# Picea rubens Sarg. Red Spruce

# Pinaceae Pine family

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Red spruce *(Picea rubens)*, also known as yellow spruce, West Virginia spruce, eastern spruce, and he-

balsam, is one of the more important conifers in the northeastern United States and adjacent Canada. It



Figure 1—*The native range of red spruce.* 

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is a medium-size tree that may grow to be more than 400 years old. The wood of red spruce is light in color and weight, straight grained, and resilient. It is used for making paper, for construction lumber, and for musical stringed instruments. Its many uses rival those of eastern white pine (*Pinus strobus*) (21).

## Habitat

#### Native Range

The range of red spruce (fig. 1) extends from the Maritime Provinces of Canada west to Maine, southern Quebec, and southeastern Ontario, and south into central New York, eastern Pennsylvania, northern New Jersey, and Massachusetts. It also grows south along the Appalachian Mountains in extreme western Maryland, and eastern West Virginia, and north and west in Virginia, western North Carolina, and eastern Tennessee. Discontinuous stands may also be found in Haliburton Township, in Algonquin Provincial Park, and near Sturgeon Falls in Nippising Township, and in the southwestern Parry Sound District in Ontario, Canada.

#### Climate

Red spruce grows best in a cool, moist climate. The climate of the northeastern part of its range can be summarized as follows: annual precipitation (total), 910 to 1320 mm (36 to 52 in); annual snowfall, 203 to 406 cm (80 to 160 in); days with snow cover, 100 to 140; January temperature, -7" to  $-1^{\circ}$  C (20" to 30" F) maximum and -18" to -13" C (0° to 8" F) minimum; July temperature, 21" to 27" C (70" to 80" F) maximum, and 11" to 14" C (52° to 58" F) minimum; frost-free days, 90 to 150 (28). Red spruce attains maximum development in the higher parts of the southern Appalachian Mountains where the atmosphere is more humid and the rainfall heavier during the growing season than in other parts of its range (47). Local extension of the range of red spruce, as along the southern Maine coast, is related to marine exposure, which provides a cool growing season and ample moisture supply (8).

#### Soils and Topography

The soils where red spruce and its associates grow are mostly acid Spodosols, Inceptisols, and sometimes Histosols with a thick mor humus and a welldefined  $A_2$  horizon-characteristics commonly associated with abundant rainfall, cool climates, and softwood cover (11). Commonly, the pH of these soils ranges from 4.0 to 5.5. In northern New England, red spruce is found predominantly on shallow till soils that average about 46 cm (18 in) to a compact layer. It will grow on many sites unfavorable for other species, such as organic soils overlying rocks in mountainous locations, steep rocky slopes, thin soils, and wet bottomland (26). On poorly drained soils, lack of aeration limits growth (22).

In the northern part of its range, red spruce (fig. 2) grows at elevations from near sea level to about 1370 m (4,500 ft) (22). In the southern Appalachian Mountains it comes in at elevations as low as 1370 m (4,500 ft) and from there to about 1520 m (5,000 ft) it is mixed with hardwoods and eastern hemlock (*Tsuga canadensis*). At 1520 m (5,000 ft) balsam fir (*Abies balsamea*) joins with red spruce to form the dominant spruce-fir climax type. In West Virginia, spruce-fir stands are found as low as 980 m (3,200 ft) about 1520 m (5,000 ft) balsam fir (*Abies balsamea*) found for the spruce for the dominant spruce-fir stands are found as low as 980 m (3,200 ft) balsam fir (*Abies balsamea*) found for the spruce for the spruce for the spruce-fir stands are found as low as 980 m (3,200 ft) balsam fir (*Abies balsamea*) for the spruce for the spruce-fir stands are found as low as 980 m (3,200 ft) balsam fir (*Abies balsamea*) for the spruce-fir stands are found as low as 980 m (3,200 ft) balsam fir (*Abies balsamea*) for the spruce-fir stands are found as low as 980 m (3,200 ft) balsam fir (*Abies balsamea*) for the spruce-fir stands are found as low as 980 m (3,200 ft) balsam fir (*Abies balsamea*) for the spruce-fir stands are found as low as 980 m (3,200 ft) balsam fir (*Abies balsamea*) for the spruce-fir stands are found as low as 980 m (3,200 ft) balsam fir (*Abies balsamea*) for the spruce-fir stands are found as low as 980 m (3,200 ft) balsam fir (*Abies balsamea*) for the spruce-fir stands are found as low as 980 m ft) balsam fir (*Abies balsamea*) for the spruce-fir stands are found as low as 980 m ft) balsam ft (*Abies balsamea*) for the spruce-fir stands are found as low as 980 m ft) balsam ft) balsam



Figure Z-A red spruce stand.

ft). Above 1890 m (6,200 ft) in the southern Appalachians, red spruce appears less frequently than Fraser fir *(Abies fraseri)* (47). In the White Mountains of New Hampshire, balsam fir is the predominant species above 1220 m (4,000 ft) but red spruce is well represented from about 790 to 1010 m *(2,600* to 3,300 ft) (27).

### **Associated Forest Cover**

Pure stands of red spruce comprise the forest cover type Red Spruce (Society of American Foresters Type 32). Red spruce is also a major component in 5 and a minor component in 13 other forest cover types (10):

- 5 Balsam Fir
- 12 Black Spruce
- 16 Aspen
- 17 Pin Cherry
- 18 Paper Birch
- 21 Eastern White Pine
- 22 White Pine-Hemlock
- 23 Eastern Hemlock
- 25 Sugar Maple-Beech-Yellow Birch
- 30 Red Spruce-Yellow Birch
- 31 Red Spruce-Sugar Maple-Beech
- 33 Red Spruce-Balsam Fir
- 34 Red Spruce-Fraser Fir
- 35 Paper Birch-Red Spruce-Balsam Fir
- 37 Northern White-Cedar
- 60 Beech-Sugar Maple
- 107 White Spruce
- 108 Red Maple

Some of the shrubs associated with red spruce are: blueberry (Vaccinium spp.), hobblebush (Viburnum lantanoides), witherod (V. cassinoides), rhodora (Rhododendron canadense), lambkill (Kalmia angustifolia), mountain-holly (Nemopanthus mucronata), speckled alder (Alnus rugosa), red raspberry (Rubus idaeus var. strigosus), creeping snowberry (Gaultheria hispidula), wintergreen (G. procumbens), fly honeysuckle (Lonicera canadensis), gooseberry (Ribes spp.), witch-hazel (Hamamelis virginiana), downey serviceberry (Amelanchier arborea), beaked hazel (Corylus cornuta), and Canada yew (Taxus canadensis).

A number of mosses and herbs are also found growing in red spruce forest types. Certain mosses, herbs, and shrubs, however, have been shown to be related to site quality of red spruce (22). The three main associations, **Hylocomium** / **Oxalis**, **Oxalis** / Cor**mus**, and Viburnum / **Oxalis**, in that order, indicate increasing site productivity and increasing hardwood competition. Similar site types in the higher elevations of the Appalachian Mountains of North Carolina include *Hylocomium / Oxalis* on north-facing slopes above 1520 m (5,000 *fit), Oxalis/Dryopteris* at high elevations and all exposures, and the best site type for red spruce and Fraser fir, *Viburnum / Vaccinium / Dryopteris* (47).

The **Oxalis** / Cornus association is considered the best for growing conditions in the northern part of the range. On these sites the soil is rich enough for red spruce but not fertile enough for the tolerant hardwoods to offer serious competition (22).

## Life History

### **Reproduction and Early Growth**

Flowering and Fruiting-Red spruce is monoecious; male and female flower buds open in May in axils of the previous year's shoots on different branches of the same tree. The pendant male flowers are bright red; female flowers are erect and bright green tinged with purple (21). Although cone buds differentiate as early as July preceding flowering in the following spring, they are difficult to distinguish until September. For experienced workers they provide a possible means of identifying seed years at that time. The cones mature from about mid-September to early October, the autumn following flowering (41). Cones are 3 to 4 cm (1.3 to 1.5 in) long, light reddish brown, with rigid, rounded scales often slightly toothed on the edges. Cones are receptive to pollen when fully open, a condition which lasts for only a few days.

**Seed Production and Dissemination-Good** seed crops occur every 3 to 8 years, with light crops during intervening years (22). Red spruce cones number about 140/liter (5,000/bu), which yields 454 to 680 g (1.0 to 1.5 lb) of seeds. The number of cleaned seeds per kilogram ranges between 220,000 and 637,000 (100,000 and 289,000/lb), with an average of about 306,000 (139,000/lb) (41).

Red spruce seeds fall about 1.2 m (4 ft) per second in still air; the following formula determines distance of travel for wind-disseminated spruce seeds at various heights (47):

## $\boldsymbol{D} = S^h \left( 1.47v \right)$

Where D = distance in feet which seed will travel, S = number of seconds required for seed to fall from a height of **h** (ft) on a tree, and v = velocity of the prevailing wind in miles per hour.

Randall (37), in a study of seed dispersal into clearcut areas, stated that at a distance of 100 m (5 chains or 330 ft) from the timber edge, the number of spruce seeds trapped were more than adequate for regeneration in a good seed year and adequate in an average year. Most of the spruce in the surrounding stands was red spruce.

**Seedling Development-Most** red spruce seeds germinate the spring following dispersal; some, however, may germinate in the fall soon after dropping from the tree. Germination is epigeal. On favorable seedbeds the usual spring germination period is from late May to early July. On duff, which is more subject to surface drying than most other seedbed materials, some seeds may lose viability by midsummer, and some may show delayed germination well into August (22). Little if any viable seeds remain in the forest floor beyond 1 year (13).

Adequate moisture is the chief factor controlling germination of red spruce. Germination takes place on almost any medium (mineral soil, rotten wood, or shallow duff) except sod. Mineral soil is an excellent seedbed for germination. Generally ample moisture is available and soil temperatures are moderate. Litter and humus are poorer seedbeds because they are likely to be hotter and drier than mineral soil (11). On thicker duff, germination may be poor also because moisture conditions are less favorable. Temperatures of 20" to 30" C (68" to 86" F) are generally favorable for germination. Seeds will not germinate satisfactorily at temperatures below 20" C (68" F) and are permanently injured by long exposure to temperatures higher than 33" C (92" F) (22).

Germination and initial establishment proceed best under cover. Seedlings can become established under light intensities as low as 10 percent of full sunlight; however, as they develop, they require light intensities of 50 percent or more for optimum growth. Seedlings starting in the open undergo heavy mortality when soil surface temperatures reach 46" to 54" C (115" to 130" F) even for a short time (11). Drought and frost heaving are major causes of mortality the first year. Crushing by hardwood litter and snow are also causes of seedling mortality. Winter drying in some years and locations can cause severe leader damage and dieback.

Natural reproduction depends more on seedling survival than on requirements for germination. Spruce seedlings have an exceptionally slow-growing, fibrous, shallow root system. Consequently, a critical factor in their survival and establishment is the depth of the 01 organic layers of the soil profile. When the combined thickness of these layers exceeds 5 cm (2 in), spruce seedlings may not reach mineral soil and the moisture necessary to carry them through dry periods. Red spruce seedlings and the commonly associated balsam fir seedlings are similar in many ways and are controlled by the same factors, but as a rule spruce is the weaker, slower growing species during the establishment period (22).

Seedlings that have attained a height of about 15 cm (6 in) can be considered established. Once established, their early growth is determined largely by the amount and character of overhead competition. Dense growth of bracken (*Pteridium aquilinum*), raspberry, and hardwood sprouts are the chief competition for seedlings on heavily cutover lands; but red spruce survives as much as 145 years of suppression and still responds to release (*11,39*).

Compared to its associates, red spruce is one of the last species to start height growth in the spring, usually beginning the first week in June and ending 9 to 11 weeks later. Radial growth usually begins about the second week of June and continues through August (22).

**Vegetative Reproduction-Red** spruce rarely, if ever, layers (*15,22,45*). Recently developed techniques facilitate propagation from stem cuttings under controlled conditions, particularly juvenile cuttings (*7,9,38,45*).

#### Sapling and Pole Stages to Maturity

**Growth and Yield-Red** spruce (fig. 3) is a medium-size tree at maturity, reaching 30 to 61 cm (12 to 24 in) in d.b.h. and 18 to 23 m (60 to 75 ft) in height in the Northeast, and up to 35 m (115 ft) in the Appalachian Mountains. Its maximum age is about 400 years (22). The American Forestry Association lists a tree 133 cm (52.5 in) in d.b.h. and 33.5 m (110 ft) tall in Great Smoky National Park in North Carolina as the largest living red spruce.

The rate of red spruce's growth is strongly influenced by light conditions. Although trees can live in dense shade for many years, once they reach sapling to pole stage nearly full sunlight is beneficial. Understory trees no more than 1.2 or 1.5 m (4 to 5 ft) tall may be more than 50 years old, whereas trees of the same age in the open may be approaching small sawtimber size (22).

Under favorable conditions, red spruce may reach an average d.b.h. of 10 cm (4 in) and height of 7 m (23 ft) in 20 years, and be over 23 cm (9 in) in d.b.h. and 19 m (62 ft) tall in 60 years (22).

Diameter growth of red spruce has been related to vigor, live crown ratio (ratio of live crown to total height), live crown length, and initial diameter at breast height (6,32). High vigor red spruce with a live crown ratio of 0.5 or better averaged 4.3 cm (1.7 in) of diameter growth in 10 years. Growth rates of trees with smaller crown ratios and less vigorous trees



Figure 3-Red spruce seeding into grassland on the mountains of West Virginia.

Tree class Live (rating as crown Average lo-yea growing stock) Vigor Crown class ratio¹ growth in d.b.l					
				сm	in
A,	superior	I Dominant and Intermediate	0.6+	4.6	1.8
В,	good	I Dominant and Intermediate	0.3 to 0.5	3.3	1.3
C,	acceptable	I I Overtopped Intermediate	0.6+ 0.6+		
		Dominant	0.6+	2.3	0.9
D,	inferior	Intermediate	0.3 to 0.5	1.5	0.6
E,	undesirable	III Intermediate All others	0.3+ 0.3 or less	0.5	0.2

 Table
 l-Classification of red spruce trees (11)

'Ratio of live crown to total height.

decreased progressively to an average of 0.8 cm (0.3 in) in 10 years for trees of low vigor or with crown

ratios smaller than 0.4 (22). A tree classification for red spruce is shown in table 1 (11).

In one study (40), average net annual growth in softwood stands (66 to 100 percent softwood species) that can be expected from stands receiving minimal silvicultural input was found to be about 3.5 m<sup>3</sup>/ha (50 ft<sup>3</sup>/acre). In mixed-wood stands (21 to 65 percent softwood species) this dropped to about 2.8 m<sup>3</sup>/ha (40 ft<sup>3</sup>/acre), although the majority of the growth was contributed by softwoods. A further breakdown of the data shows the contributions of spruce, most of which was assumed to be red spruce, to be 51 percent in softwood stands and 39 percent in mixed-wood stands.

Yields per acre, in total volumes of all trees larger than 1.5 cm (0.6 in) in d.b.h. (inside bark and including stump and top but not butt swell), are given in table 2 (33).

	Site index <sup>1</sup>				
Age	12.2 m or 40 ft	15.2 m or 50 ft	18.3 m or 80 ft	21.3 m or 70 ft	
yr	m³/ha				
20	6	8	11	14	
40	94	132	164	200	
60	244	335	422	507	
80	308	424	533	640	
100	332	456	575	691	
yr	ft³/acre				
20	80	120	160	200	
40	1,350	1,890	2,350	2,850	
60	3,490	4,780	6,030	7,240	
80	4,400	6,060	7,610	9,150	
100	4,740	6, 520	8,210	9,870	

**Table** 2-Yield of red spruce by age class and siteindex (adapted from 33)

Base age 50 years when age is measured at d.b.h.-total tree age is estimated to be 65 years at that time.

**Table** 3-Merchantable yield of red spruce (adaptedfrom 48)

	Density index (regional average 100)			
Years since cut	50	100	150	
		d/ha		
10	17.1	24.4	29.5	
20	29.8	37.7	43.3	
30	43.5	52.0	58.0	
40	<b>58.</b> 1	67.3	73.4	
50	73.8	83. 1	89.7	
		ft³∕acre		
10	245	349	422	
20	425	539	618	
30	622	743	828	
40	830	961	1,049	
50	1,054	1,187	1, 281	

These yields are normal yields from even-aged stands growing primarily on old fields. Therefore, they are higher than yields that might be expected from more irregular stands such as those developing after cutting (22).

Site index has not been of great utility in rating the potential productivity of spruce-fir sites because of the tolerance of the species and its ability to survive in a suppressed state. Site index at base age 50 years is as good a measure of productivity as any of several growth functions, however (39). Recently,

Moisture regime	Biomass		Annual production		
	t/ha	tons/acre	t/ha	tons/acre	
Dry	121.3	54.1	4.5	2.0	
Fresh	263.2	117.4	8.7	3.9	
Moist	461.3	205.8	9.9	4.4	
Wht	164 1	79 9	9 0	17	

**Table 4**—Aboveground biomass and annual production of all tree components and foliage for red spruce at latitude 45" 30' N. (adapted from *17*)

polymorphic site index curves were developed for even-aged spruce and fir stands in northern Maine; they should be valuable for estimating site productivity (20).

Other yield tables for the Northeast (48) take into consideration stand density, composition, and time since cutting. These tables give merchantable volume of spruce and fir combined in trees 15.2 cm (6 in) in d.b.h. and larger from a 0.3 m (1 ft) stump to a 7.6 cm (3 in) top, diameter inside bark, and are somewhat conservative. Yields of merchantable volume for different stand densities from 10 to 50 years after cutting, where 90 percent of the trees are spruce and fir growing on predominantly softwood sites, are given in table 3.

The development of stand projection growth models that permit computer simulation of red spruce tree growth for various management practices and silvicultural treatments over a range of stand conditions has flourished in recent years. For ex-



Figure 4-A dense red spruce stand in Maine.

ample, the model FIBER was developed in the Northeast (43) for spruce-fir, northern hardwood and a range of Mixedwood forest types between the two. Such models have proved very useful for forest management planning.

In recent years, interest in total biomass yield and productivity has increased, and in the future is likely to become more important in management considerations. As an example, above-ground biomass and productivity values of typical red spruce stands in Canada are given in table 4 for stands in a steady state, across a moisture regime catena (17).

**Rooting Habit-Spruce** and fir are shallowrooted, with most of the feeding roots in the duff and the top few centimeters of mineral soil (11). The average rooting depth for all sites in Maine was found to be 33 cm (13 in), with a maximum of 56 cm (22 in) (22).

**Reaction to Competition-Red** spruce is classified as shade tolerant in the United States and tolerant or very tolerant in Canada. Opinions differ as to whether red spruce is more tolerant than balsam fir, but the relative tolerance may vary with soil fertility and climate (22).

The species' chief competition comes from balsam fir and hardwoods that produce heavy shade, like beech and maple. Competition from aspen, birch, and other thin-crowned species is not so severe. Red spruce prunes itself about as well as most softwoods in dense stands (fig. 4). As much as one-third of the live crown may be pruned artificially without seriously affecting radial growth (5).

A number of studies have demonstrated the ability of red spruce to respond to release after many years of suppression, The vigor of this response does decline somewhat with age, however, and older trees may require about 5 years to recover before showing accelerated growth (7). Reduction of growth to about 2.5 cm (1 in) of diameter in 25 years, for a duration of 100 years, represents about the limit of suppression for red spruce. Many of its associated tree species such as balsam fir and hemlock may outgrow red spruce after release (22).

Red spruce may be grown successfully using evenage silvicultural prescriptions (11,12). Red spruce is very shallow-rooted, however, making it subject to windthrow, a major silvicultural constraint in the management of the species. As a general rule, it is recommended that no more than one-fourth to onehalf of the basal area be removed in the partial harvest of a spruce-fir stand, depending on site, to avoid excessive windthrow damage. Most of the major forest cover types previously listed in which red spruce is a component are considered either climax or subclimax.

**Damaging Agents-The** shallow root system, thin bark, and flammable needles of red spruce make trees of all ages very susceptible to fire damage (11). The acreage of red spruce originally present in the southern Appalachians has been reduced to a fraction of what it once was by fire and clearcutting (22). Many former spruce sites are occupied by inferior tree species, blackberries, and ferns after 20 years (47).

The most important insect enemy of red spruce is the spruce budworm, *Choristoneura fumiferana. Al*though red spruce is much less vulnerable to damage than balsam fir or white spruce, largely due to later bud flushing in the spring (3), much damage and mortality occur in stands containing large quantities of mature balsam fir. Blum and McLean (4) suggest that factors such as stand age, species composition, density, and vigor contribute to the vulnerability of spruce-fir stands to budworm damage and suggest steps to alleviate damage. Additional, detailed information may also be found in Sanders, *et al. (42)* for spruce-fir stands in the Northeast, the Lake States, and Canada.

The eastern spruce beetle, *Dendroctonus rufipennis*, damages mature trees of red spruce. Two species of sawflies, the European spruce sawfly, *Diprion hercyniae*, and the native yellowheaded spruce sawfly, *Pikonema alaskensis*, have severely defoliated red spruce in localized areas (22). The eastern spruce gall adelgid, *Adelges abietis*, can be a serious pest on spruce when abundant. The pine leaf adelgid, *Pineus pinifoliae*, forms unsightly but relatively harmless conelike galls on red and black spruce (*Picea mariana*), which are alternate hosts (46).

Red spruce has few diseases. Needle cast caused by *Lirulu mucrosporu* may result in severe defoliation of the lower crown and a subsequent reduction of growth. *Phellinus pini* and *Phaeolus schweinitzii*, the most destructive of red spruce wood-rotting fungi, are usually confined to overmature or damaged trees. *Climucocystis borealis* causes butt rot in overmature trees (22). Trees are occasionally attacked by *Armillaria mellea* and *Znonotus tomentosa*.

All along the eastern Appalachian mountain chain, from the New England states to Georgia, growth has declined in high-elevation red spruce since the 1960's (25). In recent years, this decline has been accompanied by increased mortality and crown damge in high-elevation red spruce. Apparently, no significant natural biotic or abiotic causal agents have been identified, although it has been hypothesized that interaction among naturally occurring insect and disease factors and anthropogenic air pollutants, or air pollutants acting alone, are at the root of the problem. Sulphur dioxide (SO<sub>2</sub>), nitrogen oxides (NO,), and volatile organic compounds are the pollutants of primary concern; secondary pollutants such as ozone and nitric and sulfuric acids are also believed to be important factors (29).

Growth decline and mortality in low-elevation red spruce in northern New England, while increasing in some areas, appear to be within the normal ranges for trees and forests of various ages, compositions, and density. However, some foliar symptoms have been detected in both red spruce and white pine, particularly from ozone exposure.

Red spruce is occasionally infected with eastern dwarf mistletoe, *Arceuthobium pusillum*, a parasite causing growth reduction, tree mortality, and degradation of wood quality (24).

Mice and voles have been found to consume and store significant amounts of spruce seeds in preference to those of balsam fir, suggesting one reason for the low ratio of spruce to fir seedlings commonly found in naturally regenerated stands (1,23). Wildlife damage to the terminal buds of young spruce, presumably by birds, also has been noted (2). Some injury and mortality are also caused occasionally by porcupines, bears, deer, and yellow-bellied sapsuckers (11). Red squirrels clip twigs and terminals and eat reproductive and vegetative buds (41).

## **Special Uses**

The wood of red spruce, white spruce (*Picea glauca*), and black spruce cannot be distinguished with certainty by either gross characteristics or minute anatomy, and all three are usually marketed simply as eastern spruce. Chief uses are for lumber and pulpwood, with limited amounts going into poles, piling, boatbuilding stock, and cooperage stock (36). Flakeboard and plywood have been made from spruce in recent years. It is also the preferred wood for piano sounding boards, guitars, mandolins, organ pipes, and violin bellies (*21*).

Forest cover types that include red spruce support a wide variety of wildlife. They are particularly important as winter cover for deer and, to a certain extent, moose. Small game includes ruffed grouse, snowshoe hare, and woodcock. Many song birds and fur bearers also frequent these forest types (44).

A unique use of red spruce was spruce gum, an exudate that accumulates on trunk wounds. This was the raw material for a flourishing chewing-gum industry in Maine during the last half of the 19th century and early years of this century (21).

## Genetics

Successful interspecific crosses with *Picea rubens* as male or female parents have been reported or confirmed for *P. mariana, F! omorika, P. glehnii, P. orientalis,* and *P. koyamai (15); P. sitchensis (14); P. glauca, F! mexicana (16); I? x lutzii* Little (*P. sitchensis x I? glauca), P. maximowiczii,* and *I? likiangensis (19).* 

Crossability of *P. rubens* with *I*? omorika is good with *P. mexicana* and *P. likiangensis* moderate; with *I*? mariana, *I*? orientalis, *I*? maximowiczii, and F! glehnii fair to poor; and with *P. koyamai*, *I*? sitchensis, *P. x lutzii*, and *P. glauca* very poor. Several species fail to cross with *I*? rubens (15, 16, 18, 19).

Hybrids between *I? rubens* and *P. mariana* occur to some extent in nature, but parental species remain phenotypically pure in their characteristic habitats (15,30,31,34,35).

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