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EFFECT OF PEAT-BASED TWO-COMPONENT GROWTH MEDIA ON THE GROWTH OF CONTAINERIZED SCOTS PINE SEEDLINGS

Kaksiosaisten turvepohjaisten kasvualustojen vaikutus männyn paakkutaimien kasvuun

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One-year-old containerized Scots pine seedlings (*Pinus sylvestris* L.) were grown in two-component growth media mixtures containing 75% (by volume) light, low humified *Sphagnum* peat and under an irrigation regime where the seedlings were abundantly reirrigated after –10 to –15 kPa matric potential was achieved in the growth media. The greatest seedling growth was in pure peat and in peat to which coarse perlite had been added. The poorest growth was in mixtures of peat and hydrogel and of peat and water repellent rockwool. Intermediate growth was found in peat to which fine perlite or water absorbent rockwool had been added. During drying in the range –2 to –90 kPa matric potential of the growth medium, the decrease in the net photosynthesis of seedlings at the bud formation phase was linear when aeration was not a restricting factor. During drying, the net photosynthesis was relatively large and was of a similar magnitude in pure peat and in peat to which coarse or fine perlite had been added. Significantly smaller net photosynthesis was observed in peat to which water repellent rockwool or water absorbent rockwool or hydrogel had been added. During drying under wet conditions (–1 to –4 kPa matric potential) when limited aeration was a restricting factor, the net photosynthesis increased linearly. Due to better aeration, the net photosynthesis was higher in the mixture of peat and coarse perlite than in pure peat.

Keywords: aeration, nutrients, photosynthesis, physical properties of soil, substrate, water retention

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INTRODUCTION

In the Nordic countries pure, low humified *Sphagnum* peat is predominantly used as growth medium in the production of containerized forest tree seedlings. *Sphagnum* peat is considered to provide favourable growth conditions, which can easily be manipulated during greenhouse management. Thus it is commonly recommended for seedling production (Puustjärvi 1973, Landis et al. 1990). However, pure peat may not provide optimal physical conditions under all management regimes and growth phases of various species (Heiskanen 1993a, b). In addition, availability and costs may restrict the use of pure *Sphagnum* peat worldwide. To save peat material and manipulate the properties of the growth medium, peat-based growth media mixtures are used in many countries (Landis et al. 1990).

For manipulation of the physical properties of peat, suitable mixture materials should be selected. Information about the properties and subsequent growth conditions of the growth media mixtures is therefore required. In principle, by mixing coarse grade materials into peat, coarse pores and thus aeration of the growth medium can be increased. Fine grade materials tend, in turn, to increase water retention. Although many studies and guides on the properties of various growth media are available (e.g. Bunt 1988, Landis et al. 1990), relatively little information exists about the properties of growth media mixtures based on peat or other organic materials. In addition, little is known about how the composition of peat-based growth media actually affects water and aeration conditions in the growth medium or seedling growth.

The aim of this study was to determine the effects of the physical properties of various *Sphagnum* peat-based two-component growth media mixtures on the growth of containerized Scots pine seedlings (*Pinus sylvestris* L.) and, in particular, the daytime response of net photosynthesis of the seedlings to drying of the growth media.

MATERIALS AND METHODS

Experiment 1

Peat-based growth media mixtures were prepared by hand mixing 25% (by volume) one of the different additive materials used and 75% peat. The peat component of the mixtures was low humified, medium grade and premix-fertilized S*phagnum* peat (Vapo E D1K2, Vapo Corp., Finland), which is commonly used in Finnish forest tree nurseries. The additive materials mixed into peat (P) were coarse perlite (cPr), fine perlite (fPr), loose, repellent rockwool (rRw), absorbent rockwool granulate (aRw) or hydrogel (Gel). In addition, peat alone was used as a control growth medium. The perlites, rockwools and hydrogel were produced by Nordisk Perlite Corp. (Denmark), Grodania Corp. (Denmark) and Waterworks America Corp. (USA), respectively. Because 1 g of the dry hydrogel was found to absorb water to a volume of about 0.25 dm^3, the hydrogel was added to peat as dry grains with proportions 1 g of gel to 0.75 dm^3 of peat, which was also within the application recommendations of the producer. The growth media were filled into containers and compressed with a pressure of 10 g cm^{-2} (Heiskanen 1993b). The containers used were type TK-708, which are made of polystyrene and have an average cell volume of 345 cm^3 (Lännen Corp., Finland). Each mixture was filled into two trays, each containing 40 container cells.

At the end of February 1992, two Scots pine seeds of half sib origin were sown into each container cell. After about a week the germinants were thinned to one per cell. A week later, when the germinants had reached a height of 2 to 3 cm, they were subjected to an irrigation regime. The total number of trays used and number of seedlings grown were thus 12 and 480, respectively. In addition, for measuring the net photosynthesis of seedlings, a tray of seedlings was grown in parallel per each growth medium.

In the irrigation regime used, the seedlings were slowly drip-irrigated by hand after an average matric potential of about –10 to –15 kPa was achieved in the growth medium and so that about 50 cm^3 excess water percolated from a seedling tray through the containers within an hour. The seedlings were irrigated with 0.125% (by mass) nutrient solution (made from 6–Superex fertilizer, Kekkilä Corp., Finland) containing macronutrients in concentrations (mg l^{-1}) of 279 N (84 NO_3, 23 NH_4, 173 Urea), 233 K, 50 P, 2.5 Mg and 3.8 S. The concentrations of micronutrients (mg l^{-1}) were 2.25 Fe, 1.21 Mn, 0.34 B, 0.29 Zn, 0.17 Cu, 0.02 Mo and 0.01 Co. The solution had an electrical conductivity (EC) of about 1 mS cm^{-1}. During the experiment, an attempt was made to keep the electrical conductivity of the percolates from the containers within about 0.8–2.5 mS cm^{-1} (see Timmer & Parton 1984, Landis et al. 1989, Rikala & Huurinainen 1990) by applying only pure water with EC values > 2 mS cm^{-1}.

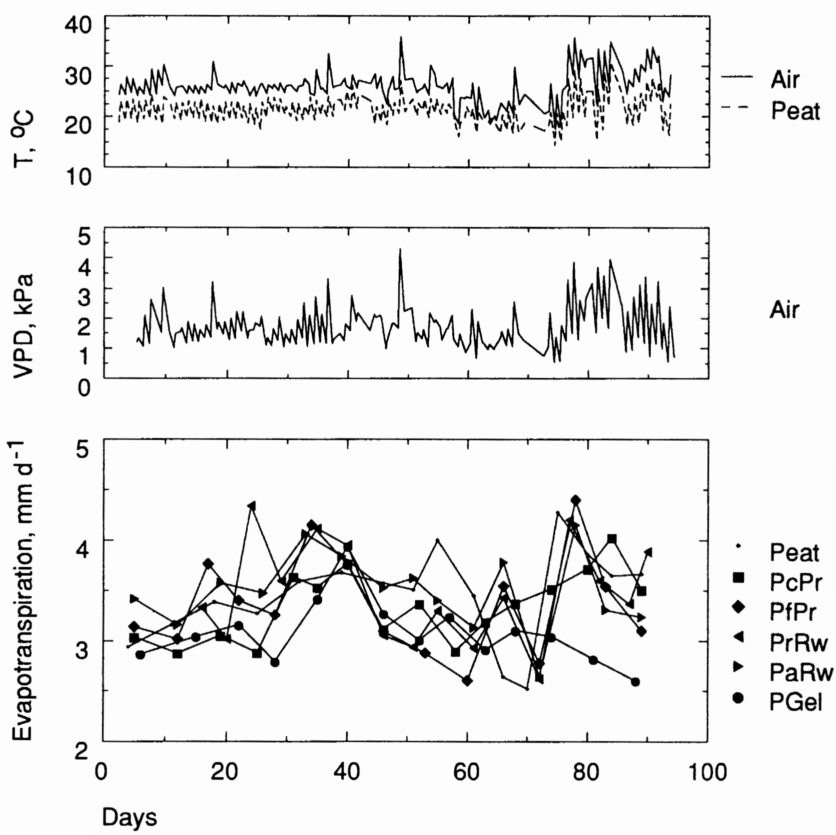
The seedlings were grown in a greenhouse (at Suonenjoki, central Finland) in which natural light was supplemented with artificial lighting to give an 18 h photoperiod. During the experiment, photosynthetically active radiation (PAR) averaged 250 mol m^{-2} s^{-1} at the seedling shoot level. Temperature (T) and relative humidity (RH) in the greenhouse varied between 15 (night) and 35°C (day) and between 30 (day) and 85% (night), respectively. The vapour pressure deficit (VPD), which was estimated from the T and RH of the ambient air at 0800 and 1400 h, varied between 1 and 4 kPa (Fig. 1). The temperature of the growth media was about 2 to 4 degrees lower than that of the ambient air at the shoot level. The evapotranspiration from the trays was estimated gravimetrically by weighing the trays before and after each irrigation.

The water potential of the growth media was measured as matric potential (kPa) every second hour during the experiment using an automated datalogger and tensiometers fitted with electrical pressure sensors. The tensiometer readings had previously been calibrated against the hydraulic head in the laboratory (Heiskanen & Laitinen 1992). The tips of the tensiometers were placed in the middle of separate container cells. Two tensiometers were installed in each seedling tray. For peat, however, only one tensiometer was used per tray. Thus, there were a total of 22 tensiometers. The relationship between water and air filled porosity of the growth media during the experiment was estimated by determining the water retention characteristics from parallel precultural media (n = 5) (Heiskanen 1993b).

The height growth of 20 randomly selected living seedlings per tray was measured once a week following the same seedlings throughout the experiment. At the end of the experiment, mortality and selected morphological characteristics of all living seedlings were measured (height, root collar diameter, shoot and root dry masses, needle length). In addition, the seedlings from each tray were harvested and pooled for nutrient analysis. The needles were dried at 65°C for 48 hours, pulverized and stored at room temperature. The concentrations of elements in the needles and in a hydrogel water suspension

Fig. 1. Mean evapotranspiration (mm d^{-1}) from the evaporative surface of the growth medium in the seedling trays (n = 2 for each growth medium) during growing. Evapotranspiration for the total tray area can be calculated by dividing the values shown by 1.144. Vapour pressure deficit (VPD) was estimated from the temperature (T) and relative humidity of the ambient air at 0800 and 1400 h.

Kuva 1. Keskihaihdunta (mm vrk^{-1}) kasvualustan pinta-alaa kohti kasvatuksen aikana (n = 2 kasvualustaa kohti). Haihdunta voidaan laskea arkkien pinta-alaa kohti jakamalla esitetyt arvot 1.144:llä. Ilman kyllästysvajaus (VPD) laskettu ilman lämpötilasta (T) ja suhteellisesta kosteudesta klo 8.00 ja 14.00.



were determined using plasma emission spectrometry (ARL-3580 OES, Fisons Instruments Corp., USA) and TGA-500 analyzer (LECO Corp., USA). The N concentration was determined with a CHN-600 analyzer (LECO Corp., USA).

At the end of the experiment, the net photosynthesis of a seedling was measured as the mean of three values recorded within one minute using a LI-6200 gas-exchange measurement system (LI-COR Corp., USA) after five to ten minutes stabilizing time in constant conditions (200 mol m^{-2} s^{-1} PAR from above, 347 ppm CO2, 26°C T). After apical buds had formed on the seedlings, the growth media were allowed to dry out freely after an abundant irrigation. During drying (within a week), the net photosynthesis of random seedlings and the corresponding matric potential of the growth medium were measured daily between 0900 and 1400 h, after which the water potential and silhouette area of the shoots (vertical projection from above) were instantly measured using a pressure chamber and a video camera system according to the techniques described by Turner (1988) and Oker-Blom & Smolander (1988), respectively. The silhouette area of the shoots was used as the light absorbing area, against which the absolute net photosynthesis of the seedlings was also estimated (Smith et al. 1991). These photosynthesis values thus indicate the photosynthetic capacity of seedlings in vertical light rather than the photosynthetic capacity of the total needle area.

Experiment 2

To study, in particular, the effect of drying at high matric potential range of the growth medium on net photosynthesis, 40 seedlings were grown in peat and in a mixture of peat (67% by volume) and coarse perlite (33%) in a tray in parallel with Experiment 1 and in similar conditions. After apical bud formation, the growth media were allowed to dry from –1 to –4 kPa matric potential (within 3–4 days), during which time the net photosynthesis of the seedlings was measured as described previously for Experiment 1.

Data analysis

Means and standard deviations (Sd) of the variables were calculated from the values obtained for seedlings within the various growth media (n 80). In addition, due to correlation within trays, the mean values for each container tray were used as independent observations (n = 2). One-way analysis of variance (ANOVA) and Tukey's test were used to evaluate differences between growth media. ANOVA and t-test were used to test the differences in regression equations between growth media.

RESULTS AND DISCUSSION

During growth of the seedlings, the temporal mean matric potential of the growth media in individual trays varied between –0.2 and –45 kPa. Median values were nearly –3 kPa in all media (Table 1), indicating adequate and rather similar water availability to seedlings (Heiskanen 1993a, 1994). Air filled porosity at –3 kPa, which was estimated by interpolation from the water retention characteristics of the media (Table 2), was about 40%, which indicates sufficient aeration in the growth media (Heiskanen 1993a, 1994). At –3 kPa, however, PGel had less than about 35% air filled porosity,

Table 1. Temporal variation in mean matric potential in different growth media during growing.

Taulukko 1. Kasvualustojen keskimääräisen matriisipotentiaalin ajallinen vaihtelu kasvatuksen aikana.

Medium *Alusta*	Matric potential (kPa) *Matriisipotentiaali (kPa)*			
	Median *Mediaani*	Mean *Keskiarvo*	Range *Vaihteluväli*	Sd *Sd*
Peat	–2.6	–5.0	–0.2...–34.1	6.4
PcPr	–2.8	–4.9	–0.2...–44.1	6.1
PfP	–2.9	–4.1	–0.2...–22.2	3.4
PrRw	–3.2	–4.9	–0.3...–26.0	4.5
PaRw	–3.7	–4.7	–0.3...–27.5	3.6
PGel	–3.0	–4.2	–0.4...–24.8	3.6

Table 2. Volumetric water retention characteristics (mean + Sd, n = 5) at desorption for different growth media. The reference volume of the medium is that at –0.1 kPa (≈ volume of filled containers). Different letters within columns indicate significant difference (P <0.05) according to Tukey studentized range test.

Taulukko 2. Kasvualustojen tilavuuspohjainen vedenpidätyskyky (keskiarvo ± Sd, n = 5). Vertailutilavuus on tilavuus –0.1 kPa:ssa (≈ paakkujen täyttötilavuus). Eri kirjaimet sarakkeilla osoittavat merkitsevää eroa (P <0.05) Tukeyn testin mukaan.

Medium Alusta	*Water retention (%) at matric potentials* Vedenpidätyskyky (%) matriisipotentiaaleilla –0.1 kPa	–1 kPa	–5 kPa	–10 kPa	–50 kPa
	89.9±2.2 ab	72.6±8.1 a	37.3±1.8 a	29.9±1.4 a	20.8±0.8 ab
PcPr	85.1±2.4 b	64.9±4.7 a	36.8±1.8 a	28.4±1.5 ab	22.2±3.7 b
PfPr	87.1±2.0 ab	74.9±2.1 a	36.8±2.1 a	29.6±1.4 ab	19.5±1.7 ab
PrRw	84.5±1.5 b	72.6±3.5 a	33.0±1.9 a	26.3±1.4 bc	18.4±2.8 ab
PaRw	92.1±2.5 a	73.9±4.6 a	37.1±1.4 a	24.9±0.5 c	16.5±0.7 a
PGel	90.1±7.1 ab	75.7±5.3 a	46.0±4.5 b	35.8±2.7 d	27.2±1.4 c
P-value P-arvo	0.006	0.106	<0.001	<0.001	<0.001

which may have caused slightly restricted aeration in this medium. Water retention characteristics and related physical properties of peat growth medium are described in detail elsewhere (Heiskanen 1993b, c).

The proportions of nutrients in the nutrient solution of the fertilizer used in reirrigations were similar to those recommended by Ingestad (1979) for Scots pine seedlings. The nutrient concentrations in the seedling foliages were rather similar in the various growth media, and their ratios to N were fairly close to those recommended by Ingestad (1979) (Table 3). In PGel, however, foliar concentrations of N and Na were

Table 3. Average concentrations of elements (mg g^{-1} for N to S and mg kg^{-1} for Fe to Na on a dry mass basis) and ash content (%) in the needles of seedlings grown in different growth media. Replicates are the mean values for the seedling trays (n = 2) of each medium.

Taulukko 3. Taimien neulasten keskimääräiset ravinnekonsentraatiot (mg g^{-1} N:stä S:iin ja mg kg^{-1} Fe:sta Na:iin massasta) sekä tuhkapitoisuus (%) eri kasvualustoissa. Toistoina arkkikeskiarvot (n = 2).

Element *Ravinne*	Peat	PcPr	PfPr	PrRw	PaRw	PGel	*P*-value *P-arvo*
N	37.5	37.5	39.8	37.2	37.8	41.3	0.049
P	3.9	3.7	3.7	3.4	3.1	3.6	0.005
K	14.6	15.0	16.2	14.7	15.8	15.8	0.376
Ca	1.1	1.0	1.0	0.9	1.0	0.9	0.706
Mg	1.2	1.1	1.0	1.0	1.0	1.0	0.661
S	1.3	1.2	1.1	1.0	1.0	1.1	0.097
Fe	69	72	77	74	75	70	0.172
B	51	60	62	51	51	60	0.003
Cu	9.5	5.7	6.1	5.5	3.6	4.6	0.054
Mn	285	217	213	173	119	266	0.001
Zn	49	56	48	51	47	44	0.608
Al	28	19	–	20	23	–	0.009
Na	41	22	39	28	28	221	<0.001
Ash *Tuhka*	3.3	3.5	3.9	3.4	3.7	3.6	0.124

significantly higher (P <0.05, Tukey's test) than in the other growth media. In addition, foliar concentrations of N were relatively high in general. It is probable that the urea applied with the nutrient solution dissolved slowly in the growth media and had only a small effect on the EC of the percolates from the containers (Puustjärvi 1991). Thus, the actual nutrient concentration in the growth media was higher than could be determined from the EC of the percolates. Still, the EC of the percolates (Fig. 2) was occasionally above that which can be considered to be favourable (1^{-2} mS cm^{-1}) (Landis et al. 1989, see also Puustjärvi 1980, 1991, Timmer & Parton 1984, Rikala & Huurinainen 1990). The decreasing acidity of the percolates during growing indicates slowly dissolving Ca from the base fertilizer of peat (Fig. 2).

In general, the seedling growth was greatest in pure peat and PcPr (Fig. 3, Table 4). The poorest growth was in PrRw and PGel. The root mass was greater and the shoot to root ratio lower in Peat, PcPr and PfPr than in the other three media. With PGel the mortality was rather high (Table 4).

During drying, the net photosynthesis of the seedlings decreased with decreasing water availability (Fig. 4, Table 5). The slopes of the regression equations for net photosynthesis did not differ between any of the media (P> 0.080, t-tests) but the intercepts did (P <0.001, F-test). The regressions (intercepts) of net photosynthesis at drying were significantly lower in PaRw, PrRw and PGel than in pure peat (P <0.001, t-tests). The respective regressions in PcPr and PfPr did not differ from that in peat (P> 0.700, t-tests). Because transpiration decreased almost similarly to photosynthesis in all growth media, the decrease in water use efficiency (photosynthesis / transpiration) during drying did not differ markedly between growth media (averaging from 5 to 0 mol CO_2/mmol H_2O).

The water retention characteristics as such did not seem to affect the growth responses

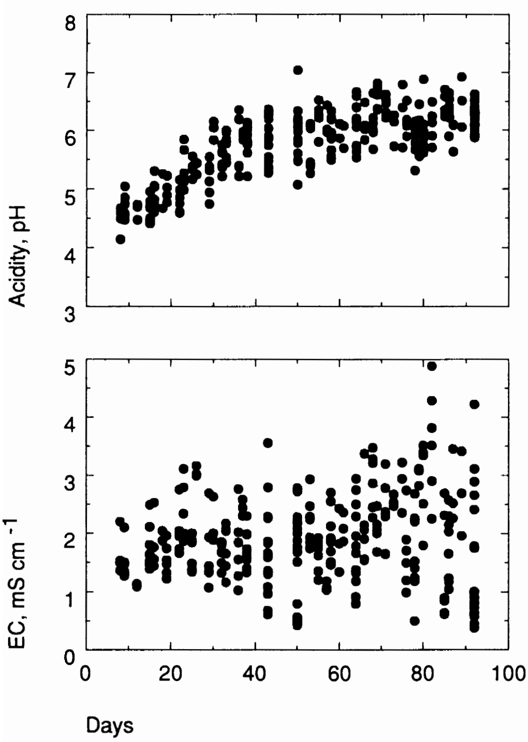


Fig. 2. Electrical conductivity (EC, mS cm^{-1}) and acidity (pH) of the percolate from the containers during growing.

Kuva 2. Paakkujen suodosveden sähkönjohtokyky (EC, mS cm^{-1}) ja happamuus (pH) kasvatuksen aikana.

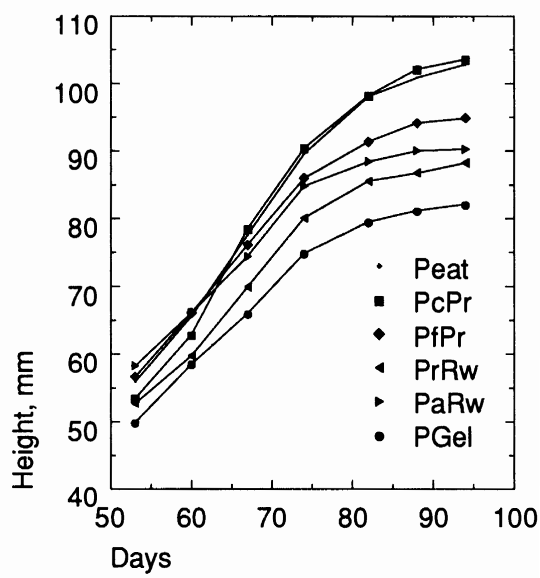


Fig. 3. Mean height growth of the seedlings (n = 20) in different growth media during growing.

Kuva 3. Taimien keskikasvu (n = 20) kasvatuksen aikana eri kasvualustossa.

Table 4. Means for the morphological characteristics and mortality of seedlings grown in the different growth media studied (mean ± Sd). All seedlings in each growth medium are used as replicates (n 80). Different letters within columns indicate significant difference (P <0.05) according to Tukey studentized range test.

Taulukko 4. Taimien morfologisten tunnusten keskiarvot ja kuolleisuus eri kasvualustoissa (keskiarvo ± Sd). Toistoina kaikki taimet tietyssä kasvualustassa (n 80). Eri kirjaimet sarakkeilla osoittavat merkitsevää eroa (P <0.05) Tukeyn testin mukaan.

Medium *Alusta*	Height *Pituus* (mm)	Root collar diameter *Tyviläpimitta* (mm)	Shoot dry mass *Verson kuivamassa* (g)	Root dry mass *Juuriston kuivamassa* (g)	Shoot/Root-ratio *Verso/Juuri-suhde* (g/g)	Needle length *Neulasen pituus* (mm)*	Mortality *Kuolleisuus* (%)
Peat	104.2±18.5 a	2.28±0.32 a	0.72±0.15 a	0.16±0.04 a	4.66±1.0 a	46.7±5.8 ab	0.0 –
PcPr	104.1±22.8 a	2.26±0.33 ac	0.85±0.22 b	0.19±0.05 b	4.52±0.8 a	46.9±7.2 ab	0.0 –
PfPr	93.6±22.4 b	1.92±0.33 b	0.75±0.20 a	0.15±0.05 a	5.07±1.2 a	44.2±6.0 a	5.0 –
PrRw	91.7±21.8 b	2.11±0.31 c	0.73±0.20 a	0.11±0.04 cd	6.87±1.6 b	48.2±10.5 b	0.0 –
PaRw	94.6±25.3 ab	2.23±0.39 ac	0.85±0.23 b	0.13±0.04 d	7.28±2.5 b	49.9±9.8 b	1.3 –
PGel	92.8±20.0 b	1.95±0.35 b	0.59±0.17 c	0.09±0.03 c	7.05±2.7 b	43.5±5.8 a	10.0 –
P-value *P-arvo*	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	–
P-value** *P-arvo***	0.446	0.067	0.025	0.001	0.005	0.009	0.017

* From two random needles in the middle of the shoot. **For tray means (n = 2).
* *Kahdesta satunnaisesta neulasesta verson keskeltä. **Arkkikeskiarvoista (n = 2).*

during the growing experiment or the net photosynthesis to drying in peat and PcPr, because these responses were about the same even though PcPr retained less water than peat did (Table 2). Nevertheless, the slightly larger proportion of coarse pores and the lower shrinkage probably provided better aeration in wet conditions in PcPr, which compensated for the lower water retention and availability compared with that in peat. In addition, growth in PfPr was lower, although the water retention characteristics and also the net photosynthesis at drying were about the same as in peat. This may be due to lower aeration in PfPr after reirrigations, which may have resulted from the increased wettability observed at reirrigation.

The differences in seedling growth found between growth media during the growing experiment and in net photosynthesis during drying may have been due to the physical properties of the growth media. However, water availability as determined by water retention (Table 2) within various matric potential ranges (e.g. –1 to –10 and –10 to –50 kPa, see Heiskanen 1993b) did not differ markedly between media. The difference in water retention between –0.1 and –3 kPa was, however, slightly lower in PGel (29%) than in the other media (> 32%). This may indicate somewhat decreased air filled porosity in PGel at matric potentials higher than the median value (Table 1), which may be the reason for the decreased intercept of the net photosynthesis response compared with that in peat (Fig. 4). Reduced aeration due to elevated water retention in growth media containing hydrogels has also been suggested in several other studies (Flannery & Busscher 1982, Lennox & Lumis 1987, Tripepi et al. 1991).

The hydrogel used here was found to contain maximally about 6 mg of water soluble Na per gram of dry mass of the hydrogel. No other soluble elements were detected. Thus, the increased availability of sodium obviously explains the increased foliar concentrations of Na in PGel (Table 3). On the other hand, many studies indicate increased levels of monovalent ions in particular and also decreased levels of divalent cations in seedling foliages grown in growth media into which hydrogel has been incorporated (Johnson 1984, Taylor & Halfacre

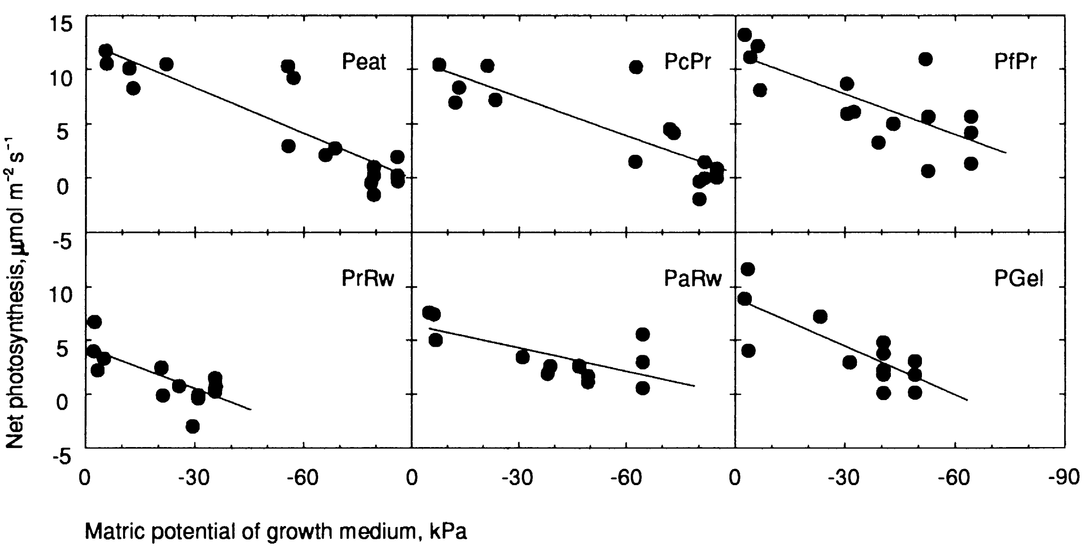


Fig. 4. Relationship between the net photosynthesis of the seedlings and the matric potential of different growth media during drying from –2 to –90 kPa (Experiment 1).

Kuva 4. Taimien nettofotosynteesin ja kasvualustan matriisipotentiaalin välinen suhde kasvualustojen kuivuessa –2:sta –90:een kPa (Koe 1).

1986, Wang & Boogher 1987, Wang & Gregg 1990, Tripepi et al. 1991). This suggests that hydrogels commonly possess selective cation exchange capacity, which may cause the availability of various nutrients to differ and even a decrease in the dry matter production of seedlings (Taylor & Halfacre 1986). The increased foliar concentration of Na, and possibly N, in PGel may thus also be caused partly by the increased adsorption of ions by the hydrogel particles compared with that of peat. Furthermore, due to soluble Na and possibly to a large nutrient retention, the hydrogel used may have markedly concentrated salts during drying, which increased the osmotic potential. This, in turn, may have decreased the water availability to the roots at the surfaces of the hydrogel particles. Despite the relatively great water retention of the medium, water may therefore not be easily available to seedlings (see Tripepi et al. 1991). Thus, decreased water availability probably contributed to the poorer root and shoot growth (Table 4) and to the lower net photosynthesis observed in PGel (Fig. 4) compared with that in peat. Moreover, the decreased water availability may also have contributed to the increased sodium uptake by the seedlings for balancing internal water status through stomatal regulation (Marschner 1986). On the other hand, the high foliar concentration of Na in PGel may have been close to the phytotoxic level.

The net photosynthesis at drying was poorest in PrRw (Fig 4). Because the initial level was low, zero level of photosynthesis was achieved already at about –30 kPa (Table 5). Seedlings grown in PrRw had rather poorly developed roots (Table 4). After the drying period, it was also found that the rockwool granulates were fairly tough and dry. Therefore, the resistance of the rockwool particles to penetration by roots was probably relatively high, causing restricted root growth and water conduction to the shoot. Furthermore, due to the presence of the dry blocking rockwool particles, water conduction during drying within the growth medium was probably decreased, which restricted water availability and hence seedling photosynthesis and growth in PrRw compared with that in pure peat. In PaRw, pore continuity may also have been blocked to some extent, which may subsequently have restricted seedling growth and photosynthesis compared to peat. Decreased root length accompanied by increased root thickness has been reported for tree seedlings grown in rockwool (Högberg 1984), which indicates increased resistance to root penetration. Decreased root growth of seedlings and cuttings has also been shown in rockwool, in which water

Table 5. Parameters for the regression equations $y = a + bx$ showing the relationship between the net photosynthesis (y, µmol m^{-2} s^{-1}) of seedlings and the matric potential (x, kPa) of different growth media during drying from –2 to –90 kPa. RMSE indicates root mean square errors (standard errors of the estimates). The regression equations differ significantly between media ($P < 0.001$, F-test).

Taulukko 5. Regressioyhtälöiden $y = a + bx$ parametrit nettofotosynteesin (y, µmol m^{-2} s^{-1}) ja kasvualustan matriisipotentiaalin (x, kPa) väliselle suhteelle kasvualustojen kuivuessa –2:stä –90:een kPa. RMSE osoittaa keskineliövirheen juurta (estimaattien keskihajontaa). Regressioyhtälöt poikkeavat toisistaan merkitsevästi (P < 0.001, F-testi).

Medium *Alusta*	a	b	x(y = 0)	RMSE	r	n	P
Peat	12.5	0.14	–89.7	2.3	0.88	17	<0.001
PcPr	10.9	0.12	–93.3	2.5	0.83	16	<0.001
PfPr	11.4	0.12	–92.2	2.7	0.73	15	0.002
PrRw	4.3	0.15	–29.5	2.4	0.64	15	0.010
PaRw	6.4	0.07	–89.5	1.7	0.69	13	0.009
PGel	9.0	0.15	–59.7	2.2	0.79	13	0.001
Pooled *Yhdistetty*	7.5	0.08	–91.7	3.5	0.54	89	<0.001

retention and availability are usually suggested to be low (van der Boon & Niers 1980, Wilhelmsson 1984, Langerud & Sandvik 1987).

The net photosynthesis of the seedlings increased with decreasing matric potential under wet conditions (matric potential > –5 kPa) (Fig. 5, Table 6). The measured response of the net photosynthesis to drying differed significantly in pure peat and peat-perlite mixture (Table 6). The intercepts of the regression equations for photosynthesis differed (P = 0.008, F-test), while the slopes did not (P = 0.665, F-test). At a matric potential of –1 kPa, for example, the net photosynthesis was about 6 and increased to about 10 µmol m^{-2} s^{-1} when the matric potential decreased to –4 kPa. At matric potentials persistently higher than –1 kPa, however, net photosynthesis would be close to zero due to excess water and hypoxia or anoxia (Heiskanen 1994). Compared with peat-perlite mixture, the lower net photosynthesis of the seedlings in peat probably resulted from low aeration due to the higher water retention between –1 and –5 kPa (Table 2). The water use efficiency also increased significantly during drying, but the variation was rather large (1 to 4 mol CO_2/mmol H_2O).

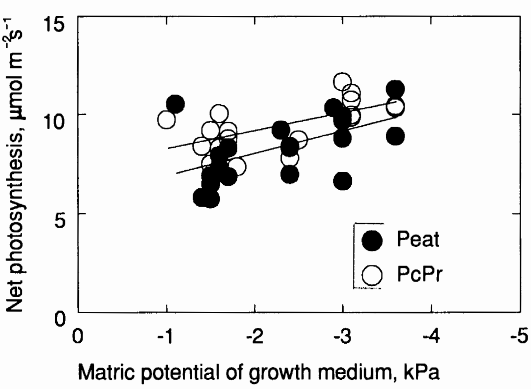


Fig. 5. Relationship between the net photosynthesis of the seedlings and the matric potential of peat and the mixture (PcPr) of peat (67%) and coarse perlite (33%) during drying from –1 to –4 kPa (Experiment 2).

Kuva 5. Taimien nettofotosynteesin ja kasvualustan matriisipotentiaalin välinen suhde puhtaan turpeen sekä turpeen (67%) ja karkean perliitin (33%) seoksen kuivuessa –1:sta –4:ään kPa (Koe 2).

In none of the growth media did the seedling water potential seem to change during drying (data not shown). Within the range –2 to –90 kPa matric potential of growth medium, the seedling water potential averaged about –1.5 MPa. Probably the seedlings could maintain rather constant internal water potential by osmotic adjustment of cells; but at the same time, a decrease in stomatal conductance decreased gas exchange and photosynthesis (Seiler & Casell 1990, Timmer & Miller 1991). In addition, the growth phase (bud formation) may also have had an effect on metabolism and the level of water potential. In wet conditions, however, the seedling water potential decreased from –0.2 to –0.8 MPa when the matric potential of the growth medium decreased from –1 to –4 kPa, thus increasing aeration. According to Zaerr (1983), if the roots are completely flooded for a few days, containerized Scots pine seedlings may show only a slight decrease in net photosynthesis, probably due to the ability of Scots pine seedlings to transfer oxygen from the shoot to the roots.

The seedling water potential, especially when measured before dawn, is widely used to measure water stress and water availability from growth medium to tree seedlings (Kaufmann 1977, Schulte & Marshall 1983, Landis et al. 1989). The seedling water potential has, however, been suggested to be a poor indicator of seedling water stress (Langerud & Sandvik 1991). In addition, the pressure chamber technique does not measure the osmotic potential of cells and therefore may partly give varying results (Turner 1988, Bennett 1990). On the other hand, in this study further drying to below –100 kPa matric potential of the growth media might have decreased the seedling water potential. Havranek & Benecke (1978) reported that the seedling water potential (at equilibrium with soil water) with the net photosynthesis of three containerized conifer seedlings (*Larix decidua* Mill., *Picea abies* (L) Karst., *Pinus cembra* L.) showed a marked decrease at soil matric potentials <–150 kPa in a humic sandy loam. During drying, the seedling water potentials were –50 to –400 kPa lower than the soil matric potential down to –800 kPa soil matric potential. Rutter & Sands (1958) showed reduced transpiration and water content in the needles of containerized Scots pine seedlings when the soil (probably mineral soil) matric potential decreased from –10 to –500 kPa.

Table 6. Parameters for the regression equations x = *a* + bx showing the relationship between the net photosynthesis (x, µmol m^{-2} s^{-1}) of seedlings and the matric potential (x, kPa) of peat and the mixture of peat (67%) and coarse perlite (33%) during drying from –1 to –4 kPa. RMSE indicates root mean square errors (standard errors of the estimates). The regression equations differ significantly between media (P = 0.03, F-test).

Taulukko 6. Regressioyhtälöiden x = a + bx parametrit nettofotosynteesin (x, µmol m^{-2} s^{-1}) ja kasvualustan matriisipotentiaalin (x, kPa) väliselle suhteelle puhtaan turpeen sekä turpeen ja karkean perliitin kuivuessa –1:stä –4:ään kPa. RMSE osoittaa keskineliövirheen juurta (estimaattien keskihajontaa). Regressioyhtälöt poikkeavat toistaan merkitsevästi (P = 0.03, F-testi).

Medium *Alusta*	a	b	RMSE	r	n	P
Peat	5.8	–1.12	1.39	0.54	20	0.014
PcPr	7.4	–0.90	1.01	0.61	19	0.006
Pooled *Yhdistetty*	6.6	–1.03	1.31	0.53	39	0.001

With decreasing water contents in peat growth medium, the water potential of containerized red pine seedlings (*Pinus resinosa* Ait.) at midday as well as transpiration and stomatal conductance have also been shown to become markedly lower (Timmer & Miller 1991).

CONCLUSIONS

It was shown that the net photosynthesis of containerized Scots pine seedlings decreased linearly with the matric potential of the growth medium. At the bud formation phase, daytime seedling water potential was not, however, found to clearly indicate seedling water stress and consequent photosynthesis. Compared with pure, low humified *Sphagnum* peat growth medium, the growth and net photosynthesis of the seedlings were found to be affected by the addition of different medium materials to peat. However, the slight differences found in the water retention characteristics of the growth media mixtures were considered to be too small to markedly affect growth directly. Nevertheless, great water retention at high matric potentials decreases aeration of a growth medium and may lead to hypoxia and hence to decreased growth and photosynthesis as may be the case, for example, in pure peat or in peat to which hydrogel has been added. At low matric potentials, low water retention and mechanical impedance causing poor root growth may markedly reduce water availability to seedlings and therefore depress growth, as in peat to which water repellent rockwool has been added.

Although the average water retention characteristics in the bulk growth medium appear to be favourable, additive materials, such as water repellent rockwool particles, may block water movement in pores within the growth medium to such an extent that water availability to seedlings is severely restricted. Furthermore, such particles may considerably increase the resistance of the growth medium to root penetration, thus causing poor root growth, reduced nutrient and water availability and low photosynthesis. In addition, especially in dry conditions, hydrogels may contain high soluble levels of some nutrients (like Na here) and also possess great selective nutrient retention, which may decrease the availability of both nutrient and water from the growth medium or even cause phytotoxicity. In dry conditions, the addition of perlite to peat improves the wettability of the growth medium. Perlite additions also diminish settling and shrinkage of the growth medium during drying. In addition, in wet conditions additions of coarse perlite to peat increase the amount of coarse pores and the percolation of excessive water and may therefore markedly improve aeration of the growth medium.

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TIIVISTELMÄ:

KAKSIOSAISTEN TURVEPOHJAISTEN KASVUALUSTOJEN VAIKUTUS MÄNNYN PAAKKUTAIMIEN KASVUUN

Yksivuotisia männyn paakkutaimia kasvatettiin kahdesta materiaalista koostuvissa kasvualustoissa, jossa oli 75% tilavuudesta vaaleaa rahkaturvetta. Taimia kasteltiin runsaasti aina kun kasvualustan matriisipotentiaali oli alentunut n. –10...–15 kPa:iin. Taimet kasvoivat eniten puhtaassa turpeessa sekä turpeen ja karkean perliitin seoksessa. Heikointa kasvu oli turpeessa, johon oli lisätty hydrogeeliä tai vettähylkivää kivivillaa. Kohtalaista kasvu oli turpeessa, jossa oli hienoa perliittiä tai vettäimevää kivivillaa. Kasvualustojen kuivuessa –2:sta –90:een kPa taimien silmunmuodostusvaiheessa, taimien nettofotosynteesi aleni lineaarisesti. Fotosynteesi oli korkea ja lähes sama puhtaassa turpeessa, turpeen ja karkean sekä turpeen ja hienon perliitin seoksissa. Muissa seoksissa fotosynteesi oli merkittävästi alempi kuivumisen aikana. Märissä oloissa (–1...–4 kPa) kasvualustan ilmanvaihdon ollessa kasvua rajoittava tekijä, fotosynteesi kohosi lineaarisesti kuivumisen edetessä. Fotosynteesi oli korkeampi turpeen ja karkean perliitin seoksessa kuin puhtaassa turpeessa, mikä johtui korkeammasta kasvulustan ilmanvaihdosta. Tutkimuksessa tarkasteltiin lisäksi kasvualustaseosten fysikaalisten sekä ravinnetekijöiden vaikutusta taimien kasvuun.

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Corrections

In the article "Effect of peat-based two-component growth media on the growth of containerized Scots pine seedlings" by Juha Heiskanen, which appeared in Suo 45(1), due to the technical reasons a part of the table 2 was omited.

Table 2. Volumetric water retention characteristics (mean ± Sd, n = 5) at desorption for different growth media. The reference volume of the medium is that at –0.1 kPa (volume of filled containers). Different letters within columns indicate significant difference (*P* <0.05) according to Tukey studentized range test.

Taulukko 2. Kasvualustojen tilavuuspohjainen vedenpidätyskyky (keskiarvo ± Sd, n = 5). Vertailutilavuus on tilavuus –0.1 kPa:ssa (paakkujen täyttötilavuus). Eri kirjaimet sarakkeilla osoittavat merkitsevää eroa (P <0.05) Tukeyn testin mukaan.

Medium *Alusta*	Water retention (%) at matric potentials *Vedenpidätyskyky (%) matriisipotentiaaleilla*				
	–0.1 kPa	–1 kPa	–5 kPa	–10 kPa	–50 kPa
Peat	89.9±2.2 ab	72.6±8.1 a	37.3±1.8 a	29.9±1.4 a	20.8±0.8 ab
PcPr	85.1±2.4 b	64.9±4.7 a	36.8±1.8 a	28.4±1.5 ab	22.2±3.7 b
PfPr	87.1±2.0 ab	74.9±2.1 a	36.8±2.1 a	29.6±1.4 ab	19.5±1.7 ab
PrRw	84.5±1.5 b	72.6±3.5 a	33.0±1.9 a	26.3±1.4 bc	18.4±2.8 ab
PaRw	92.1±2.5 a	73.9±4.6 a	37.1±1.4 a	24.9±0.5 c	16.5±0.7 a
PGel	90.1±7.1 ab	75.7±5.3 a	46.0±4.5 b	35.8±2.7 d	27.2±1.4 c
P-value *P-arvo*	0.006	0.106	<0.001	<0.001	<0.001

Page 20 left column row 13 (200 mol m^{-2} s^{-1}...), should be (200 μmol m^{-2} s^{-1} ...).
Page 20 left column row 14 CO2..., should be CO_2 ...
Page 20 right column row 14 (n 80), should be (n ≤80).
Page 22 left column row 12 was (1^{-2} mS cm^{-1}), should be (1–2 mS cm^{-1}) and page 26 left column row 26 was (1 to 4 mol CO_2/mmol H_2O), should be (1 to 4 μmol CO_2/mmol H_2O).
Page 22 right column row 22 5 to 0 mol... should be 5 to 0 μmol.
In Table 4, (n 80), should be replaced with (n ≤80).