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Effects of the removal of shelterwood on the foliar nutrient concentrations of Norway spruce (*Picea abies* (L.) Karst.) on drained peatlands

Neulasten pääravinnepitoisuuksien muutokset turvekankaan alikasvoskuusikossa ylispuuhakkuun jälkeen

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The foliar chemical composition of a Norway spruce underwood was analysed one year before and three years after the removal of a downy birch (*Betula pubescens* Ehrh.) shelterwood on an old drainage area. The most remarkable change due to the release was considered to be the significant decrease in potassium concentrations. The nitrogen concentrations increased very strongly, and phosphorus increased slightly but not significantly during the first growth period after the release, decreasing later to a level approaching the deficiency limit. Consequently the nutrient balance between N and K was strongly shaken by the increased N/K-ratio. One reason for that might be the increased use of K in the growing points of roots after the root competition of shelterwood was eliminated.

Key words: foliar analysis, nutrients, peatlands, *Picea abies*, shelterwood, underwood

INTRODUCTION

In several studies of shade-grown trees, Norway spruce was found to be quite adaptable to new conditions after the removal of shelterwood (Cajander 1934, Katrusenko 1965, Skoklefald 1967, Bergan 1971, Andersson 1988, Koistinen & Valkonen 1993). There are also opposing observations, according to which spruce has suffered severe damage (Ståfelt 1935, Andersson 1984). When comparing these results, changes caused by cuttings in soil moisture (Heikurainen & Päivänen 1970, Päivänen 1974, 1982), and air humidity and temperature conditions (Multamäki 1942, Perttu 1974, Leikola 1975, Leikola & Rikala 1983) should be taken into account. It is possible that many of the chlorotic symptoms observed after the release may be explained by environmental factors other than the increased illumination (Katrusenko 1965, Gnojek 1992, Seryakov 1994). Also differences in the viability, height and earlier growth of spruce, as well as weather conditions before and after the release, have a strong influence on the survival and growth reaction of spruce (Cajander 1934, Koistinen & Valkonen 1993).

However, the suddenly increased illumination causes changes in the physiology of spruce underwood. Photoinhibition may occur, which means a reduced photosynthetic capability. Chlorophyll bleaching or at least the inhibited build-up of chlorophylls over the growth period are secondary reactions (Gnojek 1993). Water stress and lack of some mineral nutrients like potassium, magnesium and zinc can make plants more susceptible to photoinhibition and chlorophyll bleaching (Laatsch & Zech 1967, Björkman & Powles 1984, Marschner & Cakmak 1988).

Both the increased illumination and the other environmental changes might find expression also in the foliar nutrient concentrations after the removal of shelterwood. Russian studies have shown increased nitrogen and phosphorus concentrations in Norway spruce (Katrusenko 1967, Koshelkov 1982). At the same time, however, the K concentrations decreased. After the third growth period the N concentrations were restored, whereas P decreased to a lower level than before the release. The decrease of K continued down to the deficiency limit (Koshelkov 1982).

In an old drainage area trees may suffer from a shortage of mineral nutrients already before cuttings (Kaunisto & Paavilainen 1988, Kaunisto 1989). On those peatlands the main nutrient imbalance may become more critical after shelterwood cuttings. The aim of this study was to investigate the effects of the removal of shelterwood on the foliar chemical composition and the annual height increment of underwood on drained mire sites.

MATERIAL AND METHODS

The site is located in Kiikoinen, southern Finland (61°29´N, 22°31´E). According to the Finnish mire classification by Heikurainen and Pakarinen (1982), it was originally a wet and sparsely stocked herb-rich sedge birch–pine swamp. Drainage was carried out in 1964. However, the area has long been under the influence of the main ditch coming from a nearby field. The stock before cuttings, mean height of 18 m and volume of 180 m^3 per hectare, consisted mainly of downy birch (*Betula pubescens* Ehrh.). This birch stand suppressed an uneven-aged Norway spruce underwood, the height of which varied from one to eight metres.

The experimental area was composed of two parallel strips between ditches, the width of which were 40 m and the length 120 m. The other of these strips has probably been under a stronger drainage effect of the old field ditch. These strips were both divided into four plots (30 × 40 m) and the shelterwood was then removed from two of them in winter 1991. This led to an experiment of four released underwood plots and four suppressed underwood ones as controls. After the removal of shelterwood all ditches were cleaned with an excavator.

Twelve sample spruces from each plot were randomly selected for needle analysis. Two of them represented the highest height class (height over 5 m at the beginning of the experiment), four of them the middle height class (2.5–5 m) and the last six represented the smallest and the most suppressed spruces (1–2.5 m).

Needles were collected by cutting one sample branch from the third branch whorl. The last three needle year-classes were separated later in the laboratory. The needle samples were combined to represent three different needle year-classes in three different height classes for each plot. Needles were collected before the removal of shelterwood and in three years after it (1991–1993). The same trees were sampled each year. Also the dry mass of one hundred needles and the height of the sample spruces were measured annually.

The analyses of foliar K were performed after HCl extraction of dried and ground material with flame atomic spectrophotometry (Varian AA-30). Phosphorus was determined spectrophotometrically in dry ashed material. Nitrogen was determined with the Kjeldahl method (Halonen et al. 1983).

Volumetric samples of soil were taken for analysis from the uppermost (0–10-cm) peat layer. One subsample per each sample spruce was taken from the distance of 1–2 m. This was carried out before and one year after the cuttings at the same time of the year (November 1989 and 1990). The total N concentrations were determined using the Kjeldahl-method and those of P and K with a spectrophotometer and atomic absorption spectrophotometer after dry ashing and HCl extraction. Ammonium and nitrate were determined by distilling and the H_2SO_4-titration from KCl-extraction, whereas exchangeable K and soluble P with ICP from the acid (pH 4.65) NH_4OAc-extraction. (Halonen et al. 1983)

The multivariate analyses of variance with repeated measures (BMDP 4V) were used to test the parameters of the following model:

$$Y = R + C + N + T + T \times R + (TR) \times C + (TR) \times N + \varepsilon \quad (1)$$

where Y = foliar concentrations of N, P and K, foliar dry mass or annual height increment, R = release cutting, N = needle year class, C = height class, T = growth period and ε = error.

The design had one grouping factor (R) and three repeated measure factors (N, C and T). Contrasts across time were used to test the effect of the release on the nutrient concentrations and the dry mass of the current needles and annual height increment during each separate growth period after the cuttings. These contrasts were used also to test the same effect on the total amounts of nutrients per one hundred needles (mg per dry mass).

The release effect on the foliar nutrient concentrations and dry mass, as well as height increment, were tested in the form of the following three hypotheses:

1. Changes in the follow-up period (time effect) on the released plots differ from those on the control ones (release effect). Interaction between the time and release [T × R] is significant.
2. Changes in the time after the release depend on the height of the underwood spruces (height effect). Interaction between the height class, time and release effects [(TR) × C] is significant.
3. Changes in the time after the release depend on needle year-classes. Interaction between the needle, time and release effects [(TR) × N] is significant.

RESULTS

The main nutrient concentrations of peat as their total and NH_4OAc-extractable components (mg l^{-1}, *in situ*) are shown in Table 1. When comparing the NH_4OAc-extractable concentrations before and after the release, only nitrogen showed a significant increase. Before the removal of shelterwood the total concentrations of each nutrient on the control plots were higher than on the plots to be released.

Spruces on the control plots grew better before the cutting than those to be released (Fig. 1). Compared with the growth period before cuttings, released spruces increased their height increment almost threefold during the third growth period after the release, especially among the most suppressed spruces. Differences between the height classes due to this effect were, however, not significant (Table 2).

The N concentrations increased very strongly during the first growth period after the release (Fig. 2, Tables 2 and 3). The concentrations in the needles of the smallest sample spruces were as high as 22 mg g^{-1} compared with the control concentrations of 15–16 mg g^{-1}. There was only a slight decrease during the following years. Phosphorus increased slightly but not significantly during the first growth period. The following periods showed a decrease approaching the deficiency limit (1.5 mg g^{-1},

Table 1. Total and NH_4OAc- extractable nutrient concentrations (mg l^{-1}, *in situ*) of peat (0–10 cm) before (1990) and after (1991) the removal of shelterwood.

Taulukko 1. Pintaturpeen (0–10 cm) kokonaisravinnepitoisuudet sekä ammoniumasetaatilla uuttuvien ravinteiden pitoisuudet (mg l^{-1} häiriintymättömässä tilavuusnäytteessä) ennen (1990) ja jälkeen (1991) ylispuuhakkuita.

	N		P		K	
	Control *Vertailu*	Released *Hakkuu*	Control *Vertailu*	Released *Hakkuu*	Control *Vertailu*	Released *Hakkuu*
Total nutrient concentrations, mg l^{-1} – *Kokonaisravinnepitoisuudet, mg l^{-1}*						
1990	3337	2898	128.5	106.3	53.2	35.0
1991	2704	3045	93.8	126.9	51.4	36.3
NH_4OAc-extractable nutrient concentrations, mg l^{-1} – *NH_4OAc-uuttuvat ravinnepitoisuudet, mg l^{-1}*						
1990	7.8	10.5	6.9	6.2	36.5	27.4
1991	8.1	16.9	6.9	6.8	37.9	32.0

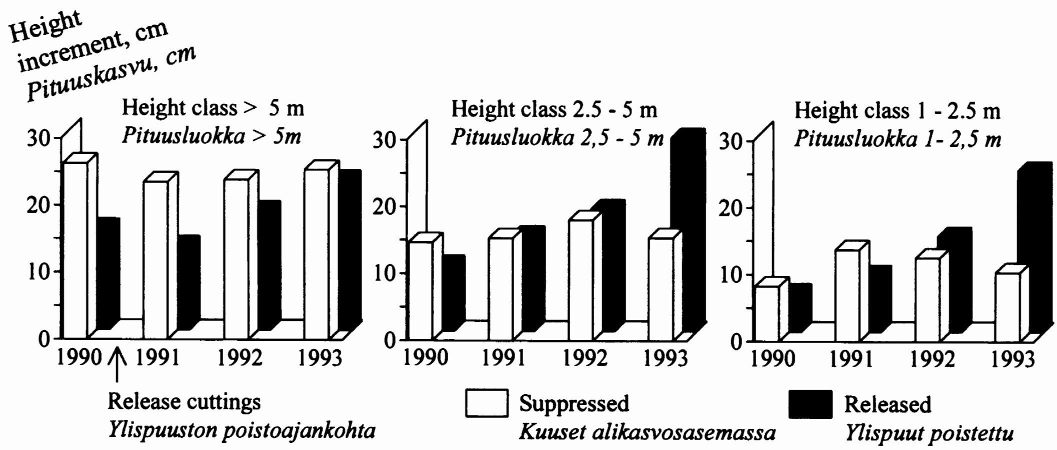

Fig. 1. Annual height increment of the sample spruces in three height classes.

Kuva 1. Koepuiden vuotuinen pituuskasvu kolmessa eri pituusluokassa.

Paavilainen 1974). The most remarkable change after the release was considered to be the decrease in the K concentrations. They were 5–7 mg g^{-1} before the release and close to the deficiency limit (4 mg g^{-1}, Paavilainen 1974) after it. These changes (hypothesis 1: interaction between the time and release treatments) were significant only in the case of N and K. It is important to notice that this effect on the dry mass of needles was not significant (Table 2).

Release effects across time on the total amounts of nutrients per one hundred needles were nearly the same as described above in the case of N and P, whereas the K amounts significantly decreased only in the first year after the release (Table 3).

Changes in the time after the release did not depend on the height class of the underwood spruces (hypothesis 2, Table 2). Instead, the changes were dependent on the age of needles concerning the K concentrations and needle mass (hypothesis 3). The interaction in the K concentrations was due to differences between the current (C) and C + 1 or C + 2 needles. The decrease after the release was the strongest in the current nee-

Table 2. Results of Greenhouse-Geisser tests of three hypotheses explained in the text. F-, p- and adjusted df-values of height increment, concentrations of foliar nitrogen (N), phosphorus (P) and potassium (K) and needle dry mass.

Taulukko 2. Tekstissä esitettyjen ennakko-oletusten testaus Greenhouse-Geisser-testillä. Pituuskasvusta, neulasten typpi- (N), fosfori- (P) ja kaliumpitoisuuksista sekä neulasten kuivamassasta laskettujen testisuureiden F- ja p-arvot sekä korjatut vapausasteet (df).

	Hypothesis (interaction) – *Ennakko-oletusten mukaiset yhdysvaikutukset*								
	1			2			3		
	Time × Release *Aika × Hakkuu*			(TR) × Height class *(AH) × Pituusluokka*			(TR) × Needle *(AH) × Neulasvuosik.*		
	F	p	df	F	p	df	F	p	df
Height increment – *Pituuskasvu*	11.0	0.001	2.38	0.97	0.402	1.82	–	–	–
Concentrations in current needles – *Nuorimman neulasvuosikerran ravinnekonsentraatiot*									
N	25.1	< 0.001	1.86	2.47	0.113	2.40	4.22	0.047	1.81
P	4.49	0.036	1.98	0.52	0.566	1.55	2.61	0.125	1.72
K	12.7	0.001	2.13	1.60	0.233	2.54	11.2	< 0.001	3.33
Needle dry mass – *Neulasten kuivamassa*	0.74	0.495	1.94	0.73	0.536	2.78	6.87	0.003	2.90

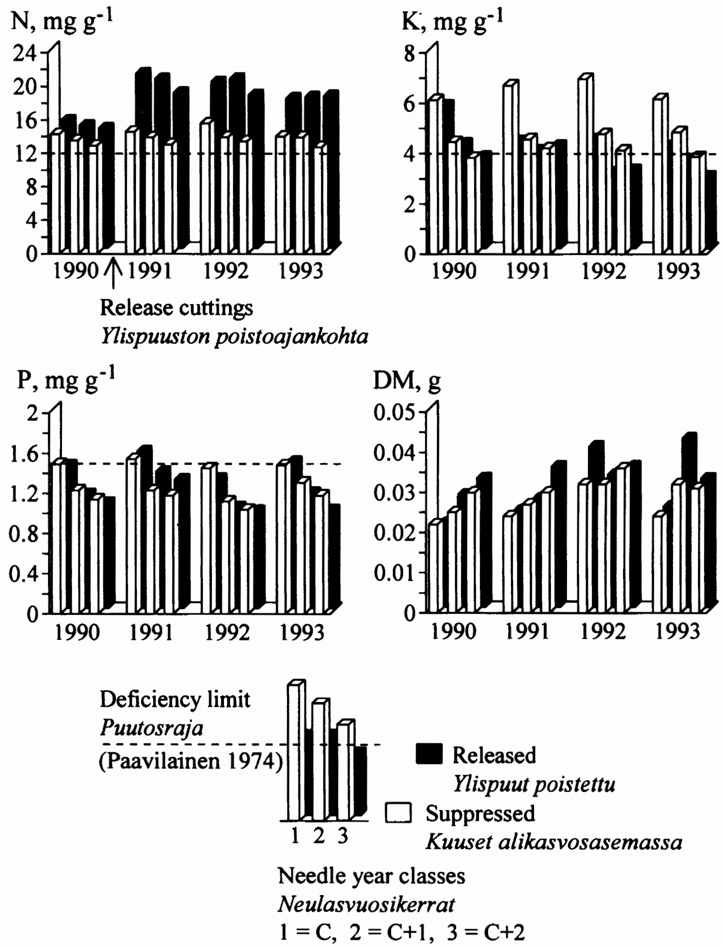

Fig. 2. Foliar nitrogen (N), phosphorus (P) and potassium (K) concentrations and dry mass (DM) of one hundred needles of the sample spruces.

Kuva 2. Koepuiden neulasten typpi (N), fosfori (P) ja kaliumpitoisuudet sekä sadan neulasen kuivamassa (DM).

dles. Concerning the needle dry mass, the same interaction was caused by the increase of dry mass in the third growth period, but only in those two years older than current needles (Fig. 2).

Table 3. F- and p- values of the statistical tests (contrasts of release effect across time) concerning height increment, foliar nutrient concentrations and dry mass.

Taulukko 3. Pituuskasvusta sekä neulasten ravinnepitoisuuksista ja kuivamassasta laskettujen hakkuuvaikutuksen aikakontrastien F- ja p-arvot ja vapausasteet (df).

	Years after release cuttings – *Hakkuun jälkeiset vuodet*								
	1991			1992			1993		
	F	p	df	F	p	df	F	p	df
Height increment – *Pituuskasvu*	0.01	0.925	1	2.0	0.231	1	15.4	0.017	1
Concentrations in current needles – *Nuorimman neulasvuosikerran ravinnekonsentraatiot*									
N	32.8	0.005	1	14.5	0.019	1	20.0	0.022	1
P	0.5	0.510	1	0.4	0.544	1	0.5	0.504	1
K	21.9	0.009	1	25.8	0.007	1	31.3	0.005	1
Needle dry mass – *Neulasten kuivamassa*	0.9	0.396	1	6.2	0.067	1	0.8	0.414	1

DISCUSSION

Comparing the total main nutrient concentrations of peat before the removal of shelterwood to the studies made on old drainage areas of corresponding site types, it was found that the N and P concentrations did not differ from the typical levels (N: 3 610 mg l^{-1}, P: 122 mg l^{-1}; Kaunisto & Paavilainen 1988). The total K concentrations, however, were higher than the average level (23 mg l^{-1}).

Comparing the foliar nutrient status before the release to the deficiency limits (N 12 mg g^{-1}, P 1.5 mg g^{-1}, K 4.0 mg g^{-1}) defined in experiments concerning spruce fertilization on peatland (Paavilainen 1974), the P concentrations were considered to be relatively low. They were either close to the limit values or, especially in the sample trees representing the highest height class (> 5 m), even a bit lower than the limit (Fig. 2). There was no shortage of N and K.

The improvement of the N status of released spruces may be related to a decreased competition for nutrients and increased mineralization in warmer soils. The concentrations of soluble nitrogen in peat increased about 60% after the cuttings. According to Russian studies, the increase in the foliar N concentrations was related to released soluble nitrogen in soil and also to an improved capability of nutrient uptake due to the strongly developed root system (Koshelkov 1982). In the same studies the temporary increase of both N and P was supposed to be related to the internal nutrient translocation of trees. A corresponding translocation from needles one and two years older (C + 1 and C + 2) to the current (C) ones could not be found in this experiment. Simultaneously with the increase of the concentrations in the youngest needles (current), an improvement in the nutrient status also in two older needle classes was found. It is, however, possible that N and P had translocated from shoots more than two years older (C + 3 or older).

In principle, the availability of K in peat could have been affected negatively by the cleaning of ditches (leaching of nutrients) and positively by nutrients released by cuttings. There were not, however, such changes in the NH_4OAc-extractable K concentrations in peat which could have explained the decrease in the foliar potassium concentrations. The decrease of the foliar K concentrations, coinciding with the increase of nitrogen, may be related to the so-called dilution effect of mineral nutrients (Veijalainen 1979). Since any simultaneous increase of foliar dry mass did not occur in these data, the dilution of K might only be due to increased shoot elongation. On the other hand, a significant increase of the height increment did not start until the third growth period after the release.

The free growing space for roots of underwood must have strongly increased after the competition of shelterwood was eliminated. It is thus obvious that also the growth of roots has strongly increased. The use of K in the growing points of roots might be one reason for decreased foliar concentrations. Probably the relative allocation of nutrients into roots will remain on a high level until the root system of spruces is adapted to new conditions. Expecting the recovering time to be dependent on the K nutrition before the removal, new experiments on different site types and/or with K fertilization treatments should be established to examine its variation.

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TIIVISTELMÄ:

Neulasten pääravinnepitoisuuksien muutokset turvekankaan alikasvoskuusikossa ylispuuhakkuun jälkeen

Useissa tutkimuksissa kuusen on todettu sopeutuvan hyvin ylispuiden poiston jälkeisiin uusiin ympäristöoloihin (Cajander 1934, Katrusenko 1965, Skoklefald 1967, Bergan 1971, Andersson 1988, Koistinen & Valkonen 1993). Toisaalta on tehty myös päinvastaisia havaintoja, joiden mukaan kuuset ovat kärsineet vakavia vaurioita (Ståfelt 1935, Andersson 1984). Verrattaessa näitä tuloksia keskenään on otettava huomioon muutokset maan vesitaloudessa (Heikurainen & Päivänen 1970, Päivänen 1974, 1982) sekä ilman kosteudessa ja lämpöoloissa (Multamäki 1942, Perttu 1974, Leikola 1975, Leikola & Rikala 1983). Onkin mahdollista, että monet hakkuun jälkeen ilmenevistä kuusen kloroottisista oireista johtuvat muista syistä kuin valaistuksen lisääntymisestä (Katrusenko 1965, Gnojek 1992, Seryakov 1994). Myös erot kuusten elinvoimaisuudessa, pituudessa ja ennen hakkuuta vallitsevassa kasvussa vaikuttavat voimakkaasti alikasvoskuusten elpymiseen ja kasvureaktioihin (Cajander 1934, Koistinen & Valkonen 1993).

Auringon säteilyn äkillinen ja voimakas lisääntyminen vaikuttaa kuitenkin alikasvoskuusten fysiologiaan mm. neulasten yhteyttämistehokkuuden tilapäisenä heikentymisenä (Gnojek 1993). Samalla tiettyjen kivennäisravinteiden puute voi vaikuttaa valosopeutumiseen, sillä esim. viherhiukkasten tuhoutuminen valaistuksen lisääntyessä on voimakkaampaa kaliumin, magnesiumin ja sinkin puutteesta kärsivillä kasveilla (Laatsch & Zech 1967, Björkman & Powles 1984, Marschner & Cakmak 1988).

Ympäristömuutokset saattavat myös heijastua neulasten ravinnepitoisuuksissa. Venäläisissä tutkimuksissa kivennäismailla kasvavien alikasvoskuusten neulasten pääravinnepitoisuuksien suhteet olivat muuttuneet voimakkaasti ylispuuhakkuun jälkeen (Katrusenko 1967, Koshelkov 1982). Tämän tutkimuksen tarkoituksena oli tutkia typen, fosforin ja kaliumin pitoisuuksien hakkuun jälkeisiä muutoksia sellaisella turvemaan kasvupaikalla, jolla em. ravinteiden suhteet ovat usein jo ennestään puille epäedulliset.

Kiikoisten kunnassa sijaitsevalla ruohoisen sararämeen vanhalla ojitusalueella koivuvaltainen puusto hakattiin alikasvoskuusten päältä talvella 1990–91. Koekenttä jakautui kahteen vierekkäiseen 40-m sarkaan, joista kumpikin jaettiin neljään koealaan. Ylispuusto poistettiin kummallakin saralla kahdelta koealalta. Jokaiselta koealalta valittiin otannalla kaksitoista koepuuta neulasten ravinnepitoisuuksien seurantaa varten.

Ylispuustosta vapautettujen alikasvoskuusten neulasten typpipitoisuudet kohosivat voimakkaasti heti hakkuun jälkeisen kasvukauden aikana (Kuva 2). Samalla neulasten kaliumpitoisuudet laskivat. Fosforipitoisuuksissa ei esiintynyt merkitseviä muutoksia. Neulasten typen ja kaliumin pitoisuuksien suhde (N/K) säilyi korkeana koko hakkuun jälkeisen kolmivuotisen seurantajakson ajan. Ravinnepitoisuuksien muutokset ilmenivät samanlaisina kaikissa tutkituissa kolmessa alikasvoskuusten kokoluokassa sekä kolmessa eri neulasvuosikerrassa (C, C + 1 ja C + 2).

Turpeen liukoisen typen pitoisuudet kohosivat selvästi hakkuun jälkeisenä kasvukautena. Se selittänee osittain neulasten kohonneet typpipitoisuudet. Mahdollista siirtymää kaikkein vanhimmista neulasvuosikerroista (C + 3 ja vanhemmat) ei kuitenkaan tutkittu. Turpeen liukoisesta typestä poiketen sen kaliumpitoisuuksissa ei tapahtunut muutoksia. Myöskään neulasten kuivamassan perusteella ei voitu selittää neulasten kaliumpitoisuuksien laskua, koska kuiva-ainetiheydet (sadan neulasen kuivamassa) eivät merkitsevästi kohonneet hakkuun jälkeen ja pituuskasvukin elpyi voimakkaimmin vasta kolmannen kasvukauden aikana (Kuva 1). Maaperän vapaan juuristotilan lisääntyminen kilpailevan puuston poiston ja kunnostusojituksen ansiosta on todennäköisesti aiheuttanut alikasvoskuusten juurten voimakkaan kasvun. Tämä saattaa olla yksi syy havaittuun neulasten kaliumpitoisuuksien laskuun kaliumin siirtyessä nopeasti kasvavien juurten kärkisolukoihin.

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