv. 1955; Rawlings 1948; Scott 1960.

³¹ Martinez, Jose Benito. *Op. cit.* See footnote 22.

³² Anon. 1957b; Bancroft 1911; Birch 1936, 1937; Capretti 1956; Curtis 1926; Eldridge 1957; Ferreirinha 1953; Gibson 1958; Gryse 1955; Hutchinson and Henry 1957; Laughton 1937; Purnell 1956, 1957; Rawlings 1948, 1955; Waterman 1943; Young 1936.

³³ Anon. 1957b; Allsop 1954; Hutchinson and Henry 1957; Rawlings 1955; Scott 1960.

³⁴ Birch 1935, 1937; Rawlings 1955; Scott 1960; Storate and Bednall 1953.

³⁵ Coleman, George A. *Op. cit.* See footnote 11.

³⁶ Coleman, George A. *Op. cit.* See footnote 11.

³⁷ Coleman, George A. *Op. cit.* See footnote 11.

beetles, but may become primary, especially in plantations (Keen 1952; Struble 1961).

Monterey pine weevil (*Pissodes radiatae* Hopk.).—Larvae mine the cambium layer of the tops, stems, or bases (above or below ground) of young trees³⁸ (Essig 1926; Keen 1952).

Other important insects in native stands are:

Spittlebug (*Aphrophora permutata* Uhl.).—The young stages of the spittlebug work on the windward sides of exposed trees in the sand dunes, denude branches, and sometimes injure cones³⁹ (Keen 1952).

Monterey pine cone beetle (*Conophthorus radiatae* Hopk.).—This major pest in central California attacks and aborts second-year cones. It has killed as much as 90 percent of the cones in some stands at Monterey, but has not been found at Cambria or Swanton (Schaefer 1962).

Silver-spotted halisidota (*Halisidota argentata* Pack. var. *sobrina* Str.).—These tent caterpillars feed on the foliage and sometimes denude many branches in protected areas⁴⁰ (Essig 1926; Keen 1952).

Twig beetles of the *Pityophthorus* group, possibly *P. carmeli* Sw. (Keen 1952), are sometimes abundant and destructive. This minute bark-boring insect saps the strength of trees by killing small branchlets.⁴¹

Monterey pine tip moth (*Rhyacionia montana* Busck).—Larvae infest the terminals of Monterey pine (Essig 1926).

Monterey pine midge (*Thecodiplosis piniradiatae* Snow & Mills).—A common and serious pest that can practically denude heavily infested trees (Essig 1926). It works at the bases of newly formed needles and causes them to become swollen and shortened. Heavily attacked twigs are sometimes killed (Keen 1952).

Sequoia pitch moth (*Vespamima sequoiae* Hy. Edw.).—The larvae bore into the cambium layer of branches and boles where they feed and cause the flow of pitch in which they live⁴² (Essig 1926).

Many insects also have been identified in exotic stands of Monterey pine. They include 30 insects

in Australia (Minko 1961), and 7 in South Africa (Tooke 1943) that are capable of causing economic losses. Present attacks are confined mainly to nursery stock and natural regeneration growing under maturing stands.

The two most commonly mentioned insects that attack Monterey pine abroad are:

Hylastes ater Payk., a common bark beetle.—Lives and breeds in recently felled slash and attacks young seedlings.⁴³

Sirex noctilio Fabr., a horntail or wood wasp.—Found in Tasmania and New Zealand. Successful insect attack requires the rapid growth of a symbiotic fungus, which is inoculated into the tree during oviposition; and successful invasion by the fungus depends upon a weakened sap flow within the tree. An insect build-up, therefore, is favored by a series of dry years.⁴⁴ Attacks sometimes only kill trees which should have been removed by earlier thinning (Entrican 1960).

No animals have been reported as serious pests in native Monterey pine forests. Some young trees in plantations in California have been browsed. And some have been broken or girdled by rubbing by the Columbia black-tailed deer (*Odocoileus hemionus columbianus* (Richardson)); and others have had bark removed from limbs by the dusky-footed woodrat (*Neotoma fucipes monochroua* Rhoades) (Sindel 1963). In general, mice, rats, rabbits, hares, opossums and deer have caused minor damages overseas (Crutwell [Crutwell] 1953; Davis 1942; Goudie 1925). But in South Australia, rabbits—unless controlled—can cause severe seedling losses (Fielding 1947).

Fire is one of the enemies of Monterey pine. Young trees, with their thin bark are especially susceptible to fire damage, and older trees are easily scorched (Lindsay [1932]; Pryor 1940). Fire risk is always grave in plantations (Anon. 1956a). Pruning in young stands to a height of 7 to 8 feet is a desirable measure for fire protection. Otherwise, the lower limbs persist and become festooned with needles, creating a situation ideal for crowning fires. Removal of the lower limbs helps to keep a fire on the ground and makes control comparatively easy (Chapman 1949a).

³⁸ Coleman, George A. *Op. cit.* See footnote 11.

³⁹ Coleman, George A. *Op. cit.* See footnote 11.

⁴⁰ Coleman, George A. *Op. cit.* See footnote 11.

⁴¹ Stevens, R. E. (*Pityophthorus* twig beetles on Monterey pine.) 1958. (Unpublished report on file at Pacific SW. Forest and Range Exp. Sta., U.S. Forest Serv., Berkeley, Calif.

⁴² Coleman, George A. *Op. cit.* See footnote 11.

⁴³ Anon. 1957b; Boomsma and Adams 1943; Fenton 1951; Kennedy 1957; New Zealand Forest Service 1955.

⁴⁴ Anon. 1957b; Coutts 1965; Gilbert and Miller 1952; Hutchinson and Henry 1957; New Zealand Forest Service 1955; Rawlings 1953, 1955; Rawlings and Wilson 1949.

Climatic factors are sometimes hostile to exotic Monterey pine stands. The most adverse weather conditions are summer rainfall, unseasonable frosts, hail and wind (Rawlings 1957). Summer rainfall favors attack by leaf-cast fungi and *Diplodia pinea*, particularly when high temperatures and humidity are maintained for long periods (Rawlings 1957).

Temperatures below 12° F. and unseasonable frosts of much less severity are liable to damage Monterey pine. This tree sometimes will tolerate temperatures as low as 0° F., but frost rings may form which destroy the timber's usefulness for lumber (Rawlings 1957).

Monterey pine is particularly susceptible to injury by hail. Direct damage consists of defoliation and splitting of bark on twigs and branches (Rawlings 1957). These injuries attract attacks by *Diplodia pinea*.⁴⁵

Wind is one of the most important factors in the growth of Monterey pine as an introduced species—both in direct and in indirect effects. In some instances wind may be a limiting factor in the use of this species for forestry. It sometimes determines the form of the tree and the structure of the wood (Rawlings 1957). Prevailing west winds in Australia have caused windthrow, lean, and eccentric growth, but soil moisture, aspect, and exposure were contributing factors (Pryor 1937). Southeast and northwest winds caused leans and defects, including elliptical stems, irregular growth, sweep, sloping grain, and compression wood (Fielding 1940; Millet 1944). Windthrow may be severe where trees are grown on non-forest land where rooting is notoriously shallow ([Hocking] 1945). The whipping of crowns while the cambium is active may bark the boles which leads to dead tops (Hocking 1947).

Special Features

Monterey pine is the most important conifer yet introduced to the Southern Hemisphere. Its rapid growth and adaptability to a wide range of conditions prove it valuable for providing softwoods to that region, particularly Australia, New Zealand, and South Africa (Lindsay [1932]).

The most remarkable quality of Monterey pine may be its extreme variation of tree types (Thom-

son 1950). These widely different types within small uniform areas suggest a wide genetical variation between individuals. Because this variation includes characteristics important to foresters, such as vigor, stem form, and limb size and angle,⁴⁶ the possibility of establishing elite strains seems good.

In California, young Monterey pines have become favored as Christmas trees (Metcalf 1955).

Races and Hybrids

The two-needled pine found on Guadalupe Island usually is considered to be *Pinus radiata* var. *binata* (Engelm.) Lemmon (Lindsay [1932]; Newcomb 1959). Another variety, the golden-leaved Monterey pine (var. *aurea*), is propagated from layers and cuttings as an ornamental tree in New Zealand and has no significance for foresters. Considerable morphological diversity within the species has been recognized in both natural and exotic stands,^{47 48} but no other varietal names are now used, except rarely. However, *P. radiata* var. *macrocarpa* Hartw. has been suggested to designate the form at Cambria (Fielding 1961).

Monterey pine has been hybridized artificially with knobcone pine and bishop pine (Righter and Duffield 1951; Rodger 1957; Stockwell and Righter 1946). In vigor, the knobcone cross (*Pinus* × *attenuradiata* Stockwell and Righter) is between the parental species. It resembles Monterey pine in appearance, but has heavier branches (Fielding 1950). An interesting feature is its resistance to frost injury. At 3 years seedlings were undamaged by a 15.4° F. temperature, which

⁴⁵ Bryan 1954; Laughton 1937; Legat 1930; Rawlings 1957.

⁴⁶ Bannister 1959; Chapman 1949b; Pawsey 1950; Poole 1947; Thulin 1957.

⁴⁷ Bannister 1954, 1958, 1959; Fielding 1953, 1961, 1962; Jacobs 1937, 1961; Lindsay 1932; Pawsey 1960b; Sherry 1947.

⁴⁸ Forde, M. B. *Op. cit.* See footnote 2.

either killed or permanently deformed Monterey pine seedlings, and at 8 years the hybrids withstood a minimum temperature of 11.8° F. (Stockwell and Richter 1946).

The bishop pine cross has good form, but has no advantages over Monterey pine. It has bishop pine's undesirable habit of producing many cones on the main stem (Fielding 1950).

Natural hybrids of Monterey and knobcone

pinus have been found near Point Año Nuevo⁴⁹ (Bannister 1958; Lindsay [1932]; Stebbins 1950) and the possibility of natural hybridization between Monterey and bishop pines at Monterey has been discussed⁵⁰ (Stebbins 1950). Putative hybrids between Monterey pine and knobcone pine were spontaneous in five widely separated areas in New Zealand (Bannister 1958; New Zealand Forest Service. 1960).

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⁴⁹ Forde, M. B. *Op. cit.* See footnote 2.

⁵⁰ Duffield, John Warren. *Interrelationships of the California closed-cone pines with special reference to *Pinus muricata* D. Don.* 1951. (Ph.D. thesis on file at Univ. Calif., Berkeley.)

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