of 60 cm and a root collar diameter of 10.0 mm in 7 months. Black spruce seedlings of this size will normally yield approximately 140 cuttings each.

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THE ROOTING STIMULUS IN PINE CUTTINGS

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Abstract. Occurrence, distribution, and function of the "endogenous root-forming stimulus" (ERS) were examined in jack pine (*Pinus banksiana* Lamb.) seedling cuttings via surgical treatment and application of indole-3-butyric acid (IBA). Removal of terminals or needles markedly reduced rooting, indicating that both terminals and needles contained substantial amounts of ERS and that ERS was rather generally distributed in the cuttings. However, terminals contained much more ERS per unit dry weight, compared to needles. ERS consisted of an auxin and non-auxin component. Applied IBA did not replace the effects of terminals on rooting and, therefore, was largely ineffective when non-auxin ERS was limiting. Auxin ERS was initially required for the development of callus in which primordia initiated. Subsequently, auxin and non-auxin ERS were required for primordium development. However, limiting the supply of non-auxin ERS was primarily responsible for reduced rooting after terminals were removed.

About 100 years ago the idea arose that chemical factors in the aerial portion of plants controlled the formation of roots (26). Subsequently, it was learned that auxin, indole-3-acetic acid (IAA), and one or more non-auxin chemicals accumulated

in the bases of cuttings during propagation (4, 28). Together, auxin and the non-auxin factors comprise the "endogenous root-forming stimulus" (ERS), which is the primary initiator and controller of adventitious rooting (16, 28).

Most research concerning the nature, location, and functions of ERS has been conducted with dicotyledonous species, whereas less work has concerned conifers. Jack pine (*Pinus banksiana* Lamb.) is a commercially important forest tree in the North Central U.S. and Canada, but is extremely difficult to propagate from cuttings when ortets reach the age of 5 to 7 years (25). The present work examined the occurrence, distribution, and some functions of auxin and non-auxin ERS in cuttings of jack pine. The present examination was conducted as part of a comprehensive study to determine the relationships between the "predisposition" of cuttings to root, cellular "competence" to form root initials, and ERS. These relationships are described in the following rationale.

The potential for adventitious rooting increases concomitantly with what has been termed the "predisposition" of cuttings to root (14). Cuttings are predisposed to root after minimum anatomical and physiological thresholds have been exceeded (14). See Figure 1. Various types of cells form root primordium initials, depending on the species of plant and type of cutting (14). However, only a few cells of the anatomically suitable type within a cutting will form root initials, which indicates a special physiological status plus the particular cellular morphology. This cellular morphology and physiological status makes some cells "competent" progenitors of root initials, but the ontogeny and nature of the competence re-
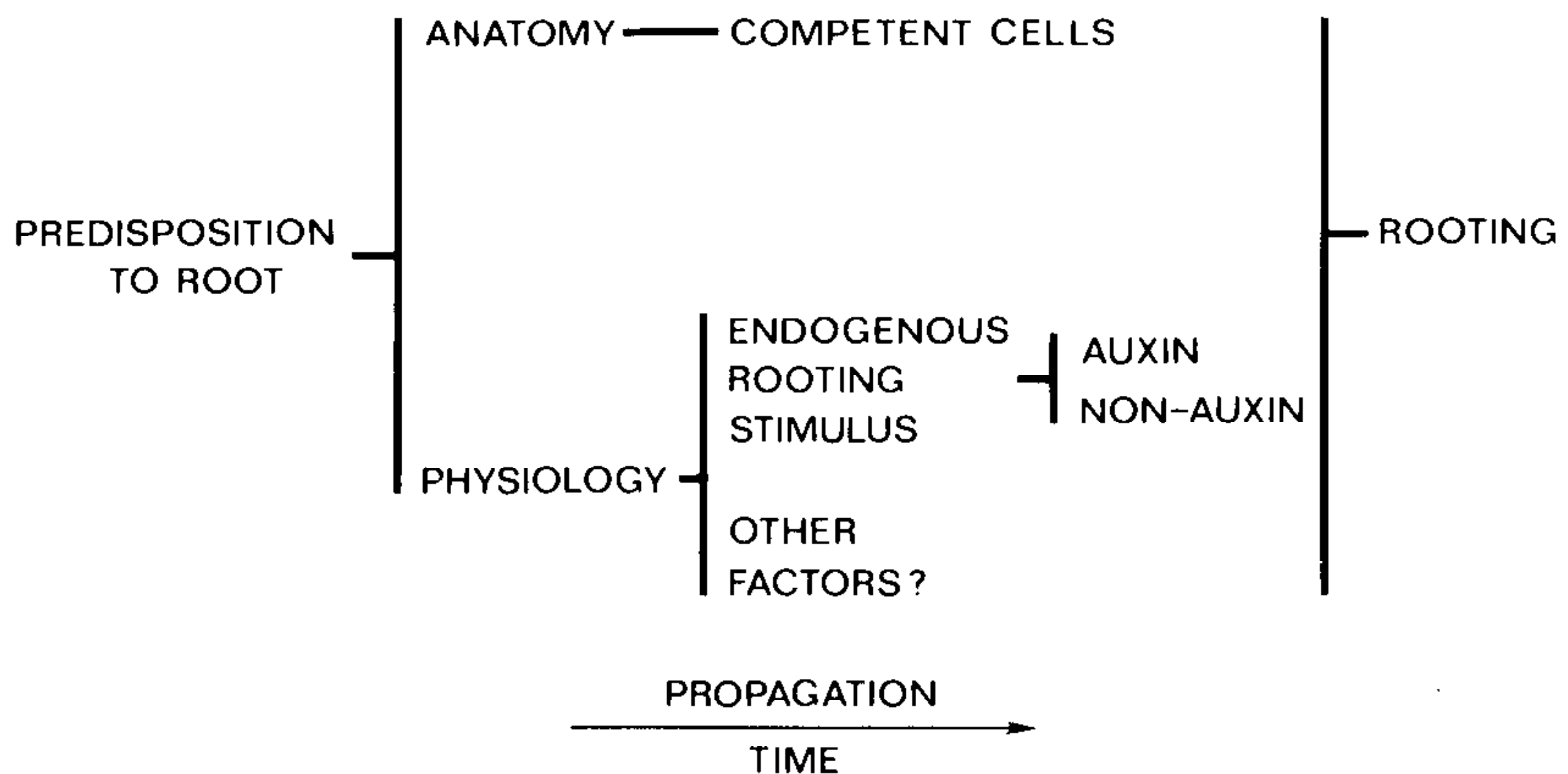

Figure 1. Relations between some anatomical and physiological factors that determine the ability of cuttings to complete the rooting process.

main obscure (14). See Figure 1. Nevertheless, the presence of competent cells is part of the minimum status that predisposes cuttings to root (14). See Figure 1.

Rooting occurs in two different ways, depending upon the species of plant. In "non-callusing" species, such as pea (*Pisum sativum* L.) and bean (*Phaseolus vulgaris* L.), primordia initiate from competent cells that exist at the time a cutting is severed (9). See Figures 1 and 2. In "callusing" species, which initiate primordia in or adjacent to developing callus tissue, competent cells do not exist prior to propagation (14). See Figures 1 and 2. In comparison with many non-callusing species, callusing species have ortets with a long life span, undergo secondary vascularization (wood formation), and require relatively long periods for successful propagation of cuttings. See Figure 2. Compare Figure 4 with Figure 1 of (16). For example, jack pine cuttings root slowly and initiate primordia only in or adjacent to basal callus tissue formed during propagation (20), even in cuttings from seedlings as young as 20 days old (5,21,27). Based on the foregoing, the predisposition of callusing species to root depends both on normal plant development and the presence of factors that allow the formation of callus, which directly or indirectly yields competent cells (14).
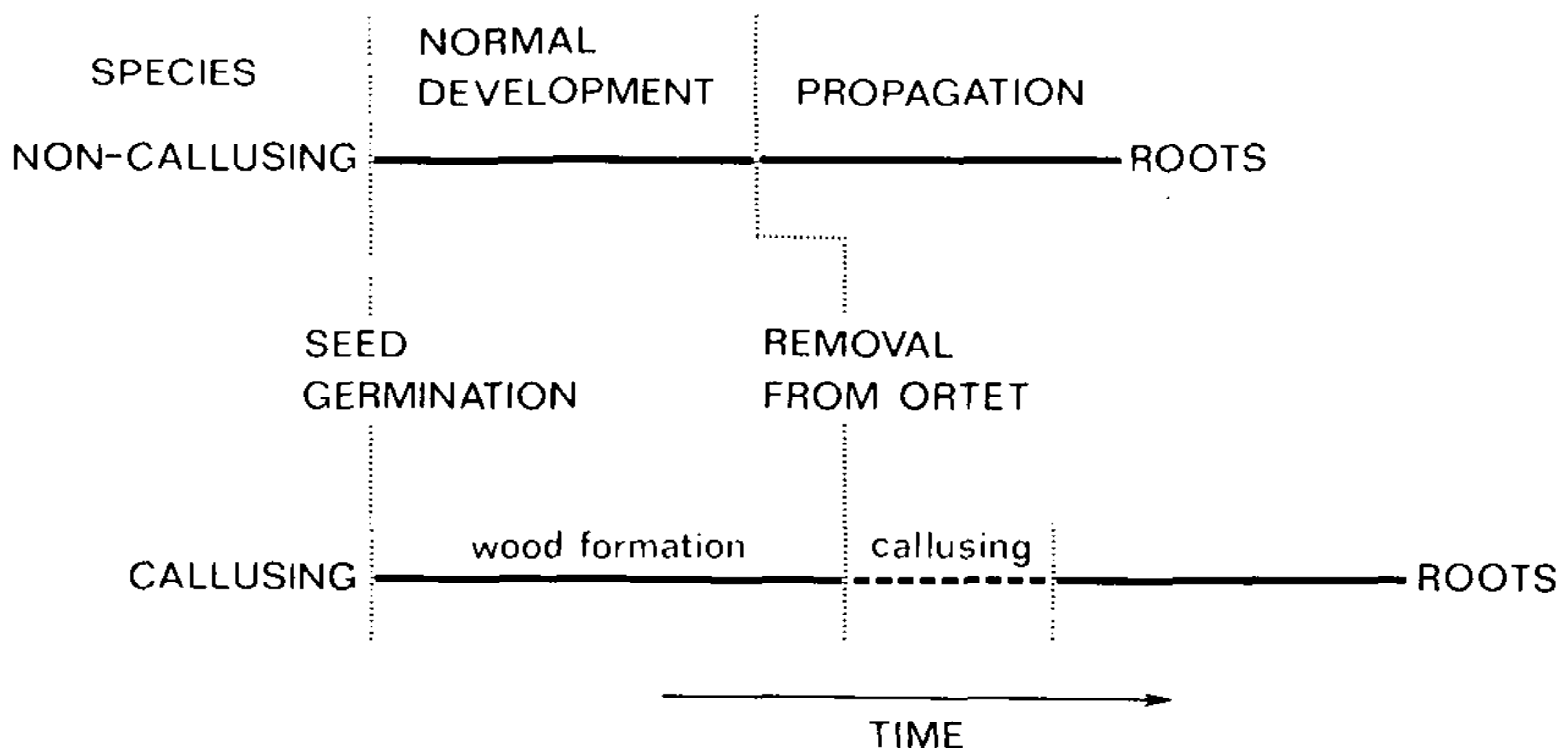

Figure 2. Relations between normal plant development and rooting characteristics of cuttings from species that do and do not initiate root primordia in or adjacent to callus tissue.

Formation of root initials requires physiological stimulation in the form of ERS (16). See Figure 1. Auxin and non-auxin ERS exist in leaves, embryonic shoots, and cotyledons (1,3,6,7,10,11,12,13,15,24); are basipetally transported in the cutting [(4) and previous references]; and are separately required for initiation (auxin ERS) and development (non-auxin ERS) of primordia (7,11,12,13,14,15). The minimum physiological status that predisposes non-callusing species to root is the

presence within cuttings of enough auxin and non-auxin ERS (Figure 1). In callusing species, the minimum additionally requires factors that promote callus formation (i.e., the development of competent cells).

The actions of ERS on primordium initiation-development appear to occur in substantially different time-frames in non-callusing and callusing species, although these matters are largely unstudied. In non-callusing species, the basipetal movement of ERS occurs quickly, resulting in root primordia after 1 or 2 days propagation [compare Figures 1 and 8 of (16)]. However, in callusing species, either the basipetal movement of ERS is delayed or the actions of basipetally transported ERS on primordium initiation are delayed, awaiting callusing and the development of competent cells. For example, significant production of callus requires 7 days in untreated and at least 2 days in auxin-treated jack pine seedling cuttings [see Figure 6 of (18)], and rooting occurs substantially later (18). See Figure 4.

Shortly after the discovery of auxin, it was learned that applied auxin often stimulated adventitious rooting (4,28). However, cuttings of certain age classes or species of plants have shown little or no positive response to applied auxin, which resulted in their classification as "poor or non-rooters" (2). Such species apparently lack sufficient non-auxin ERS, an essential predisposing them to root for which applied auxin cannot substitute (11). Based on available information, only normal plant development predisposes cuttings to root and only modifications of normal development can enhance or diminish a prevailing predisposition to root. For example, etiolation and surgical treatment both modify normal plant development and can enhance or diminish rooting responses, respectively (7,8,10,11,16,22,23).

MATERIALS AND METHODS

Jack pine seedlings were grown from a single lot of open pollinated seed in a growth chamber and propagated in a greenhouse (17). Cuttings were made from 90-day-old seedlings that were randomly selected for treatment (as described in Table or Figure captions). In some experiments, "needles" or "terminals" were removed before or after cuttings were severed from the original seedling root system. The terminal consisted of the terminal bud and about 1 cm of subtending stem plus needles (Figure 3). Therefore, some needles remained on those cuttings from which "needles were removed" (Figure 3). When used, indole-3-butyric acid (IBA) in 100% ethanol was applied as a one μl drop to the apical stump of cuttings from which terminals were removed or in 100% ethanol by the basal quick dip method [(19), see Table and Figure captions].
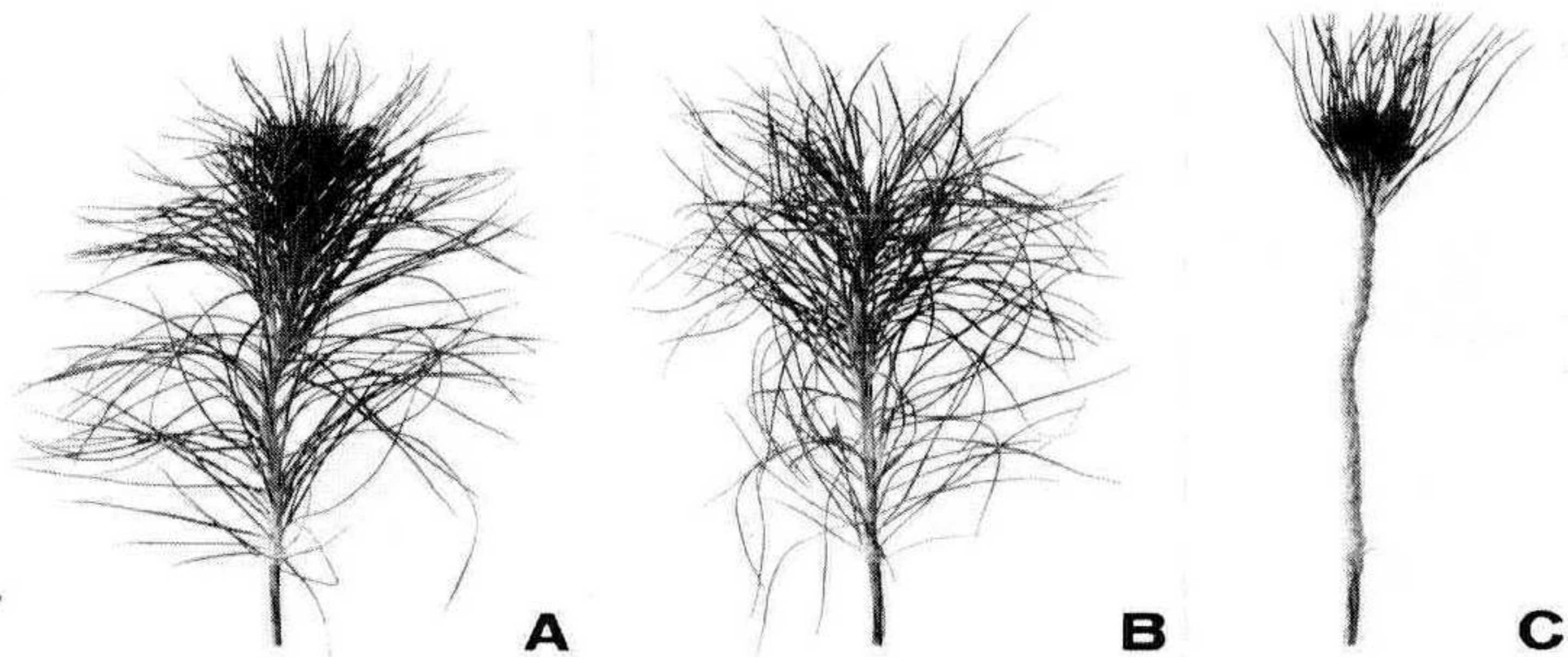
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Figure 3. Jack pine cuttings produced from 90-day-old seedlings: (A) untreated, (B) terminal removed, (C) needles removed.

Surgical treatment can remove the possible influences of both auxin ERS and non-auxin ERS, whereas applied auxin can mimic the effects of auxin ERS (1,7,8,11). Therefore, rooting data were evaluated in the following ways (16): 1) effects of ERS alone — determined from the difference between data for non-auxin-treated, surgically-treated cuttings compared to non-auxin-treated, non-surgically-treated cuttings; 2) effects of auxin treatment alone — determined (a) from data for non-auxin-treated, non-surgically-treated cuttings compared to auxin-treated, non-surgically-treated cuttings; or (b) from data for non-auxin, surgically-treated cuttings compared to auxin-treated, surgically-treated cuttings; 3) combined effects of ERS and auxin treatment — determined from data for auxin-treated, non-surgically-treated cuttings compared to non-auxin-treated, non-surgically-treated cuttings; 4) non-auxin ERS — determined from data for non-auxin-treated, non-surgically-treated cuttings compared to auxin-treated, surgically-treated cuttings; 5) auxin ERS — from (2b) above.

Experiments were repeated at least twice in time and data were analyzed via paired comparisons with a Mann-Whitney U-test and sometimes with correlation analysis. The following presentation has been limited to statistically significant (P > 0.95) differences between means or to statistically significant (P > 0.95) correlations.

RESULTS

Basal application of IBA resulted in earlier rooting (between 10 and 16 days), more roots per cutting, and a higher percentage of rooted cuttings, all in comparison with untreated cuttings at the same time (compare same days, IBA-treated vs. Untreated, Figure 4). For both IBA-treated and untreated cuttings, rooting percentages, number of roots, and basal fresh weight were positively correlated with time; number of roots and basal fresh weight were positively correlated with rooting percentages; and, number of roots was positively correlated

with basal fresh weight (Figure 4). Finally, rooting percentages and basal fresh weights were positively correlated in comparisons of untreated with IBA-treated cuttings (Figure 4).
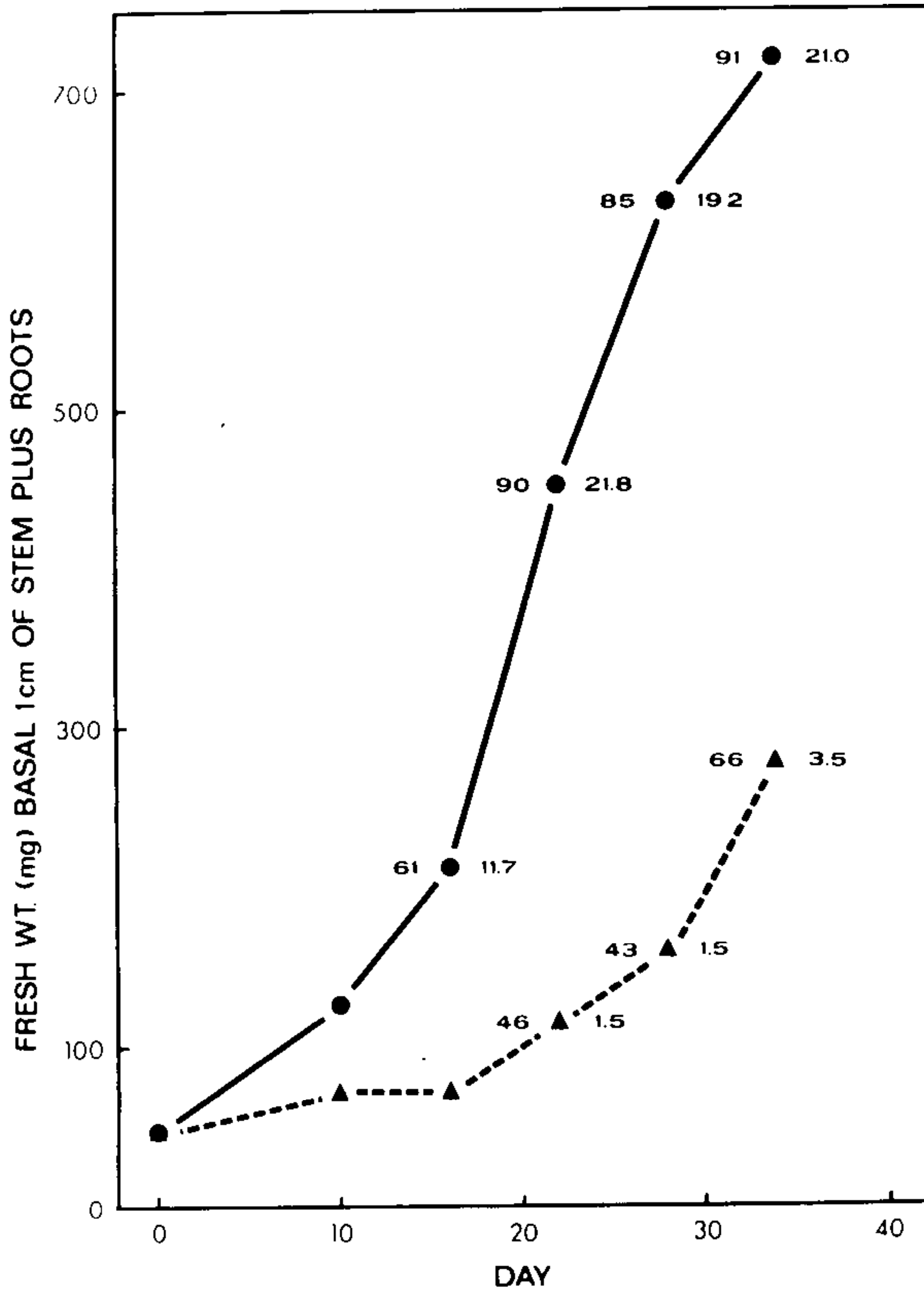

Figure 4. Effect of indole-3-butyric acid (IBA) treatment on fresh weight of basal one cm of stem plus roots of non-surgically-treated, 92-day-old jack pine seedling cuttings. Treatment by basal quick dip in 100% ethanol with (circles) or without (triangles) 25 mmol/l IBA. For each day, percentage rooted (left) and mean number of roots per cutting (right) appear adjacent to symbols. No rooting was found on days without numbers next to symbols. At day 10, mean fresh weights for untreated and IBA treated cuttings differed significantly (P > 0.95, n = 100) from each other and from the mean for day 0. Mean number of roots per cutting differed significantly between treatments at and after day 22.

In the experiment to determine the general locations of ERS in jack pine cuttings, removing needles or terminals (Figure 3) on the individual test days resulted in fewer rooted cuttings, fewer roots per cutting, and shorter roots per cutting, compared to the control, except when needles were removed

at day 10 (Control vs. Needles Removed and Terminal Removed, Table 1). Lesser rooting after removing terminals, compared with no treatment, was also found in other experiments (Tables 2-5).

Table 1. Rooting data after 44 days propagation of 89-day-old jack pine seedling cuttings. Cuttings were untreated (Control), or their terminals or needles were removed at the indicated times after cuttings were severed from the original seedling root system. Data are means expressed on a per cutting basis. Means with different letters differed significantly (P > 0.95, n = 30). Means for pooled data for all treatment times for Terminal Removed and for Needles Removed differed significantly (P > 0.95, n = 210).

Time of treatment	Percent rooted	Number of roots	Longest root length (mm)
Control			
—	93%	4.2a	30.5a
Terminal Removed			
+ 1 min	23	0.6b	3.4b
+ 2 days	43	1.1b	10.8b
+ 4 days	70	2.0b	18.0b
+ 6 days	63	1.8b	14.0b
+ 8 days	40	1.0b	9.8b
+ 10 days	70	2.0b	17.0b
+ 12 days	57	1.3b	16.1b
Mean	52	1.4	12.7
Needles Removed			
+ 1 min	60	1.8c	13.9c
+ 2 days	77	2.8c	18.1c
+ 4 days	53	1.4b	13.2b
+ 6 days	67	2.5b	26.0b
+ 8 days	67	1.9b	15.7c
+ 10 days	80	3.1a	24.6a
+ 12 days	83	1.9c	21.2b
Mean	70	2.2	19.0

Overall, removing needles was less effective in diminishing rooting (i.e., ERS) than was removing terminals. Firstly, removing needles early in the experiment (up to +2 days) or late in the experiment (+8 to +12 days) resulted in either more roots or longer roots per cutting, or both, compared with removing terminal (needles removed vs. terminal removed, Table 1). Secondly, removing needles resulted in more roots per cutting and longer roots per cutting, compared with removing terminals based on a comparison of pooled data for all days that each treatment was tested (compare means, Needles Removed vs. Terminal Removed, Table 1). Thirdly, the mean percentage of rooted cuttings during the whole experiment (+1 min to +12 days) was greater when needles were removed than when terminals were removed (compare means, Needles Removed vs. Terminal Removed, Table 1).

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Table 2. Rooting data after 41 days propagation of 93-day-old jack pine seedling cuttings. Cuttings were untreated (Control), or their terminals were removed at the indicated times after cuttings were severed from the original seedling root system. Data are means expressed on a per cutting basis. Means with different letters differed significantly (P > 0.95, n = 40).

Time of treatment	Percent rooted	Number of roots	Longest root length (mm)
Control			
—	80%	2.2a	26.0a
Terminal Removed			
+ 1 min	30	0.6b	8.1b
+ 1 day	32	0.8b	10.9b
+ 2 days	32	0.7b	6.2b
+ 3 days	35	0.6b	7.7b
+ 7 days	48	0.9b	9.2b
+ 8 days	28	0.5b	2.3c
Mean	34	0.7	7.4

The time at which terminals were removed after cuttings were severed from the original seedling root system had no effect on the number of roots or root length per cutting (+1 min through +12 days, Terminal Removed, Table 1; see also Tables 2-5). Similar results were obtained when terminals were removed up to one hour before cuttings were severed (Table 4). However, removing terminals 1 day before cuttings were severed, compared to removal later, resulted in better rooting, although results were somewhat conflicting. In one experiment, removing terminals 1 day before cuttings were severed resulted in a greater percentage of rooted cuttings, number of roots per cutting, and root length per cutting, compared with treatment from 1 hour before to 1 min after cuttings were severed (−1 day vs. −1 min and +1 min, Table 4). Also in the foregoing experiment, a greater percentage of rooted cuttings and longer roots per cutting were obtained when terminals were removed one day before cuttings were severed, compared with treatment 1 day after cuttings were severed (−1 day vs. +1 day, Table 4). In a second experiment, a greater percentage of rooted cuttings was obtained when terminals were removed 1 day before cuttings were severed, in comparison with treatment 1 min or 1 day later (Terminal Removed, Table 5). However, no differences were found in number of roots or root length per cutting (−1 day vs. +1 min and +1 day, Terminal Removed, Table 5).

Application of IBA to the cut apex of cuttings after removing terminals increased the number of rooted cuttings but, with few exceptions, had no effect on the number of roots or root length per cutting, compared to removing terminals alone (compare same days, Terminal Removed vs. Terminal Removed + Apical IBA, Table 5). However, when data for all

treatment times were pooled, which greatly increased sample size, IBA treatment significantly increased rooting, using all bases of comparison (compare means, Table 5). Nevertheless, IBA treatment did not fully counteract the negative effects on rooting of removing terminals (Control vs. Terminal Removed + Apical IBA, Table 5).

Table 3. Rooting data after 33 days propagation of 90-day-old jack pine seedling cuttings. Cuttings were untreated (Control), or their terminals were removed at the indicated times before (−) or after (+) cuttings were severed from the original seedling root system. Data are means expressed on a per cutting basis. Means with different letters differed significantly (P > 0.95, n = 150).

Time of treatment	Percent rooted	Number of roots	Longest root length (mm)
	Control		
—	57%	1.8a	17.5a
	Terminal Removed		
− 1 min	21	0.6b	2.9b
+ 1 min	15	0.3b	2.2b
+ 1 day	21	0.5b	3.9b
Mean	19	0.5	3.0

Table 4. Rooting data after 38 days propagation of 95-day-old jack pine seedling cuttings. Cuttings were untreated (Control), or their terminals were removed at the indicated times before (−) or after (+) cuttings were severed from the original seedling root system. Data are means expressed on a per cutting basis. Means with different letters differed significantly (P > 0.95, n = 50).

Time of treatment	Percent rooted	Number of roots	Longest root length (mm)
	Control		
—	82%	3.3a	43.4a
	Terminal Removed		
− 1 day	54	1.7b	31.9b
− 1 hour	38	1.0c	20.7c
− 1 min	38	1.2c	18.2c
+ 1 min	32	1.1c	16.0c
+ 1 day	28	1.5b	20.2c
Mean	38	1.3	21.4

A final experiment tested the effect of removing terminals combined with immediate apical or basal application of IBA on fresh weight of the basal 1 cm of stem prior to macroscopically visible root development. Basal fresh weight of control cuttings and cuttings from which terminals had been removed increased initially at day 9, compared to day 0, and were equal during the test (C vs. TR, Figure 5). Apical and basal application of IBA after removing terminals resulted in faster and greater increases in basal fresh weight, compared with non-IBA-treated cuttings (Figure 5). However, apical application of IBA was less effective than basal application (Figure 5).

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Table 5. Rooting data after 33 days propagation of 93-day-old jack pine seedling cuttings. Cuttings were untreated (Control), or their terminals were removed at the indicated times before (−) or after (+) cuttings were severed from the original seedling root system. IBA (5.7 nmol per cutting) was apically applied to some cuttings immediately after the terminals were removed. Data are means expressed on a per cutting basis. Means with different letters differed significantly (P > 0.95, n = 30). Means for pooled data for all treatment times for Terminal Removed and Terminal Removed + Apical IBA differed significantly (P > 0.95, n = 300).

Time of treatment	Percent rooted	Number of roots	Longest root length (mm)
	Control		
—	80%	2.8a	20.2a
	Terminal Removed		
− 1 day	37	0.8b	3.9b
+ 1 min	17	0.5b	3.2b
+ 1 day	17	0.3b	1.0b
+ 2 days	23	0.6b	2.5b
+ 3 days	40	1.0b	5.9b
+ 4 days	27	0.4b	1.3b
+ 5 days	20	0.6b	2.3c
+ 6 days	33	1.0b	6.5b
+ 7 days	40	0.7b	3.8b
+ 8 days	27	0.5b	3.6c
Mean	28	0.6	3.4
	Terminal Removed + Apical IBA		
− 1 day	47	1.7b	9.6b
+ 1 min	28	0.7b	3.5b
+ 1 day	30	1.2b	6.6b
+ 2 day	33	1.1b	4.2b
+ 3 day	33	2.0b	8.6b
+ 4 day	33	1.2b	6.5b
+ 5 day	43	1.4b	6.8b
+ 6 day	30	1.5b	10.5b
+ 7 day	43	1.0b	3.1b
+ 8 day	53	1.8b	8.2b
Mean	37	1.4	6.8

DISCUSSION

The present results indicated that removing needles or terminals (Figure 3) greatly reduced rooting of jack pine seedling cuttings and, therefore, substantially reduced levels of ERS. On a per part basis, terminals contained substantially more ERS than needles, assuming a linear relation between rooting data and concentration of ERS (compare means, Table 1). On a dry weight basis, the content of ERS in terminals was even greater, compared to needles, because the dry weight of terminals was about one-half that of needles (data not shown). Overall, the data indicated that ERS was rather generally distributed in jack pine seedling cuttings, probably because all of
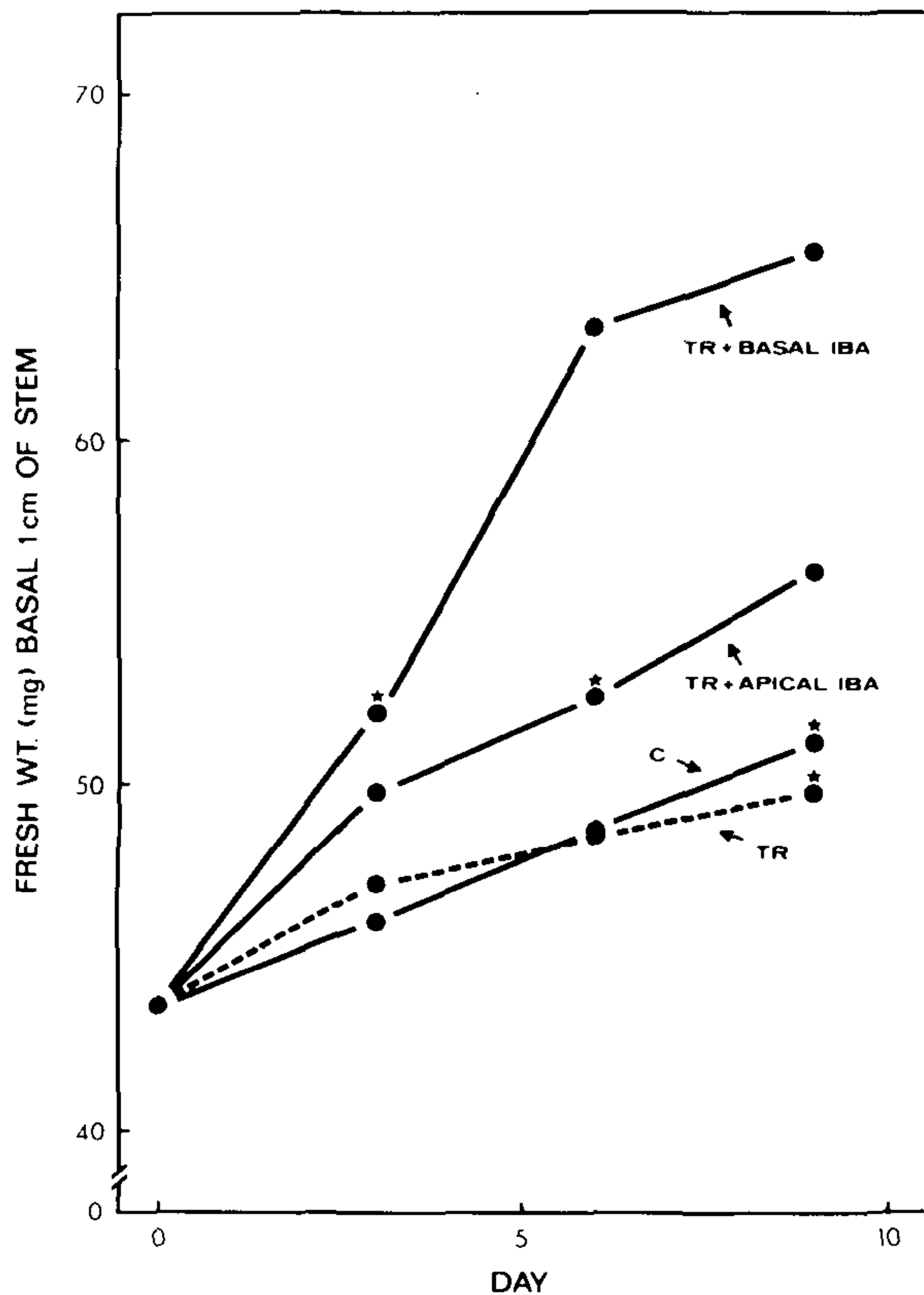
Figure 5. Effect of indole-3-butyric acid (IBA) treatment on fresh weight of basal one cm of stem of 92-day-old jack pine seedling cuttings. Terminals were not (C) or were (TR) removed immediately after cuttings were severed, immediately after which some cuttings were apically (+ Apical IBA, 500 nmol/cutting) or basally (+ Basal IBA, 25 mmol/l) treated with IBA in 100% ethanol. Stars indicate the initial significant (P > 0.95, n = 30) change within each treatment in comparison with day 0. By day 8, means for TR + Basal IBA and TR + Apical IBA differed significantly from means for C and TR, which were equal.

the needles were relatively young and borne on the entire epicotyl (Figure 3A).

The present experiments indicated that auxin ERS enhanced rooting of jack pine seedling cuttings. For example, basally applied IBA increased rooting, in comparison with untreated cuttings (Figure 4). However, applied IBA only partially replaced the effect of terminals (i.e., ERS). As an example, apical application of IBA to cuttings without terminals enhanced rooting, in comparison with similar non-IBA-treated

cuttings, but rooting of the IBA-treated cuttings was still markedly less than in control cuttings with terminals (Table 5). Therefore, ERS in jack pine seedling cuttings consisted of an auxin and a non-auxin component, and applied IBA would not substitute for the non-auxin component, as determined for other species (cf. previous references).

Partial removal of ERS by surgical treatment could have reduced rooting in the present tests by: 1) limiting the rate of callus formation, thereby delaying or preventing the differentiation of cells that were competent to respond to ERS; 2) reducing levels of auxin ERS and/or non-auxin ERS too much to support primordium initiation-development, even though competent cells were present; or 3) a combination of (1) and (2). The following three observations indicated the correctness of postulate (2) and, additionally, that diminished rooting occurred mostly because surgical treatment lowered levels of non-auxin ERS.

Firstly, applied IBA only partially reversed the deleterious effects on rooting that resulted from removing terminals, as discussed previously. Secondly, significant callusing occurred in control cuttings with terminals as early as day 8 in the present experiments, and rooting occurred between day 16-23 (Figure 4). Other tests with identical cuttings have detected a significant increase in basal fresh weight at day 7, when weights were determined daily (18). If removal of terminals (i.e., limiting ERS) had primarily influenced callus formation, the surgical treatment would have been increasingly less deleterious to rooting as the period of propagation increased before treatment. However, the results indicated that rooting was equal when terminals were removed from 1 hour before to 12 days after cuttings were severed from the original seedling root system (Tables 1-5). Thirdly, basal fresh weight was identical in non-IBA-treated cuttings with or without terminals (Figure 5) but removing terminals reduced rooting (e.g., Table 1).

Thus, removing terminals seemed to reduce rooting by direct effects on primordium initiation-develpment. Nevertheless, formation of competent cells was determined by influences of auxin ERS. Firstly, basal application of IBA to non-surgically-treated cuttings resulted in greater callusing-rooting, compared with similar but non-IBA treated cuttings (Figure 4). And, callusing-rooting by untreated and IBA-treated cuttings were positively correlated (Figure 4). The foregoing results indicated that applied IBA acted in the same manner as auxin ERS but, probably because of the higher auxin levels attained at the base of cuttings, applied IBA enhanced the "normal" callusing-rooting responses. Secondly, application of IBA to

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cuttings without terminals increased basal fresh weight, in comparison with similar non-IBA treated cuttings (Figure 5).

In summary the present results indicated for jack pine seedling cuttings that: 1) ERS was more generally distributed throughout the cutting than has been reported for dicotyledonous species (cf previous references); 2) non-auxin ERS was the limiting factor in adventitious rooting; and 3) auxin ERS had roles in both callusing and primordium initiation, whereas auxin ERS is only needed for primordium initiation in non-callusing species.

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