

northern red oak, such as the creation of the Hardwood Tree Improvement and Regeneration Center (HTIRC) in Purdue (Indiana). HTIRC aims to improve the genetic quality and regeneration of *Q. rubra* through application of classical breeding, genomics, and advanced propagation technology.

Exotics

Oaks have been transferred to various regions in the world. Red oaks from the eastern USA have been introduced in Europe, and *Q. rubra* is currently used throughout western Europe, not only as an ornamental tree but also as a plantation species for veneer or timber production. Hence tree improvement activities in *Q. rubra* were implemented in France, Germany, and the UK, starting with the installation of combined provenance and progeny tests. As the introduction in Europe began at the end of the eighteenth century, there have been only a few generations since the species was introduced in Europe but landraces (a landrace is a population that became adapted in a new environment to which it was transferred) have already been genetically differentiated in Europe. Similarly, *Q. robur* was introduced in many countries throughout the world, but no genetic improvement program has been reported outside its natural range and Europe.

See also: **Genetics and Genetic Resources:** Cytogenetics of Forest Tree Species; Genecology and Adaptation of Forest Trees; Genetic Systems of Forest Trees.

Genetics and Genetic Resources: Molecular Biology of Forest Trees; Population, Conservation and Ecological Genetics. **Temperate Ecosystems:** Fagaceae. **Tree Breeding, Principles:** Breeding Theory and Genetic Testing; Conifer Breeding Principles and Processes.

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Pinus radiata Genetics

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Introduction

Pinus radiata is arguably the most domesticated of all forest trees. It is grown in exotic plantations occupying over 4 million ha, an area roughly 500 times its natural extent. Overall these plantations are highly productive, and many are intensively managed. Associated with the intensive management, several large-scale, intensive genetic improvement programs have developed, which have prompted a large volume of genetic research on the species. Indeed, this genetic research, and commercially motivated research on most other aspects of the species' biology, have led to the species assuming the role of a model species for research into forest trees. The genetics of the species are of twofold interest. On the one hand, the story typifies that of many conifers, and pines in particular, in respect of karyotype, genomic characteristics, and genetic system in general. On the other hand, there are a number of features that are highly distinctive of the species. Notable among these are the biogeography, with five discrete natural populations that are differentiated by a combination of adaptive features and apparent founder effects, and the conspicuously high level of functional genetic variation from tree to tree. Intensive genetic improvement began from around 1950, and is now being pursued at varying levels of sophistication in at least five countries. It has delivered major genetic gains, in growth rate, tree form, and disease resistance. Improvement work is shifting in emphasis towards improving wood properties, while differentiated breeds are being developed. Challenges remain in the management of gene resources.

The Genetic System

Breeding System

Like almost all pines (*Pinus* spp.), *P. radiata* is an outbreeder. Effective self-fertility, reflected in filled

seed produced upon selfing, is very incomplete, but highly variable from tree to tree. This is consistent with the postulated mechanism of a fairly high 'load' of recessive embryo lethal genes, combined with the archegonial polyembryony – with this polyembryony, the set of viable seed can be much higher than the percentage incidence of viable zygotes resulting from inbreeding.

The viable offspring produced by self-pollination show, on average, marked inbreeding depression, with poorer growth and competitive ability than outcross progeny. This inbreeding depression reflects sublethal deleterious recessive genes. It varies markedly according to parents and individual offspring. This variability, in both effective self-fertility and inbreeding depression in viable offspring, is consistent with random variation among parents in the load of deleterious recessive genes.

Matings between relatives that are less extreme than selfing also cause inbreeding depression, roughly in proportion to the relatedness between the seed- and pollen parents.

Seed collections made from natural stands show appreciable inbreeding depression, resulting from neighborhood inbreeding whereby neighboring trees tend both to be related to each other and to interpollinate. In plantations, the natural neighborhood structures are typically broken down, and seed collections from plantations show negligible signs of inbreeding. Self-thinning evidently eliminates inbred individuals preferentially during the life of a natural stand.

Genomic Characteristics

Pinus radiata is strictly diploid with a haploid chromosome number of 12. Any departure from the diploid state evidently reduces natural fitness to zero. Regarding the karyotype, the chromosomes are extremely large, all of similar size and metacentric, with only subtle distinguishing features. In these respects the species is typical of pines (*Pinus* spp.) in general, and also of most other conifer genera.

In keeping with the size of the chromosomes, the genome is enormous, around 2×10^{10} basepairs, but over 95% noncoding. However, despite the extremely stable karyotype, it appears that there is a relatively high mutation rate, judging from the level of the genetic load and the general sensitivity of pines to gamma rays. In keeping with the genomic stability, DNA analysis has revealed a very high level of homologies, in respect of functional genes and their loci within chromosomes, between *P. radiata* and *P. taeda*, which has become another main 'model-species' pine.

Crossing-over of chromosomes in meiosis is high – estimated map length is around 1800–2000 centi-Morgans – and is evidently slightly higher in male than female meiosis.

Genetic Architecture

Taxonomic Position and Crossability

Pinus radiata belongs within the subgenus *Pinus* (syn. *Diploxylon*) or the 'hard pines.' It has recently been assigned to a section *Attenuatae* van der Burgh (the 'California closed-cone pines') which has recently been separated from the section *Oocarpae*, which now comprises a group from Mexico–Central America. Within the *Attenuatae*, it is readily crossable with *P. attenuata* and moderately crossable with some southern populations of *P. muricata*, but tends to be reproductively isolated from both species by pollination season and distance. However, there is one area where hybrids with *P. attenuata* occur naturally, but without conclusive signs of long-term introgression. *Pinus radiata* is also known to be weakly crossable with three or four members of the *Oocarpae*.

Population Differences

The pattern of natural population differences reflects the distinctive natural distribution. The species occurs in just five discrete natural populations (Figure 1). While all populations exist in a particular variant of a Mediterranean climate, created by a cold ocean current reducing summer temperatures and causing summer sea fogs, the habitats of the populations differ significantly (Table 1). In addition, the geographic separation between populations varies widely. In keeping with that, the degree of taxonomic separation varies. The southernmost populations, from Cedros and Guadalupe Islands, are recognized as separate varieties, vars *cedrosensis* and *binata* respectively, both having their needles usually in pairs rather than threes. The three northern populations, on the mainland, are assigned to var. *radiata*; that from Cambria is apparently the most distinct.

Chemotaxonomic information is very incomplete, but it serves to reinforce a picture of highly multi-dimensional differentiation among the various natural populations. In this pattern, the apparent affinities between individual populations can depend greatly on the trait in question, such that many traits have to be considered simultaneously, preferably in common-garden experiments, for the overall pattern to become clear. However, immunoassay techniques have been used to give a measure of genetic distances

between populations, with results that generally match the classical taxonomic picture.

The populations differ not only in traditional taxonomic traits and phytochemistry but also in tree morphology, growth rate, site tolerances, and pest and disease resistance (which are often the effective manifestations of site tolerances).

Some population differences for morphological traits, turpentine composition, and wood density are summarized in Table 2. Corresponding differences in growth rate, site tolerances and disease and pest

resistance are summarized in Table 3. In some morphological features, such as cone size and branching pattern, marked population differences are superimposed upon large tree-to-tree differences. However, for needles per fascicle (except on vigorous shoots of young trees) and bark thickness (except in old trees), tree-to-tree differences are totally subordinate to population differences.

The pattern of population differences can in part be interpreted in terms of adaptation to the different environments. For example, the strong taproot development of the Cedros population, and to a lesser extent the Guadalupe population, are presumably an adaptation to more intense drought on the islands. The greater palatability of Guadalupe to browsing animals can be readily interpreted as reflecting a lack of browsing mammals on the island. However, there are other population differences that are difficult to interpret as being adaptive. It therefore appears that some of the differences reflect founder effects and genetic drift occurring in the processes of colonizations, local extirpations, and coalescences that evidently resulted from climatic fluctuations and eustatic sea-level changes that have occurred since the Pleiocene.

Marker and Genomic Differentiation

Some strong population differences exist within *P. radiata* with respect to the standard isozyme systems, in contrast to the norm of isozyme variation within species being almost entirely among individuals within populations. Indeed, there are electromorphs that represent high-frequency private alleles for some of the populations. Actual DNA marker differentiation has not been studied thoroughly. Markers (simple sequence repeats or SSRs) have been developed that give excellent 'fingerprinting' of individual genotypes and pedigree verification, but such markers, because they are so polymorphic within populations, are inherently unsuited to differentiating among populations. Thus, while populations will surely be differentiated by DNA markers,

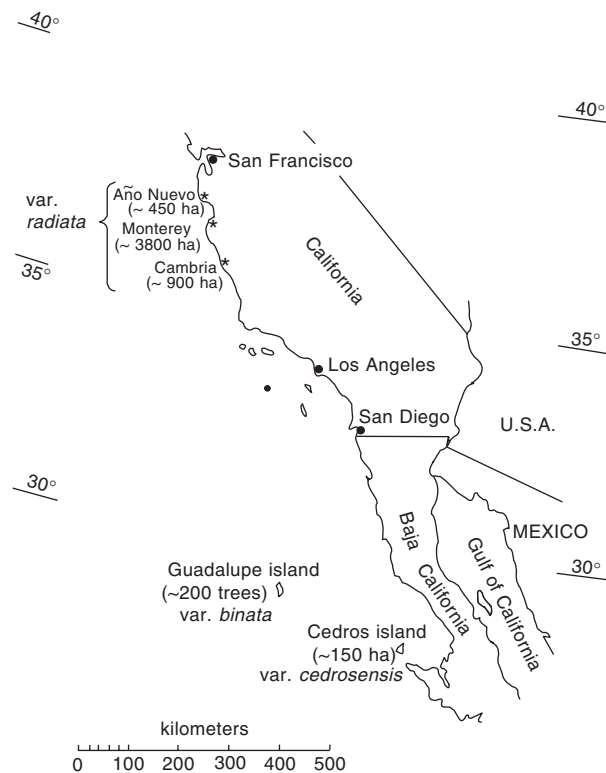


Figure 1 Map showing natural distribution of *Pinus radiata*. Current extent is shown for each population, being reduced by urbanization at Monterey and Cambria and grossly reduced on Guadalupe island. Adapted with permission from Burdon RD (2000) *Pinus radiata*. In: Last FT (ed.) *Ecosystems of the World*, vol. 19. *Tree Crop Ecosystems*. Amsterdam, The Netherlands: Elsevier.

Table 1 Natural occurrence and habitats of *Pinus radiata*

Population	Latitude (°N)	Altitude (m)	Exposure	Rainfall (mm)	Geology/soil	Extent (ha)	
						Historic	Current
Año Nuevo	37	0–330	Very varied	675–900?	Argillite-derived, slightly calcareous	450	450
Monterey	36½	0–420	Generally moderate	400–650?	Very varied geology and soils	7400	3800
Cambria	35½	0–180	Varied	450–575?	From single sandstone formation	1400	900
Guadalupe	29	330–1200	Severe	150–500?	Basaltic, rocky	250?	200 trees
Cedros	28	380–640	Locally severe	150–250?	Skeletal, old sediments and metamorphics	150	150

Adapted from Burdon RD (2000) *Pinus radiata*. In: Last FT (ed.) *Ecosystems of the World*, vol. 19: *Tree Crop Ecosystems*, pp. 99–161. Amsterdam, The Netherlands: Elsevier.

Table 2 Native-population differences within *Pinus radiata* in some morphological traits, turpentine composition, and corewood density

Trait	Population				
	Año Nuevo	Monterey	Cambria	Guadalupe	Cedros
Bark thickness (young trees)	Thinnish	Thickish	Medium	Thin	Thin
Cone length (cm)	8–15	5.5–13	10–19	5–11.5	3.5–9.5
Mean seed weight (mg)	42	23	48	29	29
Needles per fascicle	3	3	3	2	2
Persistence of juvenile features	Low	High	Very high	Very low	Low
α -pinene (% pinenes) in wood turpentine	23	35	34	21	14
Inner corewood density (site-dependent)	325	330	320	360	360
Sinker root development	Medium	Medium	Least	Strong	Greatest

(Adapted from Burdon RD (2000) *Pinus radiata*. In: Last FT (ed.) *Ecosystems of the World*, vol. 19: *Tree Crop Ecosystems*, pp. 99–161. Amsterdam, The Netherlands: Elsevier.)

Table 3 Differences between natural populations of *Pinus radiata* in growth potential, site tolerances, and resistance to pests and pathogens

Feature	Grade of evidence	Population				
		Año Nuevo	Monterey	Cambria	Guadalupe	Cedros
Growth potential	a	+	+	+	–	– –
Ease of transplanting	bc	+	o	–	+(+)	– –
Resistance to/tolerance of:						
Frost	b	++	+	–	o?	– –
Snow damage	c	+	o	–	n.d.	n.d.
Boron deficiency	b	+	+	+	–	– –
Phosphorus deficiency	b	–	++	++	–?	n.d.
Soil salinity	bc	o	+	++	– –	–
Damage by pathogens						
<i>Dothistroma pini</i>	ab	++	++	– –	o	– –
<i>Cyclaneusma minus</i>	a	+	++	– –	–	–?
<i>Sphaeropsis sapinea</i>	b	++	++	– –	– –	–
<i>Phytophthora cinnamomi</i>	b	– –	+	++	n.d.	n.d.
<i>Endocronartium harknesii</i>	b	o	–	– –	++	+
Damage by invertebrates						
<i>Pineus pini</i>	c	+	+	– –	– –	+
Damage by mammals						
Deer/rabbit browse	bc	o	o	o	–	+
Deer browse	b	–	o	+	n.d.	n.d.
Porcupines	b	+	+	– –	n.d.	n.d.

o, average; +, better than average; ++, markedly better than average; –, worse than average; – –, markedly worse than average; n.d., no firm data available.

a–c denote decreasing weight of evidence.

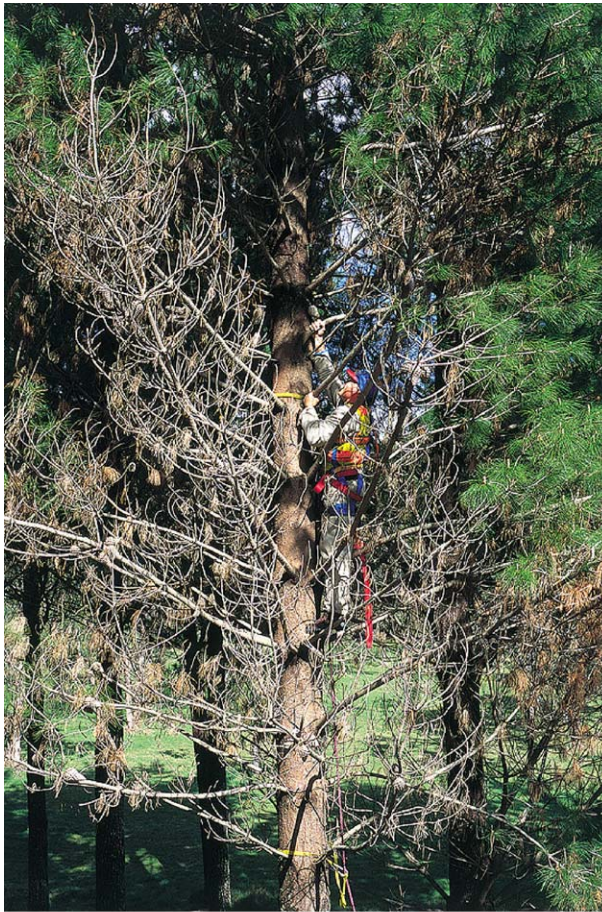
(Reproduced with permission from Burdon RD (2000) *Pinus radiata*. In: Last FT (ed.) *Ecosystems of the World*, vol. 19: *Tree Crop Ecosystems*, pp. 99–161. Amsterdam, The Netherlands: Elsevier.)

there are not yet the markers identified whereby a tree can be assigned unequivocally to a single native population, let alone to its correct hybrid ancestry.

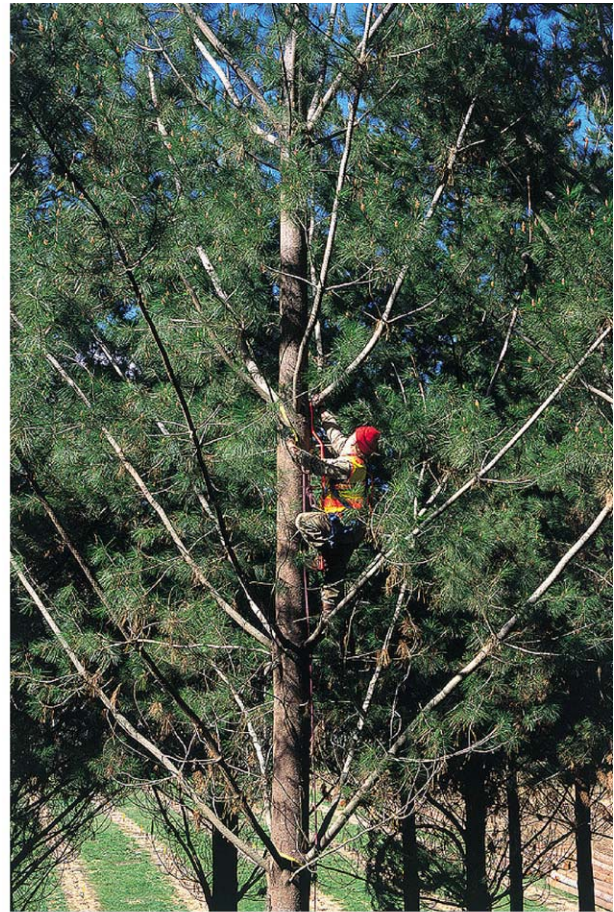
Within-Population Genetic Variation

Tree-to-tree genetic variation, both visible and cryptic, is a striking feature of *P. radiata*, which has led to much past confusion among taxonomists. Cone size and shape show much variability, which is superimposed upon the considerable population

differences. Dramatic variation exists in branching pattern (**Figure 2**), with neighboring trees often ranging from being monocyclic or uninodal (with only one cluster of branches produced in a year's growth on the leader) to highly polycyclic (with up to six such clusters); this variability is of profound importance for breeding programs and wood utilization. Considerable tree-to-tree genetic variation is also evident for growth rate, resistance to some diseases, stem straightness, a wide range of wood properties, turpentine composition, rate of onset of



(a)



(b)

Figure 2 *Pinus radiata* trees of contrasting branching patterns. (a) This tree has a highly polycyclic (or multinodal or short-internode) branching habit, producing several quite closely spaced branch clusters on each year's growth of the leader. In consequence, the branches are relatively small, giving a dispersed pattern of knots in timber, which favors producing structural grades. It is usually associated with less susceptibility to malformation and often better straightness and faster growth, at least early in the rotation. This sort of habit has been favored for the main breeding programs of New Zealand and Chile. Preferable for structural timber, it requires pruning in order to produce clear timber, which has been widely practiced in New Zealand. (b) This tree has an essentially monocyclic (or uninodal or long-internode) branching habit. The branches are large and steep-angled, but clearcuttings can be obtained between branch clusters without pruning. Prone to malformation and general poor form on many sites, this habit has been pursued in a subsidiary breeding program in New Zealand to produce a long-internode breed. This variation is strongly heritable, with the two trees representing extremes of an essentially normal distribution. For many sites, the ideal might be two co-equal branch clusters per year's leader growth, but that can only be expected reliably through mass propagation of well-proven clones. Courtesy of New Zealand Forest Research Institute Ltd.

some adult characteristics, and soil tolerances. Soil tolerances can generate substantial genotype–site interactions among phosphorus-deficient sites and elsewhere.

Estimated heritabilities and additive genetic coefficients of variation (which between them encapsulate the scope for genetic improvement) are shown for a range of traits in Table 4. While some of the values relating to branching pattern and cone characteristics may be exceptional, those for other traits seem fairly typical for the genus. For many additional wood properties only broad-sense estimates are available; while generally very high, they are unlikely greatly to

exceed narrow-sense heritabilities. Some of the wood properties, e.g., grain spirality and percentage heartwood, can show very high coefficients of variation, but such figures need to be interpreted with caution. As always, heritabilities for individual traits can depend, to varying degrees, on both the populations and the environments.

Relatively few between-trait genetic correlations are known at all well (Table 5), although, as with heritabilities, the values may vary according to both population and environment. Those best known involve positive associations between growth rate, frequency of branch clusters, light, wide-angled

Table 4 Estimated heritabilities and phenotypic coefficients of variation among individuals within base populations in *Pinus radiata* for different traits, together with likely economic significance for genetic improvement

Trait	Heritability	Coefficient of variation (%) ^a	Economic significance
Turpentine composition	>0.9		Negligible
Wood density (cores or disks)	0.7	7	Sometimes major
Cone characters ^b			
Volume, seed weight	>0.5	20–35	Minimal
Length, shape, scale no.	>0.5	12–18	Minimal
Grain spirality	0.3–0.7	~45	Sometimes major
Branch clusters on bole	>0.5	20–30	Often high, but indirect
Stem sinuosity ^c	0.4		Not major (– ve)
Wood density (penetrometer or torsionmeter measurements)	0.3–0.4		As for wood density
Branching habit overall ^c	0.3		Generally high
Height to first cone	0.3	20–30	Little direct importance
Dothistroma attack ^c	0.3		Locally major
Cyclaneusma needle cast ^c	0.1–0.35		Considerable (– ve)
Branch angle (steepness) ^c	≤0.2		Considerable (– ve)
Height	0.2	12	Limited in itself
Stem diameter	0.1–0.3	15	Major
Stem volume	0.1–0.3	30	Major
General stem straightness ^c	0.1–0.3		Generally major
Branch diameter	0.2		Major (– ve)
Frost resistance (growth room)	0.2		Minor overall
Butt sweep ^c	0.1–0.2		Often major (– ve)
Forking, etc.	0.05–0.1		Major (– ve)
Wind damage	0.05		Locally major (– ve)
Leader dieback	0.05		Sometimes important

^aWhere measurement scale allows valid estimate.^bBroad-sense heritability, instead of narrow-sense, but unlikely to be much greater than narrow-sense.^cBased on visual scores, with observer error depressing effective heritability values.Reproduced from Burdon RD (1992) Genetic survey of *Pinus radiata*. Part 9. *New Zealand Journal of Forestry Science* 22: 275–298, with permission.**Table 5** Approximate values of the better-estimated between-trait genetic correlations in *Pinus radiata*

	Height	Wood density	Stem straightness	Branching frequency	Forking (incidence)	Branch diameter	Branch angle
Stem diameter	0.7	– 0.2 to – 0.4	0.1	0.15–0.45	0.1		0.1
Height		0.15	0.2	0.2–0.45	0.35		0.25
Wood density			0	– 0.05	0		
Stem straightness				0.4	0.5		0.15
Branching frequency					0.3–0.5	0.75	0.6
Forking						0.3	0.4
Branch diameter							0.65

Note: Positive signs denote favorable genetic correlations in relation to ideal of fast growth, high wood density, small, wide-angled branches, zero forking, and polycyclic (multinodal or short-internode) branching habit. Hence there are a number of adverse correlations in relation to an ideal of long internodes that would allow significant clear cuttings without pruning, more so on some sites than others.

After Burdon RD (1992) Genetic survey of *Pinus radiata*. Parts 1–9. *New Zealand Journal of Forestry Science* 22: 275–298.

branching, stem straightness, and freedom from malformation, and a negative association between wood density and stem diameter. Significant constraints therefore face the breeder in trying to pursue long internodes (which offer clear cuttings without pruning) along with improved growth and form, or both increased wood density and volume production.

Genotype–environment interactions are evident in respect of both variation among sites in expression of

genetic variation and rank changes among sites in performance of genotypes. Differences in tree form can be more strongly expressed on fertile sites. Rank changes are strongly evident between phosphorus-deficient sites and elsewhere (pointing to genetic variation in tolerance of this deficiency) but otherwise tend to be limited.

Within-population variation in genetic markers (isozymes, restriction fragment length polymorphisms

(RFLPs), randomly amplified polymorphic DNA (RAPDs), amplified fragment length polymorphisms (AFLPs), SSRs) is significant, but it does not stand out from other conifer species in the way that much of the morphological variation does.

Early Domestication Genetics

Domesticated stocks of the species have arisen since the species was first introduced as an exotic, around 1850–1860 for South Africa, Australia, New Zealand, and Spain, and in 1885 for Chile. New Zealand evidently became self-sufficient for seed by the early 1880s, and made significant exports of unimproved seed to South Africa at least in the 1920s and to Australia until the middle of the twentieth century. Documentation of follow-up seed importations by Chile and Spain has not been traced. It appears that the two northernmost of the natural populations, Año Nuevo and Monterey, have been the progenitors of almost all the domesticated stocks, with a disproportionate contribution from the small Año Nuevo population. For many purposes these are the natural populations that are best adapted to the exotic environments, but even broader adaptation can presumably be obtained from drawing germplasm from the other populations.

While domesticated stocks may have come from a very incomplete and unbalanced representation of the natural range, seed importation records for New Zealand and genetic evidence indicate a fairly broad ancestral base in terms of numbers of individuals.

Even before intensive breeding began, some genetic improvement occurred in a process of land-race development. Release from the ‘neighborhood inbreeding’ of natural stands has evidently been a positive factor. There have also been some genetic shifts in response to pressures of natural and silvicultural selection in the adoptive environments, although it is difficult to quantify these shifts accurately. Heterosis, or hybrid vigor, from crossing between two natural populations, has been postulated but not proven.

Intensive Genetic Improvement

General History

Pioneering research on genetic variation in *P. radiata* began in Australia during the 1930s, under the auspices of the (Commonwealth) Forestry and Timber Bureau, Canberra. Intensive breeding programs began in New Zealand, Australia, and South Africa in the 1950s. These were based on local stocks, in the belief that provenance variation would not be important. This decision was put to the test in

parallel or subsequent provenance or provenance/progeny trials. In fact, it proved to be justified, despite initial underestimation of provenance variation and the likelihood that additional germplasm from the natural range could bring long-term benefits. However, some of these benefits may only be realizable in segregating generations, after the F_1 .

Improvement began with very intensive selection of ‘plus trees,’ mainly in commercial stands (Figure 3). Selection criteria varied significantly among agencies according to perceptions of whether growth rate or form was the higher priority for improvement. The plus trees were grafted into archives prior to establishing grafted clonal seed orchards. This put tree breeders on a long ‘learning curve’ in the siting, establishment, and management of the orchards. Difficulties arose with delayed incompatibility of grafts (or else obtaining cuttings from postjuvenile trees), achieving good pollen isolation, and with seed yields.

An interim improvement measure, pending self-sufficiency for orchard seed, has been collection of seed from the best trees in stands, either at felling or on standing trees. This was much helped by the serotinous cones which could store several years’ seed crops on the trees. In addition, progeny trials were available as back-up seed sources.



Figure 3 One of the original *Pinus radiata* plus trees selected in a closed stand in New Zealand, shown well after the selection age. The outstanding vigor of this parent (‘Clone 55’) characterizes almost all its progeny. The wood of the progeny, while of low density, has some very desirable technical properties. Courtesy of New Zealand Forest Research Institute Ltd.

Progeny testing was embarked upon from the outset, with varying thoroughness and success. However, it became appreciated, by the late 1960s, that the extremely intensive selection of plus trees left little scope for reselection on the basis of progeny-test information, and severely restricted the genetic base for long-term breeding. Further selection of first-generation plus trees was done, making vastly more selections.

Despite the technical problems, clonal seed orchards came close to meeting planting requirements, and actually exceeded them in some areas. However, the slow and incomplete capture of genetic gain prompted the development of new delivery systems. Selection of orchard sites was greatly improved. Hedged seed orchards were adopted in some quarters, which allowed controlled pollination with full capture of genetic gain and greater flexibility, and they are easier and safer to manage and harvest. Other types of orchard that allow controlled pollination have also been developed (Figure 4). Vegetative multiplication of small amounts of top-quality seed is a slightly more recent development that can further speed up the capture of genetic gain. It is being done on a large operational scale using nursery cuttings, and on a smaller scale using tissue-culture plantlets, while embryogenesis from seed embryos is being pursued. Embryogenesis, while more difficult to achieve in pine than in spruces (*Picea* spp.), offers a platform for future genetic transformation. Clonal forestry, based on mass propagation of well-characterized, intensively select

clones, is being pursued by a few agencies, and is close to being fully developed, although there still remain some problems of long-term storage of clones to retain full vigor and ease of propagation.

As befits the species' commercial importance and its model-species status, it is the subject of a full-scale genomic sequencing project, but the information is proprietary.

Early improvement work was directed mainly at improving growth rate and tree form, in varying emphasis on the two. Genetic gains achieved have generally been large (Figure 5), typically reflecting



Figure 4 Clonal seed orchard of *Pinus radiata* designed to produce seed of superior genetic quality by controlled pollination. This is one of several types of orchard that has been developed to avoid the operational problems of producing seed on tall, tree-form grafts or cuttings, and is an adaptation of the meadow orchard system of producing apples. A site has been chosen that favors early and profuse seed production on the grafts. Often such seed is now produced in limited quantities for mass vegetative multiplication, still mainly by nursery cuttings. Courtesy of New Zealand Forest Research Institute Ltd.



Figure 5 Trees of *Pinus radiata* produced by early pair-crossing between intensively select parents on a very high-quality site in New Zealand. Tree form is strikingly good for the site and stocking. Planted at $750 \text{ stems ha}^{-1}$ in pasture, and thinned at age 8 to $215 \text{ stems ha}^{-1}$, 18-year predominant mean height was 33.5 m, mean breast height diameter 54 cm, with $480 \text{ m}^3 \text{ stemwood ha}^{-1}$. The better pair-crosses of similar material, kept at higher stockings but on a similar site, gave mean annual increments approaching $50 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ at age 27, compared with an expected value of $30\text{--}35 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ for unimproved stock. With large genetic gains achieved in growth and tree form, attention is shifting to improving wood properties to help produce high-quality raw material on short rotations. Courtesy of New Zealand Forest Research Institute Ltd.

the relative emphasis on growth and form respectively. Since then there has been some focus on resistance to needle-cast diseases, with local or sporadic efforts directed at resistance to some other diseases. More recently has come increasing emphasis on improving wood properties (Figure 6), to offset the impacts of various measures that cut effective growing costs, viz. shorter rotations, fertilizer use, heavier thinning regimes.

Genetic Improvement in Individual Countries

New Zealand The breeding program was initiated by the Forest Research Institute (FRI) within the New Zealand Forest Service. FRI also conducted associated research, gathering up some earlier work. A national program was effectively operated until 1987, when the Forest Service was dissolved. Following that, the New Zealand Radiata Pine Breeding Cooperative was created, with FRI doing the breeding and genetic research, but with increasing in-kind contributions from member companies after corporatization and then privatization of Forest Service plantations. Cooperative members have come to include some from Australia, the Forestry Commission of New South Wales and some smaller concerns. During 2000–2002, the Cooperative became a limited-liability company. In the meantime, some companies have developed their own propagation and clonal programs as their own intellectual property. In 2003 a decision was made to terminate state funding of breeding and gene-resource work and immediately associated research.

Intensive plus-tree selection began in the early 1950s, for establishing regional seed orchards, although the regionalization proved to be unnecessary.

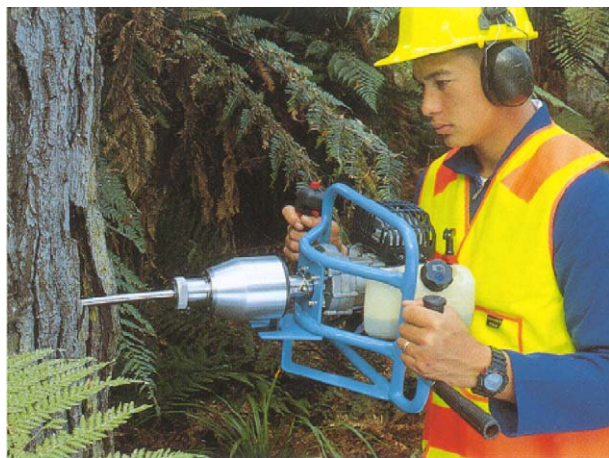


Figure 6 Sampling a *Pinus radiata* candidate for selection for determining several key wood properties by taking a core of 12 mm diameter. Courtesy of New Zealand Forest Research Institute Ltd.

The first block of orchard was planted in 1958, to start producing seed in 1968. Orchards produced enough seed for the whole country by 1986. Since then, control-pollinated orchards have become predominant, with considerable vegetative multiplication. Fully clonal systems, while still hampered by imperfect control of maturation, are being implemented on a significant scale by two companies.

Following the initial round of plus-tree selection, many more first-generation plus trees were selected in 1968–1970, to give a broadly based breeding population, with a further round during 1984–1987.

Selection was initially for growth and form, arriving at a strongly polycyclic (or multinodal or short-internode) ideotype (Figure 2a), although a side-program pursued a long-internode ideotype (Figure 2b) as an insurance. Recently a portfolio of differentiated breeds has been created, to serve different sites and end-uses as well as addressing market uncertainties.

Australia Although the federal organization (Forest and Timber Bureau, later the Division of Forestry and then Forestry and Forest Products) of the Commonwealth Scientific and Industrial Research Organisation (of Australia) (CSIRO) started the research, breeding programs began under the auspices of individual states and Australian Capital Territory (ACT). Of the states, New South Wales, Victoria, and South Australia had a major involvement in the species, with lesser involvements on the part of Western Australia, ACT, Tasmania, and Queensland. All the states and ACT began intensive breeding by 1960 or soon after, with two programs in Victoria, although some programs have effectively lapsed or been absorbed. Lack of coordination among the states, and the consequent thin spread of expertise, hampered progress, but some coordinated efforts were eventually achieved under the auspices of the Australian Forestry Council. The Council established a research working group that met biennially to address forest genetic improvement in general, and New Zealand participants were eventually admitted.

Selection emphasis has been more on growth rate and less on tree form than in New Zealand, but some shifts towards establishing new plantations on more fertile ex-pasture sites call for greater emphasis on improving tree form.

In 1978 CSIRO led a major initiative to collect seed from natural stands for *ex situ* gene resources. Numerous plantings resulted from that, but are in need of active management. Further seed collection was done on Guadalupe island in 1991.

In 1983, after disastrous fires in South Australia, the Southern Tree Breeding Association was formed,

initially to address a crisis of availability of seed of acceptable genetic quality. Members now include, in addition to various South Australian agencies, ones from Victoria, Western Australia, and Tasmania.

South Africa Despite an early start with breeding, in the 1950s, activity has been limited by the restricted areas over which the species succeeds.

Chile An abortive start by Instituto Forestal in the early 1970s was followed by the successful establishment of a Cooperative (initially Convenio) between the Southern University of Chile and industry parties. Established along the lines of the Industry/North Carolina University Tree Improvement Cooperative, it began with individual members setting up their own seed-orchard programs. However, it appears not to have led to a coordinated national program based upon free exchange of genetic material, although some interregional integration has occurred within large corporate structures.

Initial plus-tree selection was intensive, aimed at much the same short-internode ideotype as in New Zealand. Each member company established a 42-clone grafted seed orchard. Choice of orchard site was guided by experience in New Zealand and Australia, and was mostly very successful, leading to orchards meeting most members' seed requirements in about 10 years.

Among major member companies there have been separate developments, pursuing vegetative multiplication, and sophisticated biotechnology for appropriating intellectual property.

Spain In the late 1980s a breeding program was set up for the Basque autonomous region, on the northern coast just west of the Pyrenees, based in Vitoria. By far the main emphasis has been on breeding for diameter growth. Problems in finding a suitable seed-orchard site within the region have led to the establishment of an orchard far to the south, in Andalusia.

Hybridization

Experimental hybridization of *P. radiata* was undertaken as early as the 1930s, the main success being crossing with *P. attenuata*. While this hybrid had advantages, difficulties of mass production, and limited availability of sites where it had a decisive advantage prevented its large-scale planting. Interest in interspecific hybrids has been rekindled by a combination of availability of technology for vegetative multiplication of seeds or seedling stock, combined with a desire to extend site tolerances and/or improve resistance to diseases that are threats.

Genetic Transformation

Genetic transformation is being researched in *P. radiata*, initially as proof of concept, with current emphasis on control of reproduction and herbicide resistance, but with a view to other goals, notably manipulating wood properties. It is serving as a research tool. Operational use is envisaged as being in the context of clonal forestry.

See also: Genetics and Genetic Resources: Cytogenetics of Forest Tree Species; Genetic Systems of Forest Trees; Molecular Biology of Forest Trees; Population, Conservation and Ecological Genetics; Propagation Technology for Forest Trees. **Tree Breeding, Practices:** Genetics and Improvement of Wood Properties. **Tree Breeding, Principles:** A Historical Overview of Forest Tree Improvement; Conifer Breeding Principles and Processes; Forest Genetics and Tree Breeding; Current and Future Signposts.

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