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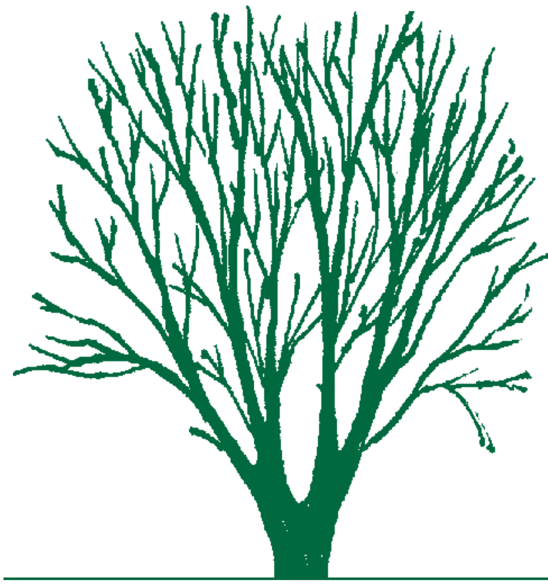
Cottonwood



Establishment, Survival, and Stand Characteristics

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Contents

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Cottonwood provides structural and functional benefits to riparian areas where it is adapted. Cottonwood is adapted to specific growing conditions. If you want to promote cottonwood establishment, it is important to understand its ecology, including site characteristics and conditions required for establishment and survival. This publication is not intended to be a "how-to" guide. It is intended to describe site characteristics and the conditions necessary for cottonwood to establish and sustain itself naturally. Artificially establishing cottonwood is possible and will be addressed in a subsequent publication.

Cottonwood belongs to the genus *Populus*, which also includes aspens and other poplars. Black cottonwood is the species native to Oregon. In most references, the scientific name is *Populus trichocarpa* Torr. & Gray (DeBell 1990). On the U.S. Department of Agriculture Natural Resources Conservation Service Web site (http://plants.usda.gov/), the scientific name is *Populus balsamifera* L. ssp. *trichocarpa* (Torr. & Gray ex Hook.) Brayshaw.

The range of black cottonwood encompasses much of the interior and coastal Northwest, including Oregon, except most of the southeast quarter of the state. The best growth occurs in the humid coastal forests (DeBell 1990). In the Blue Mountains, black cottonwood populations are found up to approximately 3,500 to 4,000 feet elevation (Crowe and Clausnitzer 1997). In the Wallowa Mountains, populations are found at elevations higher than 4,000 feet, perhaps as a result of the more moderate climate.

Black cottonwood, a member of the *Tacamahaca* section within the *Populus* genus (Eckenwalder 1996), expresses a high degree of genetic variation, and natural hybridization within the section is common (Farmer 1996). Black cottonwood is the largest of the American poplars, with exceptional individuals exceeding heights of 200 feet on the best sites (DeBell 1990).

Much of the discussion below relates to cottonwoods throughout North America because research relating to establishment, survival, and stand characteristics has been conducted on a variety of cottonwood species throughout the continent. Various species seem to share the characteristics discussed below. If the discussion is specific to black cottonwood, it is noted as such.

Site conditions

Black cottonwood grows primarily on moist sites, the most productive of which are bottomlands of major streams and rivers (DeBell 1990). It can grow on a variety of soils and sites, ranging from moist silts, sands, and gravels on islands and new river bars to rich humus soils, loams, and occasionally clay soils on upland sites. Optimum growth requires abundant moisture, nutrients, oxygen, and nearly neutral soil reaction (pH 6.0 to 7.0) (Everitt 1968, DeBell 1990). Growth is best at low elevations on deep, moist, alluvial soils (those made up of material deposited by running water).

Black cottonwood is a drought- and shade-intolerant pioneer species (DeBell 1990). In drier areas such as eastern Oregon, cottonwood usually is limited to protected valleys and canyon bottoms, along streambanks, and edges of ponds and meadows. West of the Cascades, Farmer (1996) cited studies that found decreased branchiness and increased growth and leaf size at higher latitudes (corresponding to increasing water availability from south to north). Reduced height, decreased leaf size, and increased branchiness are associated with the drier conditions of interior river systems east of the Cascades.

Methods of reproduction

Cottonwoods reproduce by both seed and vegetative means, including root and shoot sprouting.

Reproduction by seed is a primary means of cottonwood establishment (Hines 1999). Cottonwoods are dioecious; male and female flowers (catkins) are borne on separate trees (DeBell 1990). Large, mature trees yield millions of seeds, which normally are released during spring flooding. Seeds are extremely light and can be carried great distances by wind or water (DeBell 1990).

Read (1958) reported high seed viability (near 100 percent) for plains cottonwood during the first 5 days following dispersal, but viability dropped rapidly if seeds were not kept moist. Braatne et al. (1996) described seed viability for cottonwoods as short, generally lasting only 1 to 2 weeks under natural conditions. Once a seed becomes wet, viability is lost in 2 to 3 days if a favorable microsite is not encountered. The ideal environment for germination typically is found on moist silt, sand, or gravel in full sunlight along river and stream floodplains (DeBell 1990).

Vegetative reproduction (sprouting from roots, stumps, or branches) occurs both in low, moist environments and on higher terraces where moisture is more limiting (Wilson 1970). It often is associated with disturbance stress caused by fire, beaver, ice scouring, animal browsing, or the burial or toppling of saplings during floods (Rood and Mahoney 1990). Sprouting ability is excellent from both roots and stumps of young trees, but declines as trees grow older. Regrowth from stumps with an established root system often is more rapid than seedling growth (Rood and Mahoney 1990).

Winter wind and snow can break off branches, which may fall at the water's edge. These tree parts represent potential sources for new tree establishment (Braatne et al. 1996). High water may bury the branches, either onsite or after transporting them downstream. As the high water recedes, the branches may sprout, forming new plants.

Black cottonwood also can shed branchlets (twigs and small branches) throughout the winter and early spring as part of a natural pruning process called cladoptosis (Galloway and Worrall 1979). Cladoptosis is the physiological abscission (removal) of lateral branchlets brought about by the formation of a corky layer of young cells at the base of a branchlet. The branchlet eventually breaks off at this "ball and socket" abscission zone. Shed branchlets usually consist of short shoots (5 to 10 cm or 2 to 4 inches long) 3 or 4 years old. Galloway and Worrall (1979) found that black cottonwood twigs that had been shed by cladoptosis could form new plants, and that such twigs could remain viable during water transport for great distances downstream.

In research conducted at a variety of sites, Galloway and Worrall found that most regeneration from areas already forested with black cottonwood and understory conifers was from root suckers. Most reproduction on new gravel and sand bars was from seedlings. Of the rest, most originated from twigs and branches that had been removed mechanically from the parent plant (e.g., by ice, heavy snow, or wind breakage). During each of their searches, they found at least one 1- to 2-year old plant that arose from twigs shed by cladoptosis.

Seedling establishment

Cottonwood flowering and pollination generally coincides in the spring with rising water in riparian systems. Seed development and dispersal follow as water levels recede (DeBell 1990). The timing of these events is critical to cottonwood seedling establishment. Seed germination and establishment require a specific environment and have a narrow window of opportunity.

Black cottonwood germination is favored by conditions at the water's edge. However, seedlings there are threatened by flooding, burial, and scouring. Seedlings at higher point bar locations are less likely to be disturbed, but are more likely to succumb to the rapid drainage of a temporarily elevated water table (Hines 1999).

As high flows recede, freshly deposited mineral substrate (fine sand or a fine sand/gravel mix) on active point bars provides moist, bare conditions ideal for seed germination. Moss (1938) and Noble (1979) noted that cottonwood seed germination typically occurs within 8 to 24 hours on moist surfaces. The seedling crop will fail if the surface dries during the first several days after germination. Moisture must be available in the upper layer of soil for 1 to 3 weeks because seedling root growth is slow. Seedling water absorption depends largely on a brush of delicate hairs (collet-hairs) located near the soil surface. The collet-hairs also anchor the plant by attaching to sand particles, making seedling displacement difficult.

The best conditions for establishment are associated with sustained high flows during the establishment period (Bradley and Smith 1986). Noble (1979) suggested that a halt in the drop of water enhances seedling survival by keeping seedlings moist. This combination of conditions yields an environment free of competition, a mineral soil in which roots can maintain contact with a zone of moist substrate as waters slowly recede, and an environment that is not subject to additional erosion, deposition, or prolonged flooding during the first growing season.

These conditions tend to recur on a 5-year return (or longer) interval. A 5-year return interval implies that a given discharge occurs in only 20 percent of the years based on the historical record. Actual occurrence can be quite variable, and one should not expect a regular 5-year spacing between events.

From a stream classification perspective (Rosgen 1996), these conditions generally are seen on C and low-gradient B channels. These streams provide colonization opportunities through point bar formation and the deposition of substrate in remnant channels that also carry floodwater. The stream gradient in this scenario likely is less than 2 percent, allowing fine sands or a sand/gravel mix to form the surface layer of exposed point bars. Skeletal layers of mixed and coarse material are found beneath, having been deposited during periods of higher stream velocity. The low gradient suggests that floodwaters tend to pond within such stream reaches and then recede more slowly than on steeper gradient streams. This sequence of events might occur only once in 5 to 10 years or longer (Bradley and Smith 1986, Hines 1999).

As a river or stream migrates, it erodes sediments from the concave side of meanders and deposits them downstream on the convex side, creating point bars (Leopold 1994). Point bars are potential cottonwood habitat, as are migrating edges of midchannel islands in larger rivers (Barnes 1985, Everitt 1968).

Survival

Cottonwoods are susceptible to both extended drought and flooding. Young plants are especially susceptible to drought when the water table drops below their rooting zone. This is a major cause of seedling death on point bars that have built up too high and on steep stream gradients where water levels can drop faster than roots can grow. Most seedling mortality occurs in late summer as sites begin to dry and stream levels and water tables drop (Rood and Mahoney 1990, Stromberg and Patten 1996).

There exists a critical elevation zone on point bars where seedbeds are high enough to avoid drowning, but low enough to avoid drying out. By the end of the first growing season, cottonwood seedlings lower on the point bar have a better chance of surviving than those higher on the point bar if the higher positioned seedlings' roots have not kept pace with the lowering water table. However, rapidly rising floodwaters can scour and uproot young cottonwoods; therefore, seedlings on point bar surfaces high enough to escape mortality from flooding during the first few years following recruitment have a better chance of surviving than those at lower elevations.

Hosner (1958) reported that plains cottonwood seedlings survived a period of 8 days of inundation, but most died after 16 days. Black cottonwood has been observed to persist under longer periods of inundation (David Hibbs, professor, Forest Science Department, Oregon State University, personal communication).

If cottonwood seedlings escape mortality from desiccation or flooding during the first few years of growth, their chances of survival probably are very good. Roots will have grown enough to ensure a stable water supply during dry periods and to anchor the sapling against all but extreme floods. As point bars expand laterally and build up vertically, the saplings will be in less danger of extreme flooding (Bradley and Smith 1986).

Because seedlings on point bars are highly vulnerable to flooding and scouring, Hines (1999) postulated that the majority of colonization on point bars results from vegetative reproduction as opposed to seed. Barnes (1985) suggested that colonization depends on sprouting and resprouting of seedlings rather than the number of successful instances of seedling establishment. Vegetative propagation allows immediate local colonization of cottonwood following the successful establishment of a few seedlings.

Cottonwood seedlings remain vulnerable to drought in the year following establishment because of their small root systems. Growth accelerates during the second year and, after 2 years, roots may be almost 3 meters long (Ware and Penfound 1949). The longer roots improve the sapling's ability to tolerate flooding and drought stress (Pezeshki and Hinckley 1988).

Growth rates tend to slow after this initial growth period and then remain relatively constant for several decades. Flowering occurs after about 7 years (Rood and Mahoney 1990).

Juvenile and mature trees, while less susceptible to drought, can show signs of pruning, leaf drop, and yellowing due to cavitation (formation of air bubbles in water-transporting tissue). Extended periods of drought will result in stunted growth and/or death in both juvenile and mature trees (Albertson and Weaver 1945, Rood and Mahoney 1990).

Cottonwood has several adaptations that allow it to survive floods, but it is not as well adapted to prolonged flooding as some riparian species. Mature cottonwoods typically show signs of stress when flood conditions last more than a few weeks (Neuman et al. 1996). Cottonwood often is associated with soils that contain a layer of coarse substrate (Crowe and Clausnitzer 1997). These soils drain more quickly than fine-textured soils, reducing the length of time a root system must survive in a flooded environment (Richardson and Vepraskas 2001).

The roots on mature trees survive flooded conditions by utilizing anaerobic respiration (respiration without oxygen) to continue essential metabolic functions. However, anaerobic respiration cannot be continued indefinitely. It is roughly 20 percent as efficient as aerobic (oxygen-based) respiration, and it produces toxic by-products that accumulate within plant tissue. Reliance upon anaerobic respiration requires a slowing or stoppage of plant growth and is limited by the amount of carbohydrate reserves stored within the roots and by the subsequent accumulation of toxic compounds.

A second way that cottonwood overcomes the lack of oxygen in flooded soils is through the presence of shallow adventitious roots and lenticels along the stem and root crown area (Nilsen and Orcutt 1996). Lenticels are small cracks or pores in the bark. Oxygen entering the tree through these pores migrates toward areas of low oxygen concentration. In most cases, oxygen supplied to adventitious roots enters via lenticels or is obtained directly from shallow, oxygenated layers within the soil. All of these adaptations can take place within the plant at the same time but in different portions of the root system.

Aerenchyma, a special type of oxygen-conducting tissue found in herbaceous species such as sedges and rushes, is a much more efficient means of delivering oxygen to flooded roots than through lenticels. Consequently, species utilizing aerenchyma tend to dominate on sites that are flooded for extended periods of time and on flooded soils composed primarily of silt and clay-sized particles.

Cottonwoods are susceptible to a number of other damaging agents. Seedlings and young saplings can be injured or killed by unseasonably early or late frosts (Crowe and Clausnitzer 1997, DeBell 1990). A variety of insects and fungi can cause problems for black cottonwoods, but most damage has been observed in plantations rather than in natural stands, especially if the trees are vigorous (DeBell 1990). Excessive browsing by wildlife and livestock can suppress both seedlings and sprouts (Crowe and Clausnitzer 1997). Seedlings and saplings are highly susceptible to intense fire because of their thin bark and shallow root systems (Crowe and Clausnitzer 1997). After 10 to 20 years, thicker bark may provide some protection against low-intensity fires, but fire wounds can allow heartwood decay to begin (Crowe and Clausnitzer 1997). Sprouting from stumps can follow top kill by fire.

Stand characteristics

Maintenance of a riparian cottonwood forest depends on establishment of new trees to compensate for those that die. Forests rely principally on seedling establishment for expansion to keep up with river and stream migration. As discussed above, successful seedling establishment does not occur regularly, as it requires complementary seed production and hydrologic events. Thus, we often find arc-shaped bands of even-aged trees parallel to the river channel. Each band contains trees similar in height and size because a large number of seedlings tend to become established at the same time and then thin as the band of trees matures.

Everitt (1968) described bands of even-aged trees on point bars that could be associated with specific hydrologic events. He noted that tree age increased with distance from the channel. Each band began as a thicket of seedlings on a bar at the channel's edge and was "transported" inland as the channel migrated and more trees were established on newer sandbars.

Within these bands, asexual (vegetative) reproduction through suckering and stump regrowth may contribute to forest maintenance (Rood and Mahoney 1990). If vegetative reproduction does not occur, old cottonwood stands eventually die out and are replaced by other species. Observations indicate that this is the more common outcome (Hibbs, personal communication).

As discussed above, cottonwood establishment is determined largely by reach type and stream flow. Differences in geology, elevation, climate, and tributary influence (Frissell et al. 1986) produce differences in cottonwood distribution along various reaches of the same stream. Thus, high flow along one reach might promote cottonwood establishment, while an equivalent flow along a second reach might scour away established cottonwood (Everitt 1968, Bradley and Smith 1986).

Conditions for cottonwood establishment and survival also vary throughout a basin as flood frequency, timing, and magnitude interplay with the structure of stream channels (Asplund and Gooch 1988, Scott et al. 1996, 1997). Conditions vary across time as well, occurring at irregular intervals of about 5 to 10 years (Bradley and Smith 1986, Braatne et al. 1996). As a result, a shifting mosaic of cottonwood patches in the riparian landscape reflects the pattern of stream disturbance cycles.

In a study of vegetation dynamics of woody plants (including cottonwood) on an island in Wisconsin, the height of woody species seemed to be correlated with island elevation (Barnes 1985). Height seemed to be a result of time elapsed since the last disturbance rather than of the growth rate. Height generally indicated the average length of time since the last resprouting from a damaged clone. Island elevation was related to the frequency of disturbance, at least by flooding, and plants that were at higher elevation were less likely to sustain damage.

Riparian cottonwoods often have a ragged shape because of the death of branches during dry periods. This may be an adaptation to deal with occasional droughts. The plant apparently drops branches during periods of limited water supply to reduce the shoot mass and leaf area supported by the root system (Rood and Mahoney 1990).

Longevity of mature cottonwoods is influenced by environmental factors, especially drought stress. During the drought of the 1930s, many older cottonwoods died across the western prairies (Albertson and Weaver 1945). The largest and oldest trees generally were found on the most favorable sites, where drought stress was avoided.

Summary of life history traits

- Black cottonwood can reproduce either by seed or vegetative means.
- Reproduction by seed is the primary means of initial establishment. Trees produce millions of seeds, which are very light and can be carried long distances by wind or water. Seed viability is high for 1 to 2 weeks, then drops off rapidly if seeds are not kept moist. Once a seed becomes wet, viability is lost in 2 or 3 days if a favorable microsite is not

encountered. Reproduction as seedlings tends to occur on moist sand, gravel bars, or scoured streambanks.

- Vegetative regeneration typically is associated with disturbance stress caused by fire, beaver, ice scouring, animal browsing, or burial or toppling of saplings during floods. It also can be a means of colonizing bare surfaces when conditions do not permit establishment by seed. As distance from the stream increases, shoot suckers tend to be more prevalent than seedlings, probably due to the increased presence of established trees farther from the water's edge.
- Black cottonwood is a drought- and shade-intolerant pioneer species.
- Long-term survival generally is associated with high flows during the period of establishment. These discharges tend to recur on a 5- to 10-year (or longer) return interval. As these flows recede, the large amounts of freshly deposited mineral substrate (fine sand or a fine sand/gravel mix) on active point bars provide moist conditions ideal for seed germination. The environment must be free of competition, consist of a mineral soil in which roots can maintain contact with moist substrate as waters slowly recede, and be free of additional erosion, deposition, or prolonged flooding during the first growing season.
- Cottonwood seedlings remain vulnerable to drought in the year following establishment because of their small size and small root systems. Growth during the second year is more rapid than during the initial year. After the first 2 years, cottonwood saplings become increasingly tolerant of flooding and drought stress as they develop larger root systems.
- Cottonwoods can tolerate substantial flooding, but not as well as many herbaceous riparian species. Cottonwood trees survive flooded environments through anaerobic respiration, the production of shallow adventitious roots, and the presence of lenticels along the stem and root crown. Cottonwood often is associated with soils that contain a layer of coarse substrate, which drains more quickly than fine-textured soils, providing a quick return to aerobic conditions.
- Cottonwood stands tend to form as separate, arc-shaped bands of even-aged trees on point bars. The age of each band increases with distance from the channel because of channel migration. Older, larger trees tend to be farther from the water's edge than younger, smaller trees and seedlings.
- Cottonwood establishment is determined largely by reach type and stream flow. Differences in geology, elevation, climate, and tributary influence can exist between two reaches of the same stream. Thus, cottonwood distribution also varies among different reaches of the same stream.

Concluding remarks

A riparian corridor is a complex mosaic of moisture and disturbance patterns. Plants that form communities within these corridors survive on sites where their basic requirements for establishment, growth, and reproduction are satisfied. Restoration efforts in riparian areas require an understanding of both the environmental mosaic and the life history/adaptations of riparian species.

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