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A Literature Review

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ACKNOWLEDGEMENT

Research supported by the College of Natural Resources, the Minnesota Extension Service, the Minnesota Agricultural Experiment Station under Projects MN-42-40 and MN-42-18, and the Telecommunications Development Center, all of the University of Minnesota, St. Paul, MN 55108. Published as Station Bulletin 587-1988, by the Minnesota Agricultural Experiment Station.

FACTORS AFFECTING THE REGENERATION OF QUAKING ASPEN: A LITERATURE REVIEW

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ABSTRACT

Quaking aspen is the most widely distributed and one of the most studied tree species in North America. It is a fast-growing, very intolerant species that is valuable for commercial forestry, wildlife management, soil and water conservation, and aesthetics.

Although aspen does reproduce from seed, suckering is the most common mechanism of regeneration following harvest. A number of studies have shown that harvesting activities can affect the physiological and environmental factors which control suckering. This paper summarizes literature on the mechanisms of aspen suckering, and how the number and vigor of suckers may be influenced by activities associated with timber harvesting operations.

INTRODUCTION

Quaking aspen (*Populus tremuloides* Michx.) is the most widely distributed forest tree species in North America. It's a fast-growing, very intolerant species that grows on a wide variety of soil types, although it grows best on deep, well-drained soils (Jones and DeByle 1985, Perala 1977, Wenger 1984). While aspen can produce high quality sawlogs on better sites, it generally reaches physiological maturity before reaching sawlog size and thus is most often used for pulp and chipboard (Brinkman and Roe 1975).

Aspen can reproduce both from seed and by suckering. Suckers have a competitive

advantage over seedlings as they can draw on the parent root system for moisture and nutrients (Day 1944). Consequently, the recommended management system is complete clearcutting with the intention of allowing suckers to regenerate the stand (Brinkman and Roe 1975, Perala 1977, Shepperd and Engelby 1983). The potential success of this management system has been demonstrated many times. For example, Bella (1986) reported regeneration densities of over 80,000 suckers per acre two years after clearcutting in east-central Saskatchewan.

Commercial demand for aspen is increasing in many parts of North America, sparking renewed interest in the study of aspen management. The physiological and environmental factors that affect suckering have attracted considerable research. This paper summarizes some of these studies, particularly those that deal with the effects of timber harvesting on aspen suckering.

THE ASPEN ROOT SYSTEM AND SUCKERING

The aspen root system has several shallow, lateral roots that have very little branching and taper once they are more than several feet away from the trunk of the tree. Sandberg (1951) estimated that there were over 13.5 miles of roots larger than 0.3 inches in diameter per acre for an aspen stand in northern Minnesota. In the same stand, he estimated that 63 percent of the length of the main lateral roots were within 4.5

inches of the soil surface, and only 4 percent were deeper than 1 foot.

After harvest, aspen suckers emerge primarily from newly initiated meristems or preexisting primordia, although a few less vigorous suckers also originate from suppressed buds (Farmer 1962; Sandberg 1951; Schier 1973b, 1981; Schier *et al.* 1985a). Schier (1973a) reported that the physiological requirements for meristem development prior to the primordial stage are separate from those for shoot growth and extension, and that growth is often arrested at the primordial stage until shoot extension is stimulated.

There may be thousands of suppressed shoot primordia found on aspen roots since primordia develop almost continuously during periods of active root growth. It is unknown how long an adventitious meristem can remain in the primordial stage (Schier 1981, Schier *et al.* 1985a). There is a positive correlation between individual root suckering capacity and number of shoot primordia on the roots (Schier 1978).

Suckers often arise in clumps from points on the root that are closest to the soil surface (Farmer 1962, Sandberg 1951, Schier and Campbell 1978, Schier *et al.* 1985a). Suckers originate from roots that are on the average 20 feet away from the base of the parent tree (Perala 1981), but they may originate up to 80 feet away (Graham *et al.* 1963). A majority of suckers originate from aspen roots that are from 0.5 to 2.0 inches in diameter and located in the soil humus or in the extreme upper part of the mineral soil (Farmer 1962, Kemperman 1978, Maini 1972, Sandberg 1951). Parent roots of aspen suckers in the Rocky Mountains may be deeper than those in the Lake States and Ontario; however, the mean depth of parent roots in western clones was still about 3 inches (Schier and Campbell 1978).

Investigators have not found any significant correlation between parent root diameter and soil depth (Kemperman 1978, Schier and Campbell 1978), sucker height and parent root depth, and sucker height and parent root diameter (Kemperman 1978).

PHYSIOLOGICAL FACTORS THAT AFFECT SUCKERING

Growth Regulators

There is a clear relationship between aspen

suckering and apical dominance. Auxin transported to the roots from aerial portions of the plant effectively suppresses suckering (Eliason 1971a, 1971b; Farmer 1962; Schier 1973c; Steneker 1974).

While it is clear that auxin can act to inhibit suckering, the fact that aspen suckers are often found in the understory of undisturbed aspen clones demonstrates that apical dominance does not have complete control over suckering (Barnes 1969, Schier 1982, Schier and Campbell 1980). Auxin is an unstable compound that does not persist for long periods of time in aspen roots and must be transported to the roots continuously if inhibitory levels are to be maintained (Eliason 1971a, Schier 1981).

There may be periods when suckering can occur in undisturbed clones, particularly in early spring before bud burst, when root auxin levels are not inhibitory and moisture and temperature conditions are favorable for sucker growth and survival (Schier 1973c, 1981).

Other growth compounds affect the stimulation and suppression of suckers in addition to auxin. Wolter (1968) found that cytokinins synthesized in root tissue can stimulate suckering. High root cytokinin to auxin ratios are associated with increased shoot initiation (Winton 1968, Wolter 1968, Schier 1981). Gibberellin-like compounds have differing effects on sucker initiation depending on the stage of development. Gibberellic acid can inhibit the continued development of newly initiated meristems, yet it stimulates shoot elongation from established primordia (Schier 1973a).

Carbohydrate Reserves

Root carbohydrates are largely responsible for sustaining emerging shoots until the sucker produces leaves and photosynthesis begins (Schier 1981, Schier *et al.* 1985a). In greenhouse studies, there was no significant correlation between root carbohydrate reserves and the number of suckers produced from aspen root cuttings (Schier and Zasada 1973, Tew 1970). These studies demonstrated there was a positive correlation between: 1) root carbohydrate reserves and sucker dry weight (Schier and Zasada 1973), and 2) time required for root cuttings to deplete carbohydrate reserves (Tew 1970). However, repeated destruction of new suckers can exhaust carbohydrate reserves and reduce production of additional suckers (Buckman and Blankenship 1965, Perala 1974b, Schier *et al.* 1985a).

ENVIRONMENTAL FACTORS THAT AFFECT SUCKERING

Soil Temperature

Soil temperature plays an important role in aspen suckering. Steneker (1974) found that while changes in soil temperature alone had a negligible affect on suckering in undisturbed clones, soil temperature significantly affected the number of suckers produced once apical dominance was removed. Maini and Horton (1966) concluded that insolation-induced increases in soil temperature following the removal of apical dominance was the primary factor influencing sucker initiation.

Controlled environment studies indicate that there appear to be minimum, optimum, and maximum soil temperatures for sucker formation. However, these values are not constant for all aspen clones within an area or between geographic regions. Maini (1967) found significant interclonal differences in the suckering responses of four clones maintained at 60°F, 75°F, 85°F, and 95°F. A study of root cuttings from four Ontario clones where treatment temperatures were 58°F, 64°F, 74°F, 87°F, and 95°F found that sucker production increased with increasing temperature up to 87°F (Maini and Horton 1964, 1966). In this study, sucker initiation occurred first in the cuttings maintained at 87°F and was progressively delayed at warmer and colder temperatures. Constant soil temperatures above 73°F appeared to be inhibitory to sucker formation on root cuttings from Alaskan aspen clones (Zasada and Schier 1973).

It is not clear whether sucker response is controlled by average temperatures, maximum temperatures, minimum temperatures, diurnal temperature change, or accumulated heat units (Hungerford 1988). It appears that suckering is inhibited by soil temperatures greater than 95°F or less than 60°F (Maini and Horton 1966, Maini 1967). While the optimum soil temperature for suckering may vary, it appears that temperatures above and below the optimum will act to delay sucker initiation, with the effect becoming more pronounced as you move further away from the optimum (Maini and Horton 1966, Zasada and Schier 1973).

Soil Moisture and Aeration

Aspen roots require a proper balance between soil moisture and aeration to survive and be productive. Only well aerated root cuttings are

capable of producing suckers (Maini and Cayford 1968, Schier 1976).

A study of root cuttings incubated for 34 days at 75°F, with 7, 10, 15, 20, 25, and 27 percent moisture, found that the maximum number of suckers developed at the 7 percent moisture content (Maini and Horton 1964). No suckers were produced at the 25 and 27 percent moisture conditions which represented saturated and flooded conditions, respectively. In fact, these cuttings started to rot after less than two weeks. Suckers emerged after 8, 6, 10, and 10 days for the 7, 10, 15, and 20 percent moisture treatments, respectively. Although the earliest suckering occurred at 10 percent moisture, the maximum number of suckers at the end of the experiment was at 7 percent moisture (Maini and Horton 1964).

Parent Stand Condition

Suckering is generally more prolific from denser parent stands (Sandberg 1951) which may be attributed to higher root densities (Schier *et al.* 1985a). Graham *et al.* (1963) found the following relationship between basal area of aspen in the parent stand and sucker density one year after logging:

Parent Stand Basal Area (ft ² /acre)	Suckers/acre
< 50	5,200
51 to 100	7,000
> 101	9,900

Ek and Brodie (1975) conducted an extensive review and modelling synthesis of the literature that was combined with additional data they collected and found maximum sucker reproduction at approximately 50 ft²/acre of parent stand basal area. They found that sucker production was not asymptotic with respect to increasing parent stand basal area which might be explained by diminished individual tree suckering in older stands; however, the relationship between parent stand basal area and sucker production was relatively flat (Ek and Brodie 1975).

It is important to note that while there may be a direct relationship between suckering and parent stand density, excessive stocking levels are not required for adequate regeneration. In Wisconsin, shearing aspen stands that had as

little as 18 ft² of basal area per acre resulted in sucker stands that were 100 percent stocked after one growing season (Perala 1983).

There is no clear relationship between suckering capacity and parent stand age. Parent stands representing a wide range of ages are capable of producing an adequate number of suckers to regenerate most stands. Clearcutting 2-, 4-, and 8-year-old Minnesota stands resulted in 30,000, 35,000, and 41,000 suckers per acre, one year after harvest (Perala 1972). Suckering increased in Minnesota and Wisconsin as parent stand age increased from 30 to 70 years (Kittredge and Gevorkiantz 1929). Adequate suckering in northern Wisconsin clearcuts was reported in all cases where the parent stand age was between 26 and 55 years (Stoekeler and Macon 1956). Graham *et al.* (1963) reported that maximum suckering capacity in Michigan was at age 35. However, individual trees more than 100 years old produced abundant suckers after harvest. A study in Minnesota found no relationship between sucker abundance two years after logging and parent stand age when comparing stands that were less than 50 years old with stands that were greater than 50 years old (Sandberg 1951).

Clone condition or vigor may also influence suckering. A greenhouse study comparing the suckering capacity of root cuttings from deteriorating clones with cuttings from adjacent, healthy clones reported no clear relationship between deterioration and the ability to sucker (Schier 1975). Deteriorating clones were characterized by having few living ramets, many dead stems, no associated conifers, and little sucker injury caused by wildlife or livestock. Two of the deteriorating clones produced significantly fewer suckers than their healthy counterparts, two produced about the same number, and one produced significantly more. Schier (1975) hypothesized that poor sucker reproduction in deteriorating clones is a function of root die-back caused by less photosynthate being channeled to the roots as more stems weaken and die, and invasion of the clone by insects and disease which may eventually lower suckering capacity. *Armillaria mellea* is a common fungus known to cause root disease in aspen and decrease the ability of the root to sucker (Hinds 1985).

CLONAL VARIATION IN SUCKERING

Investigators have found large differences in the suckering capacity of different clones. This has been true in comparisons between undisturbed

clones (Barnes 1969, Schier 1982, Schier and Campbell 1980), between clones that had been harvested or burned (Farmer 1962, Schier and Campbell 1978), and in greenhouse studies of incubated root cuttings from several different clones (Farmer 1962, Maini 1967, Schier 1974, Tew 1970, Zufa 1971).

The relative suckering capacity of different clones is not solely an inherent trait. It is also affected by non-genetic factors such as the age and condition of the trees and the environmental conditions present at the time of a disturbance (Schier 1981). Clones that are dominated by old and diseased trees may not be able to produce viable suckers (Schier 1975, Schier and Campbell 1980).

For healthy clones, the number of suckers produced following a disturbance is determined by the balance between growth regulating hormones and root carbohydrate reserves (Schier 1981). While seasonal fluctuations in the concentrations of carbohydrate reserves, auxin, and other growth regulating compounds tend to follow a general pattern, at any one time there can be distinct differences in root hormone levels (Elason 1971a, Schier 1973c) and root carbohydrate levels (Schier and Zasada 1973) between adjacent clones. Thus, the timing of a disturbance in relation to the physiological condition of the clone and the environmental conditions that are present will affect the number of suckers that may be produced (Schier 1981).

MANAGEMENT IMPACTS ON INITIAL SUCKER DENSITIES

Residual overstory

Complete clearcutting maximizes the removal of apical dominance, stimulates suckering on the greatest number of roots, and leads to the best sucker development both in terms of sucker density and growth (Brinkman and Roe 1975, Graham *et al.* 1963, Jones 1976, Perala 1972, Sandberg 1951, Schier *et al.* 1985b, Zehngraff 1949). An important effect of clearcutting is the total removal of shade which accelerates soil warm-up, sucker initiation, and sucker growth rates after emergence (Maini and Horton 1966, Sandberg and Schneider 1953, Schier and Smith 1979, Stoekeler and Macon 1956, Zehngraff 1949). Aspen management guides for both the Lake States and Rocky Mountain Regions recommend a maximum residual overstory of 10 ft² per acre following harvest (DeByle and Winokur 1985, Jones 1976, Perala 1977).

On cutover areas in northern Wisconsin, sucker density five to nine years after harvest was 2,720 stems per acre in complete clearcuts and 140 stems per acre where 100 ft² per acre of the overstory remained following harvest (Stoekeler and Macon 1956). In the same survey, height growth in open areas averaged 3.4 times that of heavily shaded areas. Similar results were found in Utah where, 12 years after harvest, stands that had only 67 percent of the overstory removed had 61 percent fewer suckers than clearcut stands (Schier and Smith 1979). Growth was 13 percent less in these partially cut stands than in clearcut areas.

Harvesting Related Disturbances

Root destruction, soil compaction and scarification, forest floor displacement, and destruction of understory vegetation are harvesting related factors that can influence suckering. Harvesting equipment can either promote or inhibit suckering depending on the type and severity of the disturbance (Graham *et al.* 1963, Jones and Shepperd 1985, Schier *et al.* 1985b). Mechanized harvesting operations can create optimum site conditions for suckering by setting back competing vegetation and by increasing soil temperature through the exposure of dark colored humus and mineral soil and the removal of insulating duff (Bella 1986, Bella and DeFranceschi 1972, Maini and Cayford 1980, Maini and Horton 1986, Perala 1972, Schier and Smith 1979, Stonaker 1974, Stoekeler and Macon 1956, Zasada and Tappeiner 1969b).

Ek and Brodie (1975) developed the following model for aspen suckering in the Lake States which suggests that sucker density is directly related to level of disturbance (site treatment).

equation 1

$$N = 5.9638 \times S \times BA \times \exp(-0.0197 \times BA) \times \{1.0 - \exp[-41.4665/(R + 1.0)]\} \times D \times T$$

N = suckers per acre at age 2 (≥ 1 ft. tall)

S = site index

BA = parent stand basal area (ft²/acre)

R = residual basal area (ft²/acre)

D = date of treatment effect ($D = 1.00$ for June, July, or August. $D = 1.17$ for all other months.)

T = site treatment effect

Killing the parent stand (hypohatchet) without removing any timber had a treatment effect (value for T in Equation 1) of 1.00. Performing a

harvest cut with no site treatment had a treatment effect of 1.32. Performing a harvest cut and knocking the residual down with heavy equipment had a treatment effect of 1.62. Performing a harvest cut, felling the residual, and burning had a treatment effect of 3.05. And, performing a harvest cut and then disking had a treatment effect of 3.46.

Most negative harvesting impacts are attributed to soil compaction and the physical destruction of roots in areas of repeated trafficking by heavy equipment (Jones 1975, 1976; Schier *et al.* 1985b; Zasada and Tappeiner 1969b). In a study of site disturbance by rubber-tired skidders in four summer logged areas in northern Minnesota, Zasada and Tappeiner (1969b) found that only heavily trafficked skid trails had less than 100 percent stocking. These trails, which had an average stocking of 65 percent, were described as "... heavily rutted and roots severed to 4 inches or more ...". However, gaps in the regenerating stand which are caused by such disturbance are often shaped and spaced in such a manner that they may not adversely affect stocking at maturity (Jones 1975, Zasada and Tappeiner 1969b).

It's difficult to evaluate the effects of parent root disturbance on final yield if sucker density is the only factor considered. Disking operations in the Lake States significantly increased sucker numbers in some poorly regenerating sucker stands (Brinkman and Roe 1975, Ek and Brodie 1975, Zehngraff 1946, Zillgitt 1951). However, the increase in sucker numbers caused by disking may have been offset by reduced sucker growth and survival on the disturbed parent root systems (Brinkman and Roe 1975, Perala 1978a).

Slash

Several investigators have suggested that areas of high slash concentrations can prevent suckering (Jones 1975, Shepperd 1987, Zasada and Tappeiner 1969a). Slash can reduce suckering by shading the ground surface and minimizing soil warm-up (Maini and Horton 1966).

In some cases, the reduction in regeneration associated with high levels of slash may not significantly reduce the final stocking because: 1) the slash concentrations are small, and 2) these failed areas may at least partially regenerate over time as the slash decomposes (Jones 1975, Zasada and Tappeiner 1969a). In Saskatchewan, Bella (1986) found that initially

high variations in stand density caused by differences in slash conditions had virtually disappeared on winter-logged sites 17 years after harvest. However, slight stocking differences were still evident between slash and no-slash areas in summer-logged sites.

Fire

Burning aspen stands following harvest affects suckering. Light to moderate burns performed shortly after harvest can accelerate sucker emergence and can increase their numbers and vigor (Brown and DeByle 1987, Horton and Hopkins 1965; Maini and Horton 1966; Shirley 1931, 1932). These results are primarily attributed to 1) the increase in soil warm-up associated with the removal of insulating duff and the blackening of the ground surface, and 2) the more complete removal of slash and competing vegetation (Brown and DeByle 1987, Horton and Hopkins 1965).

High intensity burns can produce temperatures at the ground surface that are lethal to aspen root tissue. However, killing temperatures rarely penetrate deeper than 0.5 to 1.0 inch into the soil (Horton and Hopkins 1965). In Wyoming, the mean depth of sucker-producing roots under a high intensity burn (greater than 90 percent of the litter burned) was approximately 4 inches, compared to approximately 2.5 inches under a low intensity burn (0 to 10 percent of the litter burned) (Schier and Campbell 1978). The greater depth of parent roots under the high intensity burn may also reflect increased soil warm-up with depth, caused by the more complete removal of the insulating forest floor (Brown and DeByle 1987, Jones and DeByle 1985, Hungerford 1988).

Although fire rarely completely eliminates suckering, severe or repeated burns may reduce it. Severe burns may damage the parent root system, or they may reduce site quality through such mechanisms as the volatilization of nitrogen (Brown and DeByle 1987, Horton and Hopkins 1965, Kirby *et al.* 1957, Perala 1974a, Van Cleve 1973).

Repeated burns, at two to three year intervals, can reduce the abundance and vigor of suckers by forcing the stand to resucker before it can redevelop adequate root reserves (Buckman and Blankenship 1965, Perala 1974b). In some cases, a similar effect can be caused by a single burn if the burn is delayed until after a substantial number of suckers have already developed (Perala 1974a).

Season of harvest

Season of harvest is one of the most commonly cited reasons for variations in suckering response. It is widely reported that dormant-season harvests cause more numerous and vigorous suckers than summer harvests (Steneker 1972; Stoeckeler and Macon 1956; Zehngraff 1946, 1949). However, many of the reports of increased first-year suckering on winter-harvested sites reflect the shorter first growing season associated with summer harvests. Stands may continue to sucker into the second growing season allowing summer-cut stands to make up the deficit in sucker numbers (Graham *et al.* 1963). Ek and Brodie (1975) considered this ingrowth in their model of suckering in the Lake States and found that dormant season harvests resulted in 17 percent more suckers than summer harvests at age two (*see Equation 1*).

Root carbohydrate reserves and plant competition are two factors that fluctuate with season and the phenological stage of the stand, thereby potentially affecting suckering (Maini and Horton 1966, Zasada 1950, Zasada and Schier 1973). Root carbohydrate reserves sustain suckers from initiation to the point that they develop their own leaves and begin photosynthesis (Schier 1981).

Several investigators have quantified seasonal fluctuations in root carbohydrate concentrations. Concentrations of soluble sugar and starch in eight Utah clones were lowest during June immediately after leaf flush (Tew 1970). Clones in Utah and Alaska followed the same trend with low root carbohydrate reserves in the spring and early summer, increasing levels through the summer with a peak around September, then a drop off later in the fall (Schier and Zasada 1973). The drop off in the fall was attributed to the reduced amount of photosynthate produced as leaves senesced and thereby failed to satisfy the assimilate demand in continuing metabolic processes.

The timing of sucker initiation can also affect growth and survival. Summer harvesting may stimulate suckering to occur later in the summer when competing vegetation is fully leafed out. Since aspen is a very intolerant species, shade from any source can reduce sucker production and/or growth (Brinkman and Roe 1975). Also, suckers initiated in the summer may continue to grow too late into the fall, thereby suffering frost damage (Schier *et al.* 1985b).

In some situations, summer harvesting

stimulates greater suckering. In Saskatchewan, the initial sucker densities were nearly twice as high after summer clearcutting as compared to winter clearcutting (Bella 1986, Bella and DeFranceschi 1972). These results were attributed to higher soil temperatures caused by greater removal of a heavy shrub layer and increased exposure of dark-colored humus during the summer harvest.

STAND DEVELOPMENT AFTER HARVEST

The young sucker stand is characterized by rapid shoot and root growth and quick stratification into crown classes (Jones and Schier 1985, Perala 1984, Pollard 1971). Sucker density generally reaches its maximum level within two years after harvest (Brown and DeByle 1987, Crouch 1983, 1986; Ek and Brodie 1975; Jones 1975; Jones and Trujillo 1975; Zasada 1950). The stand may produce occasional suckers after this time, however, their growth and survival are greatly reduced by overtopping from older suckers and other vegetation (Jones 1975).

As suckers mature, competition develops between individual stems for moisture and nutrients. This results in natural thinning of the stand with most of the mortality occurring in the lower crown classes (Graham *et al.* 1963, Jones 1976, Jones and Schier 1985, Perala 1984, Pollard 1971). The degree of natural thinning is a function of the level of stocking, site quality, and stress caused by environmental factors such as drought, insects and disease (Jones and Schier 1985, Graham *et al.* 1963, Perala 1984, Pollard 1971).

Sucker mortality is directly related to initial sucker density (Bella and DeFranceschi 1972, Ek and Brodie 1975, Graham *et al.* 1963). Natural thinning on some sites may occur in surges or waves and may temporarily reduce dry weight increment (Graham *et al.* 1963, Jones and Schier 1985). However, this episodic type of mortality may be restricted to sites where there is a high level of stress caused by poor moisture and nutrient conditions (Graham *et al.* 1963) or a high incidence of insects or disease (Pollard 1971).

Many stands exhibit a more continuous pattern of thinning (Bella 1986, Bella and DeFranceschi 1972). That pattern is perhaps best modelled by an approximation of the exponential decay function (see for example Ek and Brodie 1975).

Several attempts have been made to evaluate the effects of initial sucker density on yield. Graham *et al.* (1963) suggested that an initial stocking of 35,000 to 40,000 suckers per acre may result in such intense competition between suckers that excessive mortality can occur leaving the stand too scattered for optimum development. However, there is little evidence to support such a claim. A study that monitored the growth of stands that had initial sucker densities ranging from about 22,000 to 58,000 stems per acre reported that the denser stands maintained an adequate level of stocking throughout the seventeen year study (Bella 1986, Bella and DeFranceschi 1972). In Minnesota, net biomass production increased with initial sucker density up to 80,000 stems per acre, despite a rapid reduction in the number of stems through natural mortality (Perala 1973).

Analysis based on growth and fiber yield data from numerous sources in the Lake States concluded that initial sucker densities ranging from 1,250 to 30,000 stems per acre have only a slight effect on rotation length, although higher initial densities might shorten rotation length by one or two years (Ek and Brodie 1975).

Precommercial thinning can accelerate the diameter growth of selected crop trees in stands as young as 5 or 10 years (Bella 1975, Perala 1978b, Perala 1988). However, there is not a clear benefit associated with the artificial thinning of younger stands (Jones and Shepperd 1985, Schlaegel 1972). This is probably due to the inability to determine the best potential crop trees in very young stands (Sorenson 1968, Perala 1984).

A study which created densities of 260, 500, 1,500 and 10,060 (unthinned control) stems per acre in one-year-old sucker stands reported that after 15 years, the control stand, despite losses from natural mortality, had roughly four times the volume of the heavily thinned stands and that the 200 largest trees in the control stand were as large as those in the thinned stands (Sorenson 1968). Studies have not shown a significant correlation between thinning and height growth (Bella 1975, Sorenson 1968, Strothmann and Heinzelman 1957).

It's difficult to precisely specify the minimum number of suckers that will produce full stocking at maturity. It has been suggested that initial stand densities ranging from a minimum of 1,000 suckers per acre (Sorenson 1968) to 6,000 suckers per acre (Graham *et al.* 1963) to 9,000 suckers per acre (Stoekeler and Macon 1956) will produce full stocking. If the desired stocking

at rotation age is known, it is possible to estimate the initial stocking requirement from values produced by the following equation (Ek and Brodie 1975):

equation 2

$$N_t = (N_{t-1}) \times \exp\{-0.39318 \times S \times (A_{t-1})^{0.930-0.02} \times (N_{t-1}/10^7)\}$$

N = trees per acre (≥ 1 ft. tall)
 t = variable at time t
 S = site index
 A = stand age

Table 1 lists solutions to equation 2 for a range of stocking levels and site indexes.

Spacing and clumping must be considered in addition to sucker densities when assessing initial stocking requirements. Maximum utilization of the site requires relatively even spacing between stems (Perala 1972, Sorenson 1968), and clumps of two or more stems arising from nearly the same point on the root will thin to one dominant stem within a few years (Jones 1976, Maini 1966, Polard 1971, Sandberg 1951).

SUMMARY

There has been a considerable amount of research aimed at defining the physiological mechanisms that control aspen suckering and how these mechanisms are influenced by environmental conditions. It appears that virtually any kind of disturbance which kills aspen stems, without killing the roots, will stimulate suckering. However, the number and vigor of suckers is affected by the physiological and

environmental conditions present at the time of the disturbance, and by the impact of the disturbance on root and site conditions.

With respect to timber harvesting, the number and growth rate of suckers appears to be positively correlated with the degree to which the aspen overstory and other competing vegetation are removed. These results are generally attributed to the more complete removal of apical dominance which maximizes sucker initiation, and the greater growth rate resulting from less competition.

It also appears that delaying or decreasing soil warm-up may have a negative effect on suckering. Shading or insulating the ground surface, whether it be from slash, standing vegetation, or accumulated litter, may reduce suckering. On the other hand, fire or light scarification which creates a dark soil surface may increase suckering.

Aspen sucker stands undergo considerable self-thinning as the stand matures, and thus initial sucker densities should be higher than final stocking requirements. It has been suggested that initial sucker densities of as low as 1,000 stems per acre will produce fully stocked stands at maturity if the suckers are evenly distributed throughout the site.

While a majority of studies indicate that aspen will regenerate satisfactorily following harvest, it has been suggested that harvesting operations have the potential to drastically reduce suckering under certain conditions. In addition to the possible physical destruction of roots, harvesting may produce site conditions which do not favor sucker growth or survival. At the present time, however, there is little information available identifying specific mechanisms for site-wide regeneration problems or how they might be avoided.

Table 1. Estimated changes in stand density with age on different quality sites in the Lake States (calculated from Ek and Brodie 1975).

Site Index	Stems per Acre ¹						
	Initial Density ²	Age 10	Age 20	Age 30	Age 40	Age 50	Age 60
60	1000	916	725	540	401	302	233
	5000	3400	1701	940	583	394	293
	10000	5103	2029	1030	616	409	291
	20000	6736	2233	1078	633	416	295
	30000	7492	2304	1094	638	418	296
	40000	7911	2339	1102	641	419	296
70	1000	903	693	502	364	270	206
	5000	3223	1530	826	507	341	245
	10000	4705	1788	894	532	352	250
	20000	6039	1940	930	544	357	253
	30000	6625	1992	942	548	359	254
	40000	6940	2018	947	550	360	254
80	1000	890	664	468	334	245	185
	5000	3064	1389	737	449	301	215
	10000	4362	1596	790	468	309	220
	20000	5469	1715	818	478	313	222
	30000	5934	1755	826	480	315	223
	40000	6177	1774	830	482	315	223
	50000	6322	1784	833	483	315	222

¹ Only stems greater than or equal to 1 foot tall are considered.

² Initial density is the sucker density present two growing seasons after harvest.

LITERATURE CITED

- Barnes, B. V. 1969. Natural variation and delineation of clones of *Populus tremuloides* and *P. grandidentata* in northern lower Michigan. *Silvae. Genetica* 18:130-142.
- Bella, I. E. 1975. *Growth density relationships in young aspen sucker stands*. Can. For. Serv., North. For. Res. Cen. Inf. Rep. NOR-X-124. 12 p.
- Bella, I. E. 1986. Logging practices and subsequent development of aspen stands in east-central Saskatchewan. *For. Chron.* 62:81-83.
- Bella, I. E., and J. P. DeFranceschi. 1972. *The effect of logging practices on the development of new aspen stands, Hudson Bay, Saskatchewan*. Can. For. Serv., North. For. Res. Cen. Inf. Rep. NOR-X-33. 12 p.
- Brinkman, K. A., and E. I. Roe. 1975. *Quaking aspen: Silvics and management in the Lake States*. USDA For. Serv., Ag. Handbook No. 486. 52 p.
- Brown, J. K., and N. V. DeByle. 1987. Fire damage, mortality, and suckering in aspen. *Can. J. For. Res.* 17:1100-1109.
- Buckman, R. E., and L. H. Blankenship. 1965. Repeated spring prescribed burning reduces abundance and vigor of aspen root suckering. *J. Forestry* 63:23-25.
- Crouch, G. L. 1983. Aspen regeneration after commercial clearcutting in southwestern Colorado. *J. Forestry* 81:316-319.
- Crouch, G. L. 1986. *Aspen regeneration in 6- to 10-year-old clearcuts in southwestern Colorado*. USDA For. Serv., Rocky Mtn. For. and Range Exp. Sta. Res. Note RM-467. 4 p.
- Day, M. W. 1944. The root system of aspen. *Am. Mid. Nat.* 32:502-509.
- DeByle, N. V., and R. P. Winokur, eds. 1985. *Aspen: Ecology and management in the western United States*. USDA For. Serv., Rocky Mtn. For. and Range Exp. Sta. Gen. Tech. Rep. RM-119. 283 p.
- Ek, A. R., and J. D. Brodie. 1975. A preliminary analysis of short-rotation aspen management. *Can. J. For. Res.* 5:245-258.
- Eliason, L. 1971a. Growth regulators in *Populus tremula*: III. Variation of auxin and inhibitor level in relation to root sucker formation. *Physiol. Plant.* 25: 118-121.
- Eliason, L. 1971b. Growth regulators in *Populus tremula*: IV. Apical dominance and suckering in young plants. *Physiol. Plant.* 25:263-267.
- Farmer, R. E. 1962. Aspen root sucker formation and apical dominance. *For. Sci.* 8:403-410.
- Graham, S. A., R. P. Harrison, Jr., and C. E. Westell. 1963. *Aspens: Phoenix trees of the Great Lakes region*. Univ. Mich. Press, Ann Arbor. 272 p.
- Hinds, T. E. 1985. Diseases. p. 87-106. In N. V. DeByle, and R. P. Winokur (eds.) *Aspen: Ecology and Management in the Western United States Proceedings*. USDA For. Serv., Rocky Mtn. For. and Range Exp. Sta. Gen. Tech. Rep. RM-119. 283 p.
- Horton, K. W., and E. J. Hopkins. 1965. *Influence of fire on aspen suckering*. Can. Dept. Forestry, For. Res. Br. Publ. 1095. 19 p.
- Hungerford, R. D. 1988. *Soil temperatures and suckering in burned and unburned aspen stands in Idaho*. USDA For. Serv. Res. Note INT-378. 5 p.
- Jones, J. R. 1975. *Regeneration on an aspen clearcut in Arizona*. USDA For. Serv., Rocky Mtn. For. and Range Exp. Sta. Res. Note RM-285. 8 p.
- Jones, J. R. 1976. Aspen harvesting and reproduction. pp. 30-34. In *Utilization and Marketing as Tools for Aspen Management in the Rocky Mountains: Proceedings of the Symposium*. USDA For. Serv., Rocky Mtn. For. and Range Exp. Sta. Gen. Tech. Rep. RM-29. 120 p.
- Jones, J. R., and N. V. DeByle. 1985. Fire. pp. 77-81. In N. V. DeByle, and R. P. Winokur (eds.) *Aspen: Ecology and Management in the Western United States Proceedings*. USDA For. Serv., Rocky Mtn. For. and Range Exp. Sta. Gen. Tech. Rep. RM-119. 283 p.
- Jones, J. R., and G. A. Schier. 1985. Growth. pp. 19-24. In N. V. DeByle, and R. P. Winokur (eds.) *Aspen: Ecology and Management in the Western United States Proceedings*. USDA For. Serv., Rocky Mtn. For. and Range Exp. Sta. Gen. Tech. Rep. RM-119. 283 p.
- Jones, J. R., and W. D. Shepperd. 1985. Harvesting. pp. 219-222. In N. V. DeByle, and R. P. Winokur (eds.) *Aspen: Ecology and Management in the Western United States Proceedings*. USDA For. Serv., Rocky Mtn. For. and Range Exp. Sta. Gen. Tech. Rep. RM-119. 283 p.
- Jones, J. R., and D. P. Trujillo. 1975. *Development of some young aspen stands in Arizona*. USDA For. Serv., Rocky Mtn. For. and Range Exp. Sta. Res. Pap. RM-151. 11 p.

- Kemperman, J. A. 1978. Sucker-root relationships in aspen. *For. Res. Note, Min. Nat. Res., Ont. No. 12.* 4 p.
- Kirby, C. L., W. S. Bailey, and J. G. Gilmour. 1957. The growth and yield of aspen in Saskatchewan. *Sask. For. Br., Tech. Bull. No. 3.* 67 p.
- Kittredge, J., Jr., and S. R. Gevorkiantz. 1929. *Forest possibilities of aspen lands in the Lake States.* Univ. of Minn. Ag. Exp. Sta. Tech. Bull. No. 60. 84 p.
- Maini, J. S. 1967. Variation in the vegetative propagation of *Populus* in natural populations. *Bull. Ecol. Soc. Am.* 48:75-76.
- Maini, J. S. 1968. Silvics and ecology of *Populus* in Canada. pp. 20-69. In J. S. Maini, and J. H. Cayford (eds.) *Growth and Utilization of Poplars in Canada.* Can. Dept. For. Rural Dev., For. Br., Pub. 1205. 257 p.
- Maini, J. S. 1972. Silvics and ecology in Canada. pp. 67-73. In *Aspen: Symposium Proceedings.* USDA For. Serv., North Central For. Exp. Sta. Gen. Tech. Rep. NC-1. 154 p.
- Maini, J. S., and J. H. Cayford, editors. 1968. *Growth and utilization of poplars in Canada.* Can. Dept. For. Rural Dev., For. Br., Pub. 1205. 257 p.
- Maini, J. S., and K. W. Horton. 1964. *Influence of temperature and moisture on formation and initial growth of Populus tremuloides suckers.* Can. Dept. For., For. Res. Br. Proposed Publication (Project 0-2) 64-0-11. 27 p.
- Maini, J. S., and K. W. Horton. 1966. Vegetative propagation of *Populus* spp. 1. Influence of temperature on formation and initial growth of aspen suckers. *Can. J. Bot.* 44:1183-1189.
- Perala, D. A. 1972. Regeneration: Biotic and silvicultural factors. pp. 97-101. In *Aspen: Symposium Proceedings.* USDA For. Serv., North Central For. Exp. Sta. Gen. Tech. Rep. NC-1. 154 p.
- Perala, D. A. 1973. Stand equations for estimating aerial biomass, net productivity, and stem survival of young trembling aspen on good sites. *Can. J. For. Res.* 3:289-292.
- Perala, D. A. 1974a. Prescribed burning in an aspen-mixed hardwood forest. *Can. J. For. Res.* 4:222-226.
- Perala, D. A. 1974b. *Repeated prescribed burning in aspen.* USDA For. Serv., North Central For. Exp. Sta. Res. Note NC-171. 4 p.
- Perala, D. A. 1977. *Managers handbook for aspen in the north-central states.* USDA For. Serv., North Central For. Exp. Sta. Gen. Tech. Rep. NC-38. 30 p.
- Perala, D. A. 1978a. *Sucker production, survival, and growth on outplanted long and short aspen root cuttings of different diameters.* USDA For. Serv., North Central For. Exp. Sta. Res. Note NC-241. 4 p.
- Perala, D. A. 1978b. *Thinning strategies for aspen: A prediction model.* USDA For. Serv., North Central For. Exp. Sta. Res. Pap. NC-161. 19 p.
- Perala, D. A. 1981. *Clone expansion and competition between quaking and bigtooth aspen suckers after clearcutting.* USDA For. Serv., North Central For. Exp. Sta. Res. Pap. NC-201. 4 p.
- Perala, D. A. 1983. *Shearing restores full productivity to sparse aspen stands.* USDA For. Serv., North Central For. Exp. Sta. Res. Note NC-296. 4 p.
- Perala, D. A. 1984. How endemic injuries affect early growth of aspen suckers. *Can. J. For. Res.* 14:755-762.
- Pollard, D. F. W. 1971. Mortality and annual changes in distribution of above-ground biomass in an aspen sucker stand. *Can. J. For. Res.* 1:262-266.
- Sandberg, D. 1951. *The regeneration of quaking aspen by root suckering.* M.F. Thesis. School of Forestry, Univ. Minn, Minneapolis. 172 p.
- Sandberg, D., and A. E. Schneider. 1953. *The regeneration of aspen by suckering.* School of Forestry, Univ. Minn, St. Paul. Minn For. Notes 24. 2 p.
- Schier, G. A. 1973a. Effects of gibberellic acid and an inhibitor of gibberellin action on suckering from aspen root cuttings. *Can. J. For. Res.* 3:39-44.
- Schier, G. A. 1973b. Origin and development of aspen rootsuckers. *Can. J. For. Res.* 3:45-53.
- Schier, G. A. 1973c. Seasonal variation in sucker production from excised roots of *Populus tremuloides* and the role of endogenous auxin. *Can. J. For. Res.* 3:458-461.
- Schier, G. A. 1974. Vegetative propagation of aspen: Clonal variation in suckering from root cuttings and in rooting of sucker cuttings. *Can. J. For. Res.* 4:564-567.
- Schier, G. A. 1975. *Deterioration of aspen clones in the middle Rocky Mountains.* USDA For. Serv., Intermountain For. and Range Exp. Sta. Res. Pap. INT-170. 14 p.
- Schier, G. A. 1976. Physiological and environmental factors controlling aspen vegetative regeneration of aspen. pp. 20-23. In *Utilization and Marketing as Tools for Aspen Management in the Rocky Mountains: Proceedings of the Symposium.* USDA For. Serv., Rocky Mtn. For. and Range Exp. Sta. Gen. Tech. Rep. RM-29. 120 p.
- Schier, G. A. 1978. *Variation in suckering capacity among and within lateral roots of an aspen clone.* USDA For. Serv., Intermountain For. and Range Exp. Sta. Res. Note INT-241. 6 p.
- Schier, G. A. 1981. *Physiological research on adventitious shoot development in aspen roots.* USDA For. Serv., Intermountain For. and Range Exp. Sta. Gen. Tech. Rep. INT-107. 12 p.
- Schier, G. A. 1982. Sucker regeneration in some deteriorating Utah aspen stands: Development of independent root systems. *Can. J. For. Res.* 4:1032-1035.

- Schier, G. A., and R. B. Campbell. 1978. Aspen sucker regeneration following burning and clearcutting on two sites in the Rocky Mountains. *For. Sci.* 24:303-312.
- Schier, G. A., and R. B. Campbell. 1980. *Variation among healthy and deteriorating aspen clones*. USDA For. Serv., Intermountain For. and Range Exp. Sta. Res. Pap. INT-264. 12 p.
- Schier, G. A., J. R. Jones, and R. P. Winokur. 1985a. Vegetative regeneration. pp. 29-33. In N. V. DeByle, and R. P. Winokur (eds.) *Aspen: Ecology and Management in the Western United States Proceedings*. USDA For. Serv., Rocky Mtn. For. and Range Exp. Sta. Gen. Tech. Rep. RM-119. 283 p.
- Schier, G. A., W. D. Shepperd, and J. R. Jones. 1985b. Regeneration. pp. 197-208. In N. V. DeByle, and R. P. Winokur (eds.) *Aspen: Ecology and Management in the Western United States Proceedings*. USDA For. Serv., Rocky Mtn. For. and Range Exp. Sta. Gen. Tech. Rep. RM-119. 283 p.
- Schier, G. A., and A. D. Smith. 1979. *Sucker regeneration in a Utah aspen clone following clearcutting, partial cutting and girdling*. USDA For. Serv., Intermountain For. and Range Exp. Sta. Res. Note INT-253. 8 p.
- Schier, G. A., and J. C. Zasada. 1973. Role of carbohydrate reserves in the development of root suckers in *Populus tremuloides*. *Can. J. For. Res.* 3:243-250.
- Schiaegel, B. E. 1972. Growth and yield of managed stands. pp. 109-112. In *Aspen: Symposium Proceedings*. USDA For. Serv., North central For. Exp. Sta. Gen. Tech. Rep. NC-1. 154 p.
- Shepperd, W. D. 1987. Silvicultural research in Rocky Mountain aspen. pp. 23-29. In *Management of Subalpine Forests: Building on 50 Years of Research*. USDA For. Serv., Rocky Mtn. For. and Range Exp. Sta. Gen. Tech. Rep. RM-149. 253 p.
- Shepperd, W. D., and O. Engelby. 1983. Rocky Mountain aspen. pp. 77-79. In *Silvicultural Systems for the Major Forest Types of the United States*. USDA For. Serv., Ag. Handbook No. 445. 191 p.
- Shirley, H. L. 1931. Does light burning stimulate aspen suckers? *J. Forestry* 29:524-525.
- Shirley, H. L. 1932. Does light burning stimulate aspen suckers? II. *J. Forestry* 30:419-420.
- Sorenson, R. W. 1968. *Size of aspen crop trees little affected by initial sucker density*. USDA For. Serv., North Central For. Exp. Sta. Res. Note NC-51. 4 p.
- Steneker, G. A. 1972. *The growth and management of trembling aspen*. Can. For. Serv., Nor. For. Res. Cen., For. Rep. 2:5.
- Steneker, G. A. 1974. Factors affecting the suckering of trembling aspen. *For. Chron.* 50:32-34.
- Stoeckeler, J. H., and J. W. Macon. 1956. Regeneration of aspen cutover areas in northern Wisconsin. *J. Forestry* 54:13-16.
- Strothmann, R. O., and M. L. Heinselmann. 1957. *Five-year results in an aspen sucker density study*. USDA For. Serv., Lake States For. Exp. Sta. Tech. Note 490. 2 p.
- Tew, R. K. 1970. Root carbohydrate reserves in vegetative reproduction of aspen. *For. Sci.* 16:318-320.
- Van Cleve, K. 1973. Short-term growth response to fertilization in young quaking aspen. *J. Forestry* 71:758-759.
- Wenger, K. F. ed. 1984. *Forestry handbook. Second Edition*. John Wiley and Sons, New York, NY. 1335 p.
- Winton, L. L. 1968. Plantlets from aspen tissue cultures. *Science* 160:1234-1235.
- Wolter, K. E. 1968. Root and shoot initiation on aspen callus cultures. *Nature* 219:508-509.
- Zasada, J. C., and G. A. Schier. 1973. Aspen root suckering in Alaska: Effect of clone, collection time, and temperature. *NW Sci.* 47:100-104.
- Zasada, Z. A. 1950. *Aspen management problems in the Lake States*. USDA For. Serv., Lake States For. Exp. Sta. Misc. Rep. No. 10. 8 p.
- Zasada, Z. A., and J. C. Tappeiner. 1969a. *Soil disturbance from rubber-tire skidders during summer harvesting of aspen*. Univ. of Minn., Minn. For. Res. Note 204. 3 p.
- Zasada, Z. A., and J. C. Tappeiner. 1969b. *Full-tree harvesting systems aids forest management*. Univ. of Minn., Minn. For. Res. Note 205. 4 p.
- Zehngraff, P. J. 1946. *Season of cutting affects aspen sprouting*. USDA For. Serv., Lake States For. Exp. Sta. Tech. Note 250. 1 p.
- Zehngraff, P. J. 1949. Aspen as a forest crop in the Lake States. *J. For.* 47:555-565.
- Zillgitt, W. M. 1951. *Disking to increase aspen stocking in aspen stands*. USDA For. Serv. Lake St. For. Exp. Sta. Tech. Note 357. 1 p.
- Zufa, L. 1971. A rapid method of vegetative propagation of aspens and their hybrids. *For. Chron.* 47:36-39.



