

The Ecology Of Northern White-Cedar

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Northern white-cedar (*Thuja occidentalis* Linnaeus) is a small to medium sized tree typical of northern conifer-hardwood swamps. Individual trees rarely exceed 25 m in height and 80 cm in diameter. Heights of 10 to 15 m and diameters of 30 to 60cm are more typical of mature second-growth forests. Northern white-cedar (cedar) is considered shade-tolerant and individuals have the potential to live more than 500 years. Cedar often dominates the lower portion of the canopy of a swamp forest with other hardwood and conifer species dominating the upper canopy. Trunks are highly tapered and sometimes divided into two or more secondary stems. Because of the poor aeration of swamp soil, root systems are shallow and spreading, and large structural roots protrude above the ground. Windthrow is common in cedar swamps. Windthrow in combination with the ability to reproduce vegetatively results in trees of unusual form; highly curved and peculiar trunk shapes are common.

The cedar swamp association has been considered to be the final stage of plant succession on alkaline organic soil (Gates 1942). But cedar swamps are not regenerating naturally like late-successional upland forests. Why are these supposedly tolerant trees not reproducing? The objective of this paper is to review the ecological and life-history attributes of northern white-cedar. In doing so, I hope that others will be able to tackle the practical question of cedar regeneration with a better appreciation of the ecology of this important and interesting species.

LANDFORM, SOIL AND STAND COMPOSITION

Lowlands

Cedar dominated lowland swamps are critical winter habitat for the white-tailed deer (*Odocoileus virginianus borealis* Miller) in northern Michigan (Nelson 1951). They are important in terms of both thermal cover and forage. The composition of lowland cedar swamps is highly variable and cedar rarely occurs in extensive pure stands.

Depressions in glacial terrain where ground water is at or near the surface are characteristically dominated by cedar and other lowland species. These lowland habitats can occur in a variety of landscape positions: in former glacial drainways, on outwash plains, in a band around the perimeter of a kettle hole, between glacial drumlins, or along the margin of contemporary lakes and streams.

Since the close of the Pleistocene, these poorly-drained topographic depressions have filled with organic matter commonly known as peat. The ground surface is hummocky due to continual windthrow with poorly drained pits and organic mounds. Such microrelief results in substantial variability in pH and substrate composition. The result is

tremendous micro-diversity in both habitat and species composition; cedar swamps can be some of the most diverse plant communities in the Lake States.

Poorly-drained organic soils vary widely in terms of pH, dissolved oxygen, nutrient content, and degree of organic matter decomposition. The literature clearly indicates that cedar prefers organic matter where the pH is neutral to basic (pH 6.0 - 8.0) and where rates of organic matter decomposition are relatively rapid (Curtis 1946, Nelson 1951, Habeck 1958, Heinselman 1970, Schwintzer 1981). Schwintzer (1981) suggests that conifer swamps are related developmentally to water flow and chemistry. His data agree with my own personal observations. Cedar dominated forests develop where the ground water contains relatively high concentrations of oxygen and essential nutrients and where it moves laterally through the soil. These conditions result in finely decomposed organic matter and a high pH, characteristics of a good cedar soil easily identified in the field. Lateral movement of oxygen and nutrient laden water through the soil may be why cedar swamps typically occur as bands in wetlands and along lakes and streams. As soon as the hydraulic gradient lowers and water stagnates, soils become highly acidic. Acidic organic deposits are often dominated by bog vegetation, e.g. black spruce (*Picea mariana* (Miller) BSP).

The composition of cedar swamps is highly variable and these forests are some of the most diverse in Michigan. Cedar rarely forms pure stands over extensive lowland areas. Typically, cedar is found growing in association with other lowland hardwood and conifer tree species. Tamarack (*Larix laricina* (Du Roi) K. Koch), balsam fir (*Abies balsamea* (Linnaeus) Miller), white spruce (*Picea glauca* (Moench) A. Voss), black spruce, and hemlock (*Tsuga canadensis* (Linnaeus) Carriere) are common evergreen associates. Several lowland hardwoods are commonly found in cedar swamps: black ash (*Fraxinus nigra* Marshall), red maple (*Acer rubrum* Linnaeus), yellow birch (*Betula alleghaniensis* Britton), balsam poplar (*Populus balsamifera* Linnaeus) and speckled alder (*Alnus rugosa* (Du Roi) Sprengel). In addition, many upland hardwoods and conifers can be found growing well in cedar swamps; basswood (*Tilia americana* Linnaeus), sugar maple (*Acer saccharum* Marshall), trembling aspen (*Populus tremuloides* Michaux), paper birch (*Betula papyrifera* Marshall) and white pine (*Pinus strobus* Linnaeus) are good examples.

Cedar, because it grows slowly and rarely reaches 20 m in height, often is found in a subordinate canopy position. Although cedar may dominate in terms of basal area, tamarack, balsam poplar, trembling aspen and paper birch often tower 5 to 10 meters above the slow growing cedar. Thus, the cedar swamp commonly exhibits a two-storied stand structure. Black ash, red maple, yellow birch and sugar maple are usually found in the lower third of the stand diameter distribution, although large-diameter individuals do occur. White spruce, balsam fir and hardwoods occur on low ridges or elevated microsites. Alder is confined to flooded areas.

The mosaic of dominant vegetation in the cedar swamp is quite interesting. Cedar itself is typically found in small, relatively pure patches. These seem to occur in areas where the water table is at or very near the surface and is moving, such as the edge of a low ridge or along a small stream. The pure patches of cedar will give way over short horizontal distances to tamarack, spruce, and fir or patches of lowland hardwoods such as black ash, balsam poplar, and trembling aspen. This vegetation mosaic is continually changing in

both time and space --the result of microrelief, a constantly changing water regime and windthrow. Low sandy ridges dominated by upland vegetation are very typical linear features in a cedar swamp. A + change in elevation of just a meter or two can result in a completely different forest community.

The lowland cedar swamp is highly variable and discrete patches of vegetation dominated by one or more species are the exception rather than the rule. Nonetheless, large areas of wetland in Michigan are dominated by what might be best termed a “conifer-hardwood swamp on neutral to basic peat.” Cedar is often a dominant or co-dominant member of this common lowland forest.

Uplands

Upland or “old-field” stands of cedar have been reported for many years (Potzger 1941, Curtis 1946, Nelson 1951, Habeck 1958, and Musselman et al. 1975). Upland cedar forests are found growing on the following substrates: sand dunes, limestone bedrock and shallow soil overlying limestone, and rich, basic mineral soil (pH 7.0). The common denominator in all of these upland habitats is soil with a high pH. Cedar forests are more or less confined in the uplands to soils with free calcium carbonate close to the surface.

Another common observation is that upland cedar forests invade open areas: old fields, clear-cuts, sand dunes, and limestone bluffs. These situations are, in fact, the only ones where seedling establishment and recruitment are clearly the mechanism of stand regeneration. Second-growth upland cedar forests can range from relatively pure stands of cedar, to cedar mixed with virtually the entire complement of upland tree species.

Potzger (1941) suggested that cedar in northern Michigan possessed ecotypes because of its presence in upland and lowland habitats on Mackinac Island. Both Habeck (1958) and Musselman et al. (1975) further investigated the concept of localized ecotypes of cedar. Each concluded that there was evidence of genetic differentiation between upland and lowland populations. In programs of artificial regeneration, consideration should be given to the fact that local ecotypes could exist. Lowland vs. upland seed should be used to reforest the appropriate habitat.

NATURAL REPRODUCTION

Northern white-cedar is a dependable seed producer. It bears good seed crops every 3 to 5 years, with light to medium crops in the intervening years (Johnson 1977). Seed production *per se* does not appear to limit natural regeneration. Although seed viability is low, production is abundant and, compared with other tree species, relatively consistent year to year. Seed dispersal by wind starts in September with the majority of seed falling during autumn. Some seed is dispersed during winter. Most seed is dispersed within 50 meters of the mother tree. Many experts have recommended small block or strip clearcuts for this reason (Verme 1965).

Abundant seedling establishment occurs naturally on a variety of substrates (Nelson 1951, Scott 1984). Seedlings can establish on bare organic and mineral substrates, moss

mats, and down logs in various stages of decay (Nelson 1951, Curtis 1956, Scott 1984, Verme and Johnson 1986). Both Nelson (1951) and Scott (1984) report that seedling establishment is numerically greatest on logs, but Scott (1984) correctly points out that numbers of seedlings are not necessarily related to recruitment success. It is unclear if seedling establishment on logs was common in old-growth cedar forests before European settlement. It seems doubtful because “stilt rooted” individuals are uncommon and because down logs are still frequent due to blowdown (although today’s seedlings may not recruit because of browsing).

In the field, light in the forest understory is not a factor regulating seedling establishment (Nelson 1951). Seedling establishment is positively related to soil pH (Nelson 1951, Scott 1984). Verme and Johnson (1986) report the highest level of seedling establishment on sites that were burned. It is important to understand that seedling establishment is abundant under a wide variety of ecological conditions. Seedling establishment is not limiting cedar reproduction.

Recruitment of seedlings into the sapling, pole and mature tree size classes appears to be the primary factor limiting natural cedar reproduction. Scott (1984) estimated that 99% of the initial seedling cohort had died by year 13. As I examined the literature I could find no clearly documented cases where lowland cedar had been successfully regenerated through seedling establishment and recruitment. In fact, except for small seedlings that are covered by the annual snowpack, there are very few reports of any large, advanced cedar reproduction. The virtual lack of larger seedlings and saplings in lowlands is probably due to browsing by the white-tailed deer. Small cedar die when more than 15 to 20% of the foliage is removed annually (Aldous 1952). Seedlings often grow very slowly; it can take 20 years for a seedling to reach 1 meter in height (Nelson 1951). Because cedar grows slowly, seedlings are exposed to browsing pressure for a relatively long time. The only successful reports of sexual reproduction come from the uplands, exclosures, and lowlands that are not utilized by the deer for thermal reasons (Verme 1965). Interestingly, there were many references to advance cedar reproduction in the original land surveyor notes (see below).

Cedar can and often does reproduce by layering or tree tipping. Nelson (1951) reports that branch layering (where a branch of the parent stem transforms into a stem) is the predominant type of vegetative reproduction. The presence of a thick sphagnum moss mat facilitates the formation of adventitious roots and branch layering (Nelson 1951). Trees also can be blown over and the lateral branches then become main stems. When several small stems are found in a perfect row this is undoubtedly the mode of vegetative reproduction.

Vegetative reproduction via layering and blowdown appears to be a major pathway for successful regeneration in the lowlands. Reports of vegetative reproduction are abundant in the literature. Old photographs depicting advanced regeneration (e.g. Nelson, 1951) and personal observations lead me to believe that many of today’s “seedlings” and saplings are the result of vegetative reproduction, not seedling establishment and recruitment. It might well be that cedar, once established, is able to perpetuate itself on a site by vegetative reproduction. Perhaps seedling reproduction followed large-scale blowdown or fire in the primeval forest and persistence occurred through layering and

tree tipping.

The notion that “cedar typically occurs in the understory and eventually replaces the overtopping associated species” is a myth that should be eliminated. Cedar almost never “overtops” any other tree simply because it grows so slowly and rarely reaches even 20 meters in height. Cedar is long-lived and very capable of persisting in a stand. It may simply outlive most associated species. It’s occurrence in the lower portion of the canopy and ability to persist have led to the idea that cedar is very tolerant and a late successional species. In 1946 Curtis (1946) wrote:

“Evidence supports the belief that cedar is not so tolerant as formerly believed. This fact is emphasized by the scarcity of advance reproduction, especially seedlings, over one foot in height in all stands containing cedar.”

In fact, the only places seedling recruitment occurs are sand dunes, old-fields, clearcuts and burns. Perhaps cedar is a slow growing, shade tolerant, long-lived pioneer species capable of persisting by means of vegetative reproduction. Demographic studies of existing stand structure might help us understand how and when cedar established relative to its associates. Are many second-growth stands even aged? Did they establish following major disturbance at the turn of the century?

SUCCESSION

Presettlement Vegetation

Due to deforestation at the turn of the century, continued forest management and artificially high white-tailed deer populations, it is conceivable that the composition of cedar swamps today is different than those of presettlement time. To examine this possibility, I reviewed some of the original land survey records from the Upper Peninsula of Michigan. Maps published in 1977 by the Michigan Department of Natural Resources identify “core deer yards”. The original surveyor records from three of these core deer yards were examined (Table 1).

Although no quantitative study was made of the presettlement vegetation compared to the composition of present cedar swamps, it is clear that the general composition of today’s forest is very similar to the cedar swamps of presettlement time. All of the three areas examined (Arnold, Danforth, and Whitefish River) were dominated by cedar, tamarack, fir, and spruce over 150 years ago before any timber harvesting. In fact, the surveyor notes convey a picture of forest composition that is remarkably similar to contemporary cedar swamps. The original forest was a mosaic of conifer swamp and upland hardwood-conifer ridges. Cedar was a commonly recorded line tree as the surveyors established section boundaries in the lowlands (Table 1). Spruce, fir, tamarack, balsam poplar, alder, and aspen were all mentioned along with cedar as the surveyors traversed the swamps. Occasionally, cedar was recorded in the uplands. One notable difference occurs between present and presettlement forests: cedar and ground hemlock (*Taxus canadensis* Marshall) “undergrowth” were frequently mentioned in the original land surveyor notes. Such “undergrowth” is notably absent from today’s forest, almost surely due to over browsing by the white-tailed deer.

Algernon Merryweather, a Deputy Land Surveyor, recorded the following general comments as he finished surveying the boundaries of Township 42 North, Range 21 West (Whitefish River deer yard north of Rapid River, Michigan) on the 9th day of September 1842:

“The greater part of this township lies in the valley of White Fish and Rapid Rivers, which valley is enclosed by a bluff in the East from 70 to 100 feet high and on the west side from 40 to 50 feet. The first of these bluffs is very springy and generally runs into cedar swamp extending to the river. The land rises higher in the middle of the Valley where are some fine ridges of sugar, elm and basswood, but the larger portion of the valley is hemlock, cedar, tamarack, spruce, birch and poplar...”

Both the detailed line transects and general comments suggest that today's cedar swamp is very similar to those that existed in the same locations more than 150 years ago, except for today's lack of cedar and ground hemlock understory.

Windthrow

Blowdown is extremely common in cedar swamps and is a major form of natural disturbance. Completely and partially uprooted trees abound. When trees tip only partially, lateral branches assume dominance and the resulting trees are unusually shaped. Gaps range in size from an individual tree to relatively large areas. It is possible for very large areas to blow down during severe thunderstorms and as the result of occasional tornadoes.

Gap formation in the presettlement cedar swamp probably encouraged the release of vegetative reproduction (individuals that established by layering) and perhaps, when gaps were large enough, even resulted in seedling establishment and recruitment. Today, most blow-downs simply release advance spruce, fir, and hardwood regeneration, or the gaps are colonized by intolerant hardwoods and conifers like trembling aspen, paper birch, balsam poplar and tamarack. Some cedar reproduction still occurs in gaps, especially when trees are only partially uprooted and lateral branches remain beyond the reach of deer. But because there is little chance for natural reproduction to grow above the browse line, cedar does not generally regenerate in areas that are disturbed by wind. Thus, one of the primary modes of natural regeneration has been eliminated by the white-tailed deer.

Fire

The role of wildfire in cedar swamps is not well understood. Where individual investigators have attempted to burn swamps, seedling establishment has been promoted (Verme and Johnson 1986). There seems to be little doubt that cedar swamps burned naturally during exceptionally dry years. I have often noticed evidence of wildfire in the swamp; charred stumps are not unusual, especially along the edges of the low ridges that typically occur in the swamp mosaic. However, historical studies documenting the frequency of fire in cedar swamps have, to my knowledge, not been attempted.

Assuming that swamp forests did burn during exceptional years, it is likely that such fire promoted cedar establishment. We know that successful seedling regeneration today only occurs in open areas, and wildfire would have reduced competition and created an open

environment. It is my suspicion that many of today's second growth cedar forests established following logging and wildfire. The second growth forests of today established before the first explosion of the white-tailed deer population and, therefore, were not subject to such intense browsing pressure.

Detailed studies of the age of individual tree populations and the structure of today's second growth forest might help us understand how cedar regenerates naturally following logging and in the absence of intense browsing pressure. Prescribed fire is a management tool that deserves additional investigation in the cedar swamp. But any practical attempt to study silvicultural systems in cedar forests is bound to be totally confounded unless the influence of deer is factored out. It is my belief that deer are the primary force inhibiting natural cedar regeneration and their influence is so pervasive as to render most field experiments totally useless unless deer are excluded from the experimental or trial area. The effect of white-tailed deer on cedar regeneration should be our number-one silvicultural priority.

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