Aspen Root Sucker Formation And Apical Dominance

BY
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ROOT SUCKERING is the primary mode of regeneration in the aspens, *Populus tremuloides* Michx. and *P. grandidentata* Michx. When stems of these species are cut, numerous suckers originating in the root pericycle (Sandberg 1951) are formed on their extensive lateral root systems. During their first season of growth, suckers ordinarily reach a height of 3 to 5 feet. As many as 20,000 suckers per acre may occur after clear-cutting of well-stocked stands of *P. grandidentata* (Graham *et al.* 1956).

Considerable research has been devoted to the practical problem of securing adequate sucker reproduction after harvest cuts of aspen. It is now generally recognized that clear-cutting is a necessary prerequisite to successful regeneration (Zehngraff 1949). Zehngraff (1946) and Stoeckler and Macon (1956) have found that fall, winter, and early spring cuttings result in more abundant root suckers than does summer harvesting. An early study by Shirley (1931) indicated that controlled burning following clear-cutting stimulated sucker formation. More recently, disking has been shown to stimulate suckering (Zillgitt 1951).

Although numerous reports have been published dealing with the environmental conditions under which root suckering occurs, little attention has been given to the physiological mechanism which controls sucker formation. This paper presents evidence indicating that root suckering in the American aspens is closely related to apical dominance.

An intact, growing apical bud inhibits lateral shoot development; when it is removed, lateral bud growth begins. The degree of apical dominance varies with species and ontogenetic stage, and to a large degree controls plant growth habit.

In the 1930's after the discovery of auxins, several investigators showed that indole-3-acetic acid (IAA) could inhibit subapical bud development in the same fashion as does the stem apex. It was then assumed by some researchers that auxin produced in apical buds moved basipetally and directly inhibited lower shoot development (Skoog and Thimann 1934, Thimann 1937). Results of recent research indicate that the physiology of apical dominance may be more complex than originally supposed (Wickson and Thimann 1958, Gregory and Veale 1957). Audus (1959) published a thorough discussion of apical dominance theories in light of current research.

Aspen suckers appear on root systems

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TABLE 1. Occurrence of suckers in girdled and root-pruned clones of Populus grandidentata *and* P. tremuloides.

Clone no.	Suckers per acre			
	Pruned fall	Pruned spring	Girdled fall	Girdled spring
		P. tremuloides		
11	5,800		100	
10		6,000		400
25			0	0
2	1,400	2,300		
14		1,300	100	
13	5,100			300
Mean	4,100	3,200	70	250
		P. grandidentata		
16	6,500	3,700	1,700	100
21	3,000			100
22		3,200	800	
3	1,500		0	
17		2,800		700
Mean	3,660	3,200	800	300

after stems are cut or otherwise drastically disturbed, but not while trees are undamaged and vigorously growing. Consequently, it is believed that root suckering is related to apical dominance as explained in terms of the plant regulatory mechanisms discussed above (Barnes 1959). Aspen roots are visualized as "physiological" extensions of the stems; buds on these roots develop into suckers when the inhibiting influence of the shoot apex is removed. Results of the following experiments are offered as supporting evidence for this hypothesis.

Method of Study and Results

Two approaches were used in the investigation. In the first, intact plants growing under greenhouse and field conditions were subjected to treatments designed to stimulate root suckering by disrupting basipetal movement of auxin. The treatments included (1) severing lateral roots from the parent tree, (2) girdling stem phloem, and (3) girdling root phloem. In the second approach, the effect of indole-3-acetic acid (IAA) upon sucker formation was tested.

Girdling and Root Pruning

Field study. A field study was conducted in 1960 which incorporated spring and fall root pruning and phloem girdling treatments in a balanced incomplete block design (Table 1). Each of the 35-year-old clones used as an experimental block was divided into equal groups of stems, and one of the four treatments was assigned to each group.[1] Girdling was done by removing a ring of phloem 3 inches wide at a height of 3 to 6 inches above stem base. Pruning consisted of severing all lateral roots 1 to 2 feet away from the base of the trees with a sharp spade. Fall treatments were completed in October and November 1959; spring treatments were made after the trees had foliated in May and June 1960.

An isolation strip of untreated trees was left between treatments in all but the three smallest clones. These strips were designed to prevent mixture of treatment effects due to intermingling root systems of both girdled and root-pruned stems. However, root connections which are common between stems within clones (DeByle 1961) might permit transport of auxin from untreated

[1]Because of their characteristic root sucker mode of regeneration, the aspens occur under natural conditions as clonal units (Barnes 1959). These clones, covering from 0.1 to 0.5 acre and separated by open areas, were used as experimental blocks in field studies.

stems in the isolation strip to treated trees. This possibility is especially likely in the case of girdling treatments since root connections are not disturbed.

During the summer of 1960, weekly observations were made in each treated clone and suckers were marked with dated potting stakes as they appeared. On September 3, the suckers on 10 circular milacre plots in each treatment were recorded. The mean number of suckers per acre in each treatment area is shown in Table 1; individual figures are based upon the 10 milacre plots.

This study confirmed preliminary findings in that root pruning stimulated suckering in all clones. No suckers were found on root segments still attached to stems. Girdling was only moderately effective in two of the *P. grandidentata* clones and had little or no effect in the other clones of both species.

Greenhouse studies. Further study of the effect of phloem girdling upon sucker formation was carried out in a greenhouse using 1-year-old *P. tremuloides*. During vegetative propagation experiments it was observed that root systems of 1-year-old plants suckered prolifically within 2 weeks when severed from an actively growing stem. This early development of root suckering potential permitted the use of young plants (approximately 12 to 24 inches high) in the following experiments.

In an initial experiment, lateral shoot development was observed below phloem girdles. One-inch bands of phloem were removed from eight plants at points 3 inches above their root collars. Within 15 days, seven of the eight plants exhibited lateral bud growth below the girdle; the eighth plant died. Portions of the plants above the girdles remained alive during the lateral shoot development below girdles; lateral bud growth did not occur above girdles. Thus, this experiment illustrated the effectiveness of phloem girdles in blocking basipetal movement of inhibitors of lateral bud growth on small plants.

The second greenhouse experiment tested the effect of girdling root phloem upon sucker formation. Actively growing 1-year-old plants were severed 2 inches above the root collar and lateral shoots were allowed to develop for 2 weeks. The resulting plants each had a 2-inch stump supporting one or two lateral shoots 1 to 2 inches in length. The intact root systems were then gently washed free of soil. Eighteen of these plants from two clones were chosen for the experiment, and at least one lateral root on each was girdled at a point 1 inch from the root collar by removing a 0.5-inch band of phloem with a sharp scalpel. Girdled roots were at least 0.1 inch in diameter. After root girdling, the plants were placed on a sand-filled greenhouse bench under intermittent mist. This procedure allowed for daily examination of the root systems while the plants continued both root and shoot growth.

Within 20 days, root suckers formed on portions of the root systems distal to girdles on 17 of the 18 plants (Fig. 1). No suckers

FIGURE 1. *Stimulation of sucker formation by root girdling on 1-year-old* Populus tremuloides.

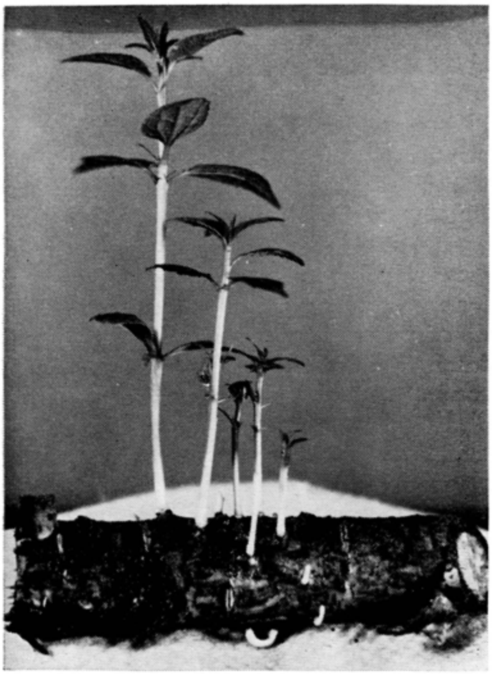

FIGURE. 2. *Three-inch-long* Populus tremuloides *root cutting with suckers.*

were observed on portions of roots proximal to girdles or on ungirdled roots.

Effect of Indole-3-acetic Acid upon Root Sucker Formation

These experiments tested the effect of IAA upon sucker formation on root cuttings of both *P. tremuloides* and *P. grandidentata* and intact root systems of the former. The assumptions basic to this approach are (1) that auxin is of controlling importance in apical dominance and (2) that auxin-like substances are found in woody plants. Both assumptions are supported by considerable experimental evidence (Audus 1959, Avery *et al.* 1937, Mirov 1941, Gunckel *et al.* 1949, Soding 1938), although there is also evidence that apical dominance may not be a simple auxin control mechanism (Gregory and Veale 1957, Champagnat 1955, Camus 1949, Went 1939). Eliasson (1961) has already observed that IAA inhibited sucker formation on root cuttings of the European aspen, *P. tremula.*

Root cuttings. Aspen root cuttings measuring 0.2 to 0.7 inch in diameter and 3 inches in length were used as experimental material (Fig. 2). These root sections were immersed for 24 hours in freshly prepared aqueous solutions of IAA, then planted horizontally to a depth of 0.3 inch in a greenhouse bench filled with coarse sand. The check treatment consisted of immersing cuttings for 24 hours in tap water before planting. During the course of experiments the sand medium was watered lightly each day; greenhouse temperatures varied from 70° to 80° F. After 6 weeks the cuttings were removed from the sand and the number of suckers on each was recorded.

Preliminary studies indicated that both IAA and indolebutyric acid (IBA) were effective in reducing sucker formation on root cuttings. Following these trials, root sections from three clones of each species were collected for experimental use in September 1959. Roots from each clone were divided into five lots of 30 cuttings each and treated with IAA solutions ranging in concentration from 10 to 100 ppm. Mean root diameter was the same for all treatment lots from a single clone. Data from this experiment (Table 2) indicate that 50 and 100 ppm solutions of IAA caused a significant reduction of suckering relative to controls. Clonal differences in response were also significant. The analysis of variance was used as a statistical test.

Intact root systems. Root systems of 1-year-old *P. tremuloides* plants (rooted suckers) used as experimental material were first washed free of soil. Then these systems were paired with respect to clonal source and root development, and the stems were severed 1 inch above the root collar. Approximately 0.5 cc of IAA-lanolin paste (8 mg/g) was applied to the freshly cut stump of one member of each pair, and the same amount of pure lanolin was placed on the second member. Both plants were then placed side by side under intermittent mist. Fresh paste was applied to stumps every 4 days for a period of 2 weeks.

Formation of suckers on untreated plants within 1 or 2 weeks, accompanied by a lack of response on the part of IAA-treated members of pairs, was considered evidence of IAA inhibition (positive results). If both members of a pair developed suckers or both failed to form suckers, results were deemed negative. The non-parametric "sign test" was used in statistical analysis (Dixon and Massey 1957).

A total of 57 pairs of plants from four *P. tremuloides* clones were utilized in three experiments. As is evident from the data presented in Table 3, IAA inhibition of sucker formation was highly significant. The treatment effect is illustrated in Figure 3. Untreated plants developed suckers within 10 to 15 days. Suckers were found on treated plants only after a period of 3 to 4 weeks (or 1 week after the last application of IAA). The delayed occurrence of suckers on treated plants is evidence that IAA had no herbicidal effect.

Discussion

The experimental results may be summarized as follows: (1) Treatment with aqueous solutions of IAA (50 and 100 ppm) reduced sucker formation on root cuttings of both species. (2) Application of 8 mg/g IAA in lanolin to stumps of young *P. tremuloides* plants inhibited suckering on root systems. (3) Under greenhouse conditions, experiments with 1-year-old *P. tremuloides* plants indicated that root girdling significantly stimulated sucker formation on portions of roots distal to girdles. Girdling stem phloem on young plants caused lateral bud development below girdles. (4) In field studies, girdling stem phloem occasionally stimulated formation of root suckers and stump sprouts in *P. grandidentata* clones, but not in those of *P. tremuloides*. (5) Lateral roots of 35-year-old *P. tremuloides* and *P. grandidentata* which were severed from their parent stems gave rise to suckers at points along

TABLE 2. Effect of indole-3-acetic acid upon (1) percentage of aspen root cuttings forming suckers and (2) number of suckers per cutting. Individual figures based on 30 cuttings.

Clone no	Control	10 ppm IAA	20 ppm IAA	50 ppm IAA	100 ppm IAA
	(1) Percentage of root cuttings forming suckers				
			P. tremuloides		
34	100.0	96.8	90.6	84.4	48.3
99	74.2	80.0	74.2	56.0	26.7
38	87.5	77.4	76.7	45.2	3.3
Mean	87.0	84.7	80.5	61.9	26.1
			P. grandidentata		
37	97.0	100.0	86.2	76.7	51.6
1M	87.1	74.2	51.5	38.7	40.6
20	80.0	80.0	86.0	77.4	46.7
Mean	88.0	84.7	74.6	64.3	46.3
	(2) Number of suckers per 3-inch-long root cutting				
			P. tremuloides		
34	10.5	10.0	8.0	4.0	2.7
99	2.7	3.2	3.6	.8	.3
38	5.8	3.8	4.9	.9	.1
Mean	6.3	5.7	5.5	1.9	1.0
			P. grandidentata		
37	7.8	8.6	5.6	4.4	1.5
1M	3.1	2.1	2.2	1.0	.8
20	3.0	2.8	3.1	1.5	1.1
Mean	4.6	4.5	3.6	2.3	1.1

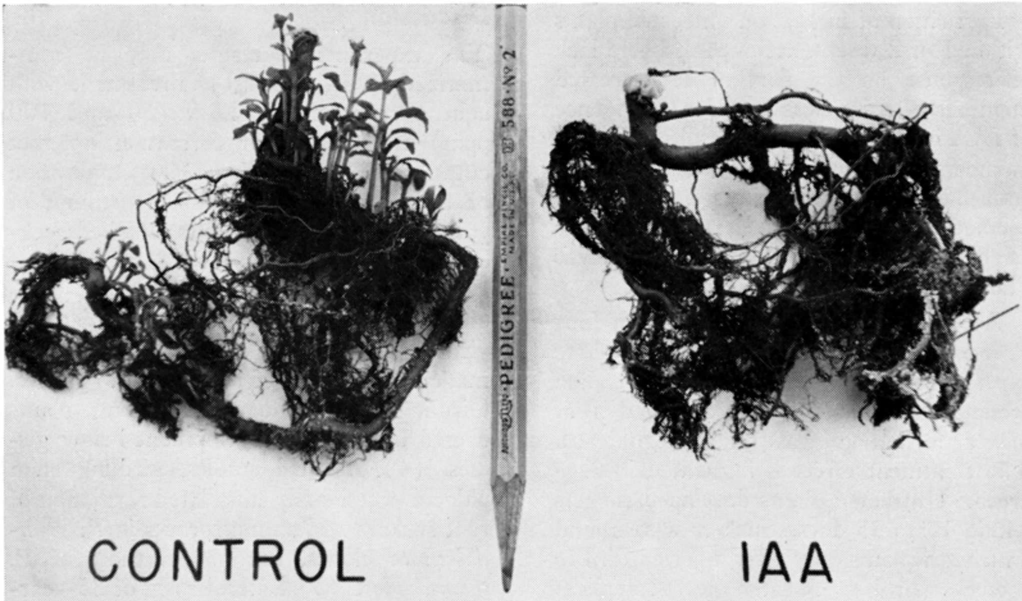

FIGURE 3. *Effect of 8 mg/g IAA-lanolin paste on suckering of 1-year-old* Populus tremuloides *root system.*

their entire length. Suckers did not occur on portions of severed roots which remained attached to stems.

Stimulation of suckering by root pruning may be interpreted as good supporting evidence for an apical dominance theory of suckering. The results suggest that growth-regulating factors transported from stem to root prevent suckering in the intact root system. Further support for this thesis exists in the fact that sprouts did not occur on portions of severed roots still attached to the stem.

Severing roots from the parent tree goes far beyond disrupting basipetal flow of a growth substance, however. In some respects it is akin to cutting the tree since the total influence of the stem upon roots, including nutritional and water relationships, is interrupted. In fact, results of root pruning taken alone may also be considered as evidence of controlling factors which move from root to stem. An accumulation of such factors in the root after pruning might stimulate sucker formation. Thus, a nutritional explanation could be based upon the data. The fact that fall treatments caused the greatest suckering could be interpreted as further evidence for a nutritional theory.

Water relations of roots are considerably disturbed by root pruning. Transport of water through roots to the stem is accompanied by a buildup of negative pressure, or moisture tension, within xylem tissue. When a root is pruned, this tension in the xylem is suddenly released, and the root attains an equilibrium with its soil medium, as far as moisture is concerned. It is con-

TABLE 3. Effect of 8 mg/g IAA in lanolin upon root sucker formation on intact root systems of 1-year-old Populus tremuloides.

Clone no.	Number of plant pairs utilized	Number of pairs exhibiting inhibition
34	24	22
38	11	10
19	17	15
18	5	4
Total	57	51

ceivable that the resulting change in cell hydration might indirectly influence sucker formation.

Results of girdling under field conditions offer less support to the apical dominance hypothesis. If growth substances are transported primarily via the phloem, as most research has indicated, then girdling should have given results similar to root pruning. However, in the field experiments, auxin may have moved downward past the girdle via the xylem. Furthermore, it is possible that living root connections with untreated stems in isolation strips may have supplied some auxin to treated root systems.

The nutritional status of roots may also have been related to girdling results. Although fall girdling was accomplished when roots were high in carbohydrate content, food materials were very likely removed from the root system with spring leaf flush. Spring girdling was done after the vernal reduction of root sugars. Thus, both treatments probably left roots with little nutritional support for suckers. These conditions coupled with a partially effective blocking of basipetal auxin movement could possibly have accounted for the weak response to girdling in the field.

The positive reaction of younger plant material to root and stem girdling is considered to be of more significance than results from field experiments. Not only are young plants generally more responsive to treatment than mature trees, but under greenhouse conditions the side effects of variation in nutrition and moisture conditions were greatly reduced. A comparison of the two types of investigation is valuable, however, in that it highlights the probable importance of the indirect role which environmental and internal factors play in sucker formation and development.

The inhibiting effect of aqueous solutions of IAA upon suckering of root cuttings furnishes considerable support to an apical dominance theory of suckering. IAA inhibition of suckering on intact root systems further substantiates the hypothesis. Although IAA concentrations used in the experiments were higher than normally found in plants, they were not toxic. In fact, physiologically effective levels were probably much lower than applied concentrations due to deactivation following treatment. This is especially so in the case of aqueous solutions.

It must also be noted that a complete and continuous inhibition of suckering by IAA was not observed. However, demonstration of such an inhibition, which would essentially involve a 100-percent effective replacement of the plant apex, seems highly unlikely when one considers the technical problems of substituting the intact apex with a chemical after the disturbance of decapitation.

Thus, data discussed above generally support the original hypothesis, that the physiology of root suckering in aspen is related to apical dominance. Environmental factors such as temperature, light, and moisture also undoubtedly play an important indirect role in the formation and development of sucker regeneration.

Summary

The hypothesis that root suckering in the aspens is controlled by apical dominance was tested. Root pruning and girdling stimulated sucker formation on portions of root systems distal to the point of treatment. Suckering of root cuttings was reduced by treatment with aqueous solutions of IAA. IAA-lanolin paste inhibited sucker formation on intact root systems of 1-year-old aspen. It was concluded that the physiological mechanism controlling root suckering is related to the apical dominance phenomenon.

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