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The effect of inorganic nutrients on water economy and hardiness of conifers

II. The effect of varying potassium and calcium contents on water status and drought hardiness of pot-grown Pinus silvestris L. and Picea abies (L.) Karst. seedlings

Samband mellan mineralämnesinnehåll, vattenhushållning och härdighet hos barrträd

II. Effecter av varierande kalium- och kalciumnivåer på vattenförhållanden och torkhärdighet hos krukodlade tall- och granplantor

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Abstract

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The effect of varying amounts of potassium and calcium on drought hardiness, transpiration rates, and water status of pot-grown seedlings of Pinus silvestris and Picea abies, 5 months old, was investigated.

An increased potassium content increased the drought hardiness of pine seedlings but not of spruce. An increased calcium content decreased the drought hardiness of pine seedlings but had no effect on spruce. When the soil of the pots dried out both pine and spruce seedlings were killed at a xylem pressure potential of about —30 bars.

Stomatal closure began at a xylem pressure potential of about —10 bars and ended at —25 bars in both pine and spruce seedlings. Different potassium contents did not affect those values. The transpiration rate of potassium-deficient seedlings of pine and spruce was about 65 per cent of that of normal- and high potassium seedlings.

The positive correlation between potassium content of pine seedlings and survival at low water potentials could not be explained by low transpiration rate or early stomatal closure as the water potential decreased. It was assumed that the potassium contents influenced the desiccation tolerance of the cytoplasm, through the colloidal properties or the metabolism of carbohydrates and proteins.

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Introduction

Plant water stress is caused either by excessive loss of water or by inadequate absorbtion or by a combination of both. The effect of water stress on plants is complex and plants respond with many protective adaptations. The physiological processes underlying the adaptation are genetically controlled, but their expression is modified by environmental factors.

Two aspects are of interest to silviculture: the capacity of different species to grow and develop under dry conditions and the ability of different species to survive dry periods. Only the latter aspect is dealt with in the present investigation.

As reviewed earlier (Christersson 1973) it has been assumed that the regimes of potassium and calcium in the plants have an important role in plant water relations and cell membrane permeability to water. These characteristics are of great importance for drought hardiness of plants.

A great many seedlings are killed in Sweden every year, for example, after planting on a clear-felled area in spring or summer, when the period just after planting is very dry. But according to experience from research in nurseries on the island of Gotland, Sweden, pine and spruce seedlings survived winter conditions better if they were fertilized with potassium (Ingestad, personal communication).

Most of our seedlings are cultivated in nurseries or in plastic greenhouses. Under such conditions it is possible to control the fertilization of the seedlings and use any desired ratio and amount of different inorganic nutrients (Sirén 1968, Ingestad 1974). In practice it is therefore of great importance to tabulate the influence of different inorganic nutrients on the drought hardiness of conifer seedlings. From a theoretical point of view such an investigation would give valuable information about the role of different ions in the water relations of cells and plants. As both potassium and calcium are thought to be of importance for drought hardiness in plants it was an obvious first step to begin with these ions. In order to analyse the effect of potassium and calcium in detail, the water content and transpiration rates have also been measured. Furthermore, the ability of conifers to become drought hardened has been investigated.

The present investigation is part of a research project on nutrient requirements, nutrient status, and fertilization effects of forest trees going on at The Royal College of Forestry, Stockholm, Sweden.

Terminology

In the present investigation the terminology follows the recommendations by Levitt et al. (1960), Parker (1969), and Levitt (1972), with one exception. The term drought hardiness is preferred to drought resistance and is used as a synonym, because of the existence of the verb to harden. It is possible to drought harden a plant, in the same sense as to frost harden, suggesting that the ability to survive unfavourable conditions is not fixed but a condition which may be changed. The term resistance implies a constant, fixed condition.

The investigations cited (Parker 1969, Levitt 1972) prefer to use the term hardiness in a more restricted sense, as the ability of the plant to survive unfavourable, internal conditions. However, during the development of a plant's ability to survive dry conditions it is very difficult to distinguish between internal and external structures and characteristics.

Drought hardiness capacity is defined here as the capacity of seedlings or of species to develop the morphological, anatomical, and physiological characteristics which allow them to survive dry conditions either by avoidance of lethal water potentials or by tolerance to dehydration of the membranes and protoplasm of their cells. Drought hardiness is the degree of development of this capacity at a particular time.

The pressure chamber method (Waring 1970) was used to determine the water status of the shoots. We have used the term xylem pressure potential or tension (Kaufmann, 1968; Tyree and Hammel 1972), rather than water potential, for the results we obtained, because of the resistance to water flow between leaf cells and xylem (Broyer 1967) and the dissolved solutes in the xylem.

Material and Cultivation Methods

The material consisted of 5 months old seedlings of Scots pine (Pinus silvestris L.) and Norway Spruce (Picea abies (L.) Karst.). The pine seeds were from a stand in central Sweden at lat. 57°45′N and altitude 200—300 m (provenance Södra Ydre). The spruce seeds were also from a stand in central Sweden (Älvan) at lat. 58°45′N and altitude 90 m.

The seeds germinated in moist vermiculite for 5—6 days at 20°C. After 3 weeks the seedlings were potted in a mixture of 50 per cent low-humified peat and 50 per cent gravel, five seedlings in each 300 ml pot. Each experiment included 90 pots, in nine groups of ten. Each group was fertilized according to Table 1. The pots were fertilized once a week for the first nine weeks and twice a week subsequently, with 20 ml of respective nutrient solution. They were not fertilized during the dormant period. The pots were watered with distilled water twice a day throughout the cultivation and the recovery period.

The seedlings were kept for the nine weeks after sowing in a glasshouse at about 20°C and 60 per cent relative humidity. Supplementary light was provided 20 hours a day by Philips HPLRH 400 W mercury lamps giving an illuminance at plant level of about 18 000 lux (irradiance 75—80 $W \cdot m^{-2}$, total radiant energy load). After these nine weeks the seedlings were comparable with one year old seedlings cultivated in the open. The length of the pine seedlings was about 5—7 cm, and of the spruce seedlings about 6—8 cm.

The seedlings then passed through a dormant period of 6 weeks in a growth chamber: 3 weeks at 20°C and short days (8 hours light) followed by 3 weeks at 3°C and short days. The light sources during the dormant period were fluorescent tubes, General Electric F 48 Power Groove 17 · CVX 100 W. The illuminance varied between 10 000 and 13 000 lux (irradiance 25—30 $W \cdot m^{-2}$).

After the dormant period the seedlings were transferred back to the glasshouse. After two weeks they began to flush and after 7 weeks the pine seedlings were about 13—16 cm long and the spruce seedlings about 15—20 cm long. The pine shoots had then stopped elongating, while the spruce shoots were elongating continously. These seedlings were comparable with 2 year old seedlings cultivated in the open.

Before the experiment, needle samples from each group were analysed for potassium, calcium, and magnesium (atomic absorbtion spectrophotometer, Perkin-Elmer, model 403), for nitrogen (Kjeldahl, micro-determination), and for phosphorus (colorimetry).

Table 1. Concentrations of the salts in the nutrient solutions used for fertilization.

	Fertilization program								
	A_1	A_2	A_3	B_1	B_2	B_3	C_1	C_2	C_3
Compound	Concentration, $mg \cdot l^{-1}$								
KCl	0	96	865	0	96	865	0	96	865
$CaCl_2 \times 2H_2O$	0	0	0	147	147	147	442	442	442
NH_4NO_3	720	720	720	720	720	720	720	720	720
$NaH_2PO_4 \times 2H_2O$	101	101	101	101	101	101	101	101	101
$MgSO_4 \times 7H_2O$	154	154	154	154	154	154	154	154	154

Experiments and results

The fertilization experiments

The fertilization program was designed to vary the internal levels of potassium and calcium in the seedlings, and the results of the analysis show that the content of potassium varied between 0.06 and 0.35 mmol per g dry matter for pine needles (Table 2) and between 0.07 and 0.39 mmol for spruce (Table 3). There was less variation in the calcium content. In pine needles it varied between 0.033 and 0.096 mmol per g dry matter and in spruce between 0.20 and 0.36 mmol. All these values can be found in natural stands, expect for the highest potassium values (Christersson 1974).

According to Ingestad (1962) these results indicate that the calcium status of the pine needles was within the optimum range for maximum growth rate, but in spruce the calcium status was in the supra optimum range.

The variation of the ratio of potassium to calcium contents in the needles was of the same magnitude in pine and spruce, but the absolute figures were lower for spruce than for pine, as a result of the higher contents of calcium in spruce needles.

The pine seedlings without potassium in the fertilization program (A_1, B_1, C_1) were about 10—15 per cent smaller than the other seedlings, and slight deficiency symptoms could be detected, such as yellow tips of the needles. The corresponding reduction in size of spruce was about 25 per cent and distinct deficiency symptoms were developed. The needles were pale green and the stem one cm below the top of the current year shoot was reddish. No reduction in size and no development of deficiency symptoms was observed in seedlings without calcium in their fertilization program (A_1, A_2, A_3). These findings agree very well with the values given for deficiency

Table 2. Potassium, calcium, magnesium, nitrogen, and phosphorus contents in mmol per g dry matter; ratio potassium/calcium contents in needles, and water contents in shoots of seedlings of Pinus silvestris, five months old, grown in pots with different fertilization programs.

	Fertilization program								
	A_1	A_2	A_3	B_1	B_2	B_3	C_1	C_2	C_3
Element	Contents of the elements, mmol per g dry matter needle								
K	0.08	0.20	0.35	0.06	0.21	0.30	0.06	0.21	0.31
Ca	0.070	0.059	0.040	0.083	0.051	0.033	0.096	0.064	0.050
Mg	0.049	0.031	0.040	0.040	0.038	0.034	0.047	0.035	0.039
N	1.03	1.02	0.90	1.04	1.03	1.03	0.98	1.02	1.05
P	0.076	0.068	0.076	0.083	0.068	0.076	0.079	0.065	0.076
ratio K/Ca	1.1	3.5	8.5	0.7	4.1	9.1	0.6	3.3	6.2
Water content of the shoot, per cent	69.9	69.1	70.5	68.7	70.5	71.0	69.4	70.3	71.4

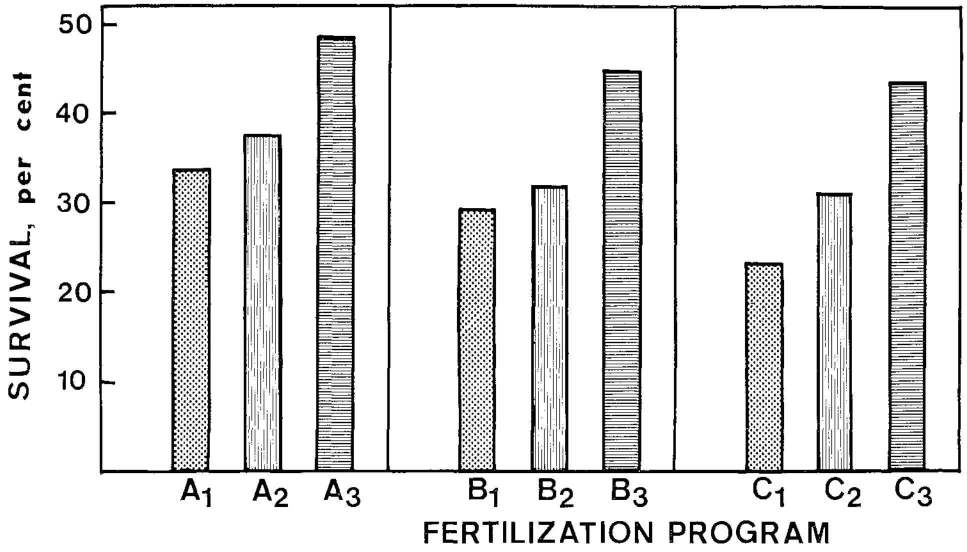

Figure 1. The percentage survival of seedlings of Pinus silvestris, 5 months old, fertilized in different ways and droughted as described in the text. The results of five separate experiments are included in the figure.

symptoms of potassium and calcium in pine and spruce seedlings by Tamm (1964).

For both pine and spruce the water content of the shoot increased at increased potassium fertilization. Calcium had no such effect (Table 2 and 3).

Drought hardiness determination

The drought hardiness of the plant material was determined in the glasshouse with a temperature of 20°C, and a relative humidity of 50 per cent. Each experiment consisted of

Table 3. Potassium, calcium, magnesium, and nitrogen· contents in mmol per g dry matter; ratio potassium/calcium contents in needles, and water contents in shoots of seedlings of Picea abies, five months old, grown in pots with different fertilization programs.

	Fertilization program								
	A_1	A_2	A_3	B_1	B_2	B_3	C_1	C_2	C_3
Element	Contents of the elements, mmol per g dry matter needle								
K	0.09	0.22	0.37	0.07	0.20	0.35	0.07	0.22	0.39
Ca	0.26	0.21	0.20	0.30	0.28	0.20	0.36	0.23	0.20
Mg	0.079	0.051	0.046	0.058	0.041	0.048	0.062	0.048	0.036
N	1.27	1.30	1.14	1.50	1.41	1.23	1.35	1.45	1.44
ratio K/Ca	0.3	1.1	1.8	0.2	0.7	1.8	0.2	1.0	2.0
Water content of the shoot, per cent	70.6	73.9	73.1	72.2	72.5	73.6	71.8	73.1	73.6

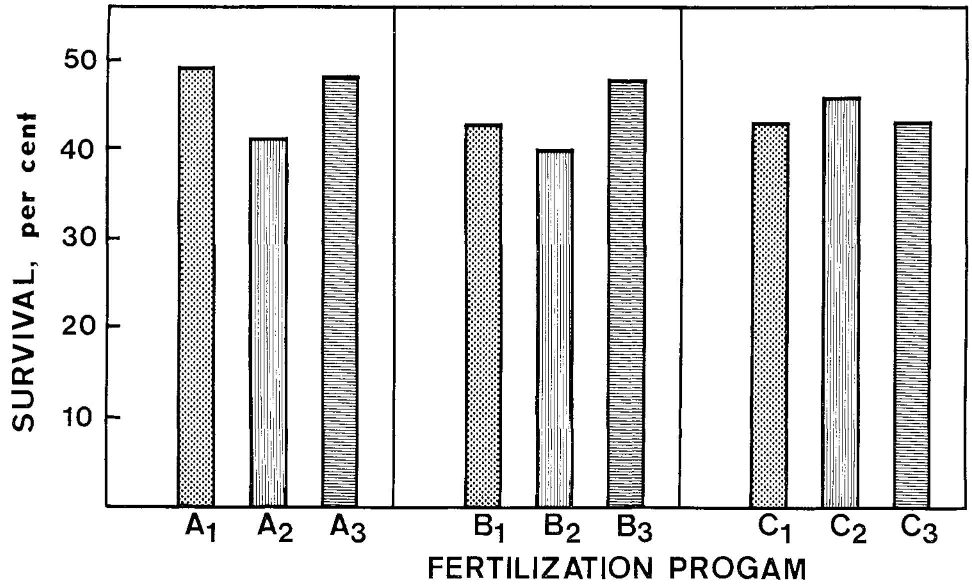

Figure 2. The percentage survival of seedlings of Picea abies, 5 months old, fertilized in different ways and droughted as described in the text. The results of five separate experiments are included in the figure.

90 pots with 4—5 seedlings in each, fertilized in nine different ways (Table 1). The soil of the pots were saturated with water and the root medium was then allowed to dry. After 10 days one pot of each fertilization program was rewatered. After 11 days another pot was rewatered, and so on. When all the pots had been rewatered the seedlings passed through another dormant period, similar to that previously described.

After this second dormant period the seedlings were transfered back to the glasshouse and after 8 weeks, survival was determined. Pine seedlings in which at least one of the top buds was flushing were listed as living; in dead pine seedlings no bud was flushing. Living spruce seedlings were those in which the top bud or lateral buds within a distance of 3 cm from the top were flushing. In dead spruce seedlings these buds were not flushing. To be able to show significant influence on drought hardiness of the investigated ions the experi-

Table 4. Mean percentage survival of seedlings of Pinus silvestris and Picea abies, 5 months old, fertilized in different ways as indicated.

	Fertilization program		
	A_1, B_1, C_1 (low K)	A_2, B_2, C_2 (medium K)	A_3, B_3, C_3 (high K)
pine	28.8	35.9	44.8
spruce	46.1	42.2	46.4
	A_1, A_2, A_3 (low Ca)	B_1, B_2, B_3 (medium Ca)	C_1, C_2, C_3 (high Ca)
pine	40.0	35.2	34.4
spruce	46.0	43.5	45.1

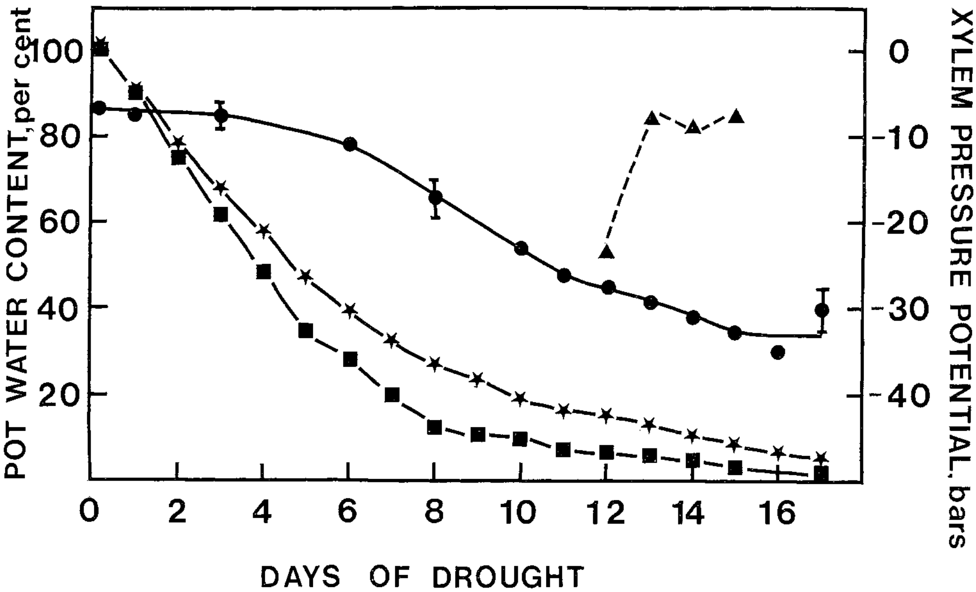

Figure 3. Determination of water status of the soil of 300 ml pots and of seedlings of Pinus silvestris, 5 months old, during a desiccation period of 17 days. Squares: Water content of the soil with seedlings, in per cent of saturation capacity. Stars: Water content of the soil without seedlings. Circles: Xylem pressure potential of shoots in bars. Triangles: Xylem pressure potential of shoots after rewatering, in bars. The first measurement was made one hour after rewatering. Vertical bars show the standard deviations.

ments were repeated four times, so that 5 000 spruce and pine seedlings were individually tested.

In Figure 1 and 2 the results, expressed as percentage survival of the seedlings of all the experiments, are put together. For pine seedlings (Figure 1) there is a positive relation between potassium contents and survival and a negative relation between calcium contents and survival. The effect of potassium is much more significant than that of calcium (Table 4). In contrast, no relationship whatsoever could be demonstrated for spruce (Figure 2 and Table 4).

Water status of soil and seedlings

The water loss during the dry period from ten pots, with or without seedlings, was determined gravimetrically, and expressed as a percentage of saturation capacity. The seedlings were fertilized according to program B_2 (Table 1). The results for both pine (Figure 3) and spruce (Figure 4) indicated that most of the water loss from the pots was by evaporation from the root substrate and that the transpiration from the seedlings played a limited role in drying the soil of the pots.

The water status of the seedlings was determined during the dry period using a pressure bomb technique, as described by Hellkvist et al. (1974), but only one measurement on each seedling was made. The first appearance of sap was easily observed in spruce, but not in pine, because of air bubbles in the xylem sap. Every second day ten seedlings (fertilized according to program B_2) were selected at random and used for determination of the xylem pressure potential. Furthermore, the change in potential was determined in some seedlings after rewatering following 12 days desiccation. The first measurement was made one hour after rewatering, with subsequent measurements once a day.

The results for pine (Figure 3) and spruce (Figure 4) show that the development of a tension in both species followed the same pattern. The rate of recovery from a low ten-

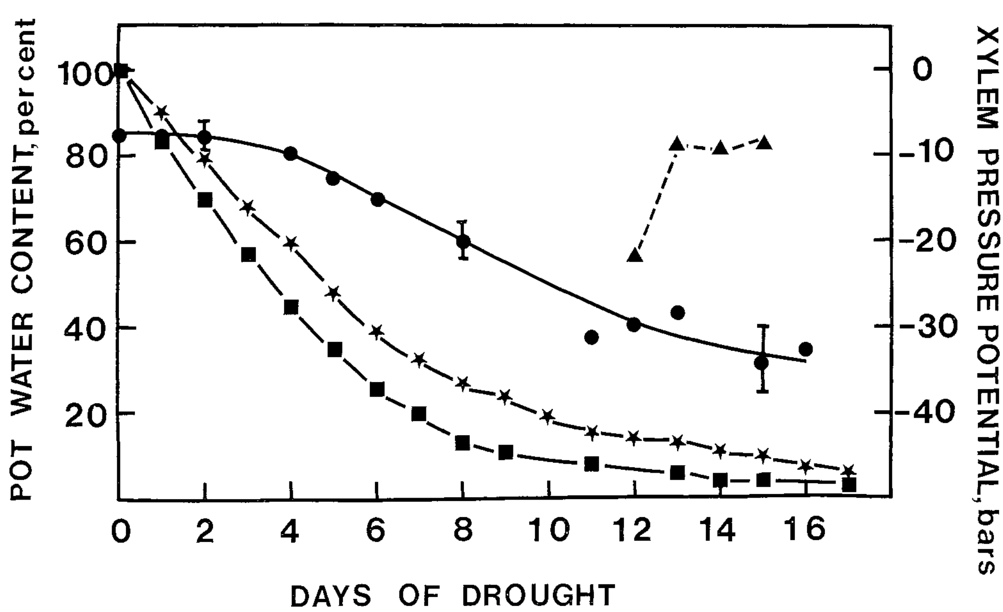

Figure 4. Determination of water status of the soil of 300 ml pots and of seedlings of Picea abies, 5 months old, during a desiccation period of 17 days. Squares: Water content of soil with seedlings, in per cent of saturation capacity. Stars: Water content of the soil without seedlings. Circles: Xylem pressure potentia of shoots, in bars. Triangles: Xylem pressure potential of shoot after rewatering, in bars. The first measurement was made one hour after rewatering. Vertical bars show standard deviations.

sion after rewatering did not differ in the two species. The pine and spruce seedlings died after 11—14 days of desiccation, indicating that the seedlings endured a xylem pressure potential of —25 to —30 bars. If there is any difference between pine and spruce, it is so small that it could not be detected by the method used. A few test samples were also taken from seedlings fertilized according to program B_1 and B_3, but the results did not differ from those for program B_2. The variation of the results of the xylem pressure potential determination increased at low values, because some of the seedlings were already dead.

These experiments were repeated once, with similar results. Only the results from one set are presented here.

Table 5. The dry weight of shoots and needles used in the transpiration experiments, expressed in g and per cent.

Fertilization program	Pine		Spruce	
	Dry weight, g		Dry weight, g	
	shoot	needle	shoot	needle
B_1	1.8 ± 0.1	1.6	1.4 ± 0.1	1.1
(low potassium)	100 %	89 %	100 %	79 %
B_2	1.9 ± 0.1	1.6	1.7 ± 0.1	1.2
(medium pot.)	100 %	84 %	100 %	71 %
B_3	2.0 ± 0.1	1.7	1.4 ± 0.1	1.0
(high potassium)	100 %	85 %	100 %	71 %

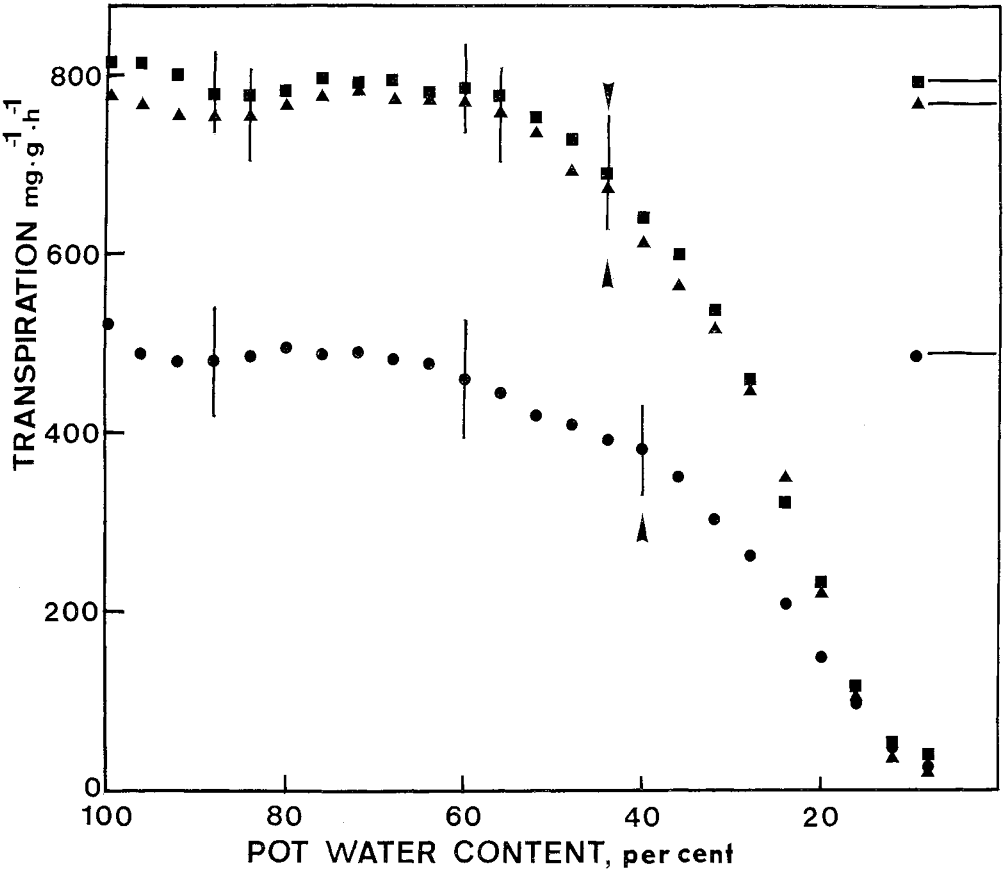

Figure 5. The transpiration rates of seedlings of pine, 5 months old, at decreasing soil water contents, expressed as per cent of saturation capacity. The seedlings were fertilized with three different amounts of potassium. The mean maximum transpiration rates are shown on the right of the figure. Arrows indicate the beginning of stomata closure (for explanation, see the text). Vertical bars indicate standard error of mean. Key to the symbols: Circles: low potassium contents (fertilization program B_1). Squares: medium potassium contents (fertilization program B_2). Triangles: high potassium contents (fertilization program B_3).

Transpiration rates and stomatal closure

The transpiration experiments were designed to determine the influence of different potassium regimes on transpiration rates and stomata closure. Seedlings fertilized according to program B_1, B_2, and B_3 (Table 1) were used, 15 seedlings from each program, carefully selected to be the same size (Table 5); one seedling in each pot. The rot medium were saturated with water and the pot covered with aluminium foil, pushed closely around the stem of the seedlings to prevent direct loss of water from the soil. The transpiration rates were determined by weighing each pot twice a day, at 10.00 h and 14.00 h in a climate chamber at 20 ± 1°C and at a relative humidity of 50 ± 10 per cent. The lighting was the same as during the dormant period. The chamber was ventilated continously with an air flow of 0.5 m · s^{-1}. The evaporation from a pot covered with aluminium foil and without seedlings was about 10 mg · h^{-1}. The transpiration rates were expressed as mg water per g needle dry weight and hour, and correction was made for the pot evaporation. The duration of the experiments was 20 days. The seedlings were not watered during this period. The

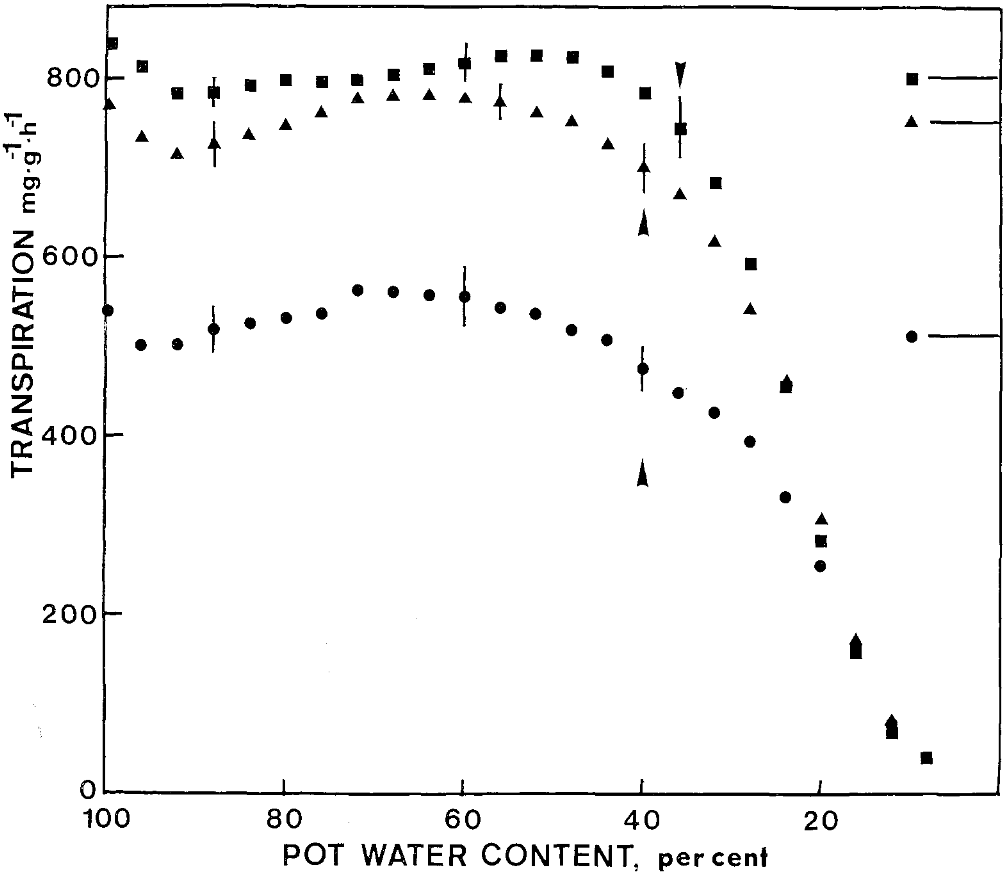

Figure 6. The transpiration rates of seedlings of spruce, 5 months old, at decreasing soil water contents, expressed as per cent of saturation capacity. The seedlings were fertilized with three different amounts of potassium. The mean maximum transpiration rates are shown on the right of the figure. Arrows indicate the beginning of stomata closure (for explanation, see the text). Vertical bars indicate the standard error of mean. Key to the symbols: Circles: low potassium contents (fertilization program B_1). Squares: medium potassium contents (fertilization program B_2). Triangles: high potassium contents (fertilization program B_3).

transpiration rates were plotted against water contents in the pots expressed in per cent of total water content.

The transpiration rates of pine and spruce seedlings with low potassium content were about 500 mg water per g dry weight and hour, while the transpiration rates of seedlings with medium and high potassium content were about 800 mg (Figure 5 and 6). As there was no relation between the differences in seedling size and the differences in transpiration rates, the size differences could not be responsible for the different transpiration rates (Table 5). Furthermore, the weight of needles varied very little with the different amounts of potassium. So it could be concluded that the results showed a direct effect of different internal potassium contents on transpiration rate.

Stomatal closure was determined in the following way. The mean values of the first ten points on the curves in Figures 5 and 6 were calculated (marked on the right frame of the figures). The beginning of stomatal closure was defined as the point where the transpiration values fell below this mean by more than double the standard error. These points are indicated by arrows. By this calculation a mean of the standard errors of the first ten points was used.

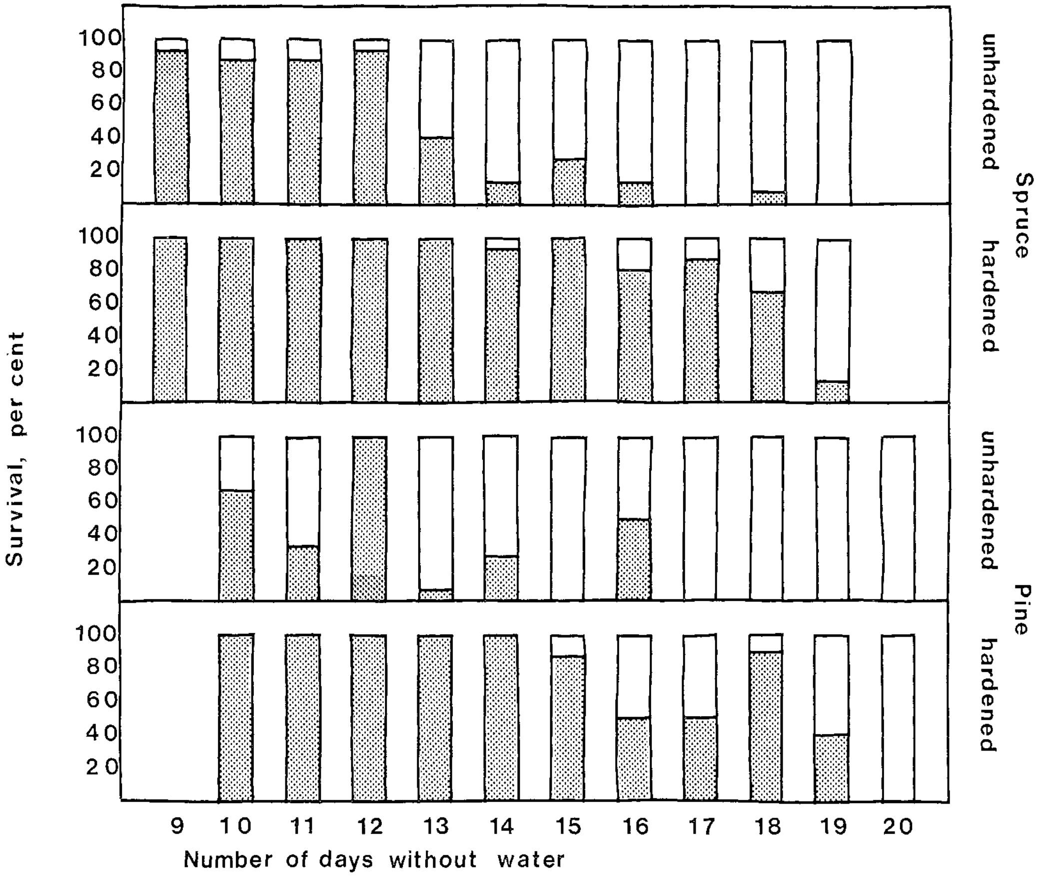

Figure 7. Drought hardiness determination of seedlings of pine and spruce, 6.5 months old, unhardened and drought hardened, for 6 weeks. The experiments were duplicated and the results are taken together. Each avlue represents 15 seedlings with exception for the four last for pine which represent 10 seedlings.

The position of this point varied very little with different potassium regimes for both pine and spruce (Figure 5 and 6), and corresponded to a soil water content in the pots of about 40 per cent of saturation capacity. Figures 3 and 4 shows that at this 40 % per cent soil water content the stomatal closure of both pine and spruce began at a xylem pressure potential of about —10 bars. In the same way the ending of stomatal closure could be calculated to about —25 bars. The differences between the species and between different contents of potassium were very small.

The experiments were repeated once with similar results. Only results from one set are presented here.

Development of drought hardiness

To find the capacity of the material to drought harden, seedlings of spruce and pine (fertilized according to program B_2) were allowed to go through a hardening period of six weeks, during which the temperature was 20°C, the day length 8 hours, and the lamp sources the same as during the dormant period. The pots were watered to saturation once a week.

The control plants (unhardened) were left in the glasshouse during the hardening period. They grew well and at the end of the period they were about 25—50 per cent bigger than the drought hardened seedlings.

After the drought hardening period the

hardiness of unhardened and hardened seedlings was determined as before, with one exception. Every fifth day the pots were weighed, and if the pots with the larger unhardened seedlings had lost more water than the pots of hardened seedlings, the difference was made good. However, these differences were very small.

The results of the experiments showed that both spruce and pine seedlings can be drought hardened (Figure 7), and that the environmental conditions used in these experiments were effective. Most unhardened seedlings of spruce survived 12 days of drought, whereas most hardened seedlings survived 18 days. The results for pine were similar but less reliable, as there were fewer seedlings. The results expressed in terms of xylem pressure potential indicate that more than 50 per cent of the unhardened seedlings were killed below a xylem pressure potential of —25 bars but 50 per cent of hardened seedlings were not killed below —35 bars (Figure 3 and 4). The experiments were duplicated.

Discussion

There are very conflicting ideas in the literature about the effect of different potassium and calcium regimes on various aspects of the water status of plants. Table 6 is an attempted summary of previously published results. Further investigations have been made in the present work.

The results presented suggest that different potassium and calcium regimes had an effect on the drought hardiness of seedlings of pine but not of spruce (Figures 1 and 2). There was a positive correlation for potassium and a negative correlation for calcium (Table 4). In considering this difference between pine and spruce, it is relevant that there were also differences in their calcium contents. Spruce seedlings contained four to six times as much calcium as pine seedlings. It is thought that calcium has a negative influence on drought hardiness and that calcium and potassium act antagonistically to each other in many physiological reactions. It is therefore probable that

Table 6. A survey of the effect of potassium and calcium on various aspects of water status and hardiness of cells and plants. Authors, working with the problem or compiling reviews, are listed.

Effects of potassium	Effect of calcium	Authors
disperses the cell colloids	coagulates the cell colloids	Biebl 1958 Van Steveninck 1965
increases the permeability of the cytoplasm and membranes	decreases the permeability of the cytoplasm and membranes	Nason and McElroy, 1963
lowers the cytoplasmic viscosity	raises the cytoplasmic viscosity	Henckel 1964
decreases (increases) the transpiration rate	increases (decrease) the transpiration rate	Biebl 1958 Keller 1967 Brag 1972
increases the cuticular transpiration	decreases the cuticular transpiration	Evenari 1962
stimulates the closing movement of stomata	inhibits the closing movement of stomata	Evenari 1962 Pearson 1975
Stimulates water absorption	—	Evenari 1962
maintains the osmotic pressure in the cell sap	—	Hawker et. al 1974
—	participates in building up and maintaining the systems of the cytoplasm and ultrastructure of the cell	Marinos 1962 Burström 1968
stimulate metabolism of carbohydrates and protein synthesis	—	Marscher 1969
activates the phosphokinase system, which produces ATP	—	Hewitt and Smith 1974
affects the proline concentration		Hewitt and Smith 1974

in spruce the effect of a high content of calcium cannot be counteracted by increased potassium content. There was no effect of increase in the potassium content from 0.07 to 0.37 mmol/g at calcium contents as high as 0.20—0.36 mmol/g. On the other hand, in pine the same increase in potassium content had a definite effect on drought hardiness when the calcium content was as low as 0.04—0.1 mmol/g.

In natural stands spruce contains much more calcium than pine (Christersson 1974); this may be one of the reasons why pine seedlings are more drought hardy than spruce even in natural conditions.

It is today generally accepted that stomatal opening involves accumulation within the guard cells of potassium ions together with organic acids and varying amounts of inorganic ions (Humble and Raschke 1971, Fischer 1972, and Pearson and Milthorpe 1974). In the present investigation a low potassium content in the needles decreased the transpiration rates of both pine and spruce (Figure 5 and 6). This can be explained by assuming that in potassiumdeficient seedlings the number of potassium ions available to be pumped in and out of the guard cells, is insufficient to open the stomata for maximum transpiration rates. It is more difficult to explain the reduced transpiration rate at very high potassium contents found for pine by Christersson (1973).

The literature in this field is very conflicting. For example, Brag (1972) found for Triticum aestivum and Pisum sativum that plants with high potassium contents had the lowest transpiration rates. The reverse effect was recovered for a clone of Populus by Keller (1967).

It is apparent that there is a difference between species but Biebl (1958) also observed differences between plants of different age; young deficient plants had a decreased transpiration rate, whereas older plants had an increased rate.

The number of available potassium ions did not influence the beginning or shape of the stomata closure curve (Figure 5 and 6). For both pine and spruce and for seedlings varying in potassium status, stomata closure begins at a xylem pressure potential of about —10 bar and is complete at about —25 bars.

The main cause of decrease in transpiration as water stress develops is stomatal closure. In conifers a water potential of less than —15 bars is required to bring about substantial stomatal closure (Jarvis and Jarvis 1963, Turner and Waggoner 1968, Lopushinsky 1969). In an investigation of detached leaves of Norway spruce and Scots pine, Jarvis and Jarvis (1963) showed that pine stomata close much sooner (at a water potential of —15 bars) than spruce stomata (—37 bars). On the other hand, an investigation by Pisek and Winkler (1953) of the same species showed that the difference in water content at the beginning and ending of stomata closure was very small. There was no difference in xylem pressure potential between pine and spruce (Figures 3 and 4) at the beginning and ending of stomata closure (Figures 5 and 6), in the present work.

The method used did not allow the measurement of the cuticular transpiration rates; low rates may be very important in the avoidance of lethal desiccation levels of the cytoplasm (Martin and Juniper 1970). There are very few published investigations of the effect of different thickness of cuticle or layers of wax. Rolf Larsen (personal communication) reports no effect of potassium concentration on cuticule thickness of 28 days old wheat leaves between 0.15—1.0 mmol potassium per g dry matter. But Martin and Juniper (1970) concluded that water loss was not correlated with the thickness of the cuticle; the structure and the chemical composition of the cuticle play a more important role.

So, in order to explain the positive correlation between potassium content in pine seedlings and survival at low water potential it is necessary to assume that potassium has a positive influence on the desiccation tolerance of the cytoplasm, probably through an effect on the colloidal properties or on the metabolism of carbohydrates and protein. In this respect calcium acts antagonistically to potassium. Although a decrease in potassium content is associated with a decrease in transpiration rate, the water conserving effect of low transpiration rates is not enough to counteract the negative effect on the desiccation tolerance of the cytoplasm also associated with a low potassium content.

In earlier reports, Christersson (1973, 1975) demonstrated that the content of potassium and calcium, or changes in the ratio of these two ions had no influence on frost hardiness development in young seedlings of Pinus silvestris. A positive relationship between drought hardiness and potassium content in pine seedlings has now been established. The positive correlation between winter survival and potassium content referred to in the introduction (Ingestad, personal communication) can be explained in the following way. Early spring is a very critical time for survival of conifer seedlings (Langlet 1960, Bärring 1967); the ground is still frozen and bright sunshine brings about very high needle temperatures (Sakai 1970). Under these conditions the seedlings lose considerable amounts of water. Increased potassium content would raise the desiccation tolerance of the cytoplasm and increase seedling survival at low water potentials.

The attempts to drought harden seedlings clearly showed that environmental conditions have an effect on the hardiness of the seedlings so that both internal and external factors play a part.

Christersson (1973) demonstrated transport of potassium from the root to the shoot in pine seedlings during development of frost hardiness and it was then assumed that an increase in potassium content of the shoot decreased the transpiration rate, and thereby assisted survival of severe water conditions. However, it has now clearly been demonstrated that the positive effect of potassium is not on the transpiration rate but on the desiccation tolerance of the cytoplasm. The transport of potassium to the shoot can therefore be regarded as a favorable adaptation for severe conditions, which may be of crucial importance in determining species distribution.

Practical application

The positive effect of potassium on desiccation tolerance of the cytoplasm can be utilized in practical silviculture during situations when pine seedlings are exposed to stress conditions, e.g. when planting takes place in spring or early summer, or when seedlings are kept at low temperatures for long periods, a common method of storage in Sweden today.

Sammanfattning

Under vårvintern, våren och försommaren utsätts ofta tall- och granplantor för extrema klimatbetingelser, vilket i många fall leder till låga vattenpotentialer inuti plantorna. Detta kan ha förödande effekt framför allt på nysatta plantor, inte bara på tillväxten utan också på överlevnaden. I dagens skogsbruk med framställning av skogsplantor under i vissa fall kontrollerade betingelser, exempelvis i plastväxthus, uppkom tidigt frågan huruvida någon eller några av de kontrollerbara ytterbetingelserna kunde antas påverka unga plantors överlevnadsförmåga efter utplantering. Från fältförsök rapporterades negativa effekter av kaliumbrist på vinteröverlevnaden. Torkhärdigheten är en del av denna överlevnadsförmåga, varför det ansågs angeläget prova kaliums inverkan på torkhärdigheten. Kalcium verkar antagonistiskt mot kalium i många fysiologiska reaktioner och borde därför undersökas samtidigt.

Tall- och granplantor odlades i växthus och klimatkammare på ett sådant sätt, att 5 månader gamla plantor motsvarande utomhusodlade 2-års plantor. Under odlingsperioden gödslades plantorna med varierande kalium- och kalciumgivor. Plantorna utsattes för varierande torkperioder.

Ett ökat kaliuminnehåll i tallplantorna påverkade torkhärdigheten positivt, medan en sådan effekt inte kunde påvisas hos gran. På motsvarande sätt minskade ett ökat kalciuminnehåll härdigheten hos tall men lämnade granplantorna utan påverkan. Någon skillnad mellan tall- och granplantors förmåga att tåla låga vattenpotentialer kunde inte konstateras. Båda arterna dog vid en vattenpotential av omkring —30 bar.

Transpirationsförsöken visade att klyvöppningarna började slutas vid ca —10 bar och slöts helt vid ca —25 bar hos både tall och gran och denna process var helt oberoende av kaliumstatus. Absolutvärdena för transpirationshastigheten varierade så att plantor av både tall och gran med kaliumbrist hade en transpirationsintensitet, som var endast 2/3 av normalplantans. Höga kaliumhalter tycks däremot inte påverka transpirationshastigheten.

Den positiva korrelationen mellan kaliumstatus hos tallplantor och förmågan att överleva långa torrperioder kan således inte förklaras av sådana vattenbesparande åtgärder som minskad transpirationsintensitet eller tidig stängning av klyvöppningarna, då vattenpotentialen i plantorna minskar. Istället måste antas att kaliuminnehållet påverkar uttorkningstoleransen hos cytoplasman antingen genom att påverka dess kolloidala egenskaper eller dess produktion av kolhydrater och protein.

I ett tidigare arbete i denna serie kunde någon effekt av varierande kaliuminnehåll på frosthärdigheten hos tall inte påvisas. Den i vissa fältförsök framkomna positiva effekten på vinteröverlevnaden av höga kaliumhalter skulle således kunna förklaras av den i detta arbete påvisade positiva inverkan av kalium på torkhärdigheten.

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