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Influence of CO_2, moisture and nutrients on the formation of Lammas growth and prolepsis in seedlings of *Pinus silvestris* L.

Inverkan av CO_2, vatten och näring på bildningen av sommarskott hos plantor av *Pinus silvestris* L.

by

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ABSTRACT

Results are presented from a study concerning the influence of environmental factors on the formation of summer shoots in young plants of *Pinus silvestris* L. grown in plastic green houses. A close relationship is found between the studied factors: CO_2, water, nutrients and the occurrence of summer shoots. Poor environmental conditions during the first year followed by improved conditions in the following year resulted in a great number of plants with summer shoots, whereas favourable conditions during the first year resulted in a low number of plants with summer shoots the following year.

According to these results the conclusion is drawn that environmental conditions and especially those of the preceding year have a great influence on the formation of summer shoots and on the shoot growth as well.

As a hypothesis it is discussed that carbohydrates in the plant may influence the formation of summer shoots and that this influence is mediated by growth regulators.

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1. Introduction

Shoot growth in most woody plants is in general a two-year process with formation of buds during the first year and development of shoots during the following year after a period of dormancy. Under certain conditions, however, summer shoot may occur, i.e. the shoot develops during the summer in the same year in which the bud is formed. So far, this phenomenon has been very rare among pine trees and in practice of small importance. In experiments with seedlings of *Pinus silvestris* L. in plastic greenhouse it has turned out that the frequency of plants with summer shoots has increased to a considerable extent in comparison with conventional growing in open air. The aim of this study has been to investigate the importance of environmental factors for the formation of summer shoots in young *Pinus silvestris.*

Second flushing has been described in the literature by many terms like "second shoot", "midsummer growth", "late season growth", "summer shoot" and "proleptic shoots". However, these terms do not distinguish between shoots formed from the terminal bud and shoots formed from lateral buds at the base of the terminal bud. As these two types of shoots influence the tree form in different ways, it is in this case of importance to distinguish between the two types of shoots. Therefore in this text the term *proleptic shoots* refers to shoots which are formed from lateral buds at the base of terminal buds after the first flushing is completed. The term *Lammas growth* refers to shoots which are formed from terminal buds in the same way. This terminology has previously been used by other authors, among others Rudolph (1964) and Kozlowski (1964 *b*). The term *summer shoot* is used when both types of second flushing are referred to.

There are different theories about factors influencing the formation of summer shoots in woody plants. Water supply as well as nutrients and accumulated carbohydrate reserves may be involved in its formation (Fraser 1958). The tendency for summer shoots is greatest in young plants and decreases with the age of the tree. Kovalenko (1960) found a comparatively great number of Lammas shoots in one to five-year-old *Pinus silvestris* and *Pinus pallasiana* Lamb. but no such shoots were found in the same species that were 10—20 years old.

Walters & Soos (1961) pointed out that the formation of Lammas growth probably was more influenced by environmental than by genetic factors. However, even genetic control may be involved. Rudolph (1964) found that in *Pinus banksiana* Lamb. Lammas growth and prolepsis and their combinations varied significantly between different provenances which had been studied in nurseries. Therefore he considered Lammas growth and prolepsis to be mainly under genetic control. Ehrenberg (1963) found in *Pinus silvestris* genetic differences between individual progenies and provenances and, moreover, a great influence of the environment on the occurrence of prolepsis.

However, the only way environmental and hereditary factors can affect tree growth is by physiological processes in the plant (Kramer & Kozlowski 1960). Experimental evidence indicates that hereditary and environmental factors can influence tree growth through growth-regulating substances. Thus, the formation of Lammas growth has been suggested to be dependent on factors influencing the concentration of growth-promoting substances in the plant (Studhalter 1955). Already in 1928 Reed suggested a connection between the occurrence of growth-promoting substances and Lammas growth in lemon. Since then many other investigators have accepted the same basic idea, e.g. Danilov (1946) and Champagnat (1954).

This study has been carried out during the years 1967 to 1969 at the Ågrena experiment nursery situated in the central part of Sweden where the Department of Reforestation at the Royal College of Forestry in 1965 started a research and development project with the working name: “Operation mechanical planting”. One of the aims of the project was to create and investigate an alternative to the conventional method of growing forest tree seedlings in open air. This was carried out in plastic greenhouses where seedlings of forest trees were grown in different levels of nutrients, water and carbone dioxide in order to bring about optimum environmental conditions. Preliminary results from these experiments have been presented by the initiator and project leader Professor Gustaf Sirén, Royal College of Forestry (Sirén 1967, 1968, 1969).

2. Material and methods

The experiments may be divided in two groups, those with the aim of studying the influence of environmental conditions during the preceding year and those with the aim of studying the influence of current conditions on the formation of summer shoots in Scots pine *(Pinus silvestris)*. For the experiments two different types of greenhouses have been used, the Finnish Usko-house in 1967 and 1968 and the Swedish Deje-house in 1969.

In all experiments peat was used as growth substrate and nutrients were supplied in solution (Wallco L-65/13; for the composition see Ingestad 1967). Ca and Mg were supplied as dolomite which was mixed in the peat before sowing in an amount of 1 kg/m^3 peat. In experiments with CO_2, nutrients and water were supplied through irrigation systems in the greenhouses while in other experiments this was done manually.

A soil moisture of 80 % of the saturation value of peat was used which has turned out to be the optimum value for growth of pine seedlings in peat (Elowson 1971).

The seed was of a Värmland provenance and of the same origin in all experiments (no. 14670).

In the following text the term 1/0-plants stands for plants which are grown one season, 2/0-plants stands for plants which are grown two seasons and are not transplanted and the term 1/1-plants stands for plants which are grown two seasons and are transplanted after the first season.

Measurements of height were made every other week according to statistical methods used in the nursery experiments. The height of the plants was measured from the ground to the terminal bud, i.e. occurring Lammas shoots are included in these measurements of two-year-old plants. This may to some extent influence the results from the height measurements in these experiments. The distribution of Lammas growth in the different experimental plots shows that they are most frequent in plots showing poor height growth and vice versa (Fig. 1, Table 2 a) which to a certain degree bring about an equalization of differences in height growth. The mean values from the height of the different plots were calculated and compared. As only one ecological factor was varied between the different plots this procedure seems to be a satisfactory way of obtaining a measure of the optimum degree which was used. The total number of summer shoots in the different plots were recorded about every fortnight.

2.1. Experiments with CO_2

After preliminary experiments in 1965 and 1966 an experiment with different levels of CO_2 was started in 1967. This experiment was arranged in 10 blocks which each consisted of 600 1/1-plants and sown plots measuring 3 m^2. Two of the greenhouses employed were divided into four sections of equal size by walls of plastic. Each section constituted an experiment block. In the different sections CO_2 was supplied at a level of 1,200, 2,400, 3,000, 3,600 ppm respectively. With an approximative level in normal air of 300 ppm these values correspond to an increased CO_2-level of 4, 8, 10 and 12 times respectively. In the following year (1968) the walls between the different sections were removed. In one house the CO_2-level was held at 3,000 ppm and in the other no CO_2 was supplied. All plastic foil in the greenhouses was PVC which has a very slight permeability to CO_2. The experiment also included reference areas in the open air and in greenhouse without CO_2-supply.

During 1967 the CO_2 was supplied from CO_2-tubes which were connected by plastic tubes with the different sections. In each section perforated tubes were connected and placed on the ground. The CO_2-supply was controlled by a timer (Micro-Matic type 6-111) which through a magnetic valve controlled the flow from the gas tubes. In addition, there was a light relay (Micro-Matic type F) which at a given light intensity increased the CO_2-supply in order to compensate the greater CO_2-consumption by the plants at higher light intensities. The timer was adjusted so that the gas flow started approximately one hour after sunrise and was closed about half an hour before ventilation began. In the afternoon the CO_2-supply was started manually when ventilation of the greenhouses had ceased and continued until one hour before sunset. In every section the CO_2-supply could be adjusted by a graduated valve. Control of the CO_2-level was made every day, at which time all values as well as adjustments were noted. A Riken-Keiki CO_2-analyzer was used for these measurements. During 1968 and 1969 the CO_2-source was propane burners which were placed in the middle of the houses. The CO_2-supply was controlled by a timer and a light relay as described above. The results from the experiments with CO_2 will be reported in a separate paper (Sirén & Aldén 1971).

2.2. Experiments with water

The occurrence of summer shoots in different levels of water was investigated in experiments carried out by Elowson (1971). The plants were sown under the standard conditions of the nursery. During their second vegetation period the plants were grown in five different levels of moisture namely 50, 60, 70, 80, and 90 per cent of the saturation value of peat. Each experimental plot consisted of a plastic container measuring 40 × 60 × 10 cm in which 50 plants were placed. The moisture was checked by weighings and the amount of water which was supplied to the containers was determined in this way. Three different series with three repetitions of each moisture level were included in the experiments which were performed in a greenhouse without CO_2-supply. In all about 2,250 1/1-plants were studied in this experiment.

2.3. Experiments with nutrients

The influence of nutrients on the formation of summer shoots was studied in a two-years experiment. During the first year the plants were sown and supplied with nutrients at four different levels namely 0.5, 1.0, 1.5 and 2.0 g N per m^2 and week. During the following year the nutrient supply was 3.0 g N per m^2 and week in all plots. Before the second year the plants were thinned so that there were 50 plants in each container. These were of the same type as described above. The experiments were carried out in a CO_2-atmosphere of 3,000 ppm. In all 1,800 plants were included in this experiment.

3. Results

The studied environmental factors: CO_2, water and nutrients all had influence on the formation of summer shoots. From the experiments it is clear that there is a connection between environmental conditions during the preceding year and the occurrence of summer shoots during the following year. Plants which were grown under favourable environmental conditions during the first year had a smaller number of summer shoots during the following year than plants which were grown under less favourable conditions during their first year.

Figure 1 shows that the height growth during the first and second year was best at a CO_2-level of 3,000 ppm. Figure 2 shows the occurrence of summer shoots in the same experiment during the second year. From Figure 3 the same tendency is obvious in spite of less optimum conditions during the second year.

In experiments with nutrients the supply was varied only during the first year. During the following year the nutrient supply was equal to all plots. Figure 4 reveals that the best nutrient conditions during the first year resulted in a decreased number of plants with Lammas growth and prolepsis during the next year, while suboptimum nutrient supply during the first year caused an increased number of plants with Lammas growth and prolepsis during the following year.

These two experiments indicate that favourable environmental conditions during the *first year* result in small occurrence of summer shoots in the following year, while the following two experiments show that improved environmental conditions during the *second year* result in an increased number of plants with summer shoots.

Elowson (1970) has proved that the optimum substrate moisture for growth of pine seedlings in peat is about 80 per cent of the saturation value. Figure 5 illustrates the fact that the greatest number of plants with Lammas growth and prolepsis occurred in plots with the most favourable moisture conditions.

In one experiment plants were sown under the standard conditions of the nursery, i.e. without CO_2-supply and with standard supply of water and nutrients. Before their second growing season the plants were placed in different CO_2-levels. During the first shoot growth in

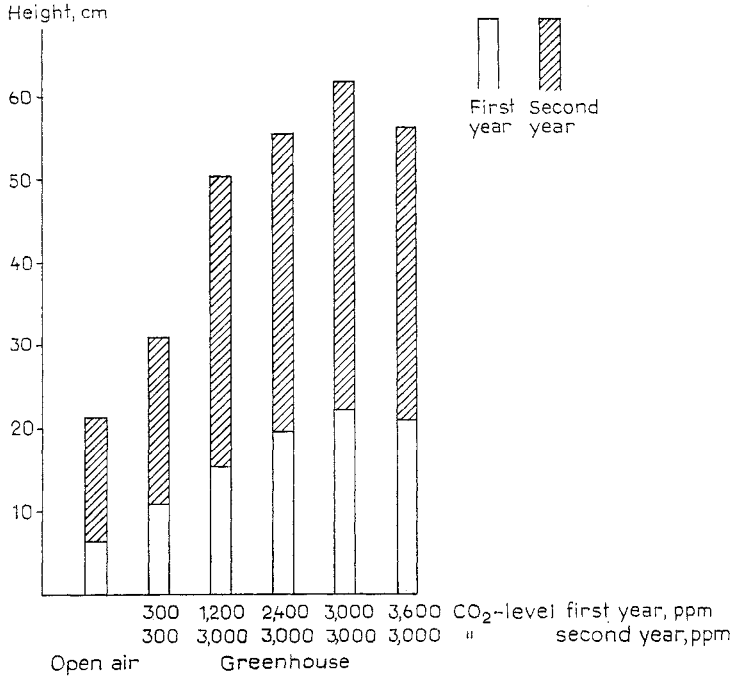

Figure 1. Height growth of Scots pine during two years in different levels of CO_2.

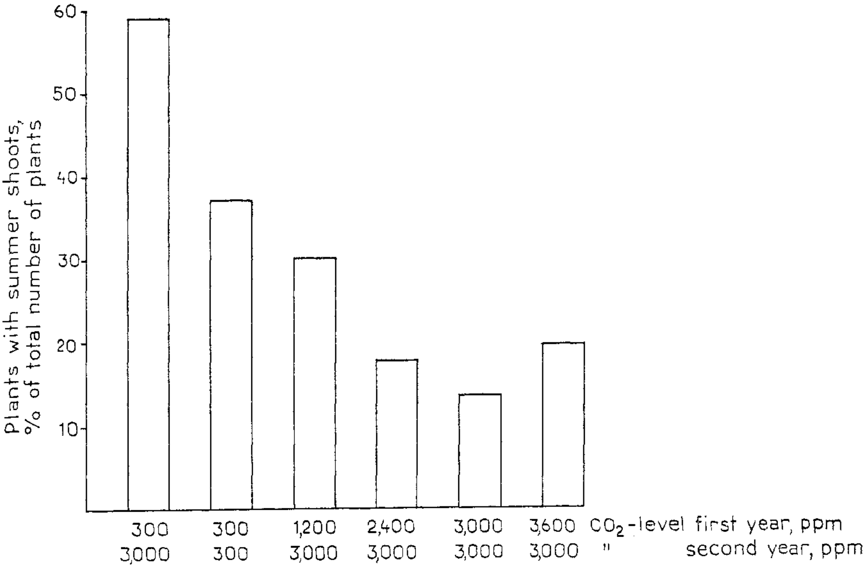

Figure 2. Occurrence of summer shoots in 2-year-old ($^1/_1$) plants of Scots pine. The plants are grown in the different CO_2-levels as indicated. No summer shoots were noted in plots in the open air.

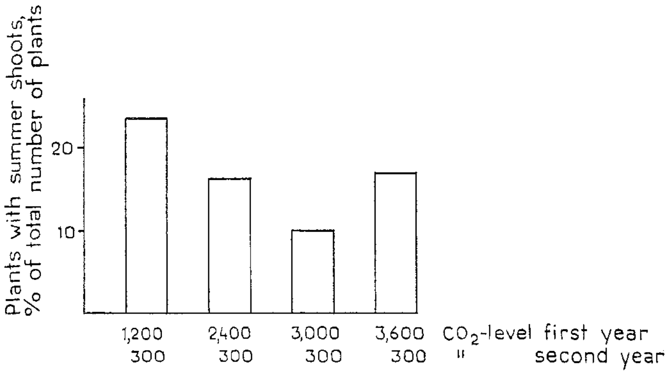

Figure 3. Occurrence of Lammas growth and prolepsis in 2-year-old ($^1/_1$) plants of Scots pine. The plants are grown during the first year in different CO_2-atmospheres and during the second year in the same CO_2-atmosphere.

spring there were only small divergences between plants in different CO_2-levels in this experiment. However, examination of the occurrence of summer shoots in the later part of the summer showed that there were great differences between the varied treatments. Figure 6 shows that the number of plants with summer shoots was greatest in CO_2-levels which previously were proved to be the most favourable for growth.

Shoot growth seems to be more dependent on the conditions of the preceding year than of current conditions (Figure 7). However, the

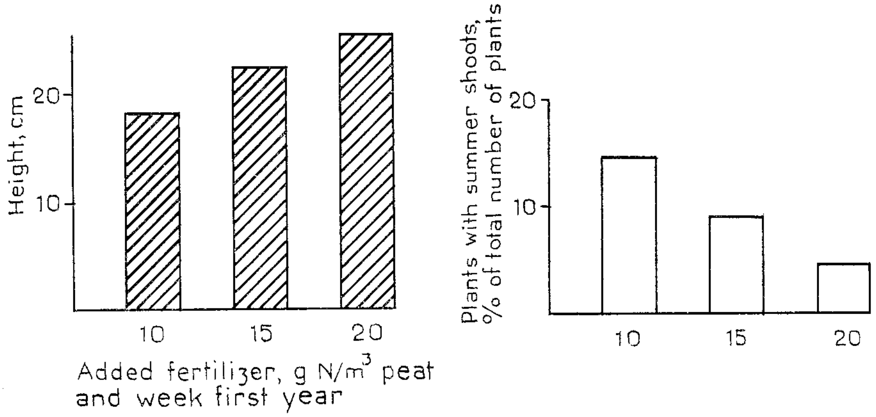

Figure 4. Influence of different nutrient supply during the first year on current height growth and on the occurrence of summer shoots during the following year. Plants not transplanted.

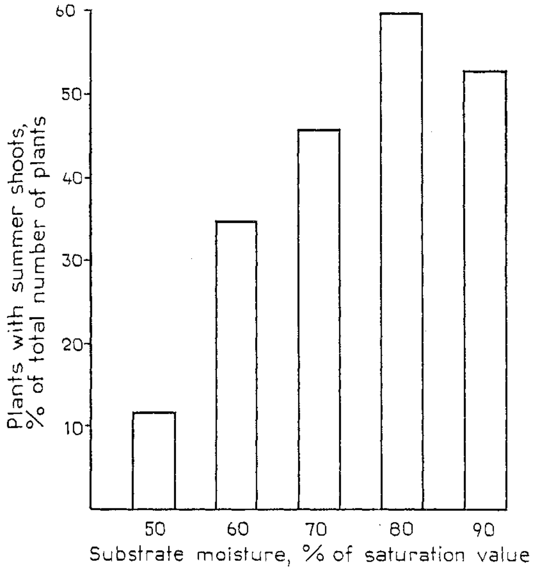

Figure 5. Influence of varied substrate moisture during the second year on the formation of summer shoots in 2-year-old ($^1/_1$) plants of Scots pine. During the first year the plants were grown under standard conditions of the nursery.

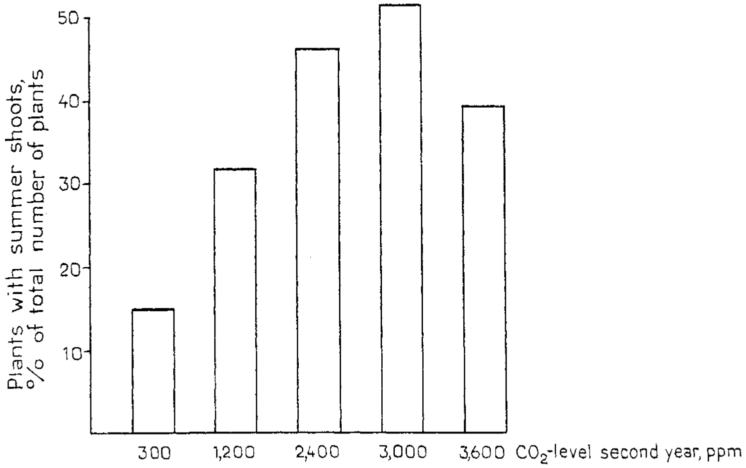

Figure 6. Occurrence of summer shoots among 2-year-old ($^1/_1$) plants of Scots pine which during their first year were grown in greenhouse without CO_2-supply and during the second year in different levels of CO_2.

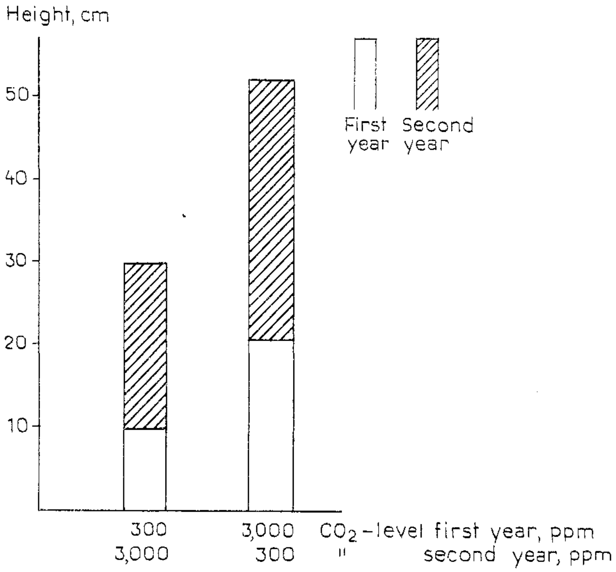

Figure 7. Comparison between the height growth of 2-year-old ($^1/_1$) plants which are grown in 3,000 ppm CO_2-atmosphere during the first and second year respectively and the other year without CO_2-supply.

Table 1. Height growth during the second year in per cent of the height growth of the first year.

CO_2-level first year, ppm	300	300	3,000	3,000
CO_2-level second year, ppm	300	3,000	300	3,000
Relative growth, %	186	200	156	180

elongation will not be entirely independent of current environmental conditions. From Table 1 it is clear that an increase of CO_2 during the second year causes an increased relative elongation growth. Lowering of the CO_2, on the other hand, causes a somewhat decreased relative growth in comparison with unchanged conditions.

In all experiments the most frequent type of late season growth was proleptic shoots, i.e. shoots formed from the lateral buds at the base of the terminal bud (Figure 8 a). In connection with the formation of proleptic shoots there is a strong inhibition of the apical dominance which thus results in a fork-shaped plant. However, in plants which have been studied for two years after the formation of summer shoots the terminal bud flushed in a normal way in the following spring. In some cases the terminal shoot has been somewhat shorter than these formed from buds on the proleptic shoot of the previous year. Occasionally a new leading shoot has been formed in this way.

When Lammas growth occurs it is generally in combination with proleptic shoots (Figure 8 b). Lammas growth alone occurred only in exceptional case which makes it possible to neglect the few occurring plants of this type in the text. The occurrence of proleptic shoots and the combination Lammas growth—proleptic shoots at different times during the summer is represented in Table 2 a. The ratio between these two types of late season growth is shown in Table 2 b. Comparing the figures of 25 June and 16 September in Table 2 b it is clear that Lammas growth in combination with prolepsis becomes an increasing part of late season growth during the later part of the summer.

In some respects summer shoots have different morphological characteristics in comparison with normal ones. Thus, commonly there are three needles in each whorl on summer shoots, while the normal number is two (Figure 8 a, 8 b). Another type of shoot is shown in Figure 8 c. This type bears single primary needles of the same type as in one-year-old plants. Even the buds in this type of shoots are the typical "juvenile" ones, i.e. one single bud without any laterals.

Table 2 a. Occurrence of summer shoots at different times during summer. Figures given in per cent of total number of plants in each plot. Figures in brackets refer to plants with both Lammas growth and prolepsis.

CO_2 level, ppm		Date of survey				
1967	1968	25/6	10/7	25/7	15/8	16/9
300	3,000	41.2(17.4)	46.4(19.6)	49.6(22.2)	53.4(24.9)	57.0(26.9)
300	300	1.0(—)	13.2(5.2)	20.6(8.5)	29.4(10.3)	36.7(15.2)
1,200	3,000	4.3(1.7)	20.1(7.5)	22.5(8.2)	26.4(9.2)	29.3(13.5)
2,400	3,000	2.6(0.2)	12.4(5.0)	14.5(4.3)	15.3(5.8)	18.3(8.1)
3,000	3,000	4.1(1.1)	9.4(3.7)	11.8(5.2)	12.0(5.4)	12.1(6.2)
3,600	3,000	5.5(1.5)	15.5(3.2)	17.8(5.7)	20.2(8.7)	20.4(11.0)

Table 2 b. Occurrence of plants with both Lammas growth and prolepsis at different times of the summer. Figures given in per cent of the total number of plants with summer shoots.

CO_2-level, ppm		Date of survey				
1967	1968	25/6	10,7	25/7	15/8	16/9
300	3,000	42.2	42.2	44.7	46.6	47.1
300	300	—	39.3	41.2	35.0	41.4
1,200	3,000	39.5	37.3	36.4	34.8	46.0
2,400	3,000	7.6	40.3	29.6	37.9	44.2
3,000	3,000	26.8	39.3	44.0	45.0	51.2
3,600	3,000	27.2	20.6	32.0	43.0	53.9

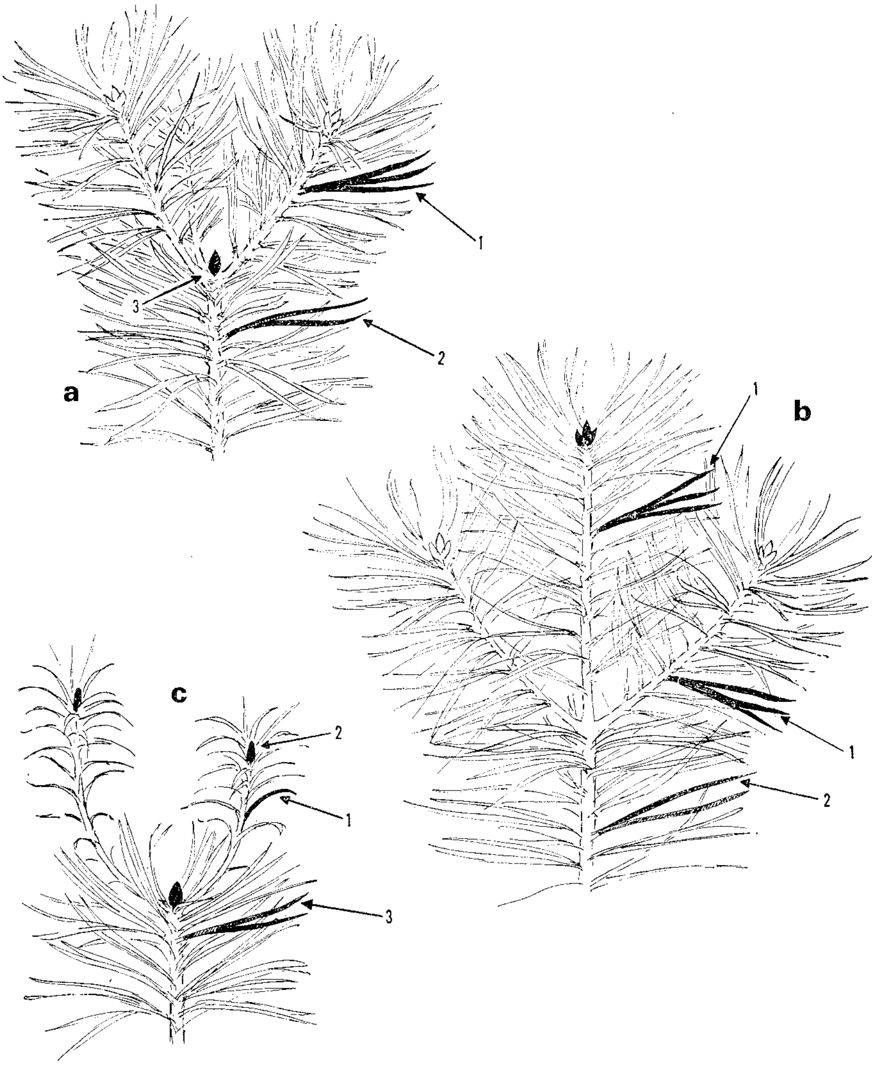

Figure 8. Different types of summer shoots in Scots pine.
(a) Proleptic shoots with three needles in each whorl (1) while the normal shoots bear two needles in each whorl (2). Terminal bud has not flushed (3).
(b) Lammas growth and prolepsis, both with three needles in each whorl (1). Normal shoot with two needles in each whorl (2).
(c) Proleptic shoot with "juvenile" shape, i.e. single primary needles (1) and without lateral buds (2). Normal shoot with two needles in each whorl (3).

4. Discussion

The results from the different experiments confirm the well-known fact that there is a strong connection between the environmental conditions during the first year and the shoot growth during the following year (Kozlowski 1964 *b*). This is valid not only for the shoot growth in spring but also for the formation of summer shoots. Thus, the frequency of summer shoots could be related to the environmental conditions of the preceding year. The results from this study indicate that a favourable constellation of environmental factors during the preceding year is followed by a strong shoot growth in spring and a small number of plants with summer shoots in the following year. On the contrary, poor environmental conditions during the first year are followed by an increased number of plants with summer shoots.

Shoot growth has previously been proved to be dependent essentially on carbohydrate reserves in the plant and not on a current photosynthesis (Kozlowski 1955, 1958, 1962, 1963, 1964 *a, b*). Newirth (1959) proved for *Pinus silvestris* that the normal shoot growth was dependent on nutrient reserves in older needles. If these were removed the shoot growth was inhibited. Kozlowski & Clausen (1965) found a rapid decrease in dry weight in one-year-old needles of *Pinus resinosa* during shoot growth mainly because of translocation of carbohydrates from the needles to the expanding shoot. Rutter (1957) found shoot growth of young *Pinus silvestris* to be completed in the middle of June. On 26 May, when approximately half the shoot growth was completed, the whole plants had decreased in dry weight.

The results unequivocally show that environmental factors have influence on the formation of summer shoots. Favourable current conditions seem to be a prerequisite for its formation. Evidently there is also a connection between the shoot growth in spring and the formation of summer shoots as well as between the conditions during the previous season and the shoot growth in the following spring.

Thus, if the plant owing to suboptimum environmental conditions has no possibilities of storing enough carbohydrate reserves in the roots, stem and needles, this will influence the development of the shoot the following year. The foregoing may be summarized in the following schedule.

First year	A	Growth.
	B	Nutrient reserves are built up and stored.
Second year	A	Nutrient reserves are used for shoot growth.
	B	Some of the growth is performed by products from a current photosynthesis.
	C	Nutrient reserves are built up and stored.

In the normal case the steps A and B during the second year seem to be close to each other and not distinguishable as two different steps but as a continuous growth. If during the first year the plant owing to poor environmental conditions can neither produce nor consequently store adequate amounts of nutrients, the step A during the following year (second year) results in a poor shoot growth.

Kozlowski & Keller (1966) divide species of woody plants in the temperate zone into two different groups with respect to shoot growth characteristics and dependency on carbohydrate reserves for shoot elongation. In the first group—which includes the *Pinus* species—the shoots are predetermined in the winter bud. According to this theory shoot formation involves bud differentiation during the first year and extension of the preformed parts within the bud into a shoot during the second year. In the second group the shoots are not fully preformed in the winter bud and both early and late leaves are produced. Ranked under this group are, for instance, several *Populus* species.

According to the foregoing the number of leaf primordia and cells in the future shoot is fixed already in the bud (Sacher 1954, Kozlowski 1958, 1963). This means that improved environmental conditions during the shoot growth cannot influence the size of the shoot by an increased cell number but by affecting the cell enlargement. Of course this is possible only up to a certain limit. A high photosynthetic activity after the buds are formed may cause an enrichment of carbohydrates in the plant to such an extent that the capacity for the plant to store it is wholly utilized. This in turn may affect the formation of a new shoot. Probably there is some mechanism involved which is influenced by the carbohydrate state of the plant and which can affect bud break and shoot growth. If such a pathway exists, this is not the normal way for control of bud break and shoot growth but neither are summer

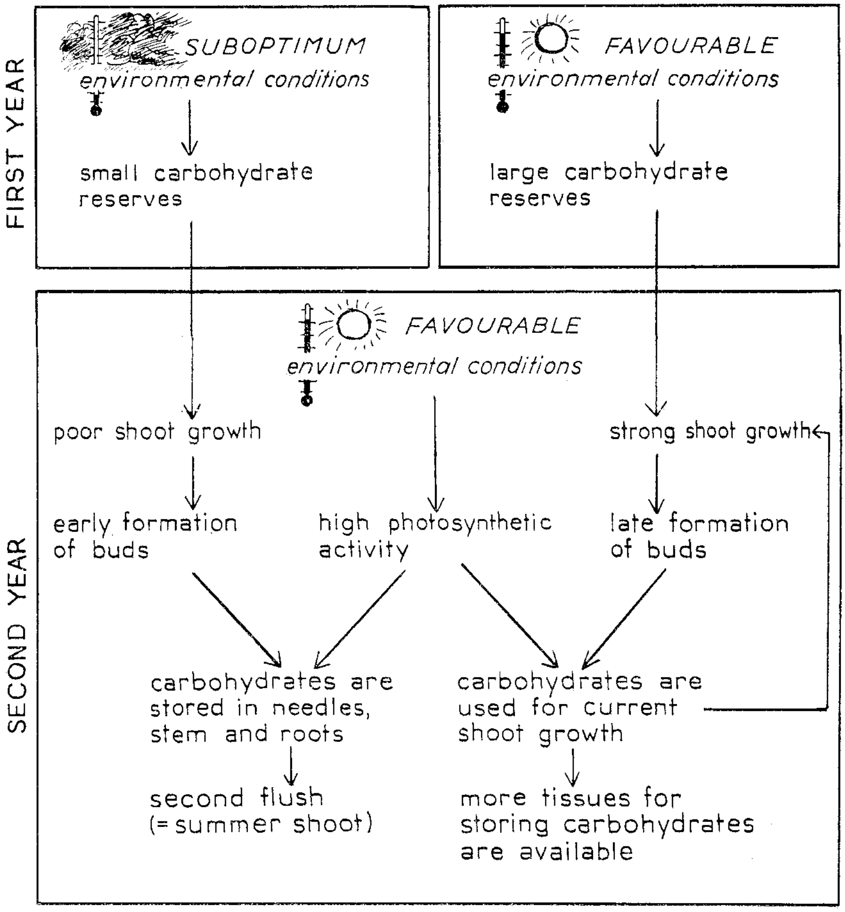

Fig. 9. Proposed possibilities for influence of environmental factors on the formation of summer shoots in seedlings of Scots pine.

shoots a normal occurrence. In fact, there are two abnormal phenomena involved in the formation of summer shoots which both are affected by growth regulators. Firstly, the bud break and formation of shoots without passing a complete dormancy period and, secondly, the inhibited apical dominance.

Day length and light conditions are in addition to temperature factors which have been proved to influence the onset and termination of dormancy. The effects of these factors are probably mediated by growth regulators such as gibberelins, cytokinins, auxins and inhibitors. A possible explanation of the formation of summer shoots seems to be that the levels or functions of one or more of these growth regulators are affected by carbohydrates which are stored in the plant and that this mechanism exists beside the normal pathway.

This hypothesis might be connected to the above-mentioned observation of Kovalenko, that summer shoots are most frequent in young plants and that the tendency for their formation decreases with the age. In other words, small plants with limited space for storage of nutrient reserves are furnished with a mechanism which enables them to use a surplus of carbohydrates for a second flush, while bigger plants or trees have better possibilities for storage of such a surplus in needles, stem and roots. The schedule in Figure 9 illustrates the behaviour of plants in different environmental conditions according to this theory.

As far as apical dominance is concerned there are several theories about its control (Brown, McAlpine & Kormanik 1967). Most of these theories involve influence by growth regulators while other show influence by nutrient metabolites in the plant. However, the inhibited apical dominance which occurs in connection with the formation of proleptic shoots must be regarded as a special case where the terminal bud is temporarily blocked. All theories concerning apical dominance deal with the problem of how axillary buds are depressed in one way or another. As this is not the case in regard to proleptic shoots, other explanations of this phenomenon might be possible. Differences in the concentration of growth regulators between terminal and lateral buds are one possibility which has formed the basis for a present investigation (Aldén 1971, Aldén & Eliasson 1970).

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Sammanfattning

Inverkan av CO_2, vatten och näring på bildningen av sommarskott hos plantor av *Pinus silvestris* L.

Den normala skottskjutningen är hos flertalet vedväxter en tvåårig process med knoppbildning under det första året och skottskjutning under påföljande år. Under vissa betingelser kan emellertid s. k. sommarskott bildas vilket innebär att skottskjutningen sker samma år som knoppen bildats. Förekomsten av sommarskott hos tallplantor har hittills varit av ringa omfattning och i praktiken saknat betydelse. I och med införandet av nya drivningsmetoder i plantskolor har dock problemet fått större aktualitet. I försök med drivning av tallplantor i plastväxthus har antalet sommarskott ökat mycket starkt i jämförelse med dess förekomst vid konventionell odling på friland.

Den föreliggande undersökningen har utförts under åren 1967 till 1969 vid Skogshögskolans försöksplantskola i Ågrena, Laxå där institutionen för skogsföryngring vid Skogshögskolan under år 1965 påbörjade ett forsknings- och utvecklingsprojekt med arbetsnamnet: »Operation maskinplantering». Ett av syftena med detta projekt var att jämföra olika miljöfaktorers betydelse för tillväxten av skogsträdsplantor vid drivning i plastväxthus.

Resultaten visar att de undersökta faktorerna CO_2, vatten och näring påverkade bildningen av sommarskott hos tvååriga tallplantor samt att en gynnsam miljö under det år sommarskotten bildas torde vara en förutsättning för deras uppkomst. En inoptimal miljö under såddåret med en förbättrad miljö under följande år medförde en hög frekvens, medan en gynnsam miljö under såddåret resulterade i en låg frekvens av plantor med sommarskott.

Skottbildningen hos vissa vedväxter — däribland *Pinus*arter — är enligt Kozlowski & Keller (1966) förutbestämd redan vid knoppbildningen (Sacher, 1954; Kozlowski, 1958, 1963). Enligt denna teori är antalet bladanlag och celler i det blivande skottet fixerat redan i knoppen. Detta medför att en gynnsam miljö under skottskjutningsåret inte kan påverka skottets storlek genom ett ökat antal celler utan endast cellernas storlek. En hög fotosyntetisk aktivitet i plantan kan därvid medföra en anriktning av kolhydrater som inte används för skottskjutningen utan lagras upp som reservnäring. Som en hypotes och möjlig förklaring till uppkomsten av sommarskott diskuteras möjligheten av att en sådan ansamling av kolhydrater i plantan kan påverka utbildningen av sommarskott. En sådan påverkan bör rimligtvis ske via tillväxtregulatorer.

Electronic version

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