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BESTÄMNING AV NÄRINGSPROPORTIONER HOS BOK, *Fagus sylvatica* L.

DETERMINATION OF THE NUTRIENT PROPORTIONS FOR BEECH, *Fagus sylvatica* L.

by

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Abstract

The preliminary nutrient proportions for beech were established, using a growth-technique developed by Ingestad (1979). The growth-technique is described (Ingestad & Lund, 1986) and consists of a closed growth unit where culture solution is circulated and nutrients are being added in the same relative rate as the uptake rate. Nutrients or culture solution are never replaced from the system during the experiment. During the whole experiment the shoot- as well as the root-climates are controlled and held at predefined levels.

Sammanfattning

De preliminära näringsproportionerna för bok fastställdes, med hjälp av en odlingsteknik som utvecklats av Ingestad (1979). Odlingstekniken som är beskriven (Ingestad & Lund, 1986), består av en sluten odlingsenhet, där näringslösningen cirkulerar och näringsämnen tillförs i samma takt som upptagningshastigheten. Näringsämnen eller lösning tas aldrig bort ur systemet under experimentets gång. Under hela experimentet hålls både skott- och rotklimat konstant på fastställda värden.

Introduction

Properties describing plant utilisation and handling of the environmental conditions for growth and development in quantitative and unambiguous terms are few and only known for a few species (Ingestad et. al., 1994ab). In order to establish these properties, specific experimental conditions must be fulfilled. The experimental plants must be in a defined and stable state, steady-state, defined as constant internal element proportions to biomass, and constant plant growth rate. The plants must be in a steady state long enough for the state to be secured. Steady state growth can thus only be achieved when the proportions of the different nutrients in the plant, in relation to the biomass, are constant (Ingestad, 1987).

One property is the maximum relative growth rate, R_{Gmax}, which is the maximum genetic capacity of species to handle and utilise nutrients, carbon and water fluxes. The relative growth rate, R_G, is expressed as the amount of biomass increase per unit of time in relation to the amount of biomass present

in the plant (Ingestad & Lund, 1986). R_{Gmax} can consequently only be accomplished when optimal nutrient proportions and lowest possible fluxes, given highest possible growth rate, are maintained. All growth limitations can be quantitatively and unambiguously expressed in terms of reduced growth related to R_{Gmax}. Thus R_{Gmax} serves as a quantitative reference value (Ingestad, 1986).

In order to keep plants in a steady state, the relative growth rate and the relative uptake rate must be equal. This is experimentally achieved by adding nutrients in a closed system with the same constant relative rate as the relative uptake rate. For optimum nutrient conditions, plants must have free access to optimal proportions of nutrients. In the experimental system of growth units (Ingestad & Lund, 1986) used in this experiment, the addition was controlled by a lower conductivity set point. Free access then means that each time a lower conductivity limit is reached, nutrients will be added. The aim of this work was to establish the preliminary nutrient proportions for optimal nutrient uptake for beech (*Fagus sylvatica* L.).

Theory

Abbreviations

n, nutrient amount in plant
R_A, relative addition rate
R_G, relative growth rate
R_{Gmax}, relative growth rate at non-limiting conditions (growth potential)
R_U, relative uptake rate
W, plant biomass
t, time

Steady state

When plants grow under steady state, this means that the internal nutrient concentration of any nutrient, n/W, must be unchanged, i.e. the internal nutrient proportions in relation to the biomass are constant. This condition is expressed (Ingestad & Ågren, 1992):

$$\frac{d\left(\frac{n}{W}\right)}{dt} = 0 \qquad (1)$$

Thus, as a consequence of (1) the nutrient uptake in relation to the nutrient amount, n, in the plant, must equal the growth in relation to the biomass, W, (Ingestad & Ågren, 1992) according to mathematical laws:

$$\frac{dn}{dt} \times \frac{1}{n} = \frac{dW}{dt} \times \frac{1}{W} \qquad (2)$$

Plant growth is thus determined by the net influx of nutrients, water and carbon (Ingestad & Ågren, 1992):

$$R_U = R_G \qquad (3a)$$

The above expression states the fact that the relative growth rate, R_G, is determined by the relative uptake rate, R_U. As long as uptake of nutrients are not being so called excess luxury uptake, the relative growth rate will equal the relative uptake rate and steady-state can be maintained.

When nutrients are being added to the plant with the same relative rate as it is taken up, the relative growth rate will equal the

relative addition rate, R_A, (Ingestad & Ågren, 1992):

$$R_A = R_U = R_G \qquad (3b)$$

When the initial nutrient amount in the plant is known and the nutrient amount taken up is known, the relative uptake rate can be calculated (Ingestad & Lund, 1986):

$$R_U = \frac{1}{n} \times \frac{dn}{dt} = \frac{d(\ln n)}{dt} \approx \frac{\ln n_2 - \ln n_1}{t_2 - t_1} \qquad (4)$$

As stated in 3a, during steady-state, R_G equals R_U. Thus, analogous to 4, R_G can be calculated:

$$R_G = \frac{1}{W} \times \frac{dW}{dt} = \frac{d(\ln W)}{dt} \approx \frac{\ln W_2 - \ln W_1}{t_2 - t_1} \qquad (5)$$

Materials and Methods

Seedlings

Seeds were collected in the park at Alnarp, in the very south of Sweden, and pregrown in washed sand at 4 ± 0.2 ^{O}C with a relative humidity of 90 ± 1 % and a daylength of 12 hours. The photon flux density, PFD, was 200 µ mol s^{-1} m^{-2} which gives 17 mol - $m^{-2}day^{-1}$. When the roots were 1-2 cm long, 50 seedlings were planted in a growth unit (Ingestad & Lund, 1986). The plants were held by cylindrical foam-rubber stoppers with holes in the middle for the seedling to grow through. Before planting, the plants were washed in distilled water and gently brushed with a paint brush to get the sand off the roots. They were then weighed five plants at a time and the weight of each group was noted. Then the seedlings were planted in the growth unit. The layout of the groups is presented in figure 1.

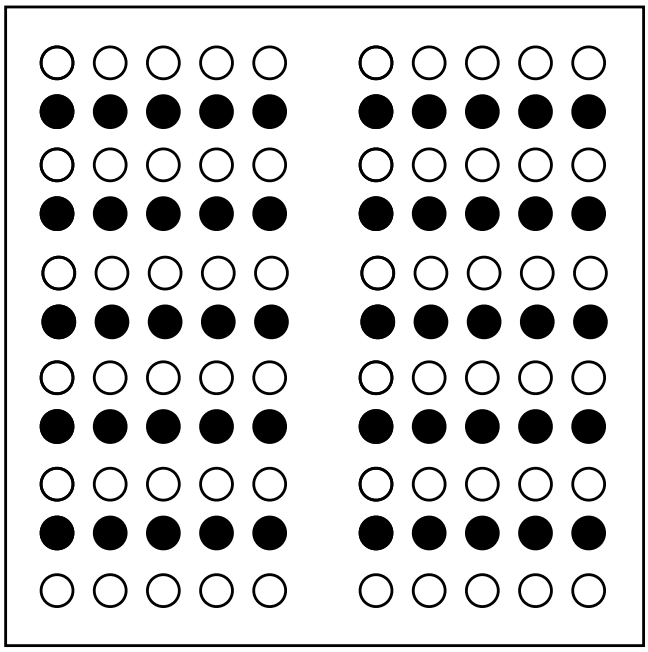

Figure 1. The layout of the seedlings in the growth unit. Dark spot corresponds with a seedling.

Experimental technique

The experimental system consists of a unit for plants where the root compartment is closed and nutrients are being added to a culture solution. The growth units, are controlled by a personal computer and every 10 minutes, conductivity, pH and temperature in the root environment are measured. Calculated amounts of nutrients are titrated from stock solutions, into the culture solution according to R_A. In order to optimise nutrient availability for uptake, the culture solution is continuously sprayed on the roots.

The culture solution is continuously filtered for rootcaps etc., but is not removed from

the system during an experiment. The culture solution is also continuously aerated to keep the CO_2 level down and to secure oxygen for the roots. The system has been developed by Ingestad & Lund (1986).

With this system, nutrients can be added in either of two ways, by free access addition rate or controlled limited addition rate. Free access, optimal uptake, means that nutrients are being added with no limitations. A controlled limited addition rate means that growth is limited by the addition rate, thus the set value for this rate must be less than the value of the free access rate with otherwise the same environmental conditions.

No matter which of the two addition methods that are being used, the nutrient proportions must be optimal. Otherwise the result will be growth limitations, so called excess luxury uptake (Ingestad & Lund, 1986) with accumulation of nutrients in the plant and in the culture solution, with an increase of the conductivity as a result.

Environmental conditions

The root-temperature was 17-22 ^{O}C.

The air temperature outside the growth unit was 18.0 ± 0.2 ^{O}C and the relative humidity was 80 ± 1 %. The light intensity was 150 µ mol m^{-2} s^{-1} and the photoperiod was 24 hours, which gave 13 mol m^{-2} day^{-1}. The light sources were fluorescent tubes (215 W, CW, Sylvania, Canada). The air inside the controlled environmental room was circulated and changed with outside air continuously and the carbon dioxide level was kept at ambient level, approximately 350 ppm.

Stock solutions

Three stock solutions for conductivity and pH titration were used for addition of nutrients to the culture solution, appendix 1. The only nitrogen source in all solutions was NO_3^-. The first solution contained all necessary nutrients and was based on HNO_3 for lowering the pH in the culture solution. The second and third solutions, were complementary solutions and together they contained all nutrients and were therefore titrated in even amounts. Because NO_3^- was the only nitrogen source, these stock solutions contained excessive but equal amounts of Ca^+ and Mg^+ to balance the cations.

Culture solution

The culture solution used in the growth unit, consisted of seven liters of distilled water to which were initially added nutrients from the stock solutions to a conductivity of approximately 110 µ S cm^{-1}. The higher conductivity used in the start was due to the small root area on the seedlings.

The pH was adjusted with the separate stock solution to 4.9. It was important that the pH was not higher than 5.3 because otherwise the solubility of iron would have been decreased.

During the experimental period the conductivity was kept between 40-50 µ S cm^{-1} and pH between 4.6-5.0.

Experimental planning

The seedlings were analysed five at a time except for the last analyse that consisted of the best eight seedlings remaining. This, because it was essential to get as large biomass as possible, in order to get a clear view

of the systematic change in nutrient proportions over time.

Each time plants were analysed, every second row were harvested. The reason for this was, that during the growth, the seedlings would shade each other if they were not given more space, and removing every second row, solved the problem of shading.

The first harvest was made when the seedlings started to absorb nutrients, which was established with conductivity measurements.

The time for the second and the third harvest were determined visually. It was important to get the change in biomass as large as possible, between the different analyses, so that the change in nutrient proportions over time would become clear.

Water analyses were taken every week. The water analyses were taken in order to show systematic changes in the nutrient proportions over time. The water analyses were taken independent of the seedling analyses.

Analyses and measurements

The fresh weight were measured on each group of five plants. The fresh weights measured were: the whole plant, the shoot, the stem and the cotyledon. From theese measurements, the fresh weights of the roots and the leaves were calculated.

During harvest the leaves and cotyledons were photocopied and the photocopies were used to calculate the group's total leaf and cotyledon area. Leaf areas were calculated with a computerised image processing system (Micro Macro Image Analyzing System, Gothenburg, Sweden).

The dry weights were measured on the stems, the cotyledons, the leaves and the roots. The dry weight of the shoot (including cotyledons) and the plant (including cotyledons) were calculated from the measured dry weights.

The nutrient proportions in plants without the cotyledons, were analysed by Agro Lab, Kristianstad, Sweden. C and N were determined with an elementary analyser (Carlo Erba N/A 1500, Italy) and the other nutrients were determined using an ICP (Thermo Jarrell Ash, USA).

The culture solution analyses were done by Lennart Månsson International, LMI, Helsingborg, Sweden, using a Segmented Flow Analyzer (Traac:s) for NO_3^- and NH_4^+ and an ICP (ARL, Switzerland) for the other micro and macro nutrients. The nutrient proportions in the seeds were analysed by Stjernquist 18-07-2012, I. (personal communication).

Results

Visual observations

The roots started to grow immediately after planting. The seedlings emerged approximately 24 hours after planting. The stems were about 1 mm long at the start. Three days after planting several seedlings had straightened. The first seedling showed the cotyledons five days after planting, but at this stage they had not unfolded. The last seedling showed the cotyledons 21 days after planting. When the cotyledons started to be visible the roots also started to branch. The first pair of leaves had completely unfolded 13 days after planting and the last pair 24 days after planting. At this time, all roots were branched from approximately 20 cm from the root-tip and upwards, and they had a white colour.

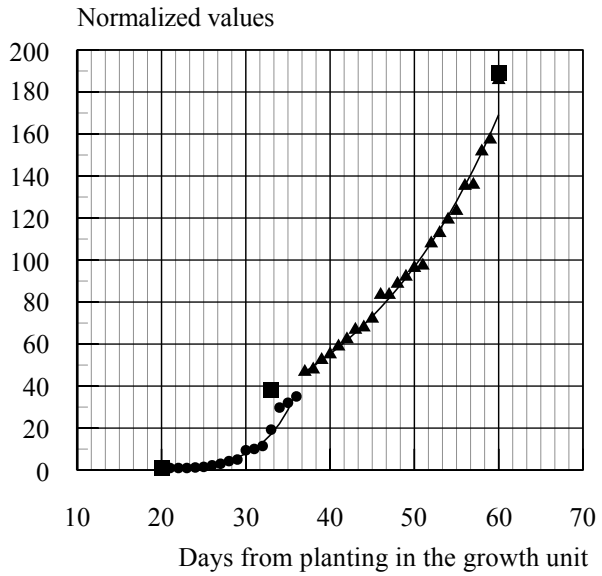

Figure 2: The relative values of the nitrogen uptake and (■) plant dry weight. Two different phases in the nutrient uptake can be noticed. (●)Phase one with an extreme nutrient uptake rate and (▲) phase two with a slower uptake rate. Correlation: First phase $r^2 = 0.984$, second phase $r^2 = 0.994$.

Figure 3: The seedlings started to branch from the first pair of character leaves.

Nutrients and growth

The seedlings started to take up nutrients approximately 15 days after planting. At this time the leaves showed deficiency symptoms. No symptoms were visible on the following leaves. In figure 2 the normalised values of the increase in dry weight per seedling and the nitrogen uptake per seedling are shown. It is in the figure possible to state that two different phases in the nutrient uptake is taking place. Phase one is recognised by it's high uptake rate. Phase two is recognised by it's slower uptake rate. Phase two seemed to start 37 days after the nutrient uptake had started. Most seedlings branched from the character leaves (Figure 3).

Nutrient proportions in nutrient solution

The results from the analyses of the nutreint solution (shown numerically in tables 2 and graphically in figures 4A and 4B), show an increase of K and a decrease of Ca in the solution.

Nutrient proportions in the plants

As shown numerically in table 3 and graphically in figures 4C and 4D, there is a systematic decrease of S, P and K in the plants. Ca increased systematically in the plants.

Fresh weight, dry weight & leaf areas

The results of the fresh and dry weights are presented in table 4 and 5 and the results of the leaf and cotyledon areas are presented in table 6. From the values can be seen that the all parts of the plant, roots, leafs and stem, have grown, throughout the eperiment. The cotyledons did not grow during the experiment.

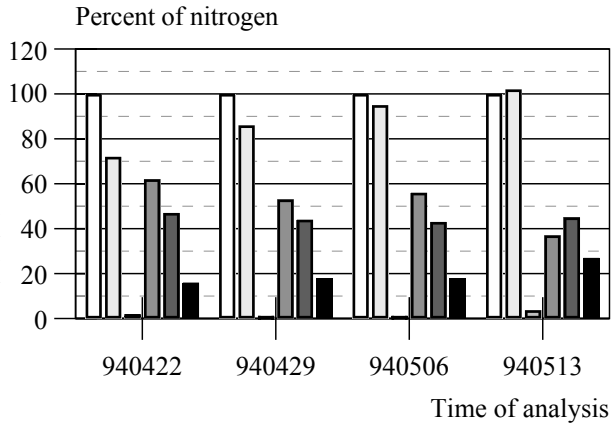

Figure 4A. The proportions of macro nutrients in the culture solution. (□) N; (□) K; (□) P; (□) Ca; (□) Mg; (□) S.

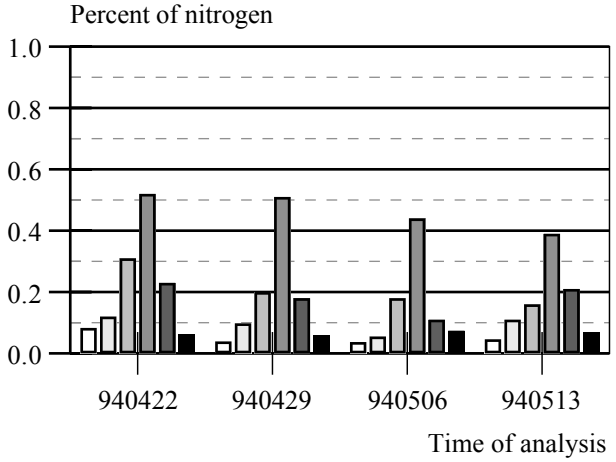

Figure 4B. The proportions of micro nutrients in the culture solution. (□) Fe; (□) Mn; (□) B; (□) Zn; (□) Cu; (□) Mo.

Table 2. Nutrient proportions in the four different samples of nutrient solution.

Nutrient	940422	940429	940506	940513
N	100	100	100	100
K	72	86	95	102
P	2.0	0.70	0.76	3.7
Ca	62	53	56	37
Mg	47	44	43	45
S	16	18	18	27
Fe	0.083	< 0.039	< 0.037	<0.046
Mn	0.12	0.098	0.055	0.11
B	0.31	0.20	0.18	0.16
Zn	0.52	0.51	0.44	0.39
Cu	0.23	0.18	0.11	0.21
Mo	< 0.062	< 0.059	0.074	<0.068

Initially a seedling develop from the nutrients contained in the seed. Compared to the needs of the seedling, the seed can contain nutrients in optimal or non optimal proportions. If the nutrient proportions in the seed are not optimal, nutrient uptake must complement the nutrients contained in the seed. Otherwise nutrient uptake need not start until the nutrients of the seed are consumed.

As can be seen in figure 2, the nutrient uptake consists of two phases. The high uptake rate of the first phase is not followed by a corresponding growth rate. It is not in this study possible two explain the behaviour of the first phase. Further studies are needed, in order to state when phase one actually starts, if it is specific nutrients that are taken up, or if it is a general uptake of nutrients. Since steady state occurs when the uptake rate equals the growth rate, and the proportions of the different nutrients in relation to the dry weight are constant, phase one can never result in a steady state.

Phase two is the phase where a steady state growth will occur. It is not, in this study, possible to confirm if steady state was achieved, because only one analysis where made of the dry weight during this phase.

It is possible that the accumulation of nutrients in phase one will influence the beginning of phase two. This should be taken into consideration in future studies of beech, no matter the experimental technique.

Since a steady state can not be confirmed, it is not possible to state anything about luxury consumption of different nutrients.

A longer experimental period was not possible, due to the fact that the seedling will reach self shading before the nutrients in the seed are consumed. This can be overcome by

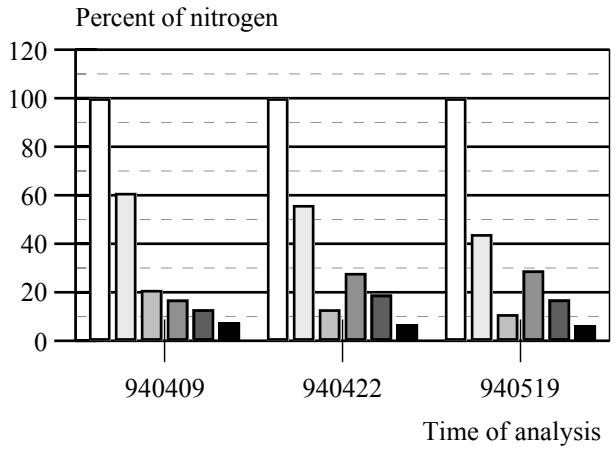

Figure 4C. The proportions of macro nutrient in the plant material. (□) N; (□) K; (□) P; (□) C a; (□) Mg; (■) S.

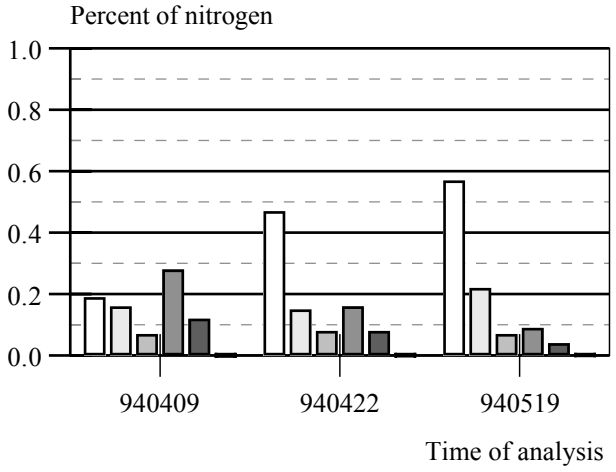

Figure 4D. The proportions of micro nutrients in the plant material. (□) Fe; (□) Mn; (□) B; (□) Zn; (□) Cu; (■) Mo.

Table 3. The nutrient proportions in the the seed and plant material. (-.- = no measurement)

Nutrient	Seed	940409	940422	940519
	[rel.]	[rel.]	[rel.]	[rel.]
N	100.0	100.0	100.0	100.0
K	33	61	56	44
P	14	21	13	11
Ca	9.7	17	28	29
Mg	7.4	13	19	17
S	7.4	7.5	6.7	6.2
Fe	0.13	0.19	0.47	0.57
Mn	-.-	0.16	0.15	0.22
B	0.072	0.07	0.08	0.07
Zn	0.091	0.28	0.16	0.09
Cu	0.050	0.12	0.08	0.04
Mo	-.-	0.001	0.002	0.003

either the use of micropropagated plants from seedlings, micro cuttings or improved technique using seedlings. The plant requirements for optimal nutrient proportions must be regarded to be the same, no matter the propagation method.

The plant analyses indicated that the proportions of S, in the nutrient solution, were high. The accumulation of K, in the culture solution, confirms the tendency of decrease in the plants. It is important to point out, that during the whole experiment the uptake continuously lowered the conductivity to 40 μ S cm^{-1}, resulting in corresponding growth. These results can be due to oscillations in the nutrient proportions in the plants. Thus values for steady-state will vary during an experiment.

The proportion of Ca increased in the plants, since the amount of Ca was deliberately high in order to get a balance between cations and anions.

The relative values of the dry weight and the nitrogen contents in the seedlings, shown in figure 2, states that the increase of dry weight follows the nitrogen contents in the plants. In the stage of development where the experiment was performed, episodic growth, as claimed by Lavarenne, Champagnat & Barnola, 1971, was not observed.

Table 4. The dry weights of the plant material. One or several groups was completely harvested at a time of harvest. Groups with the same harvest date were harvested at the same time and has thus been growing an equally long time. At the end the 8 plants, from the remaining plants, with the largest visible volume was harvested. This because it was important to get as large a biomass as possible in order to get accurate results from the analyses of the nutrient proportions.

Dry Weight of plant material							
No. pl.	**Harvest**	**Plant**	**Shoot**	**Root**	**Stem**	**Cotyledon**	**Leaf**
[pcs.]	**[date]**	**[g]**	**[g]**	**[g]**	**[g]**	**[g]**	**[g]**
5	940409	1.08	0.92	0.17	0.094	0.68	0.14
5	940409	1.06	0.9	0.15	0.099	0.65	0.16
5	940409	1.32	1.10	0.21	0.12	0.67	0.32
5	940409	0.87	0.74	0.12	0.075	0.52	0.15
5	940422	2.68	1.94	0.74	0.27	0.73	0.95
5	940422	2.27	1.56	0.71	0.26	0.53	0.77
8 best	940519	13.45	9.04	4.41	1.90	0.69	6.45

Table 5. The fresh weights of the plant material. One or several groups was completely harvested at a time of harvest. Groups with the same harvest date were harvested at the same time and has thus been growing an equally long time. At the end the 8 plants, from the remaining plants, with the largest visible volume was harvested. This because it was inportant to get as large a biomass as possible in order to get accurate results from the analyses of the nutrient proportions.The starting fresh weights of each group are shown in the column Start. These weights are the seed weight exclusive the weights of the seed shells.

Fresh Weight of plant material								
No. pl.	**Harvest**	**Start**	**Plant**	**Shoot**	**Root**	**Stem**	**Cotyledon**	**Leaf**
[pcs.]	**[date]**	**[g]**	**[g]**	**[g]**	**[g]**	**[g]**	**[g]**	**[g]**
5	940409	1.61	4.11	2.95	1.16	0.40	2.00	0.55
5	940409	1.73	3.87	2.8	1.00	0.4	1.87	0.59
5	940409	1.48	3.38	2.53	0.85	0.33	1.64	0.55
5	940409	1.86	4.72	3.31	1.41	0.45	1.79	1.07
5	940422	1.87	8.94	4.99	3.95	0.78	1.86	2.35
5	940422	1.75	7.55	3.88	3.68	0.77	1.38	1.73
8 best	940519		45.22	24.25	20.97	5.69	1.99	16.57

Table 6. The leaf and cotyledon areas of the plant material. At the end the 8 plants, from the remaining plants, with the largest visible volume was harvested. This because it was important to get as large a biomass as possible in order to get accurate results from the analyses of the nutrient proportions.

Nr .pl.	Harvest	Leaf Area	Cotyl. Area
[pcs.]	[date]	[cm^2]	[cm^2]
5	940409	48.71	77.46
5	940409	48.97	70.60
5	940409	57.67	58.85
5	940409	94.67	70.21
5	940422	231.60	73.53
5	940422	172.90	54.00
8 best	940519	1,506.00	91.83

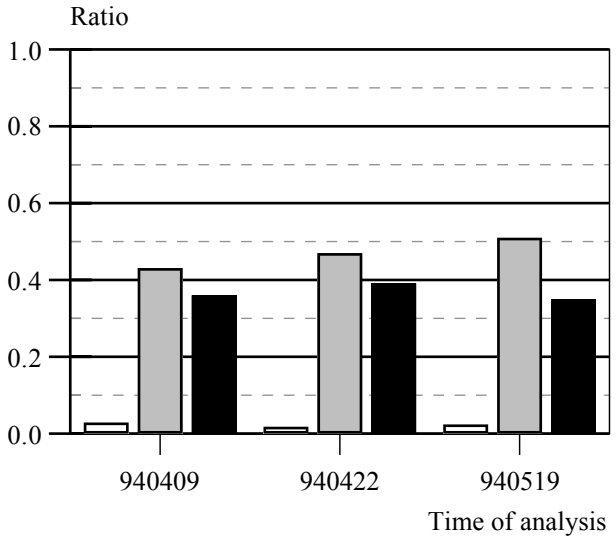

Figure 5. (□) The ratios between nitrogen and plant biomass, N/DWp; (▒) leaf biomass and plant biomass, DWl/DWp & (■) root biomass and plant biomass, DWr/DWp. The calculations are made without cotyledons. Since the ratios vary a steady-state growth can not be confirmed.

Some of the future experiments that are needed in order to establish the maximum relative growth rate, R_{Gmax}, are plant response to pH, conductivity, light intensities, daylength, temperature and also how the plant is able to handle and utilise the different nitrogen sources, NO_3^- and NH_4^+. Also the proportions of Mg and Ca compared with N must be examined, before a true steady-state and thereby the value of R_{Gmax} can be established. If any of the above mentioned conditions are not thoroughly investigated R_{Gmax} can not be accurately established.

To further investigate the nutrient proportions of beech, the nutrient proportions should be changed, such that N = 100, K = 44 and S = 6. The other nutrients should be used in the proportions used in this experiment.

Acknowledgements

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Appendix 1. The proportions of different nutrients in the three different stock solutions, pH adjusting solution, main solution, complementary solution to main. Main solution and complementary solution are given at the same time and in equal amounts, (Ingestad 1992).

Chemical compounds:	**N (NO3-N)**	**K**	**P**	**Ca**	**Mg**	**S**
Proportions [%]:	**100 (100)**	**65**	**13**	**7**	**8.5**	**9**
[mmol]:	**892.3 (892.3)**	**207.8**	**52.5**	**21.9**	**43.8**	**35.1**

Chemical compounds:	**N**	**Fe**	**Mn**	**Cu**	**Zn**	**B**	**Mo**	**Na**	**Cl**
Proportions [g]:	1000	7	4	0.3	0.6	2	0.07	0.22	0.33
[mmol]:	650	125	72.8	4.72	9.18	185	0.730	1.46	9.44

Stock solutions:

pH and conductivity adjusting solution:

Stock solution 1

		Chemical mol weight	**[%]**	**amount [g]**	**N (NO3-N)**	**K**	**P**	**Ca**	**Mg**	**S**
	K_2SO_4	174.3		6.127		70.3				35.1
	KH_2PO_4	136.1		7.145		52.5	52.5			
	KNO_3	101.11		8.594	85.0 (85.0)	85.0				
	HNO_3	63.02	65		667.9 (667.9)					
	$Ca(NO_3)_2$*	236.18		5.172	43.8 (43.8)			21.9		
	$Mg(NO_3)_2$**	256.41		11.22	87.5 (87.5)				43.8	
	Micronutrients**			6.25 ml	8.1 (8.1)					

Conductivity adjusting solution:

Stock solution 2

	K_2SO_4	174.3		6.127		70.3				35.1
	K_2HPO_4	174.18		4.206		48.3	24.1			
	KH_2PO_4	136.1		3.865		28.4	28.4			
	KNO_3	101.11		6.158	60.9 (60.9)	60.9				

Stock solution 3

	$Ca(NO_3)_2$*	236.18		46.03	389.8 (389.8)			194.9		
	$Mg(NO_3)_2$**	256.41		55.58	433.5 (433.5)				216.8	
	Micronutrients**			6.25 ml	8.1 (8.1)					

* $Ca(NO_3)_2$ X 4 H_2O

** $Mg(NO_3)_2$ X 6 H_2O

Appendix 2. The composition of the solution of micronutrients used in the Main solution, Complementary solution to main and pH adjusting solution (Ingestad 1992).

	mol weight	**amount [g]**	**N**	**Fe**	**Mn**	**Cu**	**Zn**	**B**	**Mo**	**Na**	**Cl**
$Fe(NO_3)_3$	241.9	30.24	376	125							
$Mn(NO_3)_2$	179.0	13.03	146		72.8						
$Zn(NO_3)_2$	189.4	1.739	18				9.18				
$CuCl_2$	134.5	0.635				4.72					9.44
$NaMoO_4$	205.9	0.150							0.730	1.46	
H_3BO_3	61.83	11.44						185			
HNO_3	63.03	10.55	110								
[mmol]			650	125	72.8	4.72	9.18	185	0.730		
Proportions [g]			1000	7	4	0.3	0.6	2	0.07		