

The genera *Lantana*, *Lippia*, and *Clerodendron* are also pan-tropical, contain several hundred species, and are important components of many forest ecosystems. They comprise trees, shrubs and lianes. Species of *Lantana* are important weeds and *Lippia* species are important sources of medicine.

See also: **Silviculture:** Treatments in Tropical Silviculture. **Tree Breeding, Practices:** A Historical Overview of Forest Tree Improvement; Tropical Hardwoods Breeding and Genetic Resources. **Tropical Forests:** Monsoon Forests (Southern and Southeast Asia). **Wood Use and Trade:** History and Overview of Wood Use.

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Tropical Pine Ecosystems and Genetic Resources

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Introduction

The genus *Pinus* (family Pinaceae) is one of the most widely distributed genera of trees in the northern hemisphere (Figure 1). The species often dominate the natural vegetation types in which they occur and provide some of the most important timber trees in the world. *Pinus* comprises approximately 100 species, of which about half occur naturally within the northern tropics. The tropical pines consist of two categories: first, those that occur naturally in the tropics, e.g., *P. oocarpa* (Figure 2) and, second, nontropical pines that are planted for wood production or shelter in the tropics, e.g., *P. elliottii* and *P. taeda* (Figure 3 and Table 1). This definition is

taken from the account of the tropical pines given in *Tree Crop Ecosystems* (Barnes *et al.*, 2001; see Further Reading) and on which this contribution is based.

There are virtually no natural pine forests in the southern hemisphere (Figure 1). It is not surprising, therefore, that the tropical pines have been used most extensively as exotics in the southern tropics, where some 6 million ha of plantations have been established to produce structural lumber and long-fibered pulp for particleboard, kraft paper, and newsprint manufacture (Figure 3). Unlike other crops, it is not usually economic to modify the plantation environment artificially through fertilization or irrigation. However, the extensive gene pool of tropical pine species has made it possible to establish plantations that are many times more productive than the natural forests over a great range of environmental conditions.

Taxonomy and Variation in Natural Populations of Tropical Pines

The pines are evergreen, resin-yielding, small to very large trees, usually with a single stem and strong apical dominance. If open-grown, most branches are retained and the bole tends to be conical but, under forest conditions, lower branches are shed and clean cylindrical boles are produced. Bark varies from rough and furrowed (Figure 4) to smooth and scaly (Figure 2). All pines have mature needles in fascicles (bundles) of from one to six, enclosed in a deciduous or persistent basal sheath. The fascicles are dwarf short shoots and are important in their identification. The needles contain resin canals running along their length which vary in number and position and which are also important for species identification. Needles may possess one or two vascular bundles, upon which the two major divisions of the genus are based, viz., Haploxylon and Diploxylon. Stomata (pores for gas exchange) are borne in lines on all surfaces, varying in number between species and within subspecies and ecotypes of single species.

All pines are monoecious with male and female strobili borne on the same individual tree. The female strobilus is usually terminal or subterminal and is composed of two series of spirally arranged scales, a very small bract scale and a much larger ovuliferous scale. The latter bears two pendulous ovules on its upper surface. The mature cone shows considerable variation in size, degree of woodiness, shape and size of the individual scales, and position of the apophysis and umbo (the exposed part of the scale when the cone is closed). In the Haploxylon group of



Figure 1 World distribution of the genus *Pinus*. Reproduced with permission from Critchfield WB and Little EL (1966) *Geographic Distribution of the Pines of the World*. USDA Miscellaneous Publications.

pinus (Table 1) the apophysis is terminal, whereas in the *Diploxylon* it is dorsal. The female strobilus is very important for species identification and without it an exact determination cannot usually be made. Female cone development takes from 1 year (e.g., *P. merkusii*) to 3 years (e.g., *P. leiophylla*). Pine seed is either winged or wingless (some pinyon pines).

Although the genus *Pinus* is a homogenous and natural group, its division into infrageneric and sectional groups has been the source of argument and confusion; many different schemes have been proposed. The classification adopted in Table 1 is modified from that published by Elbert Little and William Critchfield which is based on the work of Jack Duffield who segregated groups but did not give them formal names.

Information on natural hybridization among tropical pines is scattered, incomplete, and mostly unconvincing. Many species occur sympatrically and are apparently isolated by complete or almost complete genetic barriers. There are very few published examples of natural species hybrids that have sub-

sequently been verified by later controlled pollinations. Those that have are:

- *P. flexilis* × *P. strobiformis*
- *P. leiophylla* × *P. chihuahuana*
- *P. yunnanensis* × *P. tabulaeformis*
- *P. yunnanensis* × *P. kesiya*
- *P. pseudostrobus* × *P. montezumae*
- *P. montezumae* × *P. hartwegii*
- *P. palustris* × *P. taeda*
- *P. caribaea* × *P. oocarpa*
- *P. patula* × *P. oocarpa*

Ecology of Natural Stands of Tropical Pines

Natural Distribution

Geographic range Tropical pines occupy two disjunct areas in the western and eastern hemispheres (Figure 1). The smaller Latin American area has the larger number of species, and no taxon is common to both. Some species, e.g., *P. kesiya* and *P. merkusii*,



Figure 2 A natural stand of *Pinus oocarpa* at 1000 m in Honduras.

occupy enormous geographical areas in Southeast Asia. *Pinus* is almost unknown in the southern hemisphere except for *P. merkusii*, and it is absent from Africa south of the Sahara (Figure 1).

The folded mountain ranges and varied topography of Latin America provide an abundance of habitats and, although pines (36–40 species) are considered to have migrated south from the west

and east of North America in the Tertiary period, Mexico is now recognized as a center of considerable species diversity and a secondary center of endemism. No pine has ever been recorded south of latitude 12°N in Central America and the total lack of fossil records indicates that no species of pine has ever existed in South America. In Southeast Asia, tropical pines occur in southern China,



Figure 3 Exotic pine plantations of *Pinus elliotii*, *P. patula*, and *P. taeda* at 1000–1500 m altitude in the eastern districts of Zimbabwe.

chiefly in the states of Yunnan and neighboring Szechwan, the island of Formosa (Taiwan), the whole of the former Indochina peninsular, Myanmar (Burma) and Thailand, together with the north-eastern states of India.

Altitude and climate In both geographical areas, pines commonly grow under conditions that are far from tropical. Almost all are montane, some with altitudinal ranges between 700 and 4000 m. *Pinus caribaea*, in Central America and the Caribbean, rarely grows at elevations greater than 700 m, whilst *P. merkusii* in Southeast Asia and *P. strobus* var. *chiapensis* in southern Mexico and Guatemala may be found up to 1000 m or slightly higher. These three species are the most ‘tropical’ of all pines and are unable to tolerate severe frost.

All the other species are submontane or montane, although one or two survive at the timberline, sometimes in permanent snow. Most seem to be adapted to a fairly narrow altitudinal range and inhabit distinct zones. Temperature appears to be the main factor controlling the altitudinal range of a species. In Latin America, however, *P. oocarpa* extends from c. 700 m in Central America (Figure 2) to 2500 m in Mexico. The lower altitude ecotypes are always frostfree, whereas the higher populations are frequently subjected to periods of severe frost. Some of the more upland pines have equally large ranges, e.g., *P. patula* and *P. tecunumanii* from 900 to 2800 m and *P. pseudostrobus* from 2000 to 3000 m.

Pinus hartwegii is found at the highest altitude, between 2000 and 4000 m (Figure 4).

In Southeast Asia most of the species appear to have a greater range of altitudinal tolerance, several occurring from sea-level to 2500 m. Populations of *P. armandii* are found from sea level to c. 3800 m. The majority, e.g., *P. roxburghii*, are found between 1500 and 3500 m, whilst *P. densata* grows at the highest altitudes (to 4000 m).

The temperature range, therefore, over which tropical pines grow varies enormously from an annual mean of about 26°C (e.g., *P. merkusii* in Sumatra and *P. caribaea* in Nicaragua) down to treeline conditions with mean annual temperatures of 10°C (*P. hartwegii*). Mean annual rainfall also varies greatly over the areas occupied by tropical pines from as much as 10 000 mm (*P. kesiya* in the Khasi Hills, India) down to less than 600 mm (*P. caribaea* in Honduras). Almost invariably, the climate where tropical pines occur is characterized by an annual seasonal fluctuation in rainfall or temperature.

Soils Pines are able to thrive on a great variety of soils, particularly infertile, well-drained acidic soils. On richer soils, competition from broadleaved species is greater and their success in regeneration is poorer. In Central America, *P. oocarpa* tends to avoid the more alkaline soils overlying basic rocks, as does *P. caribaea* var. *hondurensis*. *Pinus caribaea* var. *bahamensis*, however, thrives on almost pure coral limestone (Figure 5).

Table 1 The tropical species of the genus *Pinus* classified according to Little EB and Critchfield WB (1969) (*Subdivisions of the Genus Pinus (Pines)*. USDA Miscellaneous Publications.) and modified by BT Styles and A Farjon (Oxford Forestry Institute)

<i>Pinus</i> subgenus <i>Ducampopinus</i> (A. Chev.) de Ferré
<i>Pinus</i> sect. <i>Ducampopinus</i>
<i>Pinus</i> subsect. <i>Krempfiana</i> Little and Critchfield
<i>Pinus krempfii</i> Lecomte
<i>Pinus</i> subgenus <i>Strobus</i> Lemm. (soft or white pines)
<i>Pinus</i> sect. <i>Strobus</i>
<i>Pinus</i> subsect. <i>Strobi</i> Loud.
<i>Pinus strobus</i> var. <i>chiapensis</i> Martinez
<i>Pinus rzedowskii</i> Madrigal & M Caballero
<i>Pinus strobiformis</i> Engelm.
<i>Pinus ayacahuite</i> Ehrenberg ex Schldtl.
<i>Pinus ayacahuite</i> var. <i>veitchii</i> (Roezl) Shaw
<i>Pinus armandii</i> Franch.
<i>Pinus dalatensis</i> de Ferré
<i>Pinus fenzeliana</i> Hand.-Mazz.
<i>Pinus wangii</i> Hu & Cheng
<i>Pinus morrisonicola</i> Hayata
<i>Pinus</i> sect. <i>Parrya</i> Mayr
<i>Pinus</i> subsect. <i>Cembroides</i> Engelm. (pinyon or nut pines)
<i>Pinus cembroides</i> Zucc.
<i>Pinus cembroides</i> var. <i>bicolor</i> Little
<i>Pinus cembroides</i> subsp. <i>lagunae</i> (Robert Passini) DK Bailey
<i>Pinus cembroides</i> subsp. <i>orizabensis</i> DK Bailey
<i>Pinus maximartinezii</i> Rzedowski
<i>Pinus pinceana</i> Gord. & Glendinning
<i>Pinus nelsonii</i> Shaw
<i>Pinus</i> subgenus <i>Pinus</i> (hard pines)
<i>Pinus</i> sect. <i>Pinea</i> Endl.
<i>Pinus</i> subsect. <i>Leiophyllae</i> Loud.
<i>Pinus leiophylla</i> Schiede ex Schldtl. & Cham.
<i>Pinus leiophylla</i> var. <i>chihuahuana</i> (Engelm.) Shaw
<i>Pinus lumholtzii</i> Robinson & Fern.
<i>Pinus</i> subsect. <i>Canariensis</i> Loud.
<i>Pinus roxburghii</i> Sarg. ^a
<i>Pinus canariensis</i> C. Sm. ^a
<i>Pinus</i> sect. <i>Pinus</i>
<i>Pinus</i> subsect. <i>Pinus</i>
<i>Pinus tropicalis</i> Morelet
<i>Pinus halepensis</i> Mill. ^a
<i>Pinus taiwanensis</i> Hayata syn. <i>Pinus luchuensis</i> Mayr
<i>Pinus massoniana</i> Lamb.
<i>Pinus yunnanensis</i> Franch.
<i>Pinus densata</i> Mast.
<i>Pinus merkusii</i> Jungh. & de Vriese
<i>Pinus kesiya</i> Gord.
<i>Pinus</i> subsect. <i>Australes</i> Loud. (southern yellow pines)
<i>Pinus caribaea</i> Morelet
<i>Pinus caribaea</i> var. <i>bahamensis</i> (Griseb.) Barr. & Golf.
<i>Pinus caribaea</i> var. <i>hondurensis</i> (S ^V sn ^V scl.) Barr. & Golf.
<i>Pinus occidentalis</i> Sw.
<i>Pinus cubensis</i> Griseb.
<i>Pinus taeda</i> L. ^a
<i>Pinus elliottii</i> Engelm. ^a
<i>Pinus elliottii</i> var. <i>densa</i> Little & Dorman
<i>Pinus palustris</i> Mill. ^a
<i>Pinus</i> subsect. <i>Ponderosae</i> Loud.
<i>Pinus engelmannii</i> Carr.
<i>Pinus durangensis</i> Martinez
<i>Pinus cooperi</i> (CE Blanco) Farjon

Table 1 Continued

<i>Pinus montezumae</i> Lamb.
<i>Pinus montezumae</i> var. <i>gordoniana</i> (Hartweg ex Gord.) Silba
<i>Pinus hartwegii</i> Lindl. (including <i>Pinus rudis</i> Endl.)
<i>Pinus devoniana</i> Lindl. (syn. <i>Pinus michoacana</i> Martinez)
<i>Pinus pseudostrobus</i> Lindl.
<i>Pinus pseudostrobus</i> var. <i>apulcensis</i> (Lindl.) Shaw
<i>Pinus douglasiana</i> Martinez
<i>Pinus maximinoi</i> HE Moore
<i>Pinus teocote</i> Schiede ex Schldtl. & Cham.
<i>Pinus lawsonii</i> Roezl ex Gord. & Glendinning
<i>Pinus herrerae</i> Martinez
<i>Pinus</i> subsect. <i>Oocarpae</i> Little & Critchfield (closed-cone pines)
<i>Pinus patula</i> Schiede ex Schlechtendal
<i>Pinus patula</i> var. <i>longipedunculata</i> Look ex Martinez
<i>Pinus jaliscana</i> Pérez de la Rosa
<i>Pinus tecunumanii</i> Eguiluz & JP Perry
<i>Pinus greggii</i> Engelm. ex Parlatore
<i>Pinus oocarpa</i> Schiede ex Schldtl.
<i>Pinus oocarpa</i> var. <i>trifoliata</i> Martinez
<i>Pinus pringlei</i> Shaw
<i>Pinus radiata</i> D. Don
<i>Pinus muricata</i> D. Don
<i>Pinus praetermissa</i> Styles & McVaugh

Authorities' names are given for precise identification. All the species listed occur in the tropics except for those followed by ^a which occur naturally only north of the tropic of Cancer but have been used operationally within the tropics.

Natural Ecosystems

Plant communities Natural pine forest ecosystems are relatively simple; species diversity is low and the number of associated taxa limited. *Pinus oocarpa* in Honduras probably forms the main forest cover over most of the country (Figure 2) whilst *P. caribaea* var. *hondurensis* is dominant in the savanna and lowlands of Belize, Honduras, and eastern Nicaragua. *Pinus densata* and *P. armandii* form dense forest masses in the mountains of southern China. As many as six different pines may grow together, e.g., in some forests in the state of Chiapas, southern Mexico. In both geographical areas *Quercus* species (oaks) are the broadleaved trees most commonly associated with pine, although other hardwoods can play the same role.

In Mexico and Central America at least, most pine communities are secondary fire climaxes. Irregular burning by anthropogenic fires or through lightning strikes prevents invasion by the broadleaved competitors that suppress pine growth. Fire also eliminates the build-up of seed- and seedling-eating animals, especially in the Central American *P. oocarpa* forests. The shade cast by dense pine growth suppresses the development of a significant ground flora. At the higher altitudes where rainfall is higher, temperatures lower, and fires less frequent, the pine



Figure 4 *Pinus hartwegii* in natural mixed pine forest at 2300 m in Honduras.

forest may be transitory and no longer part of a climax community and it merges with, and is finally replaced by, upper montane rainforest (Figure 6). A mixture of both types of forest is common in Mexico and Central America at altitudes of 2800 m and above. There is a similar transition at lower altitudes where high rainfall and fertile soils also make fire less frequent.

Mycorrhizae All pines form ectotrophic mycorrhizae with ascomycetous or basidiomycetous fungi. Fungi frequently encountered belong to genera of the Agaricales (*Amanita*, *Boletellus*, and *Suillus*); Russulales (*Lactarius*, *Russula*); Aphyllophorales (*Cantharellus*, *Thelephora*); Hymenogastreales (*Rhizopogon*); and Sclerodermatales (*Astraeus*, *Pisolithus*, *Scleroderma*). Ectotrophic associations are rare in tropical



Figure 5 Fire-maintained forest of *Pinus caribaea* var. *bahamensis* on impoverished soils over limestone rock in Bahamas.

regions, forming only in response to certain edaphic and climatic factors. Information concerning mycorrhizal fungi in these forests is very scanty (Table 2), mainly because the fruiting structures of the organisms are ephemeral in hot climates and because their taxonomic affinities are uncertain and difficult to ascertain.

Diseases Little is known about the pathology of most tropical pines in their native habitats. Natural forests generally contain trees of widely different ages, often consist of more than one pine species, and frequently contain a substantial component of non-coniferous shrubs and trees. In such areas, selection pressures are likely to operate against pathogens that give rise to severe epidemic diseases and in favor of pathogens that cause chronic low-level disease. This appears to be the case in the pine forests of Central America and the Caribbean islands where the trees are debilitated by mistletoes (e.g., *Arceuthobium* spp. and *Psittacanthus calyculatus*), heart rots caused by various basidiomycetous fungi, and cone rust (*Cronartium conigenum*). Other pathogens that have the potential to cause severe disease epidemics, such as the

fungi *Mycosphaerella dearnessii*, *M. gibsoni*, and *M. pini*, also exist at low levels in some Central American pine forests. However, they appear to be restricted by the lack of susceptible host tissues available for infection; the very susceptible individuals and species have long since been eliminated from the forests. Similarly, heteroecious leaf and stem rust diseases also occur on the pines and alternate host plants but rarely cause severe epidemics.

Predators Six orders of insects contain significant pine pests – Coleoptera, Hemiptera, Isoptera, Lepidoptera, Orthoptera, and Thysanoptera. These pests bore into the bark, wood, shoots, cones, and seed, suck sap from stem shoot or needles, and defoliate the trees. In the undisturbed natural forest they are endemic and rarely become conspicuous. However, when the forest ecology is disturbed by climate or humans, populations can build up to epidemic levels and devastation can result. For example, in 1928 the first attacks by pine bark beetles (*Dendroctonus* spp.) were noticed in remnant trees weakened by lopping in cleared sheep pastures in highland Guatemala. Damage can also be severe at high stand density, even where this does occur naturally.

Of the larger animals, humans and their domestic or feral beasts have the most profound influence on the ecology of the natural pine forests wherever they exist. Exploitation, grazing, and clearing for agriculture all involve management or mismanagement of the natural ecosystems that leads to the progressive decline of the forest.

Ecology of Artificially Created Plantations of Tropical Pines

Exotic Distribution

Species used in plantations Of the species listed in Table 1, four that occur in the tropics (*P. caribaea*, *P. kesiya*, *P. oocarpa*, and *P. patula*) are widely planted as exotics for industrial plantations. Another two (*P. massoniana* and *P. merkusii*) are extensively planted in the regions where they are indigenous and a further four (*P. greggii*, *P. maximinoi*, *P. pseudostrobus*, and one 'soft' pine, *P. strobus* var. *chiapensis*) are being used commercially on special sites. Of the eight extratropical pines that have been planted as exotics in the tropics, *P. elliottii* and *P. taeda* are the most important. Exotic pines have been widely planted in environments where the biotic, climatic, and edaphic factors are frequently unlike those in their indigenous habitats. The ecology of plantations, therefore, is in marked contrast to the ecology of the natural forest.

In 1980 it was estimated that about 3 million ha of softwood plantations had been established in



Figure 6 A natural stand of *Pinus tecunumanii*, probably established after a rare fierce fire, being replaced by hardwood species at 2000 m altitude in Honduras.

76 tropical countries of Africa, America, and Asia and this had increased to 4 million by the end of the twentieth century. About 80–90% of this area were tropical pines. In 1980, *P. elliottii* was still the largest single contributor, mainly in Brazil (c. 30%), but by 2000 it was equaled if not surpassed by *P. caribaea* followed by *P. patula*, *P. oocarpa*, *P. kesiya*, and

P. merkusii; all the remaining species will contribute less than 10%.

Climatic factors The most successful plantation schemes have been those where species have been used in monoculture homoclimally, i.e., in climates similar to those in which they occur naturally. Absence

Table 2 Fungi confirmed as symbionts of pine ectomycorrhizas in indigenous pine forests in the tropics

<i>Amanita excelsa</i> (Fr.) Kummer
<i>Amanita flavoconia</i> Atk.
<i>Amanita gemmata</i> (Fr.) Gill.
<i>Amanita muscaria</i> (L. ex Fr.) Hook. var. <i>flavivolvata</i> Sing.
<i>Amanita</i> sp. sect. <i>Lepidella</i>
<i>Fistulinella conica</i> (Rav. Apud B. & C.) Sing. var. <i>belizensis</i> Sing. & Ivory
<i>Psilolithus tinctorius</i> (Mich. Ex Pers.) Coker & Couch
<i>Rhizopogon nigrescens</i> Coker & Couch
<i>Scleroderma texense</i> Berk.
<i>Suillus cothurnatus</i> Sing.
<i>Suillus decipiens</i> (B. & C.) O Kuntze
<i>Suillus granulatus</i> (L. ex Fr.) O Kuntze
<i>Thelephora terrestris</i> (Ehrn.) Fr.
<i>Xerocomus pseudoboletinus</i> (Murr.) Sing. var. <i>pini-caribaeae</i> Sing.

Reproduced with permission from Barnes RD, Styles BT, Plumptre RA, and Ivory MH (2001) Tropical pines. In: Last FT (ed.) *Tree Crop Ecosystems*, pp. 163–192. Amsterdam: Elsevier Science.

of natural pests and diseases contributes to this success and to productivity unseen in the natural stands. There has, however, been a tendency to move species that have demonstrated excellent silvicultural characteristics in the exotic homoclimate to lower and hotter areas. The physiological stress and ecological changes that occur may not be immediately apparent but, as the plantation matures, disease and pest problems develop and the natural vegetation soon destroys the pine stand structure. Less frequently, species have been moved to higher altitudes and lower temperatures than those that occur in their natural range. Although there are significant reductions in growth rate, the ecological consequences are not as striking as when species are moved to warmer climates.

Tropical pines vary in their drought-hardiness but most species will grow with mean annual precipitation as low as 800 mm. However, species cannot be moved from winter rainfall to summer rainfall areas without severe problems; for example, *P. canariensis*, *P. halepensis*, *P. muricata*, and *P. radiata* were planted operationally in the tropics but have been abandoned.

Edaphic factors With appropriate temperature and dry season, exotic tropical pines are able to exploit the full potential of the soil and become dominant even on the very best sites. Where the climate is wrong, however, fertile soils contribute to the rapid demise of exotic tropical pine forest. In such conditions, the indigenous vegetation is not a fire climax type and there are many aggressive pioneering woody species that will take advantage of the physiologically weak pines and start recolonizing the site as the first step in reestablishing wet tropical forest ecology.

The tropical pines as exotics vary in their tolerance of soils with low nutrient status (e.g., *P. kesiya* can grow on degraded sites but *P. chiapensis* requires fertile sites) and particularly in their ability to grow on poorly drained soils (e.g., *P. kesiya* is very intolerant and *P. elliottii* very tolerant). Great depths of sandy soil can have ameliorating effects on climatic influence where rainfall is low. The most serious problems with nutrient deficiencies have been with phosphorus (e.g., *P. caribaea* in Queensland), potassium (e.g., *P. kesiya* in Madagascar), and boron (e.g., *P. caribaea* in Papua New Guinea and *P. kesiya* in Zambia).

Ecology in the Exotic Environment

Plant communities The most important biotic influences are human beings and the silvicultural practices they use to establish and maintain the pines as exotics. Initially at least, the species is nursed into its new surroundings by careful sowing, planting, and weeding techniques. On poorer soils, the pines are able to compete favorably with grass and shrubby growth but generally not with woody regrowth. On more fertile sites, it is necessary to keep woody regrowth, shrubs, and creepers cut back until the pine crop forms a canopy.

Almost invariably, when crops are harvested the area is artificially regenerated by planting. Where soil fertility is high, the second crop is often faster-growing than the first because the forest floor by that time is almost devoid of ground vegetation. On poorer sites, however, nutrient deficiencies may result in reduced production. In both cases, there are changes in the associated macro- and microflora but the long-term prognosis in this respect cannot yet be predicted. Woody weeds, both indigenous and exotic, have become conspicuous problems in pine plantations (e.g., *Acacia ataxacantha*, *Lantana camara*, and *Rubus pinnatus* in Africa).

Notwithstanding the careful cultural procedures that are used to establish exotic plantations of tropical pines, many species regenerate naturally in their new environment once they are established and some have become serious invaders of indigenous grassland and woodland, particularly where frequent fires have been preventing the local succession to climax forest communities. A good example of this is *P. patula* in the fire climax grassland and *Brachystegia* woodlands of the eastern mountainous region of Zimbabwe (Figure 7).

Mycorrhizae Pine plantations are usually planted on old forest or grassland sites where indigenous ectotrophic trees are absent or sparse and indigenous fungi rarely form a significant source of mycorrhizal



Figure 7 *Pinus patula* colonizing a hillside at 1800 m in Zimbabwe. Seed has been blown in from a nearby planted stand and many trees have already survived fires.

inoculum for introduced pines in areas remote from natural *Pinus* spp.

Exotic ectomycorrhizal fungi were probably introduced along with their native hosts by early settlers long before the importance of mycorrhizae was realized. However, when attempts were made to grow pines in new areas from importations of tree seeds, mycorrhizal deficiency problems were often encountered; uninfected seedlings would usually remain stunted and chlorotic in appearance and they would usually die in the nursery. Later, these problems were overcome by the introduction of fresh pine soil or the use of 'mother seedlings' in nursery beds.

The type of inoculum, its origin, the method of transportation, the method of inoculation, and possibly the identity of the recipient *Pinus* species, have had considerable influence on which fungi were successfully introduced to any given area. Usually only a few of the 23 commonly encountered fungi (Table 3) are observed at any one site; the range of species observed is affected by the age of the trees, the host species, and site factors, such as altitude, climate, and rotation.

Diseases Exotic pine plantations in the tropics and the southern hemisphere have mostly been established in areas that were naturally free from any specialized pine disease organisms. Thus the majority of disease outbreaks reported in pine plantations from these areas were, until recently, caused by nonspecialized pathogens with a wide host range able to spread from indigenous host species to exotic pines.

Table 3 Ectomycorrhizal fungal symbionts frequently sporulating in pine plantations in the tropics

<i>Amanita alauda</i> Corn. & Bres.
<i>Amanita muscaria</i> L. (L. ex Fr.) Hook.
<i>Boletus edulis</i> Fr.
<i>Cortinarius</i> spp. (in Sri Lanka and Kenya)
<i>Hebeloma crustuliniforme</i> (St. Amans) Quel.
<i>Hymenogaster</i> spp. (in India)
<i>Inocybe lanuginella</i> (Schrot.) Konr. & Maubl.
<i>Laccaria proxima</i> (Boud.) Pat.
<i>Pisolithus tinctorius</i> (Mich. ex Pers.) Coker & Couch
<i>Rhizopogon luteolus</i> Fr. & Nordh.
<i>Rhizopogon roseolus</i> (Corda) Fr.
<i>Rhizopogon rubescens</i> (Tul. & Tul.) Tul. & Tul.
<i>Rhizopogon villosus</i> Zeller
<i>Russula brevipes</i> Peck.
<i>Russula sororia</i> (Fr.) Romell
<i>Scleroderma bovista</i> Fr.
<i>Scleroderma citrinum</i> Pers.
<i>Scleroderma texense</i> Berk.
<i>Suillus granulatus</i> (L. ex Fr.) O Kuntze
<i>Suillus luteus</i> (L. ex Fr.) SF Gray
<i>Suillus sibiricus</i> (Sing) Sing
<i>Thelephora terrestris</i> (Ehrn.) Fr.
<i>Xerocomus</i> spp. (in India)

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These pathogens usually affect the roots or heartwood of the pines. The most notable of these diseases is *Armillaria* root disease. Following felling of infected trees the roots and stumps become extensively colonized by the fungus, which then spreads to

healthy trees. Most *Pinus* species are susceptible but *P. elliottii* appears to be exceptionally so. Several other nonspecialized pathogens also give rise to similar diseases in various parts of the tropics; these can lead to serious economic losses but they can usually be minimized. Since 1950 there has, however, been a gradual influx of specialized pine pathogens from the north into exotic plantations in the tropics and the southern hemisphere where some have already proved to be a serious threat to certain *Pinus* species. Dothistroma blight, caused by the fungus *Mycosphaerella pini*, is probably the most important of the pine diseases in the tropics to be caused by an exotic specialized pine pathogen. This fungus was identified as the cause of a severe needle blight of *P. radiata* in Tanzania in 1957 and has since been reported from many other countries in the tropics. Plantations of pines are obviously more prone to epidemic disease than natural forest; however, they also provide more scope for the avoidance or control of disease in addition to being vastly more productive than most natural forest areas.

Predators The first crops of exotic pines have been characteristically devoid of associated animal life but there is an increasing number of birds, insects, and mammals becoming associated with and adapted to the forests. Even-aged stands of trees provide ideal media for population explosions, particularly of insects, both native and introduced. There have now been epidemics of insect pests from all the main orders, e.g., bark beetles and aphids in southern Africa, termites in Malaysia, shoot moths in the Philippines, defoliating moths in Zimbabwe, grasshoppers in Malawi, and thrips in Kenya. The worst damage is frequently associated with mis-siting of the host species when environmental stress is thought to bring about high nutrient levels in the tree through remobilization of reserves; this makes it attractive to the pest and at the same time impairs the tree's defensive mechanisms. Epidemics may eventually be brought under control by local predators or diseases, e.g., coccinellids on aphids and various viruses on lepidopterous larvae.

Birds and mammals use pine plantations for shelter, particularly before they are pruned and thinned, but, surprisingly, a number of mammals find a source of food in pines and can become destructive. Elephants strip pine species in Africa and eat the inner bark; they find it convenient to work down the plantation rows. Eland antelope have similar habits in Zimbabwe and are very destructive in *P. patula* plantations. Pigs, wild or feral, in all parts of the world feed highly selectively on the roots of young *P. oocarpa*; it has been suggested that this is

due to a specific mycorrhizal association, possibly *Rhizopogon* spp., that have edible subterranean fruit bodies. Opossums feed on the young bark of *P. taeda* in Queensland, porcupines debark *P. leiophylla* by gnawing at the base in Zimbabwe, and baboons eat the bark of several pine species in southern Africa.

Genetic Resources and Adaptation

Evidence from many national and internationally coordinated comparative trials of species, varieties, populations (provenances), and progeny in many of the large number of tropical pine species have demonstrated that significant genetic variation occurs in clinal, ecotypic, and random patterns of distribution. This stresses the importance for the forester to choose the correct original natural population for exotic plantations and to monitor the change in genetic population structure under exotic conditions.

Development of landraces The possibility of genetic differences developing between the local exotic population and the original introduced sample is dependent upon the extent of heterozygosity, the genotypes of the founder members of the exotic population, the expression of the genetic variation in the new environment, and the selection pressures encountered under local conditions.

It appears that both a reduction in genotypic variation and a changed environment may, through their effect on phenotypic expression, contribute towards the rapid changes that can take place in local exotic populations. The changes may not be possible where the species is indigenous even when it is grown under plantation conditions. Such factors as endemic disease, competition with other indigenous species, and different climatic or edaphic conditions may prohibit the expression of genes that might otherwise improve commercially important characteristics.

Despite frequently small numbers of founder individuals, there is little evidence to suggest that introduced exotic tree populations are inferior to, or much less variable than, the indigenous parent populations. In fact, adaptation can take place over surprisingly few generations and the exotic population often exhibits superiority over material that is reintroduced from indigenous stands.

Development of genetically distinct exotic populations is occurring very much more rapidly now that selection and breeding in tropical pines have started. Achievements initially have been in improvements in wood yield and in stem and branch form (Figure 8). These have brought a correlated response in improved physiological adaptation to the environment and, as the environments are quite different from one country to another, a large amount of variation in



Figure 8 Seventeen-year-old plantation of *Pinus patula* from first generation of bred seed in Zimbabwe.

adaptability can be preserved in the global development of a species.

Implications for Management

Plantation silviculture aims to increase uniformity in the forest and to simplify the ecology; variation

increases the complexity of management. Uniformity invites biotic, climatic, and edaphic disasters. Uniformity can aggravate damage from drought and cyclone, lead to soil impoverishment and erosion, and provide ideal conditions for population explosions of plant competitors, diseases, and pests. These

in turn cause wild swings in the ecology and these swings themselves can sometimes prove to be beyond control through management. In the exotic environments, it is impossible to predict or even conceive of the events that may occur and to know their consequences. Introduction of diversity in the forest through mixed ages, mixed species, rotation of species, silvicultural treatment, and genetic variation may make ecology and management more complex but it will render the crop ecosystem much more stable, robust, and self-perpetuating and provide buffers against disasters. The forester must treat crop protection as part of silvicultural planning.

See also: **Pathology:** Diseases affecting Exotic Plantation Species; Diseases of Forest Trees. **Temperate and Mediterranean Forests:** Northern Coniferous Forests; Southern Coniferous Forests. **Temperate Ecosystems:** Pines. **Tree Breeding, Practices:** *Pinus Radiata* Genetics; Breeding for Disease and Insect Resistance; Southern Pine Breeding and Genetic Resources. **Tree Breeding, Principles:** A Historical Overview of Forest Tree Improvement; Conifer Breeding Principles and Processes. **Tropical Ecosystems:** Southern Hemisphere Conifers.

Further Reading

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TROPICAL FORESTS

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Bombacaceae

S Harris, University of Oxford, Oxford, UK

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Introduction

The family Bombacaceae contains trees with some of the most enigmatic of all traits, whether it is the