then drops to the muzzle of the gun where it is held ready for planting. Tests carried out since 1957 at the University of British Columbia Research Forest prove that the bullets are shattered by root growth after three or four growing seasons, depending on site quality and rate of growth.

Some of the containers described here were introduced with the sole purpose of improving survival and subsequent growth. This worthy objective is no longer adequate and must be supplemented by mechanical aids. It is already apparent that for biological and mechanical reasons each phase of a container program has important implications for other phases. Because of this, revolutionary techniques of sowing, growing, transporting, and planting will be developed in the very near future. It seems certain that many of these techniques will have applications in agriculture and horticulture as well as forestry and that each of these three sciences will benefit by learning and borrowing from the others.

VICE-PRESIDENT TICKNOR: The moderator for our second session this morning, which is on "Chemicals and Plant Growth", is Dr. J. W. Neill. Dr. Neill is in the faculty of the Division of Plant Science, University of British Columbia, Vancouver. Dr. Neill:

MODERATOR NEILL: I am most happy to be here and to give you my own word of welcome to British Columbia. The subject matter for this session is a very fundamental and important one to all of us — "Chemicals and Plant Growth." Our first speaker is Dr. Dennis Lavender, from the Forest Research Laboratory, Oregon State University, Corvallis. Dr. Lavender has spent some 20 years in forest research in the Pacific Northwest. He is going to discuss the role of growth regulators in the physiology of Douglas fir seedlings. Dr. Lavender:

THE ROLE OF GROWTH REGULATORY SUBSTANCES IN THE PHYSIOLOGY OF DOUGLAS FIR (Pseudotsuga menziesii [Mirb.] Franco) SEEDLINGS

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Douglas fir, in common with most conifers, is characterized by extremely slow seedling growth and by very heterogenous populations. Obviously it does not recommend itself as an experimental organism to physiologists studying basic processes in plant growth. It is not surprising, then, that there are little data describing chemical growth regulation of this species nor that the great majority of the existing information is derived from highly empirical trials. Unfortunately, while

such studies may define areas where more sophisticated techniques may be employed to elucidate physiological phenomena, they do not, in themselves, provide data describing the role of plant growth regulators in Douglas fir physiology.

The first part of this paper will be concerned with the aforementioned trials; the second, with problems we have encountered in our attempts to measure endogenous growth regulators; and the last, with current studies designed to define the role such endogenous regulators play in the physiology of Douglas fir seedlings.

Table 1 is a compilation of the chemicals reported which have been employed in studies of growth regulation of Douglas fir. It does not include, however, such synthetic plant growth regulators as the phenoxy group which have been used primarily as silvicides.

The term "growth retardants" is defined by Cathey (5) as "chemicals that slow cell division and cell elongation in shoot tissues and regulate plant height physiologically without formative effects". Optimum applications of these materials will result in reduced plant size but not reduced vigor or development.

The first such chemical, B-995, is a member of a new class of growth retardants which are somewhat similar to maleic hydrazide (5). It has been shown to retard growth of apples, pears, cherries, and other plants (3). In our laboratory, one-month-old Douglas fir seedlings were sprayed to the drip point six times at bi-weekly intervals with aqueous concentrations up to a maximum of 4,000 ppm. When the four-month-old seedlings were harvested, no treatment effect upon dry weight was found and only the highest concentrations re-

Table 1. Growth Regulatory Chemicals Applied to Douglas Fir Seedlings

B-995 (N-dimethyl amino succinamic acid)
CCC ([2-chloroethyl] trimethylammonium chloride)
Phosfon D (tributyl-2, 4-dichlorobenzyl phosphonium chloride)
maleic hydrazide (diethanolamine salt of 6-hydroxy-3(2H pyridazinone)
naringenin (4′, 5, 7-trihydroxyflavanone)
abscisin II (dormin) (3-methyl-5-[2′, 6′, 6′-trimethyl-1′ hydroxy-4′-keto'cyclo-hexa-2′-enyl] *cis-trans*-2,4-pentadienoic acid)
SD 8339 (6-[benzylamino]-9-[2-tetrahydropyranyl]-9H-purine)
gibberellic acid
indoleacetic acid
alpha-naphthaleneacetic acid
indolebutyric acid
kinetin (6-furfurylaminopurine)
MDB (2-methoxy-3, 6-dichlorobenzoic acid)
TPP (2,4,5-trichlorophenoxypropionic acid)

duced stem elongation (32). Further, Pharis *et al* (27) report no significant effect of an 8,000 ppm soil drench applied twice weekly for two months upon the growth of two-year-old Douglas fir seedlings.

The second compound, a quarternary ammonium compound abbreviated CCC, is an analogue of choline. It has been shown to retard the growth of the majority of plants tested (5). Lang and co-workers have concluded that the mode of action of CCC is inhibition of the biosynthesis of gibberellins which are required for growth processes (16, 25). Workers at the Earhart Plant Research Laboratory report that CCC applied as a 5,900 ppm soil drench twice weekly for two months had no significant effects upon the growth of two-year-old Douglas fir seedlings (27). Similarly we have found that this chemical is not effective in retarding the growth of Douglas fir seedlings when employed as a soil drench at concentrations up to 0.02% of soil weight of the active material. However, seedlings sprayed at bi-weekly intervals with concentrations up to 2,500 ppm active ingredient developed marked chlorosis and greatly shortened crowns. Plants treated with 2,500 ppm were very bushy and weighed less than one third of the control seedlings at the end of the four month study (32).

A second quarternary compound, phosfon-D, has been reported to reduce internode growth and to produce dark green leaves for a number of test plants (5). In common with the previous two retardants, this chemical has been most effective when applied to dicotyledons. Several trials with Douglas fir seedlings have demonstrated either no, or erratic, height growth control, but increasing levels of the chemical in the soil—up to a maximum of five grams of active material per quart of soil—resulted in increasing chlorosis of the seedling foliage (22, 27, 38).

In contrast to the above compounds, Cathey (5) describes maleic hydrazide as a "growth inhibitor", a class of compounds which may suppress growth completely in treated plants. Maleic hydrazide suppresses apical dominance and frequently results in plants with greatly shortened internodes and dark green foliage (5). One-year-old Douglas fir seedlings in nurseries in England were sprayed with 0.05, 0.1, and 0.2% aqueous solutions of maleic hydrazide during the period of bud swell in the spring (15). The purpose of such treatment was to control seedling size and late season flushing, but no significant response in seedling growth was noted. In contrast, seedlings sprayed with maleic hydrazide in late summer in the Nisqually Forest Nursery failed to form terminal buds and subsequently died during the winter[1].

The next two compounds, naringenin and abscisin II (dormin) have been shown to be associated with the biochemistry of dormancy of certain perennial plants. Hendershott and

[1]Personal communication from Dr J W Duffield, December, 1962.

Walker (18) and Phillips (28) have shown that naringenin is present in extracts from dormant peach flower buds and apparently plays a role in maintaining dormancy in this species. It is one of the flavenoids reported to occur naturally in the flowers, but not in other tissues of Douglas fir (21). However, there is no evidence that the dormant buds of Douglas fir were examined for this chemical. Two-month-old Douglas fir seedlings were sprayed to drip point at our laboratory with aqueous solutions of naringenin from 5 to 625 ppm at six bi-weekly intervals. The seedlings were maintained under an 18-hour photoperiod and a 25°-15° C. thermoperiod. A similar second trial employed 1% naringenin in lanolin applied to seedling epicotyls. No effect of the treatment on height growth or on initiation of dormancy was noted in either experiment.

Abscisin II (dormin) has been found in birch and sycamore, cotton, and a wide range of other higher plants (9, 10, 11, 13). Wareing and co-workers have shown this substance to be associated with growth inhibition or dormancy in both birch and sycamore (13, 33). In our laboratory, two-month-old Douglas fir seedlings were sprayed to drip point one, two or three times at bi-weekly intervals with concentrations of from 0 to 25 ppm. The seedlings were maintained under an 18-hour photoperiod and a 25°-20° C. thermo period for three months after treatment. No treatment effects upon seedling crown length, total dry weight, or initiation of dormancy were found at the conclusion of the study. No effects of the application of this chemical in lanolin at concentrations of 0.1 or 0.01% upon seedling growth were noted in a parallel trial. The data may reflect the low concentrations of active material employed, although one part of abscisin per billion has been reported to cause detectible inhibition of *Lemna minor* growth (26). However, without definitive data upon the absorption and translocation of this material by Douglas fir seedlings, it is impossible to determine if the lack of response was caused by the inactivity of abscisin in Douglas fir or the failure of the plant to absorb or translocate the material to an active site.

The remaining compounds in Table 1 are generally considered to be growth promoters and are termed "cytokinins", "gibberellins" or "auxins".

Cytokinins have held a fascination for plant physiologists ever since their discovery a few years ago. One of their disappointing properties, however, was that they do not seem to be translocated in the plant. If applied to a leaf, they tend to remain in that leaf. Dr. J. van Overbeek, at the Shell Development Laboratory, Modesto, California, attempted to formulate a cytokinin which would be translocated in plants. The result was SD 8339, the code number for 6-benzylamino-9-(tetrahydropyranyl)-9H-purine. This compound did appear to be translocated in plants and appeared to be a plant growth reg-

ulator. When applied to grapes, it increased fruit set and increased the size of the berries (36).

Two-month-old Douglas fir seedlings were treated with concentrations of SD 8339 as both aqueous foliar sprays and in lanolin paste, according to the schedule presented in Table 2.

Table 2. Treatment Schedule for SD 8339

Aqueous spray (*to drip point*)

(1) Control — 3% "Tween 20" and 6% ETOH.
(2) 500 ppm SD 8339 in above solution.
(3) 1000 ppm SD 8339 in above solution.
(4) 5000 ppm SD 8339 in above solution.

Solutions applied: (a) once; (b) three times (at bi-weekly intervals) or (c) 5 times (at weekly intervals).

Lanolin (*applied to either stem tip or cotyledons*)

(1) Control — pure lanolin.
(2) 0.1% SD 8339 in lanolin.
(3) 0.5% SD 8339 in lanolin.
(4) 1.0% SD 8339 in lanolin.

Lanolin paste applied: (a) once; (b) three times (at bi-weekly intervals); Control: Untreated, intact seedlings. All treatments tested on 10 Douglas fir, two-month-old seedlings.

Figure 1 illustrates the range of effect of the treatments. The first two lanolin treatments produced little change in the seedling growth and are represented by the seedlings in pots 1, 2, and 3 while the high concentration is represented by pots 5-6 (control seedlings are also represented by seedling in pot 1). In contrast the increasing concentrations of aqueous sprays resulted in the increasing effect upon seedling growth shown by the plants in pots 4 to 6 until the highest concentration resulted in dying or dead seedlings (pots 7 and 8).

A member of the second major class of plant growth promoting chemicals, gibberellic acid, has been shown to be an effective growth promoter for a wide range of plants, but, in general, the greatest response has appeared in herbaceous angiosperms (24). Gymnosperms have generally shown little or no response to applications of this compound (29). Ching and Ching (7) reported that Douglas fir pollen demonstrated greater pollen tube growth and more rapid cytological development on a nutrient agar with up to 1000 ppm of the potassium salt of gibberellic acid than did pollen germinated on a control medium. Richardson (30, 31) has shown that low (5-10 ppm) concentrations of gibberellic acid can stimulate the germination of non-stratified Douglas fir seed as well as increase the growth of radicles of newly germinated seeds.

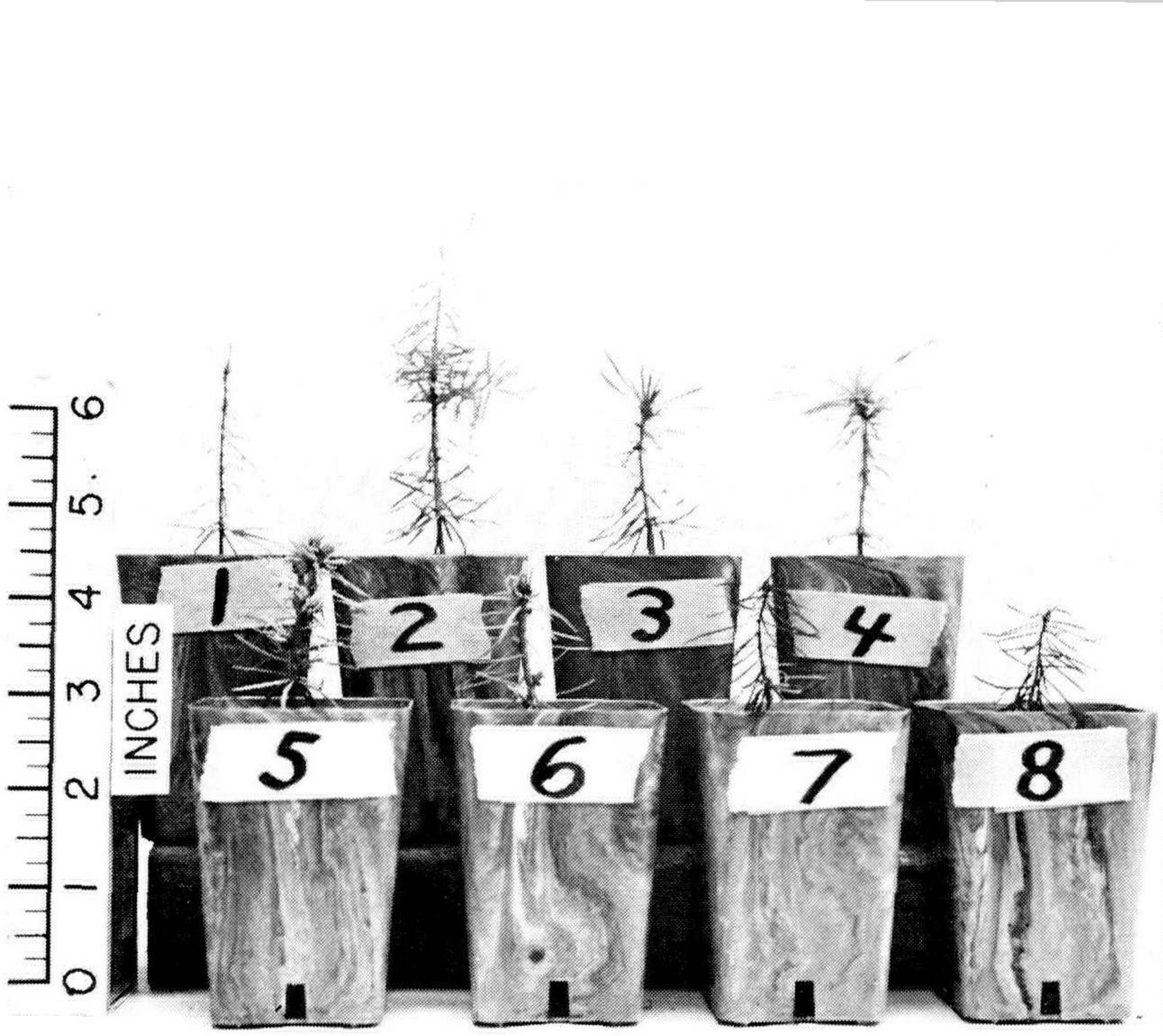

Figure 1. Effects of SD 8339 upon the growth of Douglas fir seedlings. Seedling 1, control; seedlings 7 and 8 treated with 5000 ppm aqueous spray. Note proliferation of lateral buds near apices of seedlings 3 to 6.

However, attempts to modify the growth of older seedlings, under greenhouse and under field conditions, have not only failed to produce a positive response (8, 19, 29, 35) but, in one trial (29) actually killed the seedlings. It should be noted that all these studies reported the use of gibberellic acid. It may be that one of the other more recently isolated gibberellin compounds will be found to be effective on Douglas fir (27).

Indoleacetic acid, the major native indole auxin in plants, was first reported by Went (37). This compound is thought to be universally present in higher plants, but the only recorded data on its occurrence in Douglas fir are the inconclusive chromatographic studies of Dinus (12). Experience with other coniferous species convinces us, however, that the negative data reported by Young (39) were very probably a result of the experimental procedures and not by a complete lack of diffusible indoleacetic acid in the test seedlings. Evidence that growth regulators might hasten the onset of dormancy of Douglas fir seedlings[1] prompted trials with indoleacetic acid at our Corvallis nursery. No effects upon seedling phenology were noted after treatment with aqueous sprays of 125 ppm indoleacetic acid in May, June, July, August. However, trials in a controlled environment chamber demon-

[1]Personal communication from Dr. J. W. Duffield, 1962.

strated that one-month-old Douglas fir seedlings produced twisted, rigid shoots when sprayed with indoleacetic acid solutions at 200-300 ppm. Shoot elongation and shoot dry weight were generally reduced by this treatment (32). Lavender and Hermann (23) reported that 100 micrograms of indoleacetic acid applied in lanolin paste to decapitated seedling apices significantly increased production of xylem elements.

Although naphthaleneacetic acid is not a natural plant hormone (4), it has been shown to produce many of the growth responses engendered by indoleacetic acid but is, in general, somewhat less effective (4). Dr. J. W. Duffield found that aqueous sprays of NAA at 125 to 250 ppm applied in August produced early dormancy in Douglas fir seedlings.[1] He also reported that similar spray treatments appeared to increase root regeneration of Douglas fir seedlings lifted in November and December (2). Heitmuller (17) notes that Douglas fir cuttings soaked for 24 hours in a 0.0005% (5 ppm) solution of the potassium salt of naphthaleneacetic acid rooted vigorously, while a six-hour period of soaking in 0.002% (20 ppm) naphthaleneacetic acid plus 0.002% (20 ppm) indoleacetic acid yielded slightly less favorable results.

The final compounds shown in Table 1 have been employed (indolebutyric acid both singly and in combination with naphthaleneacetic acid) in rooting trials of Douglas fir cuttings at Oregon State University's North Marion Experiment Station. Unfortunately, Dr. Ticknor reports only erratic success with indolebutyric acid and virtually none with the remaining compounds.[2]

The above discussion demonstrates that Douglas-fir is much less responsive than many angiospermous plants to the major classes of plant growth regulating compounds. This may reflect a more primitive physiology which would be consistent with the generally accepted theory of the relative primitive development of conifers in general and *Pinacease* in particular, vis-a-vis the angiosperms. This primitive physiology is also reflected by the nature of the pigments in Douglas-fir flowers. These flavanoid substances are much less complex than the pigments of angiosperms.

We are concerned with the detection of growth regulators in Douglas fir. In the past, portions of grass seedlings have been used for the assay of growth regulators, the most well-known assay being the *Avena* coleoptile curvature test. The popularity of the various *Avena* bioassays and similar bioassay systems is probably a result of the historical development of the study of hormones and the relative speed and ease with which these bioassays can be conducted compared with alternative methods. For meaningful results applicable to the intact plant, however, the bioassay tissue should be of the same species as the tissue from which the extract is made. Thus,

[1]Personal communication from Dr J W Duffield, 1962

[2]Personal communication from Dr Robert L Ticknor, August, 1967.

Douglas fir tissue is desirable as a sensing element for growth regulators extracted from Douglas fir tissue.

It would be preferable to use the entire plant in a bioassay, not just one portion of it. The intact plant would be more likely to contain all of the cofactors necessary for the manifestation of a naturally-occurring plant growth regulator. Furthermore, since our ultimate goal is to identify growth regulators which might be used to control the growth of Douglas fir, the intact plant is most likely to tell us what we want to know. If that approach fails, the next-best procedure would be to use portions of Douglas fir plants, preferably tissue such as a meristem, which would be likely to respond to growth regulators.

We have tried both these approaches in our attempt to develop a bioassay. To date we have not found a usable system. With indoleacetic acid as a standard of sensitivity, we cannot elicit a response from intact seedlings with less than about 10 micrograms of indoleacetic acid per plant. That response, which is a bending, is too variable to be useful. Flemion (14) grew excised Douglas fir embryos on filter paper to determine their germinative capacity. We tried to detect indoleacetic acid with excised embryos using her technique but got no response at all. Our attempts at adapting Allen's (1) pine hypocotyl test to Douglas fir have met with serious problems of bacterial contamination so we have not been able to evaluate that method satisfactorily. The hypocotyl section test seems to hold the most promise at this time.

Bioassays using Douglas fir tissue are not easy to conduct; seed must be stratified and germinated, germinants must be grown to the desired size, and the bioassay itself may take several days or even a week to conduct. Considerable planning is required to have plants ready for a bioassay when they are needed. In addition, a large inherent variability must be accepted. The advantages of a bioassay using Douglas fir outweigh these disadvantages, however. We plan to continue our search for a usable bioassay with Douglas fir tissue.

In his review, "Dormancy in Woody Plants", Samish (34) suggests that the dormant period of perennials is not a homogenous phenomenon, but rather a series of distinctly different physiological states. He terms these periods as "quiescence", "preliminary rest", "mid-rest", and "after-rest". Each state is defined by the growth response produced by an environment favorable to growth. The growth which may be expected during quiescence, preliminary rest, or after-rest is much more vigorous than that which occurs during mid-rest.

Interest in the natural and potential artificial regulation of dormancy in Douglas fir was stimulated at Oregon State University by evidence that seedlings disturbed during routine nursery harvest procedures in the period from late September until early December were much less able to withstand

stress than were plants harvested from December to March (20). One tenable hypothesis for these data is that physical disturbance during the "mid-rest" phase of dormancy results in a severe delay in the normal sequence of concentrations of growth regulators.

The first of a series of experiments expected to establish the validity of the above hypothesis was designed to define the seedling tissues which are the sites of growth regulator synthesis during the dormancy period. Data from this study indicated that: (a) seedling buds are the major site of synthesis of growth regulatory material; (b) the growth stimulatory substance (or substances) produced by active buds are not translocated to dormant buds; (c) lateral meristem growth is stimulated by materials exported by acropetal active buds; and (d) root growth is independent of shoot activity (23).

The second series of experiments was conducted to ascertain whether application of growth regulatory materials to decapitated seedling apices cculd change the regulatory system for the plant as a whole. These materials, (indoleacetic acid and gibberellic acid) did not affect the activity of the roots or buds nor did they stimulate lateral meristems in stems with respect to controls, except in the period of transition from mid-rest to after-rest. The effect of indoleacetic acid in this period of transition provides a clue to the manner in which the growth-regulatory system may work. In the fall buds may contain such an accumulation of inhibitors that meristems cannot be activated even with the application of exogenous growth promotors. At the end of mid-rest, the biological activity of the inhibitors seems to diminish but synthesis of intrinsic auxin is not sufficient to stimulate the growth of lateral meristems as much as does the application of exogenous indoleacetic acid. It is during this period, also, that the effect of long photoperiods in stimulating bud activity first begins to lessen, and that the foliage appears to export materials which may stimulate buds (23). In after-rest, concentrations of inhibitors in the buds are very probably sharply reduced and the production of auxin increased to a level where addition of exogenous auxin fails to stimulate meristematic activity (20).

The third year's experiment was designed to measure the effects of girdling, defoliation, and debudding of seedlings, together with applications of indoleacetic acid and gibberellic acid (19). Data obtained from this study indicate that: (a) the activity of seedling root systems, although apparently independent of measurable shoot growth is, in fact absolutely dependent upon materials exported from the shoot; (b lateral meristems of seedlings which were defoliated produced no new xylem elements until the growth of acropetal buds had produced fully expanded foliage (this is in contrast to growth of lateral meristems in intact seedlings which was stimulated

by the swelling of acropetal buds); and (c) gibberellic acid may stimulate proliferation of cortical tissue, but, unlike indoleacetic acid, does not stimulate production of xylem elements.

Future experiments will be designed to isolate and identify the substances exported from buds and foliage, to determine their levels during the different phases of the dormant period, and to elucidate the effects of nursery practice upon the endogenous rhythm in the levels of growth regulating materials in Douglas fir seedlings.

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MODERATOR NEILL: We now have Dr. Fenton Larson from the Department of Horticulture, Washington State University at Pullman. He will speak on the subject of chemical defoliation of deciduous woody plants. Dr. Larson: