Populus tremuloides Michx. Quaking Aspen

Sal icaceae Willow family

D. A. Perala

Quaking aspen ***(Populus tremuloides)*** is the most widely distributed tree in North America. It is known by many names: trembling aspen, golden aspen, mountain aspen, popple, poplar, trembling poplar, and in Spanish, alamo blanco, and alamo temblón (49). It grows on many soil types, especially sandy and gravelly slopes, and it is quick to pioneer disturbed sites where there is bare soil. This fast-growing tree is short lived and pure stands are gradually replaced by slower-growing species. The light, soft wood has very little shrinkage and high grades of aspen are used for lumber and wooden matches. Most aspen wood goes into pulp and flake-board, however. Many kinds of wildlife also benefit from this tree.

Habitat

Native Range

Quaking aspen (fig. 1) grows singly and in multistemmed clones over 111” of longitude and 48” of latitude for the widest distribution of any native tree species in North America (48). The range extends from Newfoundland and Labrador west across Canada along the northern limit of trees to northwestern Alaska, and southeast through Yukon and British Columbia. Throughout the Western United States it is mostly in the mountains from Washington to California, southern Arizona, Trans-Pecos Texas, and northern Nebraska. From Iowa and eastern Missouri it ranges east to West Virginia, western Virginia, Pennsylvania, and New Jersey. Quaking aspen is also found in the mountains of Mexico, as far south as Guanajuato. Worldwide, only ***Populus tremula,*** European aspen, and *Pinus sylvestris*, Scotch pine, have wider natural ranges.

Climate

Climatic conditions vary greatly over the range of the species, especially winter minimum temperatures and annual precipitation. The known widest range in temperatures aspen has endured in the conterminous United States is in Montana, where January lows of -57” C (-70” F) and summer highs of 41” C (105” F) have been recorded. In Alaska and northwest Canada, part of the range lies within the permafrost zone, but quaking aspen grows only on the warmest sites free of permafrost *(28,91).*

At the eastern end of the range, in the Maritime Provinces of Canada, the climate is mild, humid, and snowfall is extremely heavy, 300 cm (120 in) or more per year. Some representative climates for the northern and eastern limits of quaking aspen as well as for the warmer parts of its eastern range are as follows *(78)*:

	Interior Alaska	*Gander, NF*	*Ft. Wayne, IN*
Temperature, C:			
Minimum	-61”	-34”	-31”
January average	-30”	-7”	-3”
Maximum	38”	32”	41”
July average	16”	16”	23”
Precipitation, mm:			
Total	180	1020	860
Growing season	80	250	330
Frost-free days	81	160	176
Temperature, F:			
Minimum	-78”	-29”	-24”
January average	-22”	19”	27”
Maximum	100”	90”	106”
July average	61”	61”	73”
Precipitation, in:			
Total	7	40	34
Growing season	3	10	13
Frost-free days	81	160	176

In the central Rocky Mountains, where altitude plays an important role in the distribution of aspen, the lower limit of its occurrence coincides roughly with a mean annual temperature of 7” C (45” F). In Colorado and southern Wyoming, quaking aspen grows in a narrow elevational belt of 2100 to 3350 m (6,900 to 11,000 ft). Average annual precipitation in this belt ranges from 410 to 1020 mm (16 to 40 in). The southern limit of the range of aspen in the Eastern United States is roughly delineated by the 24” C (75” F) mean July temperature isotherm. In Canada the mean annual degree-day sum of 700” C (1260” F) with a threshold temperature 5.6” C (42” F) coincides closely with the northern limit of the species *(51,69, 70,78,80).*

Quaking aspen occurs where annual precipitation exceeds evapotranspiration. It is abundant in interior Alaska where annual precipitation is only about 180 mm (7 in) because evapotranspiration is limited by cool summer temperatures. In the interior west the 2.5 cm (1 in) average annual surface water runoff

The author is Principal Silviculturist, North Central Forest Experiment Station, St. Paul, MN.

Figure 1-*The native range of quaking aspen.*

isopleth is more coincident with the range of aspen than is any isotherm. This isopleth also is coincident with the southern limit of aspen in the prairie provinces of Canada eastward to northwestern Minnesota and south to Iowa where high summer temperatures limit growth and longevity. In summary, the range of quaking aspen is limited first to areas of water surplus and then to minimum or maximum growing season temperatures *(33,71,91)*.

Soils and Topography

Quaking aspen grows on a great variety of soils (mainly Alfisols, Spodosols, and Inceptisols) ranging from shallow and rocky to deep loamy sands and heavy clays (83). Only occasional scattered trees that seldom attain economic size occur on the coarser sands of glacial outwash, the shallowest soils of rock outcrops, and on some Histosols. In the West, it has become established on volcanic cinder cones, and in New England it is one of several species that colonizes immediately after landslides. In the Lake States, it often reforests mining waste dumps and abandoned borrow pits (78).

Growth and development are strongly influenced by both physical and chemical properties of soil. The best quaking aspen stands in the Rocky Mountains and Great Basin are on soils developed from basic igneous rock, such as basalt, and from neutral or calcareous shales and limestones; the poorest are found on soils derived from granite. Some of the best stands of quaking aspen are in the northern part of the Lake States and in Manitoba and Saskatchewan, on Boralfs that have developed from the Keewatin drift, a gray glacial drift rich in lime. Good aspen soils are usually well drained, loamy, and high in organic matter, calcium, magnesium, potassium, and nitrogen. Because of its rapid growth and high nutrient demand, quaking aspen has an important role in nutrient cycling *(2,3,18,28,78)*.

Growth on sandy soils is often poor because of low levels of moisture and nutrients. On droughty sands in the western Great Lakes region, the site index at age 50 is usually less than 17 m (56 ft). On the better sandy loams it may be about 21 m (69 ft), and on silt loams 23 to 25 m (75 to 82 ft). The best aspen sites have been found on soils with silt-plus-clay content of 80 percent or more. Wood of the highest mean specific gravity (about 0.40) is produced on well-drained, fine-textured soils, and that of the lowest mean specific gravity (about 0.35) on poorly drained soils *(28,71,78)*.

Internal drainage is critical. Water tables shallower than 0.6 m (2 ft) or deeper than 2.5 m (8.2 ft) limit aspen growth. Heavy clay soils do not promote the best growth because of limited available water and poor aeration *(35,57,78)*.

Aspen spans an elevational range from sea level on both Atlantic (Maine) and Pacific (Washington) coasts to 3505 m (11,500 ft) in northern Colorado. Near its northern limit, quaking aspen is found at elevations only up to 910 m (3,000 ft). In Baja, California, it does not occur below about 2440 m (8,000 ft). In Arizona and New Mexico it is most abundant between 1980 and 3050 m (6,500 and 10,000 ft); in Colorado and Utah, about 300 m (1,000 ft) higher. At either of its altitudinal limits the tree is poorly developed. In very high exposed places it becomes stunted, with the stem bent or almost prostrate from snow and wind; at its lower limit it is a scrubby tree growing along creeks *(28,70,78,91)*.

Quaking aspen is most abundant and grows best on warm south and southwest aspects in Alaska and western Canada. It is common on all aspects in the western mountains of the United States and grows well wherever soil moisture is not limiting. However, the best stands in the Southwest are more frequently found on the northerly slopes where more favorable moisture conditions prevail. Development is poor on physiographic positions with excessive droughtiness. In the prairie provinces of Canada, particularly near the border between prairie and woodland, the species is confined to the cooler and moister north and east slopes and to the depressions *(28,69,70,78)*.

Associated Forest Cover

Quaking aspen (fig. 2) grows with a large number of trees and shrubs over its extensive range. It is a major component of three forest cover types *(72)*, Aspen (Eastern Forest) (Society of American Foresters Type 16), Aspen (Western Forest) (Type 217), and White Spruce-Aspen (Type 251). It is a minor component of 35 other types and an occasional to rare component in 3 types.

Shrub species commonly associated with quaking aspen in the eastern part of its range include beaked hazel ***(Corylus cornuta)***, American hazel ***(C. americana)***, mountain maple *(Acer spicatum)*, speckled alder ***(Alnus rugosa)***, American green alder ***(A. crispa)***, dwarf bush-honeysuckle *(Diervilla lonicera)*, raspberries and blackberries *(Rubus* spp.), and various species of gooseberry ***(Ribes)*** and willow *(Salix)*. Additional species occurring with quaking aspen in the prairie provinces include: snowberry ***(Symphoricarpos*** spp.), highbush cranberry *(Viburnum edule)*, limber honeysuckle ***(Loniceru** dioica)*, red-osier dogwood ***(Cornus stolonifera)***, western serviceberry ***(Amelanchier** alnifolia)*, chokecherry ***(Prunus virginiana)***, Bebb willow ***(Salix bebbiana)***, and several species of rose *(Rosa).* The latter two also occur in Alaska plus such additional species as Scouler willow *(Salix scouleriana),* bearberry *(Arctostaphylos uva-ursi),* russet buffaloberry *(Shepherdia canadensis),* mountain cranberry *(Vaccinium vitis-idaea),* and highbush cranberry. In the Rocky Mountains, shrubs commonly occurring with quaking aspen include mountain snowberry *(Symphoricarpos oreophilus),* western serviceberry, chokecherry, common juniper *(Juniperus communis),* creeping hollygrape *(Berberis repens),* woods rose *(Rosa woodsii),* myrtle pachistima *(Pachistima myrsinites),* redberry elder *(Sambucus pubens),* and a number of *Ribes (69,70,72,78,85,91).*

Herbs characteristic of quaking aspen stands in the east include largeleaf aster *(Aster macrophyllus),* wild sarsaparilla *(Aralia nudicaulis),* Canada beadruby *(Maianthemum canadense),* bunchberry *(Cornus canadensis),* yellow beadlily *(Clintonia borealis),* roughleaf ricegrass *(Oryzopsis asperifolia),* sweetscented bedstraw *(Galium triflorum),* sweetfern *(Comptonia perigrina),* lady fern *(Athyrium filix-femina),* bracken *(Pteridium aquilinum),* and several species of sedges *(Carex* spp.) and goldenrods *(Solidago* spp.). In the West, the herbaceous component is too rich and diverse to describe. Forbs dominate most sites, and grasses and sedges dominate others (72).

Life History

Reproduction and Early Growth

Flowering and Fruiting-Quaking aspen is primarily dioecious. The pendulous flower catkins, 3.8 to 6.4 cm (1.5 to 2.5 in) long, generally appear in April or May (mid-March to April in New England, May to June in central Rockies) before the leaves expand *(28,66,78,91).* Local clonal variation provides early and late flowering clones of each sex in most stands. In addition, certain flowers bloom later than others, usually those on the distal end of a ·given catkin or small catkins on spurlike shoots *(13).* Maximum air temperatures above 12" C (54" F) for a period of about 6 days appear to be the principal factor governing timing of flowering. Flowers are pollinated by wind. The fruiting catkins are about 10 cm (4 in) long when mature, usually in May or June-about 4 to 6 weeks after flowering. Each catkin may bear several dozen one-celled capsules, light green, each nearly 6 mm (0.25 in) long. Each capsule contains about 10 small brown seeds, each of which is surrounded by tufts of long, white silky hairs. Although the flowers are typically unisexual, 10 to 20 percent of the predominantly female trees and 4 to 5 percent of the predominantly male trees bear perfect flowers. Trees in a given clone, therefore, are usually either all male or all female. Some studies in the eastern United States found male-to-female ratios of about 3 to 1 in natural populations; others have reported no deviation from an expected l-to-l ratio *(66,78).* In the Colorado Rockies, male clones were more common at high elevations and female clones were more common at low elevations. Furthermore, female clones had faster radial growth than male clones, especially at lower elevations. This runs counter to the theory that the high metabolic cost of sexual reproduction for females is compensated for by reduced vegetative growth (36).

Seed Production and Dissemination-Good seed crops are produced every 4 or 5 years, with light crops in most intervening years. Some open-grown clones may produce seeds annually, beginning at age 2 or 3. The minimum age for large seed crops is 10 to 20; the optimum is 50 to 70. One 23-year-old quaking aspen produced an estimated 1.6 million seeds *(51,59,78).* Seeds are very light, 5,500 to 8,000 clean seeds per gram (156,000 to 250,000/oz).

Seeds begin to be dispersed within a few days after they ripen and seed dispersal may last from 3 to 5 weeks. The seeds, buoyed by the long silky hairs, can be carried for many kilometers by air currents. Water also serves as a dispersal agent *(78,91).*

The viability of fresh fertile seeds is high (usually greater than 95 percent) but normally of short dura-

Figure *!?+A stand of 45-year-old quaking aspen with an understory of balsam fir, north-central Minnesota.*

tion. Under favorable conditions viability lasts only 2 to 4 weeks after maturity and may be much less under unfavorable conditions. When air dried and stored in polyethylene bags at -10" C (14" F), seed retains high viability for at least 1 year. Seedlings are sturdiest when germinated at 5" to 29" C (41" to 84" F) and grown at about 20" C (68" F). Ripe quaking aspen seeds are not dormant, and germination occurs within a day or two after dispersal if a suitably moist seedbed is reached. Because germintion declines rapidly after water potential exceeds -4 bars (-.4 MPa), a water-saturated seedbed is critical. Seeds germinate even when totally submerged in water or in the absence of light *(32,47,50,66,78,92).*

Seedling Development-Germination is epigeal. The primary root of a seedling grows very slowly for several days, and during this critical period the young plant depends upon a brush of long delicate hairs to perform the absorptive functions and anchor the seedling to the seedbed. Exposed mineral soils are the best seedbeds and litter the poorest seedbeds *(28,51,60,78).*

During the first year seedlings may attain a height of 15 to 30 cm (6 to 12 in) and develop a 20- to 25-cm (8- to 10-in) long taproot and from 30- to 40-cm (12- to 16-in) long laterals. During the second and third years, wide-spreading lateral roots are developed, reaching lengths of 2 m (6 ft) or more in the second year. Quaking aspen roots form ectomycorrhizae if suitable inoculum is present *(28,78,86).*

Despite the abundance of aspen seed and high germinative capacity, few aspen seedlings survive in nature because of the short period of seed viability, unfavorable moisture during seed dispersal, high soil surface temperatures, fungi, adverse diurnal temperature fluctuations during initial seedling growth, and the unfavorable chemical balance of some seedbeds *(51,52).*

Height growth of the young trees is rapid for about the first 20 years and slows thereafter. During the first several years, natural seedlings grow faster than planted seedlings but not as fast as suckers. High mortality characterizes young quaking aspen stands regardless of origin. In both seedling and sucker stands natural thinning is rapid, and trees that fall below the canopy stop growing and die within a few years *(78,93).*

Vegetative Reproduction-The aggregation of stems (ramets) produced asexually from a single sexually produced individual (the genet) is termed a clone. In aspen a clone is formed from the root system of the seedling genet following an event (cutting, fire) that destroys the genet (9).

Quaking aspen seedlings at 1 year of age are already capable of reproducing by root sprouts (suckers), and mature stands reproduce vigorously by this means *(19,431.* Root collar sprouts and stump sprouts are produced only occasionally by mature trees but saplings commonly produce them (77). Aspen clones vary widely in many characteristics, even over a small area. Members of a clone are indistinguishable but can be distinguished from those of a neighboring clone by electrophoresis and often by a variety of traits such as leaf shape and size, bark character, branching habit, resistance to disease and air pollution, sex, time of flushing, and autumn leaf color *(9,10,11,17,22,23,57,87).* Clones typically have many ramets over an area up to a few tenths of a hectare in stands east of the Rocky Mountains *(45,76).* In the Rockies, clones tend to be much larger-one Utah clone covered 43.3 ha (107 acres) and contained an estimated 47,000 ramets. Clone size in an aspen stand is primarily a function of clone age, number of seedlings initially established, and the frequency and degree of disturbance since seedling establishment *(46).*

The root suckers (fig. 3) are produced from meristems on the shallow, cordlike lateral roots within 2 to 10 cm (1 to 4 in) of the soil surface *(28,81).* In response to clone disturbance, the meristems may develop into buds and then elongate into shoots. Frequently, however, they remain in the primordial stage until stimulated to develop further. These preexisting primordia are visible as small bumps when cork is peeled off an aspen root (63).

Figure *3-One-year-old quaking aspen suckers on parent root.*

The development of suckers on aspen roots is suppressed by apical dominance exerted by auxin transported from growing shoots, while cytokinins, hormones synthesized in root tips, apparently initiate adventitious shoot development. When an aspen is cut, cytokinins accumulate in the roots, the supply of inhibitory auxins is eliminated, and suckers are initiated. If aspen is girdled, the downward transport of auxin again is stopped, but upward translocation of cytokinins via the xylem is unimpeded. Cytokinins in this case do not accumulate in the roots, with consequently less sucker production. Thus high cytokinin-to-auxin ratios favor shoot initiation while low ratios inhibit it. A gibberellic-acid-like growth regulator also stimulates shoot elongation after sucker initiation.

Carbohydrate reserves supply the energy needed by elongating suckers until they emerge at the soil surface to carry on their own photosynthesis. Therefore, the density of regeneration varies according to the level of these reserves. However, the number of suckers initiated by aspen roots is independent of variation in carbohydrate levels. Apical dominance by elongating suckers further limits the total amount of regeneration. Carbohydrates can be exhausted by grazing, repeated cropping or killing of sucker stands, or insect defoliation *(63,77,82)*.

Soil temperature is the most critical environmental factor affecting suckering. Initiation and development of suckers is optimum at about 23" C (74" F). High temperatures tend to degrade auxin and promote cytokinin production, which may account in part for the aspen invasion of grassland without apparent clone disturbance *(51,82)*.

Excess soil moisture (impeded aeration) or severe drought inhibit sucker production *(25,57,82)*.

Light is not needed for sucker initiation but is essential for secondary growth (78). Large clonal differences in ability to produce suckers may be due to differences in growth regulators, carbohydrate reserves, and developmental stages of shoot primordia (63). Some clones in the interior West are uneven-aged, suggesting weak apical control or high concentration of growth-promoting hormones so that they sucker at the least disturbance *(69,82)*.

Suckers are initially sustained by the root system of the parent tree, but they may form as much as 4.7 m (15.5 ft) of new main roots in 10 weeks. In contrast, suckers of some Utah clones produce only weak adventitious roots and depend on the distal parent root for sustenance. The parent root usually thickens at the point of sucker origin distal to the parent tree. This indicates that translocation of food produced by the sucker is toward the growing tip of the parent root, which usually becomes part of the new root system *(28,51,78,81)*. These connections readily conduct water and solutes from tree to tree *(27)*. True root grafts, in contrast, are rare in aspen.

Suckers from the roots of badly decayed trees are not infected by the parent stump. Heart rot usually terminates in the base of the stump. Deteriorating clones, however, produce few suckers.

In general, sucker regeneration is proportional to the degree of cutting, with most suckers arising after a complete clearcut *(43,57,64,65,75,78)*. Typically, from 25,000 to 75,000 suckers per hectare (10,000 to 30,000/acre) are regenerated in Alaska and the Great Lakes region and about half as many in the Rockies *(28,91)*.

Light burning on heavily cut areas increases the number of suckers and stimulates their initial growth. However, hot slash fires diminish sucker vigor. Repeated burning increases stand density because it stimulates sucker numbers and prepares mineral soil seedbeds for seedling establishment; however, it reduces stand growth *(6,19,28,56,64,78)*. Surface fires in established aspen stands are not common because of aspen's inherently low flammability. When they do occur, fire wounds and loss of shallow feeder roots substantially reduce aspen productivity. Fire is a useful tool, however, to stimulate regeneration and to reduce competition if clearcutting is not practiced. It is especially valuable for regenerating deteriorated stands and for maintaining wildlife habitat *(21,57)*.

Disking stimulates suckering, but sucker growth and survival are usually diminished because of injury to their sustaining parent roots. Rows of suckers often appear along furrows prepared for planting conifers.

Herbicides have been used to kill residual trees and to increase suckering without affecting sucker growth or vigor *(19,57,78)*.

Dormant season cutting generally produces vigorous suckers the next growing season. Summer cutting produces a sparse stand initially, but the number of suckers after 2 years is usually the same regardless of cutting season *(15)*. Suckering sometimes fails inexplicably after harvesting aspen on fine-textured soils during the growing season (59).

The number of suckers following cutting increases as stocking density of the parent stand increases up to full site utilization. The effect of age and site index on aspen suckering is not clear *(35,81)*.

Age of wood is the most important factor in rooting quaking aspen cuttings. With rare exceptions, the species roots poorly from woody stem cuttings, even when treated with indolebutyric acid (IBA). However, newly initiated shoots can usually be induced to root by dipping in IBA or other commercially available rooting powders. These softwood stem cuttings should be taken from actively growing shoots except during the period of extremely rapid mid-season elongation *(14,63,78)*. Propagation by excising succulent young sucker shoots from root cuttings is easily accomplished by treating the shoots with IBA and growing them in a suitable medium in a misting chamber until rooted, in about 2 to 3 weeks *(62)*. Quaking aspen scions can be grafted onto balsam poplar *(Populus balsamifera)*, willows *(Salix* spp.), or bigtooth aspen *(P. grandidentata)*. Quaking aspen plantlets have been produced by tissue culture *(81)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Quaking aspen is a small- to medium-sized, fast-growing, and short-lived tree. Under the best of conditions, however, it may attain 36.5 m (120 ft) in height and 137 cm (54 in) in d.b.h. The current national champion is 114 cm (45 in) d.b.h. and 26 m (86 ft) tall near Fort Klamath, OR. More typically, mature stands may range from 20 to 25 m (66 to 82 ft) tall and average 18 to 30 cm (7 to 12 in) d.b.h. A few vigorous trees attain a maximum age of about 200 years (oldest recorded is 226 years) in Alaska and the Rocky Mountain region *(28,42)*. Although individual ramets of a clone may be short lived, the clone may be thousands of years old *(46)* and longer lived than the oldest giant sequoia *(Sequoiadendron giganteum)*.

The tallest quaking aspen are found in a belt bordering the midcontinental prairie region at about latitude 55° N., and in north-central Minnesota, northern Michigan, and in the Southwest. Few quaking aspen exceed 26 or 27 m (85 to 90 ft) in Alaska *(38)*.

Growth and decay are both generally slower in Alaska and the West than in the East, hence pathological rotations are longer—80 to 90 years in Utah and 110 to 120 years for Colorado and Wyoming. In northern Minnesota, the pathological rotation is about 55 to 60 years and even shorter in southern Wisconsin and Michigan *(35,69,70)*.

Now and in the foreseeable future, most aspen will be extensively managed (complete clearing for site preparation, no thinning) for fiberboard, pulpwood, flakeboard, and some sawtimber. Aspen is harvested either as whole-tree chips or as bolewood to a nominal top size for pulpwood or sawtimber. Some of the very best stands can be thinned to increase the production of large bolts *(57,58)*.

Site quality varies regionally, being highest in the Lake States, followed by Alaska and the West. Biomass mean annual increment on the better sites in the Lake States and Canada culminates at about age 30 and at 4.4 to 4.8 mg/ha (2-2.2 tons/acre) dry weight *(16,60)*. Mature stands in Newfoundland typically carry 64 m^2/ha (280 ft^2/acre) basal area. This amounts to 376 mg/ha (167 tons/acre) at age 90 years, or 4.2 mg/ha/yr (1.9 tons/acre/year) (54). However, exceptionally good growth of quaking aspen is possible in Arizona and in Colorado and southern Wyoming (44,701. A natural triploid clone in Minnesota produced an annual yield of 14.6 m^3/ha (208 ft^3/acre) of bolewood over 38 years (59).

Aspen responds to intensive management. Production by thinned stands for a 50-year rotation, including thinnings removed at ages 10, 20, and 30, is about 511 m^3/ha (7,300 ft^3/acre), or 10.2 m^3/ha (146 ft^3/acre) per year. This is about 42 percent greater than for similar, but unthinned, stands (58). Quaking aspen growth can be further increased by fertilization and irrigation *(24,26,29,59,84)*. Sub-optimal fiber yield and the threat of *Armillaria mellea* root rot limit the practicality of rotations shorter than 15-20 years (77).

Rooting Habit-Seedlings initially have a short taproot, but a heart root system develops on deep, well-drained soils. Clonal ramets have a flat root system when young but again will develop a heart system on deep, well-drained soils. If rooting depth is restricted, a flat root system develops regardless of regeneration origin *(28,59)*.

The shallow and extensive laterals have cordlike branch roots that undulate and meander for great distances without tapering. These roots are the main producers of suckers, particularly when they are close to the soil surface. Roots tend to follow soil surface irregularities and may even grow into decaying stumps or logs. The fine feeding roots are found at all levels down to 0.6 to 0.9 m (2 to 3 ft) except in restrictive horizons. Sinker roots occur as frequently as every meter or so on the lateral roots. They may descend to depths of 3 m (10 ft) or more where they end in a dense fan-shaped fine root mass. Sinkers are capable of penetrating strongly massive soil horizons or cracks in bedrock and often use vacated root channels *(28,78)*.

Reaction to Competition-In both the eastern and western parts of its range, quaking aspen is classed as very intolerant of shade, a characteristic it retains throughout its life. Natural pruning is excellent, and long, clean stems are usually produced when side shade is present. However, this is a clonally variable characteristic and self-pruned and unpruned clones exist side by side in some stands *(69,78)*. The intolerance of aspen to shade dictates an even-aged silvicultural system, that is, clearcutting, for regenerating fully stocked sucker stands and maximizing growth *(19,57,75).*

The tree has a pronounced ability to express dominance, and overstocking to stagnation of growth is extremely rare.

Quaking aspen is an aggressive pioneer. It readily colonizes burns and can hold invaded land even though subjected to fires at intervals as short as 3 years. In the northeastern United States, it is an old-field type, and in Canada it invades grassland if fire is excluded. In the Central Rocky Mountains, it constitutes the typical fire climax at the lower elevations of the subalpine forest. The extensive stands of aspen in that area are usually attributed to repeated wildfires, and aspen is generally regarded as a successional species able to dominate a site until replaced by less fire-enduring but more shade-tolerant conifers, a process that may take only a single aspen generation or as long as 1,000 years of fire exclusion. Aspen is considered a permanent type on some sites in the intermountain region of Utah, Nevada, and southern Idaho, but conifers would invade the type if seed trees were available.

The uneven-aged character of some western aspen stands suggests that under certain conditions aspen is self-perpetuating without major disturbance. These stands are relatively stable and can be considered *de* facto climax. Seral and stable aspen stands seem to be associated with certain indicator species *(28,78,82).*

In its eastern range, aspen in the absence of disturbance is regarded as transient. Successional patterns are determined by soil water regime *(61).* Pure aspen stands gradually deteriorate to a "shrubwood" dominated by the shrub component of the stand and with only a few scattered aspen suckers. If intolerant associates are present, they will outlive the aspen and eventually dominate but in turn will be replaced again by the shrubwood type. If tolerant hardwoods or balsam fir *(Abies balsamea)* are associated with aspen, they will eventually dominate by their longevity and ability to regenerate in their own shade *(81).*

The deterioration of aspen stands begins earliest at the southern limits of its eastern range and seems to be related to summer temperatures. Deterioration begins when crowns in old stands can no longer grow fast enough to fill the voids in the canopy left by dying trees. Increased breakage accelerates the deterioration process, which may be completed in as few as 3 or 4 years *(81).* Deterioration is a much slower process in the West, where aspen often is replaced by conifers. Dry sites may revert to rangeland dominated by shrubs, forbs, and grasses. Sometimes suckers appear in a deteriorating stand and ultimately an all-age climax aspen forest develops *(28).*

Damaging Agents-Numerous factors other than competition injure or kill young stands *(25,40).* Young trees are sometimes killed by bark-eating mammals, such as meadow mice and snowshoe hares, which may girdle the stem at or near the ground line. Also, larger animals, such as mule deer, white-tailed deer, elk, and moose, frequently seriously damage reproduction by browsing and by rubbing their antlers against the stems. Elk and moose can also damage pole- and saw log-size trees by "barking' them with their incisors. Such injuries often favor secondary attack by insects or pathogens. Heavy use by overwintering big game animals can greatly reduce the number of aspen trees in localized areas. Cattle and sheep browsing is a serious problem in many areas of the Rockies because livestock are allowed to range through recent aspen clearcuts. Mature aspen stands adjacent to livestock concentrations (water holes, salt blocks, isolated stands in large open areas) often have root damage, are declining, and have few if any suckers present. Excessive use and vandalism by recreationists has caused aspen to deteriorate in many campsites *(41,70).*

Beaver feed on the young tender bark and shoots of aspen and often cut down large numbers of trees near their colonies, A high population of porcupines can greatly damage tree crowns both directly by feeding, and indirectly by increasing the trees' susceptibility to attack by insects and diseases.

The red-breasted and yellow-bellied sapsuckers may seriously scar trees with drill holes. Minor damage is caused by such woodland birds as the ruffed grouse and the sharp-tailed grouse, which feed on the buds of quaking aspen; ruffed grouse also feed on the leaves during the summer months (78).

Aspen is susceptible to a large number of diseases *(28,39,41,81,82).* Shoot blight of some aspen caused by *Venturia macularis* is periodically severe. Angular black spots appear on the leaves, enlarging until the leaf dies. If the infection occurs at the top of the tree, the entire new shoot may be infected, blackened, killed, and bent to form a "shepherd's crook." This disease is common in young stands. A similar leaf disease in Wisconsin is caused by *Colletotrichum gloeosporioides.*

Two or more species of *Ciborinia* cause a leaf spot on trees of all ages. When the disease is severe, small trees may be killed, but older ones rarely die. *Marssonina populi* causes a leaf spot and shoot blight that is especially prevalent and damaging in the western states. It is responsible for occasional severe defoliation. Severe, repeated infection can cause mortality, although susceptibility to this disease varies greatly among clones. Another leaf spot of aspen is caused by ***Septoria musiva.***

Several leaf rust fungi of the genus *Melampsora* infect aspen. *M. medusae* is common east of the Rocky Mountains. *M. abietis-canadensis* occurs throughout the range of eastern hemlock *(Tsuga canadensis)* and *M. albertensis* in the West. All can discolor and kill aspen leaf tissue and cause premature autumn leaf drop, but their damage is not serious.

Powdery mildew, *Erysiphe cichoracearum* in the West and the widespread *Uncinula salicis* can be conspicuous on aspen leaves but probably do little damage.

Recently, viruses have been detected in a few quaking aspen clones. Once trees in the clone are infected, regeneration by suckering maintains the infection, which is then impossible to eliminate except by artificially culturing virus-free tissue. The full extent and seriousness of viruses in aspen is unknown but decline of some clones has been attributed to them in both the East and the West.

Stain and decay have the greatest direct impact of the many stem pathogens on wood production. The role of microorganisms frequently associated with discoloration is poorly understood because staining also develops in their absence. Bacteria and yeast organisms are commonly associated with "wetwood," a water-soaked condition of live trees that leads to wood collapse during lumber drying.

A number of different bacteria and fungi are found in aspen tissue, apparently interacting to follow one another successionally, with bacteria appearing first. *Phellinus tremulae* causes a white rot of the heartwood at first but may eventually invade the entire stem. It causes the greatest volume of aspen decay and is so prevalent it conceals rot caused by other fungi. Sporophores (fruiting bodies) are the most reliable external indicator of decay. They provide a means to estimate present and future decay. Resistance to this fungus is strongly genetically controlled. Incidence and extent of infection increases with tree age or size but is not strongly related to site (76).

Peniophora polygonia is the second most important trunk rot fungus in the West and in Alaska, but it causes little actual cull. *Libertella* spp. is also an important trunk rot fungus in the West. Other less important trunk rot fungi found on aspen include *Radulodon caesearius, Peniophora polygonia, P. rufa,* and ***Pholiota adiposa.***

More fungi species cause butt and root rots than trunk rots-as much as one-third of the decay volume in Colorado. ***Collybia velutipes*** is found in Alaska and causes the greatest amount of butt cull in the West. ***Ganoderma applanatum*** may be as important because it also decays large roots, which leads to windthrow. Less important butt rot fungi include ***Pholiota squarrosa, Gymnopilus spectabilis, Peniophora polygonia, and Armillaria*** *mellea.* The latter is primarily a root rot which can infect a high proportion of the trees (74). Other locally important root rots in the West include ***Phialophora*** spp. and ***Coprinus atramentarius.***

Stem cankers are common diseases of aspen that have a great impact on the aspen resource. Depending on the causal fungus, cankers can kill a tree within a few years or persist for decades. Hypoxylon canker caused by ***Hypoxylon mammatum*** is probably the most serious aspen disease east of the Rockies, killing 1 to 2 percent of the aspen annually It is not an important disease in the West, nor has it been found in Alaska. The infection mode of ***Hypoxylon*** is poorly understood but seems to be related to ascospore germination inhibitors in bark. Most canker infections seem to originate in young branches with scars or galls formed by twig-boring insects *(4).* Once infected, the host bark tissue is rapidly invaded and the fungus girdles and kills the tree in a few years *(5).*

Ceratocystis canker is a target-shaped canker caused by ***Ceratocystis fimbriata, C. moniliformis, C. piceae, C. pluriannulata, C. ambrosia, C.*** *cana,* ***C. serpens, C.*** *crassivaginata,* ***C. populina, C.*** *tremulo-aurea,* and ***C. alba.*** This canker is found throughout the range of aspen, with ***C. fimbriata*** the most common causal pathogen. These cankers seldom kill aspens but can reduce usable volume of the butt log. Infection is primarily through trunk wounds and insects are the primary vectors.

Sooty-bark canker of aspen is caused by ***Phibalis pruinosa*** and is common and a major cause of mortality in Alaska and the West. The fungus infects trunk wounds and spreads rapidly, killing trees of all sizes. The fungus has been found only as an innocuous bark saprophyte on quaking aspen in the East.

Cytospora canker is caused by ***Cytospora chrysosperma,*** a normal inhabitant of aspen bark. The fungus is not considered a primary pathogen and causes cankers, lesions, or bark necrosis only after the host tree has been stressed, such as by drought, fire, frost, suppression, or leaf diseases. The disease is most serious on young trees and is found throughout the range of aspen.

Dothichiza canker, caused by ***Dothichiza populea,*** occurs in the eastern range of aspen. It is an endemic disease of young or weakened trees and is not found in vigorous stands.

In Ontario, a canker caused by *Neofabraea populi* has been found on young aspen. Few trees have been killed by it, however, and the disease is not known in the United States.

Cryptosphaeria populina cause a long, narrow, vertical canker that may spiral around an aspen trunk for 1 to 6 m (3 to 20 ft) or more. It is common in the West as far north as Alaska. Trees with large cankers have extensive trunk rot and are frequently broken by wind.

Aspen is susceptible to three types of rough-bark which are caused by the fungi *Diplodia tumefaciens, Rhytidiella baranyayi,* and *Cucurbitaria staphula.* Rough, corky bark outgrowths persist for many years but do little harm.

Quaking aspen hosts a wide variety of insects *(28,81).* One Canadian survey recorded more than 300 species, but only a few are known to severely damage trees. They may be grouped into defoliators, borers, and sucking insects.

Defoliators of aspen belong primarily to the orders Lepidoptera and Coleoptera. The forest tent caterpillar *(Malacasoma disstria)* and the western tent caterpillar *(M. californicum)* have defoliated aspens over areas as large as 259 000 km^2 (100,000 mi^2). Outbreaks usually persist for 2 to 3 years and may collapse as quickly as they begin (88). Aspen growth losses during defoliation have been as high as 90 percent and may take as long as 3 or 4 years for total growth recovery. Some trees never recover and die—as much as 20 to 80 percent of them on poor sites *(90).* On good sites mortality may be restricted to suppressed trees (59).

The large aspen tortrix *(Choristoneura conflictana)* is found throughout the range of aspen. It has defoliated trees over an area as large as 25 900 km^2 (10,000 mi^2) in Canada and Alaska. Caterpillars predominantly infest the leaves of early flushing clones (89). Outbreaks normally collapse in 2 or 3 years and, although aspen growth is reduced, few trees are killed.

In the East, aspen is a favored host for the gypsy moth *(Lymantria dispar)* and the satin moth *(Leucoma salicis) (78).*

A great number of leaf tiers defoliate aspen. *Sciaphila duplex* is one that is often associated with the large aspen tortrix and has been a major pest in Utah. Other Lepidopterous defoliators of aspen include the Bruce spanworm, *Operophteru bruceata,* and *Lobophora nivigerata.*

Three species of leaf-rolling sawflies of the genus *Pontunia* sometimes erupt in local outbreaks in the Lake States. *Anacampsis niveopulvella* is a Lepidopterous leaf roller that causes local damage in the West. Sawflies of the *Platycampus* genus chew holes in leaves.

The more common leaf miners of aspen are the aspen leaf miner *(Phyllocnistis populiella),* the aspen blotch miners *(Phyllonorycter tremuloidiella* and *Lithocolletis salicifoliella),* and a leaf-mining sawfly *(Messa populifoliella).*

Defoliating beetles include the aspen leaf beetle *(Chrysomela crotchi),* the cottonwood leaf beetle *(C. scripta),* the American aspen beetle *(Gonioctena americana),* and the gray willow leaf beetle *(Pyrrhalta decor-u).* All have similar feeding habits; the larvae skeletonize lower surfaces of leaves, and adults feed on whole leaves.

Wood-boring insects that attack aspen are primarily beetles of the Cerambycidae (round-headed borers or long-horned beetles) and Buprestidae (flatheaded borers or metallic beetles). The poplar borer *(Superda calcaruta)* is the most damaging. The larvae tunnel in the bole, weakening and degrading the wood. Breakage by wind increases and the tunnels serve as infection courts for wood-rotting fungi. *S. moesta* is a smaller related borer that attacks small suckers and aspen twigs. It is important only in the West. *Xylotrechus obliteratus* has killed large areas of aspen in the West above 2130 m (7,000 ft).

The root-boring saperda *(Saperda calcarata)* feeds on phloem and outer sapwood near the base of young aspen suckers. Oviposition incisions of the poplar gall saperda *(S. inornatu)* frequently cause globose galls to form on the stems of young suckers and on small branches of larger trees. These oviposition wounds can serve as infection sites for Hypoxylon that can then grow from a branch gall down into the bole of the tree causing a canker *(4).* The poplar branch borer *(Oberea schaumi)* attacks larger suckers and tree limbs. Damage by all these insects can lead to stem breakage. Site quality is not an important variable, and maintaining high stocking density of vigorous suckers is the best practice to minimize loss.

Two flatheaded borers, the bronze poplar borer *(Agrilus liragus)* and the aspen root girdler *(A. horni),* bore galleries that disrupt nutrient and water movement. The former attacks sucker stems and makes zig-zag galleries; the latter girdles the sucker with a spiral gallery from the lower trunk to the roots and back. *A. anxius* also girdles and kills aspen twigs in the West.

Some other Buprestids attacking aspen in the East are the flatheaded apple tree borer *(Chrysobothris femoratu),* the Pacific flatheaded borer *(C. mali),* and the flatheaded aspen borers *(Dicerca tenebrica, D. divaricata,* and *Poecilonota cyanipes).* The first two and the latter are also reported in the West, along with the aspen ambrosia beetle *(Trypodendron retusum)*. None of these cause serious injury in well-managed stands.

A widespread weevil, the poplar and willow borer, *Cryptorhynchus lapathi,* can riddle aspen stems with galleries, especially planted trees.

A clear-wing moth of the genus *Aegeria,* and willow shoot sawfly *(Janus abbreuiatus)* are examples of borers from nonbeetle families.

In the West, the fungus *Ceratocystis fimbriata* is carried by *Epurea* spp., *Nudobius* spp., and *Rhisophagus* spp. (28).

Sucking insects are represented mainly by aphids and leafhoppers. The poplar vagabond aphid *(Mordvilkoja vagabunda)* causes a peculiar curled and twisted gall of leaves as large as 5 cm (2 in) in diameter at the tip of twigs. Poplar petiole gall and twig gall aphids of the genus *Pemphigus* produce swellings on leaf petioles. Increased forking of aspen suckers may be caused by high populations of the speckled poplar aphid *(Chaitophorus populicola)* and the spotted poplar aphid *(Aphis maculatae)*. They are commonly found on expanding aspen sucker leaves *(35,81)*.

The genera *Idiocerus, Oncomtopia, Macropsis, Oncopsis,* and *Agallia* have several species of leafhoppers that cause leaf browning and slitlike ruptures in the bark of twigs. Only *Idiocerus* spp. have been found in the West. Several species of scale insects such as the oystershell scale *(Lepidosaphes ulmi)* are found on aspen but do little damage to healthy trees. Cutworms (moth family Noctuidae larvae) sometimes can cut a large number of succulent new suckers at the ground line. Black carpenter ants *(Camponotus pennsylvanicus)* frequently use and extend the tunneling made by the poplar borer, causing further damage *(35,78)*.

Aspen is highly susceptible to fire damage. Fires may kill trees outright or cause basal scars that serve as avenues of entrance for wood-rotting fungi. Intense fires can kill or injure surface roots and thereby reduce sucker regeneration *(19,56,78)*.

Early spring frosts may kill new leaves and shoots and, when especially severe, some of the previous year's shoots. Over-winter freezing can cause frost cracks. Strong wind can uproot or break mature aspen and even moderate wind can crack the bole of trees with lopsided crowns. Hail can bruise the bark of young aspen and, in severe storms, kill entire sapling stands. Aspen suffers little from ice storms or heavy wet snow, except when in leaf. Snow creep on steep slopes can bend or break aspen suckers as tall as 1.2 m (4 ft) (28).

Aspen suddenly exposed to full sunlight may suffer sunscald. Pole-size trees are more susceptible than saplings *(19,58)*.

Aspen growth and vigor suffer from drought *(79)*, and drought-stressed trees become predisposed to secondary agents such as insects and disease. Mechanical injuries inflicted on aspen bark by thoughtless recreationists can lead to infection by canker disease and eventual death in as few as 10 to 20 years.

Special Uses

Aspen provides habitat for a wide variety of wildlife needing young forests, including hare, black bear, deer, elk, ruffed grouse, woodcock, and a number of smaller birds and animals. Ruffed grouse use all age classes of aspen-sapling stands for brooding, pole stands for overwintering and breeding, and older stands for nesting cover and winter food *(53,55,67,68)*.

Aspen forests allow more water or ground water recharge and streamflow than do conifer forests. This is primarily due to lower seasonal water losses to interception and transpiration by aspen compared to conifers (34). Clearcutting the aspen type may increase streamflow by as much as 60 percent during the first year. Subsequently, water yields gradually decline to preharvest levels and stabilize when maximum leaf area is attained at about age 10 to 25 (53).

The aspen type is esthetically appealing. The light bark and autumn colors are a pleasing contrast to dark conifers. In the West in particular, the type is used by recreationists during all seasons of the year.

Aspen stands produce abundant forage-as much as 1100 to 2800 kg/ha (1,000 to 2,500 lb/acre) in the Rockies annually, or three to six times more than typical conifer stands. These amounts are comparable to forage production on some grasslands. Although the type is sought after for summer sheep and cattle range in the West, its use for grazing in the East is much more limited (28).

Aspen stands, because of low fuel accumulations, are low in flammability and make excellent firebreaks. Violent crown fires in conifers commonly drop to the ground and sometimes are even extinguished when they reach an aspen stand (28).

Whole-tree aspen chips can be processed into nutritious animal feed ("Muka") or biomass fuels (82). Aspen could be grown for such purposes in dense sucker stands on biological rotations of 26 to 30 years *(16)*.

Wood products from aspen include pulp, flakeboard, particleboard, lumber, studs, veneer, plywood, excelsior, shingles, novelty items, and wood flour. Aspen makes particularly good sauna benches and playground structures because the wood surface does not splinter.

Genetics

The vegetative cells of aspen, as well as those of nearly all aspen hybrids, contain 19 pairs of chromosomes. A number of triploid aspen (with three sets of chromosomes rather than the normal two) have been located in Utah, the Lake States, and Colorado. A few albino aspen seedlings have been observed, as have two albino aspen suckers, which were thought to result from a somatic mutation in aspen root tissue *(30,37,78)*.

Population Differences and Races

In aspen, the clone is the biological entity-a multistemmed individual that may be thousands of years old (46). The ability to propagate by root suckers assures genetic uniformity and adaptation to the present environment (73). Despite the great genetic variability among clones and the virtually infinite amount of genetic recombination in the billions of seed produced, the chance for expression of this recombination and further adaptive change in established seedlings is very small (6). Stands that are clearcut or destroyed by fire or windstorms may provide some microsites suitable for seedling establishment. However, seedlings are not likely to compete successfully with the faster growing root suckers that are also regenerated under such circumstances (93).

By definition, intraclonal genetic variability does not exist (except by somatic mutation), but interclonal variation is great on a local and regional level. Populations of aspen have undergone selection leading to better adaptation to local environments. Its extensive north to south range has induced strong racial variation along latitudinal and elevational gradients. In one study, seedlings from Saskatchewan ceased growing at a longer day-length and had heavier root systems than seedlings from Wisconsin (78). Another study found that local southeastern Michigan seedlings grew faster and later into the season than quaking aspen from more northerly or higher altitude sources (20).

Hybrids

Quaking aspen is known to hybridize naturally with the following species (hybrid names and authors are given in parentheses):

Populus alba (***P. x heimburgeri*** Boivin)
P. angustifolia (***P. x senni*** Boivin)
P. balsamifera (***P. x dutillyi*** Lepage)
P. balsamifera x deltoides
(***P. x polygonifolia*** Barnard)
P. deltoides (***P. x bernardii*** Boivin)
l? grandidentata (***P. x smithii*** Boivin,
P. x barnesii W. H. Wagner) (49).

Natural hybrids between ***P. tremuloides*** and ***P. grandidentata*** have been reported in lower Michigan, Massachusetts, and Canada *(8,13,78)*. Such hybrids are moderately fertile, and backcrosses with parent species are possible ***(13)***. Many backcross individuals are indistinguishable between ***P. tremuloides*** or ***P.*** x ***smithii*** so the true extent of hybridization, backcrossing, and gene flow between these native aspens is difficult to determine ***(31)***.

Natural hybrids between the European ***Populus alba*** and ***P. tremuloides*** have been reported from Michigan (8) and occur in a number of localities in the vicinity of Ottawa, ON (78). This cross produces viable seed, as does a cross of ***P. x canescens*** (Ait.) Sm. with ***P. tremuloides.***

Populus tremuloides also crosses readily with ***P. tremula*** L., the European aspen. Crosses between diploid ***l? tremuloides*** females and a tetraploid male ***P. tremula*** from Sweden have produced triploid progeny with exceptionally improved growth. Numerous other artificial crosses have been made but only ***l? tremuloides x dauidiana*** Dode (Asiatic aspen) has shown much promise for commercial use. Little intraspecific breeding of quaking aspen has been done *(7,78,81)*.

One particularly important limitation of almost all quaking aspen inter- and intraspecific hybrids is that rooting progeny asexually by woody stem cuttings is extremely difficult. Other ***Populus*** that root easily in this manner have a decided advantage for mass-producing inexpensive and easily handled planting stock. Nevertheless, ***P. tremuloides, P. tremula,*** and their hybrids can be propagated commercially by culturing meristematic explants from buds ***(1)***.

P. tremuloides is more closely related to ***P. tremula*** than to ***P. grandidentata (12)***.

Literature Cited

1. Ahuja, M. R. 1984. A commercially feasible micropropagation method for aspen. Silvae Genetica 33:174–176.
2. Alban, David H. 1982. Effect of nutrient accumulation by aspen, spruce, and pine on soil properties. Soil Science Society of America Journal 46:853–861.

3. Alban, D. H., D. A. Perala, and B. E. Schlaegel. 1978. Biomass and nutrient distribution in aspen, pine, and spruce stands on the same soil type in Minnesota. Canadian Journal of Forest Research 8:290–299.
4. Anderson, Neil A., Michael E. Ostry, and Gerald W. Anderson. 1979. Insect wounds as infection sites for *Hypoxylon mammatum* on trembling aspen. Phytopathology 69:476–479.
5. Anderson, Ralph L., Gerald W. Anderson, and Arthur L. Schipper, Jr. 1979. Hypoxylon canker of aspen. USDA Forest Service, Forest Insect and Disease Leaflet 6. Washington, DC. 7 p.
6. Andrejak, Gary E., and Burton V. Barnes. 1969. A seedling population of aspens in southeastern Michigan. The Michigan Botanist 8:189–202.
7. Barnes, Burton V. 1958. Erste Aufnahme eines sechsjährigen Bestandes von Aspenhybriden. [First survey of a six-year-old stand of hybrid aspen.] Silvae Genetica 7:98–102.
8. Barnes, Burton V. 1961. Hybrid aspens in the Lower Peninsula of Michigan. Rhodora 63:311–324.
9. Barnes, Burton V. 1966. The clonal growth habit of American aspens. Ecology 47:439–447.
10. Barnes, Burton V. 1969. Natural variation and delineation of clones of *Populus tremuloides* and *P. grandidentata* in northern Lower Michigan. Silvae Genetica 18:130–142.
11. Barnes, Burton V. 1975. Phenotypic variation of trembling aspen in western North America. Forest Science 21:319-328.
12. Barnes, Burton V. 1978. Pollen abortion in Betula and Populus (Section Leuce). The Michigan Botanist 17:167–172.
13. Barnes, Burton V., and Kurt S. Pregitzer. 1985. Occurrence of hybrids between bigtooth and trembling aspen in Michigan. Canadian Journal of Botany 63:1888–1890.
14. Barry, W. J., and R. M. Sachs. 1968. Vegetative propagation of quaking aspen. California Agriculture 22(1):14–16.
15. Bella, I. E. 1986. Logging practices and subsequent development of aspen stands in east-central Saskatchewan. Foresty Chronicle 62:81–83.
16. Bella, I. E., and J. P. DeFranceschi. 1980. Biomass productivity of young aspen stands in western Canada. Environment Canada Forestry Service, Information Report NOR–X–219. Northern Forest Research Centre, Edmonton, AB. 23 p.
17. Berrang, P., D. F. Karnosky, R. A. Mickler, and J. P. Bennett. 1986. Natural selection for ozone tolerance in *Populus tremuloides*. Canadian Journal of Forest Research 16:1214–1216.
18. Boyle, James R., John J. Phillips, and Alan R. Ek. 1973. "Whole tree" harvesting: nutrient budget evaluation. Journal of Forestry 71:760–762.
19. Brinkman, Kenneth A., and Eugene I. Roe. 1975. Quaking aspen: silvics and management in the Lake States. U.S. Department of Agriculture, Agriculture Handbook 486. Washington, DC. 52 p.
20. Brissette, John C., and Burton V. Barnes. 1984. Comparisons of phenology and growth of Michigan and western North American sources of *Populus tremuloides*. Canadian Journal of Forest Research 14:789–793.
21. Brown, James K., and Dennis G. Simmerman. 1986. Appraising fuels and flammability in western aspen: a prescribed fire guide. USDA Forest Service, General Technical Report INT–205. Intermountain Research Station, Ogden, UT. 48 p.
22. Cheliak, W. M., and J. A. Pitel. 1984. Electrophoretic identification of clones in trembling aspen. Canadian Journal of Forest Research 14:740–743.
23. Copony, James A., and Burton V. Barnes. 1974. Clonal variation in the incidence of Hypoxylon canker on trembling aspen. Canadian Journal of Botany 52:1475–1481.
24. Coyne, Patrick I., and Keith Van Cleve. 1977. Fertilizer induced morphological and chemical responses of a quaking aspen stand in Interior Alaska. Forest Science 23:92–102.
25. Crouch, Glen L. 1986. Aspen regeneration in 6- to lo-year-old clearcuts in southwestern Colorado. USDA Forest Service, Research Note RM467. Rocky Mountain Forest and Range Experiment Station. Fort Collins, CO. 4 p.
26. Czapowskyj, Miroslaw M., and Lawrence 0. Safford. 1979. Growth response to fertilizer in a young aspen-birch stand. USDA Forest Service, Research Note NE-274. Northeastern Forest Experiment Station, Broomall, PA. 6 p.
27, DeByle, Norbert V. 1964. Detection of functional intraclonal aspen root connections by tracers and excavation. Forest Science 10:386–396.
28. DeByle, Norbert V., and Robert P. Winokur, eds. 1985. Aspen: ecology and management in the western United States. USDA Forest Service, General Technical Report RM-119. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 283 p.
29. Einspahr, Dean W., Miles K. Benson, and Marianne L. Harder. 1972. Influence of irrigation and fertilization on growth and wood properties of quaking aspen. p. 11-19. *In* Proceedings, Symposium on the Effects of Growth Acceleration on Properties of Wood, November 10-11, 1971, Madison, WI.
30. Every, A. D., and D. Wiens. 1971. Triploidy in Utah aspen. Madroño 21:138–147.
31. Farmer, Michele M., and Burton V. Barnes. 1978. Morphological variation of families of trembling aspen in southeastern Michigan. The Michigan Botanist 17:141–153.
32. Fechner, Gilbert H., Karen E. Burr, and Joseph F. Myers. 1981. Effects of storage, temperature, and moisture stress on seed germination and early seedling development of trembling aspen. Canadian Journal of Forest Research 11:718–722.
33. Geraghty, James A., David W. Miller, Frits VanDerLeeden, and Fred L. Troise. 1973. Water atlas of the United States. Water Information Center, Port Washington, NY. Unpaged, 122 plates.
34. Gifford, Gerald F., William Humphries, and Richard A. Jaynes. 1984. A preliminary quantification of the impacts of aspen to conifer succession on water yield-II. Modeling results. Water Resources Bulletin 20:181–186.
35. Graham, Samuel A., Robert P. Harrison, Jr., and Casey E. Westell, Jr. 1963. Aspens: Phoenix trees of the Great Lakes region. University of Michigan Press, Ann Arbor, MI. 272 p.
36. Grant, Michael C., and Jeffrey B. Mitton. 1979. Elevational gradients in adult sex ratios and sexual differentiation in vegetative growth rates of *Populus tremuloides* Michx. Evolution 33:914–918.
37. Greene, K. Alan, J. C. Zasada, and K. Van Cleve. 1971. An albino aspen sucker. Forest Science 17:272.

38. Gregory, Robert A., and Paul M. Haack. 1965. Growth and yield of well-stocked aspen and birch stands in Alaska. USDA Forest Service, Research Paper NOR-2. Northern Forest Experiment Station, Juneau, AK. 27 p.
39. Hinds, Thomas E., and Thomas H. Laurent. 1978. Common aspen diseases found in Alaska. Plant Disease Reporter 62:972–975.
40. Hinds, Thomas E., and Wayne D. Shepperd. 1987. Aspen sucker damage and defect in Colorado clearcut areas. USDA Forest Service, Research Paper RM-278. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 12 p.
41. Hinds, Thomas E., and Eugene M. Wengert. 1977. Growth and decay losses in Colorado aspen. USDA Forest Service, Research Paper RM-193. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 10 p.
42. Hunt, F. A. 1986, National register of big trees. American Forests 92(4):21–52.
43. Jones, John R. 1974. Silviculture of southwestern mixed conifers and aspen: the status of our knowledge. USDA Forest Service, Research Paper RM-122. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 44 p.
44. Jones, John R., and David P. Trujillo. 1975. Development of some young aspen stands in Arizona. USDA Forest Service, Research Paper RM-151. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 11 p.
45. Kemperman, J. A. 1976. Aspen clones: development, variability, and identification. Ontario Ministry of Natural Resources, Division of Forests, Forest Research Branch, Forest Research Information Paper 101. Ottawa, ON. 11 p.
46. Kemperman, Jerry A., and Burton V. Barnes. 1976. Clone size in American aspens. Canadian Journal of Botany 54:2603–2607.
47. Krasny, Marianne E., Kristina A. Vogt, and John C. Zasada. 1988. Establishment of four Salicaceae species on river bars in interior Alaska. Holarctic Ecology 11:210–219.
48. Little, Elbert L., Jr. 1971. Atlas of United States trees, vol. 1. Conifers and important hardwoods. U.S. Department of Agriculture, Miscellaneous Publication 1146. Washington, DC. 9 p., 313 maps.
49. Little, Elbert L., Jr. 1979. Checklist of United States trees (native and naturalized). U.S. Department of Agriculture, Agriculture Handbook 541. Washington, DC. 375 p.
50. McDonough, W. T. 1979. Quaking aspen-seed germination and early seedling growth. USDA Forest Service, Research Paper INT-234. Intermountain Forest and Range Experiment Station, Ogden, UT. 13 p.
51. Maini, J. S., and J. H. Cayford, eds. 1968. Growth and utilization of poplars in Canada. Department of Forestry and Rural Development, Forestry Branch, Departmental Publication 1205. Ottawa, ON. 257 p.
52. Meyer, J. F., and G. H. Fechner. 1980. Seed hairs and seed germination in *Populus.* Tree Planters' Notes 30 (3):3–4.
53. Ohmann, L. F., H. 0. Batzer, R. R. Buech, and others. 1978. Some harvest options and their consequences for the aspen, birch, and associated conifer forest types of the Lake States. USDA Forest Service, General Technical Report NC-48. North Central Forest Experiment Station, St. Paul, MN. 34 p.
54. Page, G. 1972. The occurrence and growth of trembling aspen in Newfoundland. Canada Forestry Service, Publication 1314. Ottawa, ON. 15 p.
55. Patton, David R., and John R. Jones. 1977. Managing aspen for wildlife in the Southwest. USDA Forest Service, General Technical Report RM-37. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 7 p.
56. Perala, Donald A. 1974. Prescribed burning in an aspen-mixed hardwood forest. Canadian Journal of Forest Research 4:222–228.
57. Perala, Donald A. 1977. Manager's handbook for aspen in the North-Central States. USDA Forest Service, General Technical Report NC-36. North Central Forest Experiment Station, St. Paul, MN. 30 p.
58. Perala, Donald A. 1978. Thinning strategies for aspen: a prediction model. USDA Forest Service, Research Paper NC-161. North Central Forest Experiment Station, St. Paul, MN. 19 p.
59. Perala, Donald A. 1989. Data on file. USDA Forest Service, North Central Forest Experiment Station, Grand Rapids, MN.
60. Perala, Donald A., and James Russell. 1983. Aspen. *In* Silvicultural systems for the major forest types of the United States. p. 113-115. Russell M. Burns, tech. comp. U.S. Department of Agriculture, Agriculture Handbook 445. Washington, DC.
61. Roberts, Mark R., and Curtis J. Richardson. 1985. Forty-one years of population change and community succession in aspen forests on four soil types, northern lower Michigan, U.S.A. Canadian Journal of Botany 63:1641–1651.
62. Schier, George A. 1978. Vegetative propagation of Rocky Mountain aspen. USDA Forest Service, General Technical Report INT-44. Intermountain Forest and Range Experiment Station, Ogden, UT. 13 p.
63. Schier, George A. 1981. Physiological research on adventitious shoot development in aspen roots. USDA Forest Service, General Technical Report INT-107. Intermountain Forest and Range Experiment Station, Ogden, UT. 12 p.
64. Schier, George A., and Robert B. Campbell. 1978. Aspen sucker regeneration following burning and clearcutting on two sites in the Rocky Mountains. Forest Science 24:303–308.
65. Schier, George A., and Arthur D. Smith. 1979. Sucker regeneration in a Utah aspen clone after clearcutting, partial cutting, scarification, and girdling. USDA Forest *Service,* Research Note INT-253. Intermountain Forest and Range Experiment Station, Ogden, UT. 6 p.
66. Schreiner, Ernst J. 1974. ***Populus*** L. Poplar. *In* Seeds of woody plants in the United States. p. 645-655. C. S. Schopmeyer, tech. coord. U.S. Department of Agriculture, Agriculture Handbook 450. Washington, DC.
67. Scott, Virgil E., and Glenn L. Crouch. 1987. Response of breeding birds to commercial clearcutting of aspen in southwestern Colorado. USDA Forest Service, Research Note RM-475. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 5 p.
68. Sepik, Greg F., Ray B. Owen, Jr., and Malcolm W. Coulter. 1981. A landowner's guide to woodcock management in the Northeast. University of Maine Life Sciences and Agriculture Experiment Station, Miscellaneous Report 253. Orono. 23 p.
69. Shepperd, Wayne D. 1986. Silviculture of aspen forests in the Rocky Mountains and the Southwest. USDA Forest Service, RM-TT-7. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 38 p.

70. Shepperd, Wayne D., and Orville Engelby. 1983. Rocky Mountain Aspen. *In* Silvicultural systems for the major forest types of the United States. p. 77-79. Russell M. Burns, tech. comp. U.S. Department of Agriculture, Agriculture Handbook 445. Washington, DC.
71. Shields, W. J., Jr., and J. G. Bockheim. 1981. Deterioration of trembling aspen clones in the Great Lakes region. Canadian Journal of Forest Research 11:530–537.
72. Society of American Foresters. 1980. Forest cover types of the United States and Canada. F. H. Eyre, ed. Washington, DC. 148 p.
73. Spurr, Stephen H., and Burton V. Barnes. 1980. Forest ecology. John Wiley and Sons, New York. 687 p.
74. Stanosz, G. R., and R. F. Patton. 1987. Armillaria root rot in Wisconsin aspen sucker stands. Canadian Journal of Forest Research 17(9):995–1000.
75. Steneker, G. A. 1976. Guide to the silvicultural management of trembling aspen in the prairie provinces. Environment Canada Forestry Service, Information Report NOR-X-164. Northern Forest Research Centre, Edmonton, AB. 6 p.
76. Steneker, G. A., and R. E. Wall. 1970. Aspen clones: their significance and recognition. Canadian Forestry Service, Department of Fisheries and Forestry Liaison and Service Note MS-L-B. Forest Research Laboratory, Winnipeg, MB. 10 p.
77. Stiell, W. M., and A. B. Berry. 1986. Productivity of short-rotation aspen stands. Forestry Chronicle 62:10–15.
78. Strothmann, R. O., and Z. A. Zasada. 1965. Quaking aspen (*Populus tremuloides* Michx.). *In* Silvics of forest trees of the United States. p. 523-534. H. A. Fowells, comp. U.S. Department of Agriculture, Agriculture Handbook 271. Washington, DC.
79. Sucoff, Edward. 1982. Water relations of the aspens. University of Minnesota Agriculture Experiment Station, Technical Bulletin 338. St. Paul. 36 p.
80. U.S. Department of Agriculture. 1941. Climate and man. U.S. Department of Agriculture, Yearbook of Agriculture 1941. Washington, DC. 1248 p.
81. U.S. Department of Agriculture, Forest Service. 1972. Aspen: Symposium Proceedings. USDA Forest Service, General Technical Report NC-l. North Central Forest Experiment Station, St. Paul, MN. 154 p.
82. U.S. Department of Agriculture, Forest Service. 1976. Utilization and marketing as tools for aspen management in the Rocky Mountains: Proceedings of the Symposium. USDA Forest Service, General Technical Report RM-29. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 120 p.
83. U.S. Department of Agriculture, Soil Conservation Service. 1975. Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys. Soil Survey Staff, coord. U.S. Department of Agriculture, Agriculture Handbook 436. Washington, DC. 754 p.
84. Van Cleve, Keith. 1973. Short-term growth response to fertilization in young quaking aspen. Journal of Forestry 71:758–759.
85. Viereck, Leslie A., and Elbert L. Little, Jr. 1972. Alaska trees and shrubs. U.S. Department of Agriculture, Agriculture Handbook 410. Washington, DC. 265 p.
86. Vozzo, J. A., and Edward Hacskaylo. 1974. Endo- and ectomycorrhizal associations in live *Populus* species. Bulletin of the Torrey Botanical Club 101:182–186.
87. Weingartner, D. H., and J. T. Basham. 1985. Variations in the growth and defect of aspen (***Populus tremuloides*** Michx.) clones in northern Ontario. Ontario Ministry of Natural Resources, Forest Research Report 111. Maple. 26 p.
88. Witter, J. A. 1979. The forest tent caterpillar (Lepidoptera: Lasiocampidae) in Minnesota: a case history review. The Great Lakes Entomologist 12(4):141–197.
89. Witter, J. A., and L. A. Waisanen. 1978. The effect of differential flushing times among trembling aspen clones on tortricid caterpillar populations. Environmental Entomology 7:139–143.
90. Witter, J. A., W. J. Mattson, and H. M. Kulman. 1975. Numerical analysis of a forest tent caterpillar (Lepidoptera: Lasiocampidae) outbreak in northern Minnesota. Canadian Entomologist 107:837–854.
91. Zasada, John C. 1989. Personal correspondence. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Corvallis, OR.
92. Zasada, J. C., and R. A. Densmore. 1977. Changes in seed viability during storage for selected Alaskan Salicaceae. Seed Science and Technology 5:509–518.
93. Zasada, John C., Rodney A. Norum, Christian E. Teutsch, and Roseann Densmore. 1987. Survival and growth of planted black spruce, alder, aspen and willow after fire on black spruce/feather moss sites in interior Alaska. Forestry Chronicle 63:84–88.