1985

Morphology in Aspen: Ecology and Management in the Western United States

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MORPHOLOGY

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The term "morphology" is used broadly here to include the exterior form of the tree above ground, the root system, and the stand.

Tree Above Ground

Sources for the following description are Barry (1971), Einspahr and Winton (1976), Fechner and Barrows (1976), Harlow and Harrar (1958), Little (1950), Preston (1961), Sargent (1890), and Viereck and Little (1972).

General Characteristics

Aspen is a small to medium-sized deciduous tree with straight trunk and short, irregularly bent limbs, making a narrow dome-like crown. Trees are commonly 20 to 60 feet (6 m to 18 m) tall and 3 to 18 inches (8 cm to 46 cm) in diameter. Occasionally, trees more than 80 feet (24 m) tall and larger than 24 inches (61 cm) in diameter are found.

The bark is smooth with a greenish-white, yellowish-white, yellowish-gray, or grayish to almost white coloration. At maturity the bark may become roughened and fissured.

Small twigs are smooth, slender, flexible, and reddish-brown. Terminal winter buds are 1/4 to 1/2 inch (0.6 cm to 1.3 cm) long, conical pointed, and covered by six to seven, sometimes resinous, reddish-brown scales. The flower buds are larger and ovate (fig. 1).

Leaf blades are thin and firm, nearly round, 1 1/2 to 3 inches (4 cm to 8 cm) in diameter, short-pointed at the apex, rounded at the base, with many small rounded to sharply pointed teeth at the margin (fig. 1). The leaves are smooth, shiny, green to yellowish-green above, and dull beneath. In autumn, the leaves turn bright yellow, gold, orange, or slightly reddish. Petioles are 1 1/2 to 3 inches (4 cm to 8 cm) long and flattened perpendicular to the plane of the blade. The flattened petiole acts as pivot for the blade, which trembles in the slightest breeze. In contrast to the leaves on mature trees, the leaves of young suckers are much larger (sometimes 7 to 8 inches (18 cm to 20 cm) long)), very succulent, often twice as long as they are broad.

Aspen is dioecious, with male and female flowers normally borne on separate trees (fig. 1). Flowering commonly occurs in April or May before the appearance of the leaves. Petalless, unisexual flowers (1/8 inch (0.3 cm) long) are arranged along drooping, flexible, modified spikes (1 to 2 1/2 inches (2.5 cm to 6 cm) long)) called catkins or aments. Individual flowers are inserted singularly on a saucer-shaped disc attached to the stalk by a short pedicle, and are subtended by a brown hairy lobed scale. Male flowers have 6 to 12 stamens. Female flowers have a single ovary composed of two carpels crowned by a short stout style with two erect stigmas.

The seed capsules mature in May and June, when the catkins are 3 1/2 to 4 inches (9 cm to 10 cm) long. They are conical, light-green, thin-walled, 2-valved, and nearly 1/4 inch (0.6 cm) long. The number of capsules per catkin varies from 70 to 100, with 6 to 8 seeds in each. Seeds are pear-shaped, light brown, about 1/32 inch (0.08 cm) long, with a tuft of white hairs attached to the basal end. (See the SEXUAL REPRODUCTION, SEEDS, AND SEEDLINGS chapter.)

The Bark

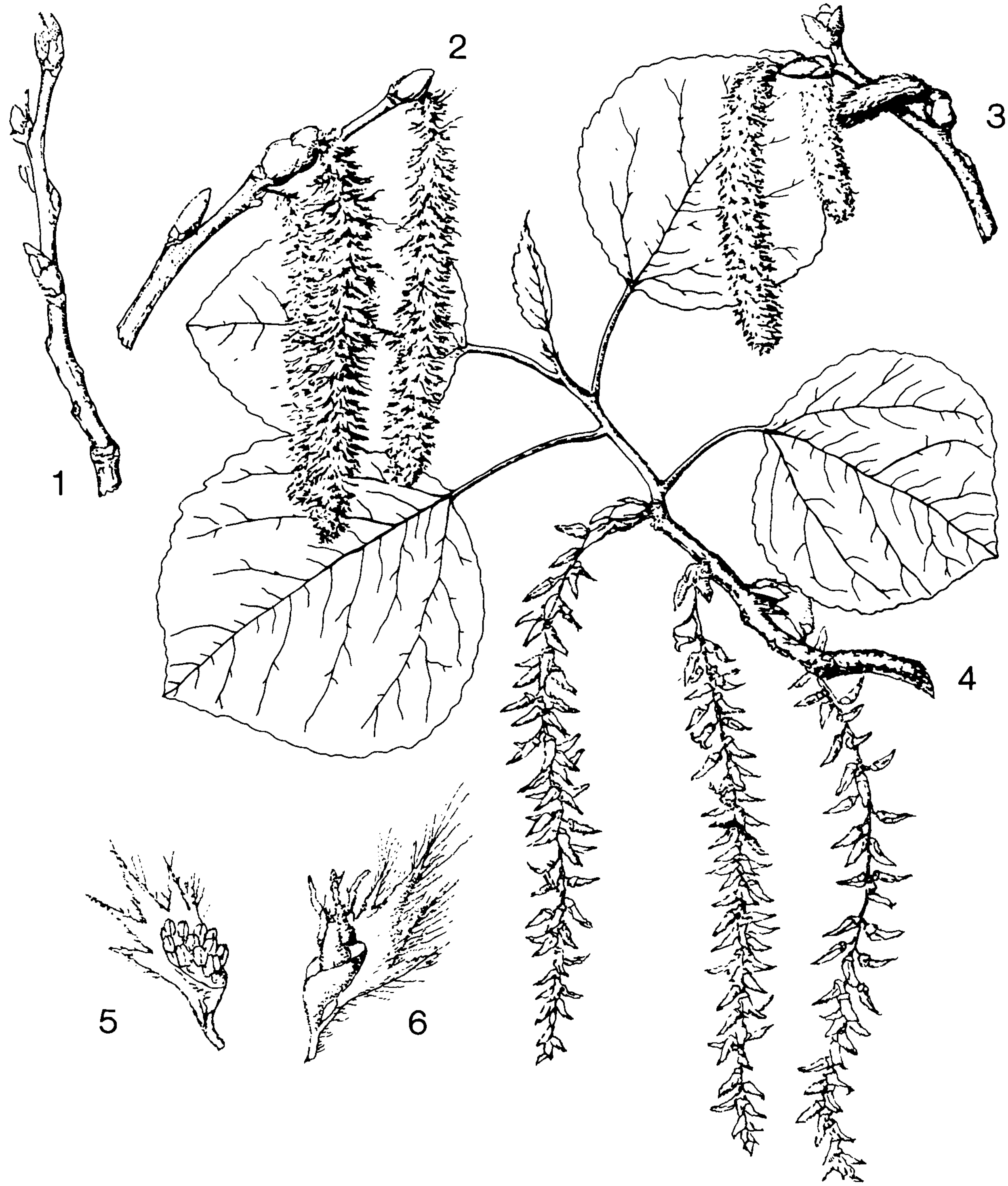
Descriptions of western aspen trees often mention several bark colors: white, yellow-brown, and green. The white bark, common in the West, results from a coating of dead cork cells that easily rub off (Strain 1961). Some yellow-brown trees have a coating of dead cork cells, too.

Chlorophyll in the bark gives the green color. In northern New Mexico, Covington (1975) found aspen bark to be darker green at higher elevations. But this darker bark actually had less chlorophyll than the lighter-colored bark of aspen at lower elevations; instead, the dead cork cells of dark green bark were more translucent.

The smooth bark characteristic of aspen results from a persistent periderm (Kaufert 1937). Rough bark on aspen in the West is restricted largely to the lower few feet of the bole and as patches higher up. Baker (1925) wrote that rough basal bark in the West results from gnawing by sheep. In the West, the rather uniform upper boundary of dark, rough, fissured bark in some stands suggests a snow line as well as a browse line. Gnawing by rodents beneath the snow surface also stimulates rough bark in aspen (fig. 2) (Hinds and Krebill 1975).

Geometry

Baker (1925) provided data on the relationship of tree height to diameter at breast height (4.5 feet (1.4 m) above ground) (table 1). Because this relationship varies strongly with site quality, there are separate values for sites 1 through 4. However, these data are from a limited geographical area, in which Baker's site 1 does not include the truly best aspen sites found elsewhere in the



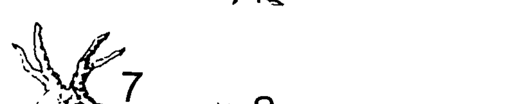


Figure 1.—Twigs, leaves, flowers, fruit, and seed of quaking aspen. (1) Winter twig, natural size; (2) a flowering branch of the staminate (male) tree, natural size; (3) a flowering branch of the pistillate (female) tree, natural size; (4) a fruiting branch, with leaves, natural size; (5) a staminate (male) flower with its scale enlarged; (6) a pistillate (female) flower with its scale enlarged; (7) vertical section of a pistil, enlarged; (8) a fruit, enlarged; (9) a fruit with open valves, enlarged; (10) a seed, greatly enlarged.

Table 1.—Average heights (feet) of aspen of different diameters (inches) on site quality classes 1-4 (Baker 1925).

d.b.h.	Site class 1	2	3	4
4	40	35	32	30
5	46	41	36	34
6	51	46	41	37
7	57	51	45	39
8	62	56	46	41
9	66	59	51	43
10	70	63	54	45
11	73	66	57	46
12	75	68	58	48
13	76	70	60	N/A
14	78	71	61	N/A
15	79	72	62	N/A
16	80	73	62	N/A
17	81	74	N/A	N/A
18	81	74	N/A	N/A
19	82	74	N/A	N/A
20	82	75	N/A	N/A
21	83	75	N/A	N/A
22	83	75	N/A	N/A

N/A = Not applicable.

West. On these, aspen with the given diameters would grow much taller.

In the West, old trees on mediocre or poor sites sometimes reach large diameters that give them a peculiarly stout-boled stubby appearance. Strain (1964) reported two extreme cases: a 226-year-old aspen that was 39 feet (12 m) tall and 17.3 inches (44 cm) d.b.h., and a 107-year-old tree that was only 10 feet (3 m) tall but 9.2 inches (23 cm) in diameter at the 1-foot (30-cm) height.

Beetle (1974) described the crown spread of aspen of different diameters in Wyoming stands.

d.b.h. (*inches*)	Crown spread (*feet*)
2	5
5	7
7	9
12	12
13–18	13–14

He noted that crown spread, while varying somewhat with stand density, was not great for aspen, even for mature trees.

Beetle (1974) described aspen crowns as round-topped and "one-sided," and "always developed toward the nearest edge of the stand." This crown description is not found elsewhere in the literature. There would seem to be a limit to how far from the edge that condition could occur.

Strain (1964) pointed out that aspen crowns may be either rounded or pyramidal. Clones with branches approximately at right angles to the trunk produce pyramidal tops; those with strongly ascending branches produce round tops. Those tendencies would be modi-

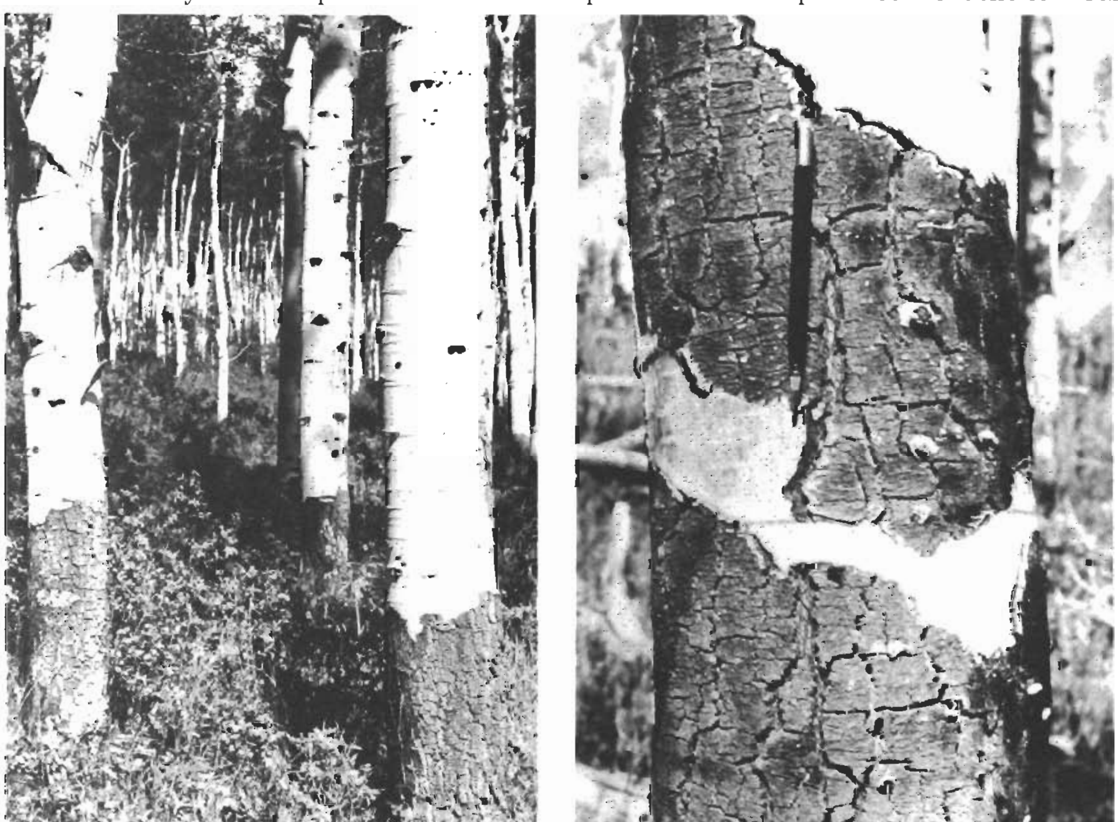


Figure 2.—Dark, rough bark resulting from feeding by voles. (A) Trees with rough bark extending upward to 4 feet (1.2 m). (B) Closeup. (Hinds and Krebill 1975).

fied or strengthened by the relative growth rates of terminals versus lateral shoots.

Aspen trees exhibiting pronounced drooping characteristics have been observed throughout the Rocky Mountain region along roadsides, in campgrounds, and in urban areas (Livingston et al. 1979). Trees affected with this malady "are characterized by pendant branches with shortened internodes and large nodes, large terminal leaves, and a lack of lateral foliage and branching." The pendant growth habit results from punky, rubbery wood in the branches. The cause or causal agents of drooping aspen are unknown. (See the DISEASES chapter.)

Aspen Clones

Barnes (1966) described the clonal habit of aspen. A clone is a group of individuals propagated vegetatively from a single individual of seedling origin, termed the "ortet". The members of a clone, termed "ramets," are genetically identical. (See the GENETICS AND VARIATION chapter.)

As an aspen seedling grows and matures, it develops a widespread root system. Under suitable conditions, typically after fire, this root system gives rise to many shoots, called "root suckers" that form new trees. (See the VEGETATIVE REGENERATION chapter.) These suckers (the ramets) are genetic copies of the original ortet. The genotype present in the ortet survives as a clone through many generations of ramets. In the West, clones apparently persist for thousands of years. By expansion of ramet root systems, a clone may expand over time to cover 100 acres or more, although the area occupied usually is much smaller (Kemperman and Barnes 1976).

The boundary of two adjoining clones is often abrupt and frequently conspicuous (Baker 1921, Barnes 1969, Cottam 1954, Jones and Trujillo 1975b). Because each clone consists of genetic duplicates, the mass uniformity within clones emphasizes the differences between clones.

The clonal habit is of major importance in the ecology and management of aspen. Stands are composed of clones. A stand may be a mosaic of clones or may be a single clone.

The Root System

Aspen seedlings (ortets) during their first year have fibrous, branching, lateral root systems with few taproots. In moist, sandy soil, Day (1944) found at the end of the first year that lateral roots were less than 16 inches (41 cm) long and taproots less than 6 inches (15 cm) deep. In the second year, lateral roots had grown to 4 to 6 feet (1.2 m to 1.8 m), and suckers appeared on them. He found an 18-year-old tree, 25 feet (7.6 m) tall, with a main lateral root 47 feet (14 m) long and branch sinker roots to a depth of 7 1/2 feet (2.3 m).

The root system of an aspen clone is characterized by relatively shallow, widespreading cord-like lateral roots and vertical sinker roots that descend from the laterals (Baker 1925, Buell and Buell 1959, Gifford 1966, Maini 1968). The lateral roots are cylindrical with little taper, except near the ramets (Sandberg and Schneider 1953). Undulating within the upper 2 to 3 feet (0.6 m to 1 m) of the soil profile, they show only occasional branching. Branches generally arise from the base of ramets (Gifford 1966). Lateral roots may extend for more than 100 feet (30 m) into adjacent open areas (Buell and Buell 1959). In Colorado, of eight plant species studied, Berndt and Gibbons (1958) found quaking aspen roots to have the greatest lateral extent, up to 48 feet (15 m) from the tree. The shallow laterals tend to follow minor soil surface irregularities (Sandberg 1951), so much so that Baker (1925) found them growing upward into decaying conifer stumps, where they often produced suckers Jones (1974a). Turlo (1963) found aspen roots in Wyoming growing along the soil surface beneath fallen logs as well as into the logs themselves.

Sinker roots may descend from points anywhere along a lateral root. In two Utah clones, Gifford (1966) observed that only 30% of the sinker roots originated from the base of ramets. They reached depths of more than 9 feet (2.7 m), often following old root channels (Day 1944, Gifford 1966). At their lower extremities, sinker roots branch profusely into a dense fan-shaped mat. Dense mats of fine roots often occur when tree roots encounter an impeding layer—rock, dense clay, or water saturated soil. Several studies of soil water depletion by aspen imply effective rooting depth to at least 9 feet on deep, well-drained soils (Johnston 1970, Johnston et al. 1969). This is similar to the depths reached by associated woody plant species on the same sites.

The quantity or weight of roots under aspen infrequently have been measured. Day (1944) found a root/shoot ratio of 2:1 in 6- to 8-year-old aspen. Vaartaja (1960) measured greater proportions of roots under 6-month-old seedling aspen from a northern (54° latitude) ecotype than from an ecotype from 46° latitude; the difference was attributed to adaptation to the cold soils of the north. Young and Carpenter (1967) found the ratio decreased with increasing aspen tree heights from 10 through 35 feet (3 m to 11 m). An open, mature stand of Minnesota aspen (200 trees per acre averaging 5 1/2 inches (14 cm) d.b.h.) was estimated to have 70,000 feet (21 km) of roots per acre that were larger than 0.3 inch (0.8 cm) in diameter (Sandberg 1951, Sandberg and Schneider 1953).

The stems in aspen clones usually are interconnected in small groups via their common parent root system (Barnes 1959, Day 1944, Kittredge and Gevorkiantz 1929). These connections can transmit water and solutes from tree to tree (DeByle 1961, 1964; Gifford 1966; Tew et al. 1969), but perhaps not carbohydrates (Strain 1961). The intraclonal connections, the extensive lateral root network, and the characteristic enlargement of the parent root on the distal side of suckers (Brown 1935) are illustrated in figures 3 and 4. These groups of stems may remain functionally interconnected throughout the life of the aspen stand (DeByle 1964, Maini 1968, Tew et al. 1969). The size of most groups will decrease in number as the stand matures and trees die (DeByle 1964). Also, some connections likely will decay and break (Barnes 1959, Gifford 1966). The development of interconnected stem groups in aspen clones is illustrated in figure 5.

Root grafts seldom are found in aspen. LaRue (1934) discovered numerous grafts in some species, but found none at all in aspen, even where roots had grown around one another or were otherwise in contact. Turlo (1963) found no actual grafts, even though there was a great deal of root crossover. DeByle (1964), using tracers and extensive excavation in several stands of bigtooth aspen and quaking aspen, found a few grafts in one bigtooth aspen stand but none elsewhere, although in all stands many roots were found growing tightly together.

A newly formed aspen sucker depends upon the parent root for nutrients and water. This ready-made root system gives aspen suckers a growth and survival advantage over seedlings of aspen and other species (Day 1944, Graham et al. 1963). As the sucker grows in diameter, the parent root distal to it enlarges, and branch roots arise from the base of the shoot itself and from the portion of the thickened root (Baker 1925, Brown 1935). The sucker literally adopts that portion of its parent root as its own. The degree of dependence suckers have on their parent roots diminish as they develop their own root systems. The rate of such development and independence seems to vary widely—from a couple of years (Sandberg 1951) to more than 20 years (Zahner and DeByle 1965). In the West, Schier and Campbell (1978a) examined 1- and 2-year-old suckers in

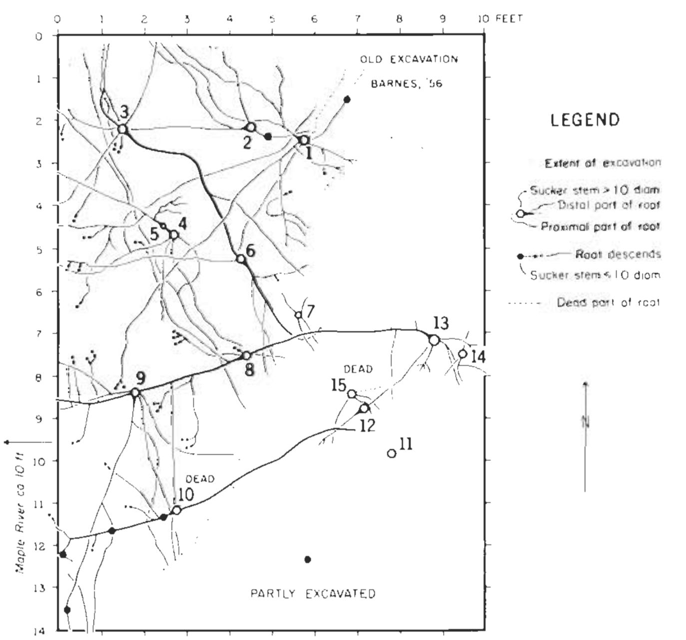


Figure 3.—Drawing of a vertical view of the root system under part of an aspen clone with 13-year-old, 3-inch (8-cm) diameter stems. (DeByle 1964).

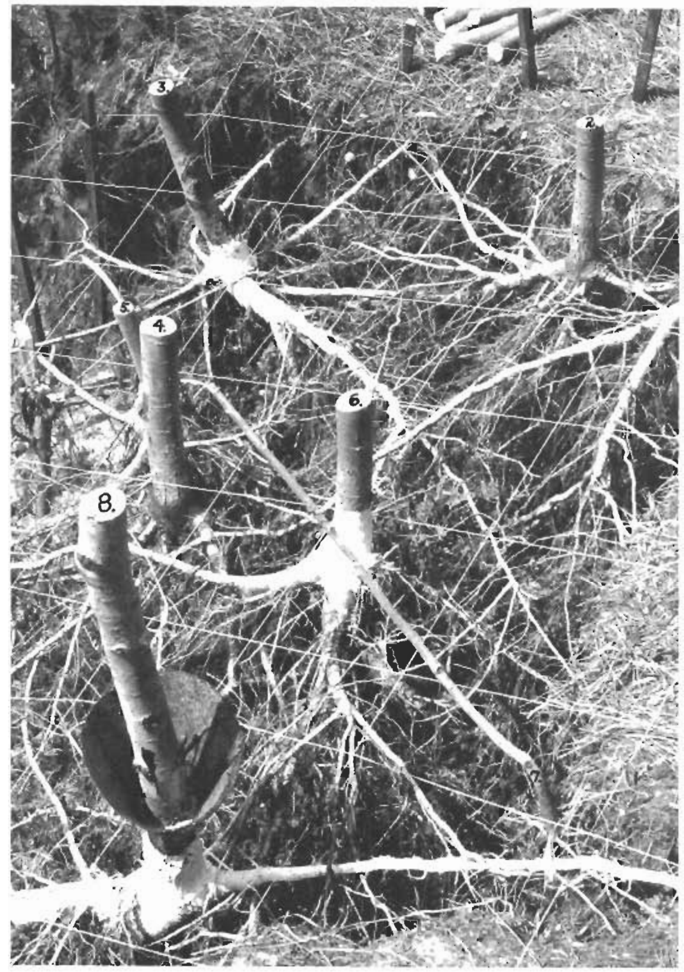


Figure 4.—North half of the root system excavation diagrammed in figure 3.

8 clones and found adventitious roots had developed under more than half of the suckers; but only 1% had well-developed root systems of their own. Those that did were on very small parent roots.

The swelling of the parent root on the distal side of suckers and the likelihood of interconnected stem groups make the root system of aspen unique among common forest tree species. The parent root and its branches often are considerably older than the sucker stems. These unique characteristics and the effect they have on both size and development of roots and stems must be taken into account when studying aspen root systems, especially those of young sucker stands.

Stand Structure

Aspen, is a shade-intolerant species that commonly grows in even-aged stands, especially on sites where competition with more shade-tolerant tree species is intense, such as throughout most of aspen's range in the East. In the West, most aspen stands are even-aged and single-storied. Nearly all of the trees in these stands originated during a period of 2 to 4 years (Baker 1918b, 1925; Jones 1975; Jones and Trujillo 1975a, 1975b; Patton and Avant 1970; Sampson 1919; Smith et al. 1972).

Sometimes these even-aged stands of aspen are the same age over some rather large areas. In the White Mountains of Arizona, for example, many aspen stands originated in 1905,[1] following widespread fires in 1904 (Kallander 1969).

The uniformity of these even-aged stands, when young, can be striking. For example, Miller (1967) found that the leaf distribution of an even-aged sapling stand in Colorado was rather homogeneous throughout the depth of the canopy, except at the very top and bottom.

In contrast, Baker (1925) described Utah stands that were only broadly even-aged, made up of trees that originated over a period of 10 or 20 years during deterioration of the previous stand. Stahelin (1943) and both Jones and Hinds[2] also found such stands in Colorado and New Mexico (fig. 6). These stands typically were mature and single-storied; their age irregularity was recognized only when the ages of individual trees were determined.

Other single-storied stands have two distinct, easily-recognized age classes. They are likely to consist of a more or less substantial scattering of old, often fire-scarred veterans standing among younger, slender trees of similar height. The old trees usually are survivors of a fire decades earlier that killed many of the aspen and gave rise to a subordinate stratum of suckers. (See the FIRE chapter.) Many of these eventually reached a height similar to the older trees, and, with them, formed a closed canopy.

[1]*Unpublished data collected by John R. Jones.*
[2]*Unpublished data.*

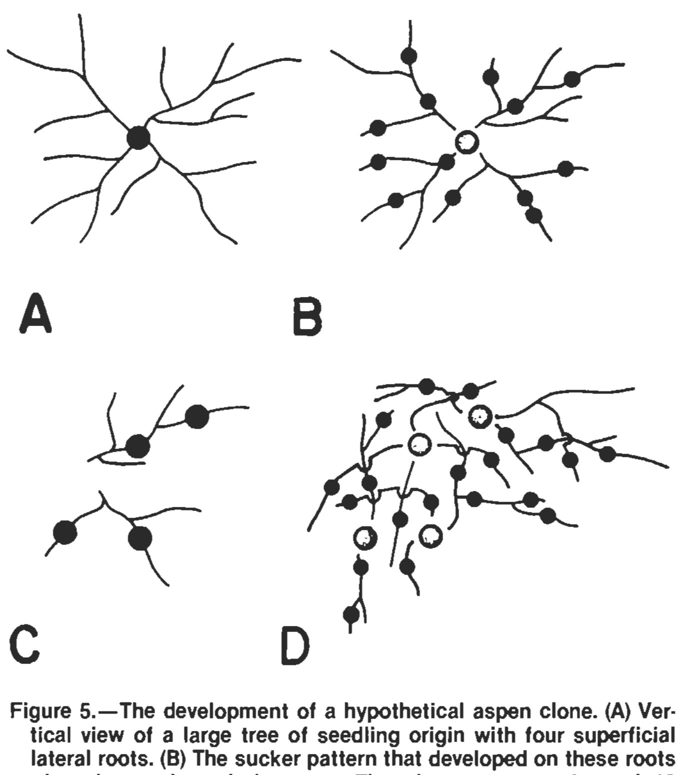


Figure 5.—The development of a hypothetical aspen clone. (A) Vertical view of a large tree of seedling origin with four superficial lateral roots. (B) The sucker pattern that developed on these roots after destruction of the ortet. The clone now consists of 13 ramets, each connected to some but not all others in the clone. (C) Four of the 13 ramets illustrated in B that survived for approximately 50 years before being removed by fire or cutting. (D) The roots of the four trees shown in (C) would give rise to numerous suckers. After 10 to 20 years, these might have thinned through natural causes to the 20 stems illustrated here. (DeByle 1964).

Figure 6.—A single-storied stand with trees ranging from 75 to 99 years old. Dark bark near bases appears to be caused by rodent gnawing beneath the snow. White River National Forest, Colorado.

Baker (1925) described two-storied stands in Utah. Surface fire in single-storied stands had killed some trees and resulted in an understory of suckers (fig. 7). Johnston and Doty (1972) mentioned two-storied stands in which the lower stratum developed beneath an open overstory when livestock were excluded after long overuse. Similar two-storied stands probably would result if big game browsing were eliminated from severely impacted mature aspen stands (Krebill 1972).

All-aged stands are more common than expected. Davidson et al. (1959) sampled 32 aspen sawtimber plots scattered through western Colorado. Only eight were even-aged; seven were "two-aged," with ages in the lower class somewhat uneven; and the other 17 were uneven-aged, with most age spreads from 20 to 70 years. Alder (1970) selected 44 uncut aspen stands in Utah and Arizona with at least two tree strata and described their age structure. A few had an age distribution resembling the classic J-shaped curve of all-aged stands (Bruce and Schumaker 1950). Packard (1942) mentioned similar all-aged stands in Colorado. However, their health and vigor many not be the best. Betters and Woods (1981) measured reduced growth rate and increased incidence of decay in suppressed trees within uneven-aged aspen stands in northwestern Colorado.

Many stands dominated by aspen contain a mixture of other species. Authors since Weigle and Frothingham (1911) have pointed out the common occurrence of coniferous understories beneath aspen canopies. In the Southwest, where many aspen stands developed after the burning of mixed conifer forests, aspen stands often include groups and scattered individuals of overmature conifers, most commonly Douglas-fir (*Pseudotsuga men-*

Figure 7.—Two-storied stand after a moderate fire in aspen (Baker 1925).

ziesii), that survived the fire. Some southwestern forests are an irregular mosaic of aspen patches and coniferous patches, reflecting in part the varying intensities of old fires.

After fire, aspen sometimes forms mixed stands with lodgepole pine. These mixes are described for northern Colorado (Clements 1910) and northern Utah (Ream 1963). Mixtures may be in small groups, with the aspen taller during early years of stand development, and the pine asserting dominance later and eventually eliminating most of the aspen (Clements 1910).

In summary, aspen in the West occurs as even-aged stands that probably originated after fire or similar perturbance, broadly even-aged stands, two-storied stands of two ages, one-storied stands of two ages, and all-aged stands. Even-aged stands predominate. For example, Shepperd (1981) sampled 140 sites in Colorado and Wyoming and found single-aged stands most frequent, two-aged stands next, and broad-aged stands made up only 4% of the sample. Choate (1966) implied that most stands in New Mexico are even-aged, too.

Stand Changes Over Time

The morphology of even-aged aspen stands changes with age. Young stands have a large proportion of their stems overtopped by others of about the same age (Pollard 1971). On six clearcut plots in Arizona heavily stocked with 3- and 4-year-old suckers, 38% were already dead—most apparently because of intense competition—and 42% of the survivors were overtopped (Jones 1975). In four fully stocked, 22-year-old-clones, 59% of the live trees were completely overtopped (Jones and Trujillo 1975a), forming a subordinate layer of very slender trees with little foliage. Conventionally, even-aged stands like these are called single-storied; the numerous overtopped trees, seriously declining, are ignored. However, in well-stocked mature and overmature even-aged stands, there are very few overtopped aspen (Stoehr 1955), except for more or less ephemeral suckers.

Barnes (1966) and Brown (1935) described stands with a somewhat domed or elliptical profile. These usually are in openings where lack of competition permits clonal expansion. The core of such stands generally consists of older trees, with progressively younger and shorter trees toward the edge. These stands often have even-aged cores surrounded by bands of younger even-aged stems. Baker (1925) ascribed these even-aged extensions to surface fires and described them as commonly only about 15 feet (5 m) wide but sometimes more than 50 feet (15 m) wide. In Wyoming, Beetle (1974) found that the older aspen in the center of such stands had died, forming what he termed a "fairy ring," or, if larger, an "aspen opening."

As an even-aged aspen stand matures, several factors may act independently or together to influence stand structure or morphology. In addition to clonal characteristics (Schier 1975a), these appear to be climate, fire history, soil or site quality, impacts of livestock and big game, incidence of disease and perhaps insects, and the presence of a conifer seed source.

Baker (1925) stated that single-storied stands regularly produced suckers. If these stands were reasonably well-stocked, the suckers normally were weak and inconspicuous and died in a few years. However, without sudden destruction by fire or a similar agent, a well-stocked, overmature, even-aged aspen stand slowly dies, the canopy opens up, and aspen suckers survive and grow in the openings. (This assumes that other species, especially conifers, do not take over the site, and that livestock or big game impacts are minimal.) These suckers typically arise over a period of several years; the resulting stand is broadly even-aged.

If such broadly even-aged stands reach old age without disturbance, their deterioration is likely to extend over a longer period than before because of the range of tree ages. That, in turn, would result in a longer regeneration period and a new stand with an even greater range of ages. Baker (1925) hypothesized that if this continued over several generations of aspen, all-aged stands would result. The all-aged stands of aspen that occur in the West probably developed through this process. The stability of aspen on some sites was recognized many years ago (Fetherolf 1917), and is considered by some as a de facto climax type (Mueggler 1976b) on these sites.