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High and dry: Consequences of drought exposure in Scots pine seedlings grown in authentic peat soil

Kasvualustan kuivumisen vaikutukset rahkasaraturpeeseen istutettujen männyntaimien ensikehitykseen

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Should the frequency of drought increase in boreal forests due to climate change, seedlings planted in prepared peat mounds could become more susceptible to soil desiccation. The resistance of Scots pine (*Pinus sylvestris* L.) seedlings to drought will thus be a key factor in the regeneration success of pine-dominated, forestry-drained peatlands. In this study, we evaluated the physiological, metabolic, and morphological responses of year-old seedlings gradually exposed to extreme drought in highly decomposed *Sphagnum-Carex* peat blocks. Drought clearly suppressed root and shoot growth as well as fractional colonization of ectomycorrhizal fungi. Sustained declines in photochemical efficiency (F_v/F_m) of previous-year and current-year needles did not occur until the volumetric soil water content had dropped to 30% and 10%, respectively. Polyamine analysis revealed that new needles are preferred in protecting the different parts of the seedlings against drought stress. Despite growth losses, the maintenance of rather high photochemical efficiency in current-year needles under severe water stress would appear to indicate a potential for seedling recovery if water availability in the peat improved. Given the high tolerance exhibited by Scots pine seedlings, death by drought seems a lesser concern.

Key words: drought, F_v/F_m, mycorrhizal colonization, *Pinus sylvestris* seedlings, polyamines, root and shoot growth, *Sphagnum-Carex* peat

Introduction

Tree seedlings planted in forest regeneration areas are most vulnerable to stress prior to gaining an established foothold in their new environment. Spells of adverse weather, e.g., drought during this time may prove fatal. Water deficit has, in fact, been identified as the main reason for unsuccessful establishment of newly planted trees (Kaushal & Aussenac 1989, Grossnickle 2005).

In a changing climate, the frequency of drought may increase in boreal forests (IPCC 2007), which further emphasizes the need to screen conifer planting stock for drought resistance which will match present and predicted drought conditions (Bigras 2005). Slowly growing genotypes of white spruce (*Picea glauca* (Moench) Voss), for instance, were shown to be better adapted to drought or dry environments than intermediate or fast-growing ones. According to Kozlowski et al. (1991), the availability of water to outplants particularly during new root regeneration is critical. Water loss through heightened transpiration combined with nonabsorption of water from soil markedly increase the internal water deficit of the outplant.

On boreal forestry-drained peatlands, clearcutting followed by soil preparation via mounding and planting is a commonly applied scheme for regenerating Scots pine (*Pinus sylvestris* L.) (Hyvän metsänhoidon… 2007). On thick-peated sites (> 30 cm), mounds lack a mineral soil component. Depending on the specific technique used, the peat mass may be inverted directly upon the excavated spot or beside the ditch (or pit) from which it was excavated. In the latter case, the lifted peat mass is placed on the intact peatland surface. Independent of the technique used, the mound bottom is typically comprised of an upturned humus layer, which is topped by more or less decomposed peat. Although peat mounds provide adequate substrate for Scots pine seedling establishment and growth during moist growing seasons, drought can radically impact regeneration success especially in mounds composed of well decomposed *Carex* peat (Saarinen 2005). Hence, increasingly drier and hotter summers would clearly enhance the susceptibility of seedlings growing in peat mounds to drought.

Plants respond to abiotic stress with changes in many physiological and metabolic processes. Chlorophyll fluorescence is indicative of the state of Photosystem II (PSII) and thus photochemical efficiency (Maxwell & Johnson 2000). Chlorophyll fluorescence provides information on the ability of a plant to tolerate stress as well as the extent of damage incurred by the photosynthetic apparatus in response to stress (e.g., Mohammed et al. 1995, Maxwell & Johnson 2000). As a technique for assessing plant physiological status, chlorophyll fluorescence is quick to determine and does not require whole-plant experimentation in addition to being renowned for its affordability and precision (e.g., Vidaver et al. 1991, Schreiber et al. 1994, Maxwell & Johnson 2000, Percival & Sheriffs 2002). In particular, of all the measurable chlorophyll fluorescence parameters, the ratio of variable to maximal fluorescence yield (F_v/F_m), i.e., the maximum potential quantum yield of PSII, has been the most widely used in interpreting plant responses to environmental stress and as an indicator of photoinhibition (Öquist & Wass 1988, Mohammed et al. 1995, Maxwell & Johnson 2000). For most plant species including trees, an average value of about 0.83 is typical when the phototosynthetic apparatus is functioning normally (Björkman & Demmig 1987). Exposure to stress will lead to values lower than this and thus F_v/F_m has been used as an indicator of photoinhibition.

With regards to Scots pine, chlorophyll fluorescence has primarily been used to evaluate physiological changes related to cold hardiness and freezing damage (e.g., Sundblad et al. 1990, Lindgren & Hällgren 1993, Taulavuori et al. 2000), elevated atmospheric CO_2 and air pollution (e.g., Saarinen & Liski 1993, Kellomäki & Wang 1997, Gielen et al. 2000). In this study, chlorophyll fluorescence served as a diagnostic tool for monitoring the physiological status of needles repeatedly from the same seedlings as the level of drought stress increased.

Polyamines (PAs) are organic compounds commonly occurring in plant cells in free and conjugated forms (Martin-Tanguy 2001). They stabilize macromolecular structures and regulate many cellular processes such as cell division, morphogenesis, senescence, and cell death, and gene expression on the whole (Bouchereau et al. 1999, Davies 2004, Kuehn & Phillips 2005). Furthermore, PAs are recognized as being crucial in a plant's defense against abiotic stresses (Alcázar et al. 2010). The PAs spermidine, spermine, and their precursor putrescine are the most common and thus also the most frequently studied, and have been reported to regulate plant growth or serve as intracellular messengers for conveying physiological responses (Davies 2004). Notably, PA concentrations are affected by drought stress in some plant species (Capell et al. 2004, Kasukabe et al. 2004, Ma et al. 2005) and tolerance to drought is associated with polyamine biosynthesis for example in eastern white pine (*Pinus strobus* L.) (Tang et al. 2007).

Morphologically, a balanced proportion of shoots to roots is important for seedling survival since it is indicative of both seedling water loss and water uptake capability at the onset of water stress (Ritchie 1984, Thompson 1985, Burdett 1990, Mexal & Landis 1990, Grossnickle 2000). Dry conditions reduce root growth: roots of conifers stop elongating and become quiescent at a soil water potential below –0.6 to –0.7 MPa (–600 to –700 kPa) (Kaufmann 1968, Leshman 1970, Day & MacGillivray 1975). When root growth is constricted by a water shortage, photosynthesis is also constrained resulting in lowered production of photosynthates (Burdett 1990, Grossnickle 2000). The circle becomes more vicious the longer the stress continues, inexorably preventing the regeneration of new roots not only due to a lack of water but also photosynthates (Ritchie 1982, Puttonen 1986). Furthermore, limited nutrient availability associated with water deficit may constrain the normal development and growth of young seedlings (Grossnickle 2005).

Mycorrhizal fungi are known to play a vital role in nutrient uptake and transport between soil and plant roots (Smith & Read 1997). Some evidence exists that they may even aid water transfer to plants (Duddridge et al. 1980, Plamboeck et al. 2007). Potentially, ectomycorrhizae could fortify a seedling's ability to overcome episodes of drought stress. However, the effect of drought even just on the ectomycorrhizal biomass present in tree roots is a sphere largely unstudied (Cudlin et al. 2007). The use of fine roots and associated ectomycorrhizae as bio-indicators of environmental stress has considerable potential, but any such studies are both time-consuming and complex (Cudlin et al. 2007). It has been suggested that such parameters as the number of root tips per unit root dry mass and fractional colonization of ectomycorrhizae (i.e., fraction of root tips that is ectomycorrhizal), for example, should be employed more often as indicators of the effects of drought (Cudlin et al. 2007).

Thus, drought stress in a plant may be interpreted in terms of carbon allocation to the root system and root-associated fungi in addition to the functional state of PSII. Furthermore, PAs, which are involved in many developmental and growth processes as well as abiotic stress tolerance, are regarded to play a role also in acclimation to abiotic stress.

In the following study, we evaluated physiological, metabolic, and morphological parameters, namely chlorophyll fluorescence, fluctuation in polyamine concentrations, and growth of Scots pine seedlings gradually exposed to drying in unprocessed peat substrate. Under intensifying drought stress, we monitored the physiological status of year-old Scots pine seedlings by measuring 1) *in vivo* chlorophyll *a* fluorescence of different needle age classes, and 2) endogenous polyamine concentrations in needles and roots. Finally, at experiment's end, we determined the consequent morphological response in terms of 3) root and shoot traits and mycorrhizal colonization of root tips. In doing so, we sought to shed more light on the potential mechanisms behind stress endurance of Scots pine, which can have far-reaching implications for regeneration success on silviculturally challenging areas, e.g., drained, nutrient-poor peatland forest in a changing climate.

Materials and Methods

Experimental design

As part of a larger investigation concerning soil preparation and forest regeneration on drained peatlands (Pearson et al. 2011), the substrate and seedling material used in this study matched those customary to peatland forestry. Fifty blocks of authentic, undisturbed highly decomposed *Sphagnum-Carex* peat (bulk density 0.22 ± 0.03 g cm^{-3}) were dug up manually from a drained, clearcut, and mounded peatland site in Western Finland (61°50′41″N, 24°17′19″E) (Fig. 1). The thickness of the peat layer there exceeded 1.5 m. According to the Finnish classification system, the peatland represented a transitional form between dwarf shrub (Vatkg) and *Vaccinium vitis-idaea* (Ptkg II) drained peatland site types (Vasander

Fig. 1. Fifty highly decomposed, undisturbed Sphagnum-Carex peat blocks were extracted from a drained peatland site in Juupajoki, Western Finland.

Kuva 1. Viisikymmentä pitkälle maatuneesta rahkasaraturpeesta koostuvaa häiriintymätöntä näytettä kaivettiin ojitetulta suolta Juupajoelta Länsi-Suomesta.

& Laine 2008). In order to simulate the surface peat of the mounds (i.e., the peat at the top of mounds) at the site, the blocks were extracted from a soil depth of approximately 10–50 cm after first stripping off the humus layer. To disengage the substrate in blocks without disturbing its inner structure, 50 individual PVC frames (25 × 20 × 20 cm) were shoved into the peat. Thereafter, the delimited peat blocks were detached from below with a peat spade. The blocks were then transported to the Parkano unit of the Finnish Forest Research Institute and planted with one-year-old containerized Scots pine seedlings (one seedling per block). Half the seedlings represented the control and were placed in a PVC tub and watered from below. The water level was maintained at 18 cm below the soil surface of the 20-cm-high blocks. This was deemed sufficient to ensure capillary water movement and thus adequate moisture conditions throughout the experiment. The other 25 planted seedlings were set on top of planks and subjected to drought stress by withholding water entirely. From mid-June till the end of August 2008, all seedlings were situated outside in a lean-to with a transparent roof and thus sheltered from the rain. Thereafter, as the weather cooled and relative humidity rose at the turn of autumn, the drought stress group was moved indoors to a heated greenhouse beside the lean-to where they remained until the end of the experiment in mid-October. This maneuver was justifiable to maintain the conditions necessary for drying of the peat substrate, i.e., sufficiently high air temperature and low relative humidity. Prior to

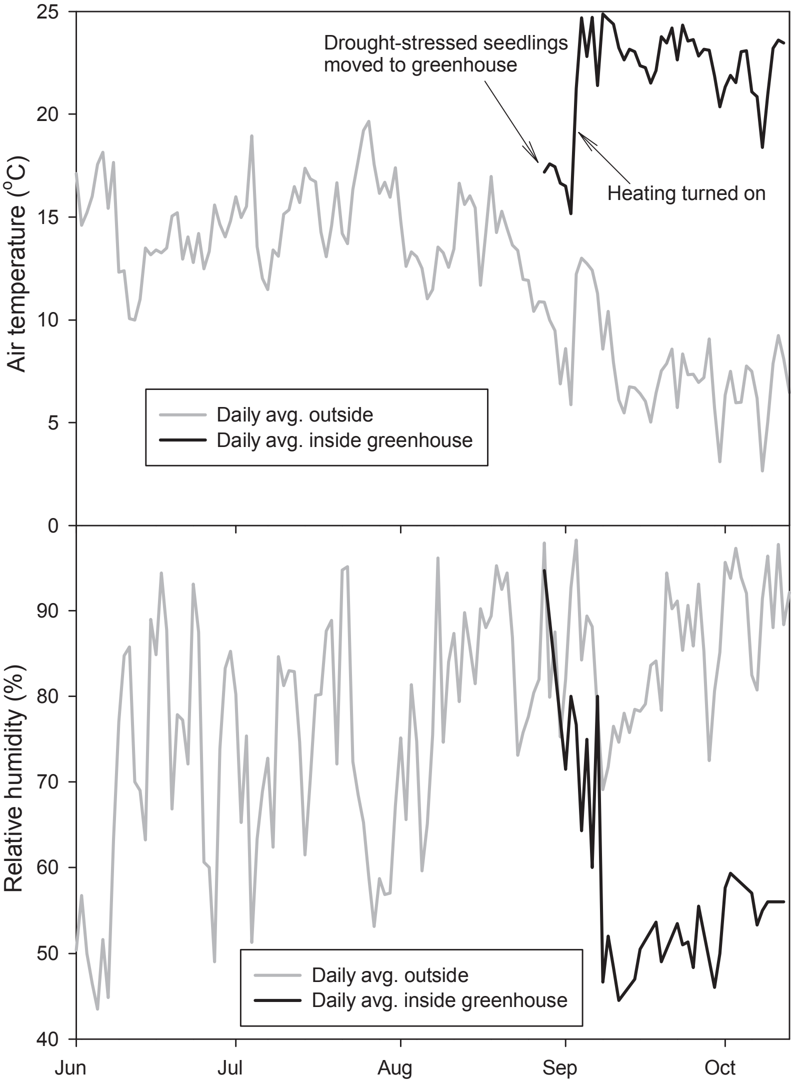

Fig. 2. Mean daily air temperature and relative humidity outside in lean-to and inside greenhouse. The drought-stressed seedlings were moved into heated greenhouse at the end of August to expedite drying of the peat substrate.

Kuva 2. Päivittäinen keskilämpötila ja ilmankosteus kokeen aikana ulkona katoksen alla (harmaat viivat) sekä kasvihuoneessa (mustat viivat). Elokuun lopussa kuivuuskäsittelyn taimet siirrettiin lämmitettyyn kasvihuoneeseen kasvualustan kuivumisen nopeuttamiseksi. Jun = kesäkuu, Jul = heinäkuu, Aug = elokuu, Sep = syyskuu, Oct = lokakuu.

being moved inside, the volumetric water content of the peat in the drought treatment was 25–30%.

The mean daily air temperature and relative humidity for the duration of the experiment are provided in Fig. 2. At the conclusion of the experiment, water retention at desorption (Fig. 3) of the *Sphagnum-Carex* peat was determined at the Suonenjoki unit of the Finnish Forest Research Institute from five, undisturbed fresh cylindrical samples taken from four of the 25 × 20 × 20 cm peat blocks (Heiskanen 1993). The aforementioned bulk density (g cm^{-3}) for this peat was ascertained from these same five cylindrical samples.

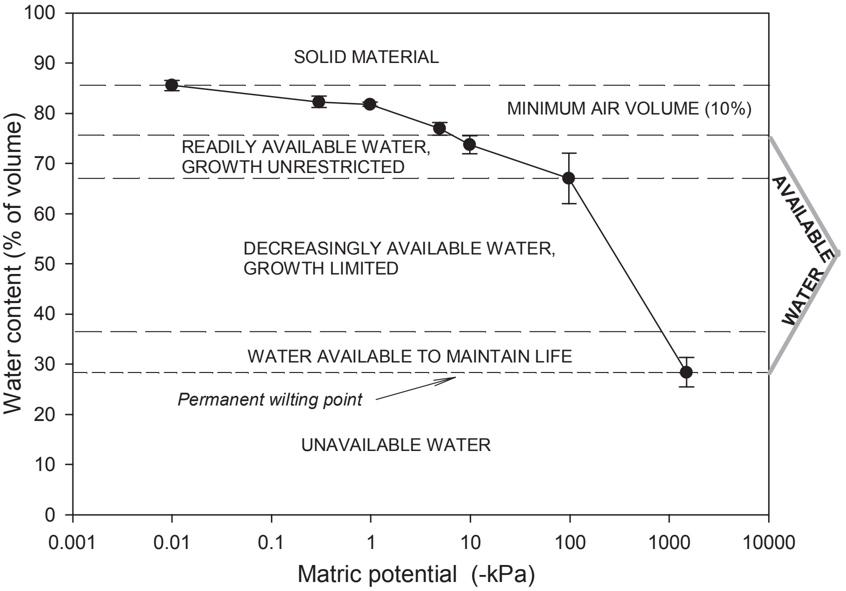

Fig. 3. Water retention at desorption (relative to wet volume at –0.3 kPa) of the highly decomposed Sphagnum-Carex peat. Each dot represents the mean ± SE of five cylindrical soil samples taken from four of the 25 × 20 × 20 cm peat blocks which served as growing substrate for the pine seedlings. The water availability distinctions at corresponding units of pressure have been modified from Päivänen (1973).

Kuva 3. Kokeessa käytetyn pitkälle maatuneen rahkasaraturpeen vedenpidätyskyky. Kuvan x-akselilla maaveden potentiaali ja y-akselilla turpeen vesipitoisuus (% tilavuudesta). Jokainen piste edustaa viiden turvenäytteen keskiarvoa keskivirheineen. Turvenäytteet on otettu neljästä männyntaimien kasvualustana toimineesta 25 × 20 × 20 cm turveprofiilista. Maassa olevan veden rajat ja niitä vastaavat paineet kasvien veden saatavuuden kannalta Päiväsen (1973) mukaan: Readily available water = käyttökelpoinen vesi jonka sitoutuneisuus ei estä kasvia ottamasta sitä, Decreasingly available water = vähenevän kasvun vesi, Water available to maintain life = elämää ylläpitävä vesi, Permanent wilting point = pysyvä lakastumisraja, Unavailable water = käyttökelvoton vesi.

Chlorophyll fluorescence measurements

Chlorophyll fluorescence was measured from detached new (current-year) and old (previous-year) needles every 1–2 weeks till the end of August, and thereafter every 4–7 days as drought stress manifested. One new needle from the current-year leader shoot and one old needle from the previous-year leader shoot per seedling were plucked approximately midway up the respective shoots between 08:00–09:00, placed in a plastic bag, and stored in a small cooler to await darkening and measurement within 6 hours. Such a storage procedure was recommended by, e.g., Mohammed & Noland (1997). Needle detachment has been shown to have no effect on the chlorophyll fluorescence of Scots pine (Otronen & Rosenlund 2001, Percival & Sheriffs 2002). Furthermore, our preliminary testing of the needle sampling procedure demonstrated that the leaf clips were too heavy for needles attached to the young seedlings to bear. Gielen et al. (2000) noted slightly lower F_v/F_m values in one-year old than in current-year Scots pine needles, thus we chose to measure both old and new needles as well.

After collection, the needles were dark-adapted for half an hour in leaf clips equipped with a shutter plate inside a black, light-impenetrable bag at room temperature 20°C. Thereafter, chlorophyll fluorescence parameters were measured using the non-modulated Plant Efficiency Analyzer (Hansatech Instruments Ltd., U.K.) with its probe set at 100% of maximum light (i.e., saturating) intensity for 15 seconds. The probe's six lightemitting diodes (LEDs) illuminate the leaf surface with red light having a peak wavelength of 650 nm. The parameters derived from the induction kinetics of chlorophyll fluorescence were as follows: F_o = minimal fluorescence in the dark-adapted state; F_v = yield of variable fluorescence in the dark-adapted state ($F_v = F_m – F_o$); F_m = maximal fluorescence in the dark-adapted state; F_v/F_m = photochemical trapping efficiency in the dark-adapted state, i.e., the maximum potential quantum efficiency of PSII if all capable reaction centers were open. In the Results section, we will focus on interpreting the parameter F_v/F_m.

Immediately after fluorescence measurements, the volumetric water content (%) of each peat block was determined by employing a soil moisture meter equipped with a sensor (Moisture Meter HH2 and ThetaProbe ML2x, Delta-T Devices Ltd., U.K.). Default coefficient values for organic soil were used (derived from Roth et al. 1992). The manufacturer reports a loss of absolute accuracy up to 4% volumetric water content with this meter setting. The sensor bears four, 6-cm-long spikes which are inserted into the soil. The top of each peat block was measured from four spots every time of measurement. Chlorophyll fluorescence and soil water content were measured on 13 occasions during the study.

Polyamine analysis

Polyamine concentrations of current and previous-year needles and fine roots were analyzed from four seedlings per treatment 1) at the start of the experiment (July 2nd); 2) before moving the drought stress group into heated greenhouse (Aug. 27th); 3) after the onset of stress observable in the chlorophyll fluorescence parameter F_v/F_m (Sept. 30th); and 4) near the end of the experiment (Oct. 7th). Seedling root systems were rinsed off and placed in distilled water. Fine roots were then excised and dried with paper towel. All samples were weighed (100–400 mg fresh mass/sample) and stored in a freezer (–80 °C) until analysis. PA samples were extracted with 5% (w/v) $HClO_4$ after which free PAs from the crude extract and soluble conjugated PAs from the hydrolyzed supernatant were dansylated and separated with HPLC (Merck-Hitachi) (Sarjala & Kaunisto 1993, Fornalé et al. 1999). The putrescine, spermidine and spermine concentrations are expressed as nmol g^{-1} fresh mass of plant tissue.

Since sampling for polyamine determination is destructive, the number of seedlings under surveillance in each treatment consequently decreased by four each time samples were taken.

Root and shoot characteristics

At the end of the experiment, four seedlings per treatment were selected from which the following morphological traits were characterized: 1) dry biomass of shoots and roots; 2) water content of shoots and roots; 3) root to shoot ratio; 4) total number of living and dead (defunct) fine root tips; 5) proportion of fine root tips colonized by ectomycorrhizae; 6) number of living fine root tips mg^{-1} root dry mass (DM). Prior to microscopic examination of the roots, the fresh mass of the roots and shoots was determined. The root samples for microscopic examination were cleaned and segmented into suitable portions for viewing and tallying root characteristics (i.e., items 4 and 5) under the microscope. Root tips appearing dark, flat, damaged, and/or lifeless were collectively classified as defunct. Thereafter, the roots and shoots were dried in an oven at 105 °C overnight and then reweighed.

Statistical analyses

The analysis of the chlorophyll fluorescence parameter F_v/F_m and free polyamine concentrations were based on linear mixed models (procedure MIXED in SPSS 17, SPSS Inc., Chicago, IL, USA). The model was structured as follows:

$$Y = m + T + N + D + T{*}D + N{*}D + T{*}N + T{*}D{*}N + s + e, \quad (1)$$

where Y is the response variable (F_v/F_m, free putrescine, spermidine, or spermine concentrations), m is constant, T is treatment, N is needle age class (or sample type for polyamine testing), D is time since the beginning of the treatment, s is seedling and e is residual term. Of these, T, N and D were treated as fixed effects and s was treated as a random effect.

The models define a split-plot structure with needle age (or sample type) as a split-plot treatment. A first-order autoregressive (AR1) covariance structure was assumed for the time correlation between the residuals of a needle age of a seedling. The Bonferroni adjustment method was applied to the confidence intervals and significance values to account for multiple comparisons. Variances of the residuals of the fluorescence parameter (F_v/F_m) depend on the expected values and the fluorescence parameter values were transformed using an arcus sine square root transformation. In spite of the transformation, the variances of the residuals were dependent on the predicted values, which was taken into account by using regression weights $w=1/(pred_u*(1–pred_u))$, where $pred_u$ is a predicted value computed by unweighted analysis. Normality and homogeneity of the variance of the residuals were checked graphically and the selection of the covariance structure was based on Akaike's information criteria.

The differences in morphological root and shoot traits between the control and drought-stressed seedlings were tested for significance with one-way ANOVA using the same statistical package mentioned above.

Results

Water retention curve of peat substrate

Water retention at desorption (relative to volume at –0.3 kPa) is presented in Fig. 3 wherein the water availability nomenclature is based on the work of Päivänen (1973). In this particular peat, the permanent wilting point (–1554 kPa, i.e., pF 4.2) (Taiz & Zeiger 1991) lay at a volumetric soil water content of approximately 28% (Fig. 3).

The estimated total porosity of the peat was 85.53 ± 2.20% of soil volume, which is equivalent to the approximation made by Päivänen (1982) for peat in an advanced stage of decomposition. In such peat, about 80% of the pores are medium (30–0.2 μm) and small (< 0.2 μm) in size (Päivänen 1973). Consequently, while the water content at saturation is lower compared to poorly decomposed peat, the loss of water with increasing matric suction is smaller (Päivänen 1973). Here, a matric suction of −100 kPa caused the peat water content to drop by only 18% (Fig. 3). Although the peat was particularly resistant to drying, soil water increasingly moved from capillary pore space and adhered to soil particles (adhesion) in effect slowing down water uptake by the drought-stressed seedlings, which then infringed on their root and shoot growth. Eventually, the inability of the stressed seedlings to uptake water culminated in the point of no return, i.e., permanent wilting point.

Chlorophyll fluorescence

Overall drought lowered the photochemical efficiency of Scots pine seedlings significantly relative to the control (Table 1, Figs. 4 and 5). The treatment effect also depended on needle age class (Table 1). F_v/F_m in drought-stressed seedlings was significantly lower for both old and new needles compared to the control (in both cases p=0.000). Furthermore, while no difference in F_v/F_m between needle age classes within the control treatment was observed (mean and SD of new and old 0.83 ± 0.02; p=0.900), drought reduced photosynthetic efficiency significantly more in previous-year than current-year needles (mean and SD of new 0.79 ± 0.15 vs. old 0.71 ± 0.28; p=0.000).

A significant three-way effect between treatment, needle age, and time was also found (Table 1). The precise stages at which peat water content began to limit photosynthesis in old and new needles can be seen in Figs. 4 and 5, respectively. When the volumetric water content of the peat in the drought treatment had dropped to approximately 25–30%, F_v/F_m of old needles plunged significantly in stressed seedlings compared to the control. For new needles, however, the difference between treatments did not become significant until more than three weeks later when the peat had dried still further to a water content of about 10%. Within the drought treatment, the needle age classes likewise began to differ significantly at 25% peat water content.

Based on the water availability distinctions in Fig. 3, the peat water content instigating a critical change in the level of F_v/F_m in the old needles of drought-stressed seedlings approximated with the permanent wilting point. By the time F_v/F_m began to descend markedly in new needles, however, the peat water content had already sunk well below this critical point. In effect, old Scots pine needles were more sensitive than new needles when oppressed by water shortage. The first registered decrease in F_v/F_m of old needles was also accompanied by visual observations of needle yellowing and shedding in drought-stressed seedlings. Although F_v/F_m in new needles eventually plummeted in response to severe drought, by then extensive damage to the seedlings, e.g., yellowing, browning, and shriveling of needles as well as wilting of shoots, was already visibly perceivable.

Here, if we define mortality as that state when all old needles have browned and died (thus fluorescence no longer measurable) and the mean F_v/F_m in new needles is < 0.50, then 6 of the 25 seedlings succumbed to death by drought over the course of the experiment. The first registered death occurred on Sept. 22nd about three weeks prior to the end of the experiment. Expectedly, control seedlings were in stable health throughout without any casualties.

Drought-induced changes in polyamine concentrations

Free putrescine

The treatment effect was significant (Table 1) wherein the free putrescine concentration in control seedlings was greater overall than in drought-stressed ones. Significant interaction between treatment and sample type was also found (Table 1); drought decreased putrescine concentrations in both new (p=0.023) and old needles (p=0.013) relative to the control (Table 2). For fine roots, however, the difference between treatments was insignificant (p=0.249) (Table 2). Notably, the effect of treatment also depended on time (Table 1, Fig. 6a,d,g). Prior to being moved into the greenhouse (Aug. 27th) with soil water content at 25–30%, the putrescine concentrations in roots and new needles of drought-stressed seedlings had risen considerably higher than their starting levels as well as in relation to the control (drought > con-

Table 1. Explanatory factors (fixed effects) and their significances in the linear mixed model for the chlorophyll fluorescence parameter (F_v/F_m), free putrescine, spermidine, and spermine concentrations. The experiment consisted of control and drought stress treatments. F_v/F_m was determined from two needle age classes, previous-year and current-year needles. Polyamine concentrations were determined from previous-year and current-year needles as well as fine roots.

Taulukko 1. Neulasten fotosynteesin tehokkuutta (F_v/F_m) sekä vapaan putreskiinin, spermidiinin ja spermiinin pitoisuuksia ennustavien sekamallien selittävät tekijät (kiinteät vaikutukset) ja niiden tilastollinen merkitsevyys. Koe sisälsi kaksi käsittelyä: kuivuusstressi ja kontrolli. F_v/F_m mitattiin sekä yksivuotiaista että uusista neulasista. Polyamiinien pitoisuudet mitattiin yksivuotiaista ja uusista neulasista sekä hienojuurista. Time = aika käsittelyn alkamisesta, Treatment = käsittely, Needle age = neulasten ikä, Sample type = näytetyyppi.

Source	F	df	p
F_v/F_m			
Time	34.50	12	0.000
Treatment	68.56	1	0.000
Needle age	8.389	1	0.004
Time* treatment	30.42	12	0.000
Time*needle age	1.917	12	0.029
Treatment*needle age	7.443	1	0.006
Time*treatment*needle age	1.878	12	0.034
Free putrescine			
Time	1.148	3	0.337
Treatment	4.335	1	0.041
Sample type	8.525	2	0.001
Time*treatment	4.660	3	0.005
Time*sample type	6.876	6	0.000
Treatment*sample type	5.722	2	0.005
Time*treatment*sample type	1.094	6	0.376
Free spermidine			
Time	3.994	3	0.011
Treatment	6.273	1	0.015
Sample type	89.89	2	0.000
Time*treatment	4.925	3	0.004
Time*sample type	20.37	6	0.000
Treatment*sample type	2.328	2	0.106
Time*treatment*sample type	1.394	6	0.231
Free spermine			
Time	18.02	3	0.000
Treatment	9.196	1	0.004
Sample type	52.14	2	0.000
Time*treatment	1.092	3	0.359
Time*sample type	4.166	6	0.001
Treatment*sample type	4.054	2	0.022
Time*treatment*sample type	1.466	6	0.204

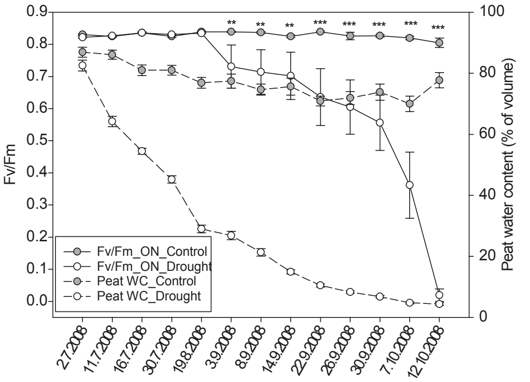

Fig. 4. F_v/F_m of dark-adapted year-old Scots pine needles (ON) and peat water content (WC) over the course of the study. Each dot represents mean ± SE. Asterisks indicate significant differences in F_v/F_m between the control and drought treatments as follows: * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

*Kuva 4. Yksivuotiaiden neulasten (ON) fotosynteesin tehokkuus (F_v/F_m) ja turpeen vesipitoisuus (% tilavuudesta, WC) eri ajankohtina käsittelyittäin. Neulaset pimennettiin puoleksi tunniksi ennen mittausta. Pisteet edustavat keskiarvoa ja pystyjana kuvaa keskivirhettä. Kontrolli- ja kuivuuskäsittelyjen väliset tilastollisesti merkitsevät erot F_v/F_m:ssä merkitty tähdellä seuraavasti: * $p<0.05$, ** $p<0.01$, *** $p<0.001$. Control = kontrollikäsittely, Drought = kuivuuskäsittely.*

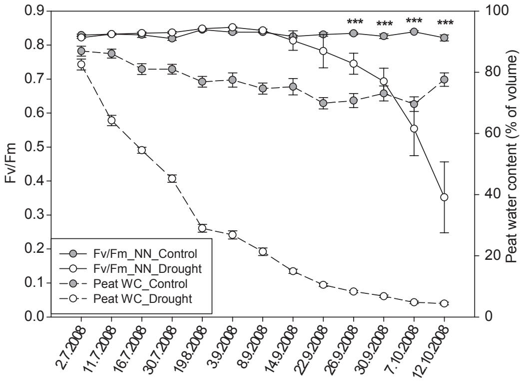

Fig. 5. F_v/F_m of dark-adapted new Scots pine needles (NN) and peat water content (WC) over the course of the study. Asterisks indicate significant differences in F_v/F_m between the control and drought treatments as follows: * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

Kuva 5. Uusien neulasten (NN) fotosynteesin tehokkuus (F_v/F_m) ja turpeen vesipitoisuus (% tilavuudesta, WC) eri ajankohtina käsittelyittäin. Neulaset pimennettiin puoleksi tunniksi ennen mittausta. Pisteet edustavat keskiarvoa ja pystyjana kuvaa keskivirhettä. Kontrolli- ja kuivuuskäsittelyjen väliset tilastollisesti merkitsevät erot F_v/F_m:ssä merkitty tähdellä seuraavasti: $p<0.05$, ** $p<0.01$, *** $p<0.001$. Control = kontrollikäsittely, Drought = kuivuuskäsittely.*

trol, p=0.049). However, by the third time samples were taken (Sept. 30th) with soil water content at < 10%, putrescine concentrations had decreased in all sample types in the stress treatment with a dramatic decrease occurring particularly in new needles (Fig. 6a,d, g). Hence, the overall concentration was significantly lower in the drought-stressed than control seedlings on this occasion (p=0.010).

Free spermidine

As with putrescine, the free spermidine concentration in control seedlings was significantly higher overall than in drought-stressed ones (Tables 1 and 2). In addition, treatment interacted significantly with time (Table 1). Drought led to significantly lower spermidine concentrations

Table 2. Mean concentrations (± SE) (nmol g^{-1} FM) of free polyamines in the Scots pine seedlings according to treatment and sample type.

Taulukko 2. Männyntaimien vapaiden polyamiinien (putreskiini, spermidiini ja spermiini) pitoisuuksien keskiarvot ja keskivirheet (nmol g^{-1} tuoremassaa) käsittelyittäin ja näytetyypeittäin. Control = kontrollikäsittely, Drought = kuivuuskäsittely. Sample type = näytetyyppi, New needles = uudet neulaset, Old needles = yksivuotiset neulaset, Fine roots = hienojuuret.

	Putrescine		Spermidine		Spermine	
Sample type	Control	Drought	Control	Drought	Control	Drought
New needles	216 ± 21	185 ± 29	69 ± 8	70 ± 11	14 ± 1	27 ± 3
Old Needles	152 ± 23	101 ± 10	30 ± 4	27 ± 4	6 ± 1	7 ± 1
Fine roots	149 ± 12	179 ± 18	121 ± 9	77 ± 5	12 ± 2	13 ± 2

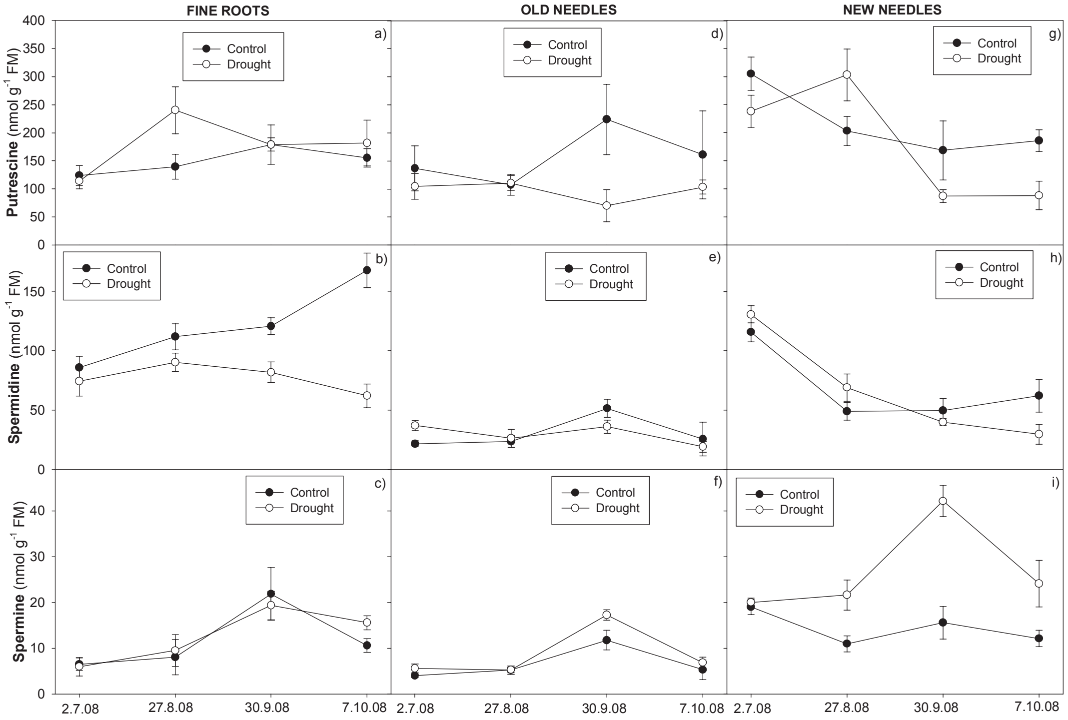

Fig. 6. Free polyamine concentrations (mean ± SE) according to treatment, sample type, and time of sampling.

Kuva 6. Vapaiden polyamiinien pitoisuudet (keskiarvo ± keskivirhe) käsittelyn, näytetyypin ja näytteenottoajankohdan mukaan. Putrescine = putreskiini, Spermidine = spermidiini, Spermine = spermiini. Control = kontrollikäsittely, Drought = kuivuuskäsittely. New needles = uudet neulaset, Old needles = yksivuotiaat neulaset, Fine roots = hienojuuret. FM = tuoremassa.

than in the control on the last two sampling occasions (p=0.033 and 0.006, respectively) when peat water content had already dropped below 10% (Fig. 6b, e, h). At this stage, namely the much lower concentration in fine roots of stressed seedlings accounted for the differences observed between treatments (Fig. 6b). For instance, the last measured spermidine concentration in the control was nearly threefold that of the drought-stressed roots. Furthermore, as opposed to the control where spermidine in roots consistently increased from start to finish, the concentration in roots of drought-stressed seedlings steadily decreased. Thus, seedling roots were the defining factor for the observed differences in the free spermidine concentration between treatments (Table 2).

Free spermine

Opposite to the treatment effect for free putrescine and spermidine, drought stress increased the spermine concentration in Scots pine seedlings in respect to the control overall (Tables 1 and 2). The treatment effect also depended on sample type (Table 1); as a result of drought stress, the spermine concentration namely in new needles rose significantly above the control level (p=0.000) (Table 2, Fig. 6c, f, i).

Soluble conjugated PAs

The changes induced by drought in soluble conjugated putrescine, spermidine, and spermine (data not shown) followed the same pattern as for free putrescine levels. However, the nature of the soluble conjugated PA data was such that the assumptions of normality and equal variances were difficult to fulfill even with transformations. Consequently, the data could not be fitted with the same MIXED model as for free polyamines, and therefore was not tested.

Root and shoot characteristics

Except for the root to shoot ratio (Fig. 7a), drought stress significantly affected all other measured seedling morphological characteristics (Figs. 7b–c and 8a–d). Clear reductions in dry biomass and water content of both shoots and roots were observed in drought-stressed seedlings relative to the control (Fig. 7b–c). Root growth markedly suffered from drought as evidenced by the dramatically smaller amount of fine root tips per seedling on average (Fig. 8a) and the nearly threefold higher proportion of defunct roots in respect to control seedlings (Fig. 8b). Furthermore, severely reduced carbon allocation to root biomass in response to dry soil conditions was likewise reflected in the frequency of root-associated ectomycorrhizal fungi (Fig. 8c). While over 80% of the fine root tips in control seedlings were colonized by mycorrhizae, less than 40% of fine roots tips in stressed seedlings had sustained a symbiotic relationship with ectomycorrhizae after exposure to drought. Finally, relative to the dry biomass of roots, drought-stressed seedlings also had a significantly lower quantity of living (i.e., not defunct) fine root tips than control counterparts (Fig. 8d).

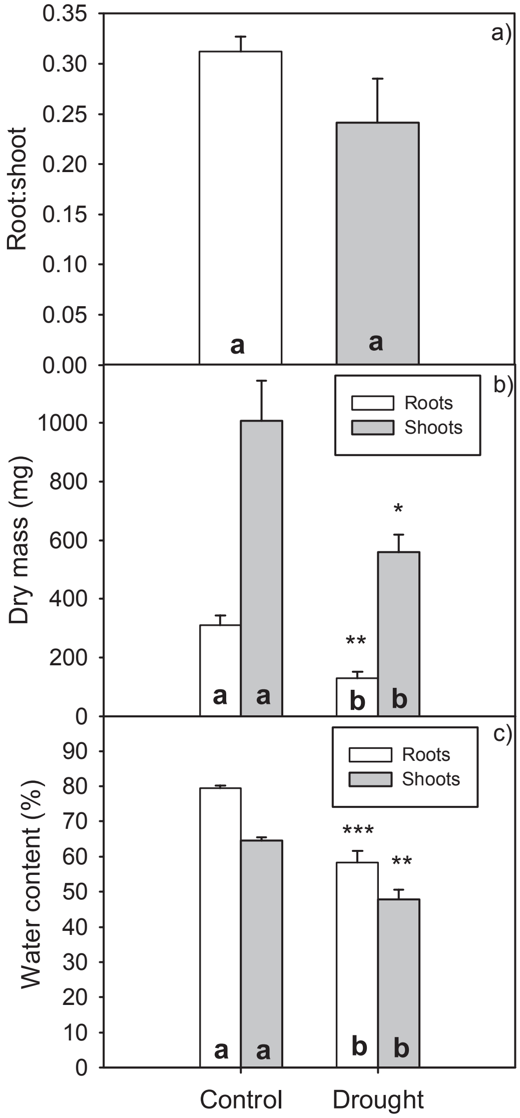

Fig. 7. Mean (± SE) a) root to shoot ratio, b) dry biomass, and c) water content of shoots and roots in Scots pine seedlings according to treatment. Significant between treatment differences are indicated in bold with different letters (a–b), insignificant ones ($p>0.05$) with the same letter (a–a). Significance levels are designated by asterisks as follows: * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

*Kuva 7. Männyntaimien a) juuriversosuhteet, b) juurten ja versojen kuivamassat ja c) juurten ja versojen kosteuspitoisuudet käsittelyittäin. Tilastollisesti merkitsevästi toisistaan poikkeavat erot merkitty eri kirjaimin. Merkitsevyystasot merkitty tähdellä: * p<0.05, ** p<0.01, *** p<0.001. DM = kuivamassa. Control = kontrollikäsittely, Drought = kuivuuskäsittely. Roots = juuret, Shoots = versot.*

Discussion

Chlorophyll fluorescence

In our study, exposure to drought affected *in vivo* chlorophyll *a* fluorescence of Scots pine seedlings in two ways. Not only did it lower the F_v/F_m ratios of both old and new needles, but it also provoked differences between needle age classes (no such differences within control) wherein previous-year needles were more susceptible to stress, i.e., reacted earlier to stress via F_v/F_m, than current-year needles. The decline in F_v/F_m, discoloration and eventual abscission of old needles allowed seedlings to reduce leaf area and hence water loss

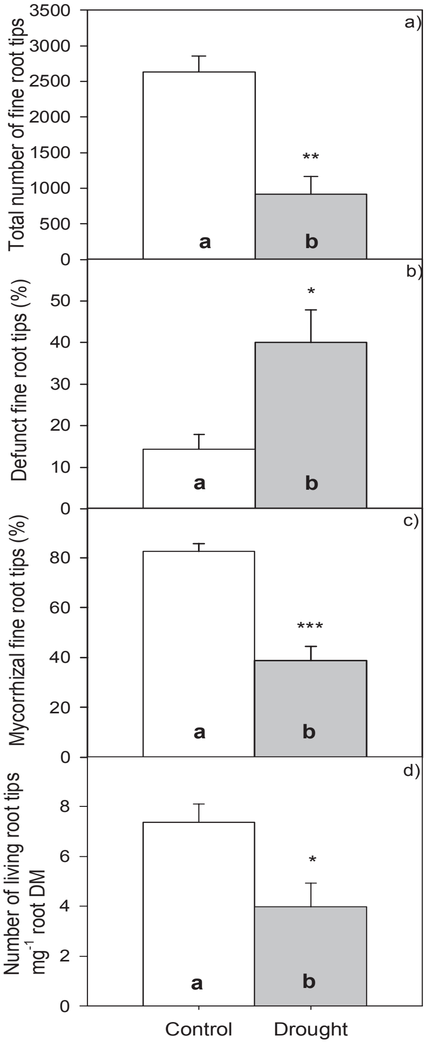

Fig. 8. Root characteristics (mean ± SE) of Scots pine seedlings according to treatment: a) number of fine root tips; b) proportion of defunct tips; c) proportion of tips colonized by mycorrhizae; d) number of living tips respective to root dry mass. Significant between treatment differences are indicated in bold with different letters (a–b), insignificant ones ($p>0.05$) with the same letter (a–a). Significance levels are designated by asterisks as follows: * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

*Kuva 8. Männyntaimien juurten ominaisuudet (keskiarvo ± keskivirhe) a) juurenkärkien kokonaismäärä, b) elottomien juurenkärkien osuus, c) mykorritsallisten juurenkärkien määrä, d) elävien juurenkärkien määrä suhteessa juurten kuivamassaan käsittelyittäin. Tilastollisesti merkitsevästi toisistaan poikkeavat erot merkitty eri kirjaimin. Merkitsevyystasot merkitty tähdellä: * $p<0.05$, ** $p<0.01$, *** $p<0.001$. DM = kuivamassa, Control = kontrollikäsittely, Drought = kuivuuskäsittely.*

through transpiration. Consequently, seedlings were seemingly able to delay the negative impact of drought on the photochemical efficiency of new needles. Notably, when a sustained decrease in F_v/F_m finally occurred in the new needles of stressed seedlings, their outward appearance already obviously attested to their suffering. Shifting growth resources within Scots pine, as we saw here, for the benefit of the youngest needles is also known to be crucial in providing developing new needles and elongating shoots with nutrients through retranslocation (Fisher & Höll 1991, Helmisaari 1992).

Although old needles provided the first indication of physiological distress as F_v/F_m fell, by the time this occurred the peat water content was astoundingly low (< 30%), especially when considering water availability for plant use (Fig. 3). Furthermore, discoloration of old needles in drought-stressed seedlings was also visibly apparent at this stage. In new needles, the decline in photochemical efficiency did not materialize until the water content of the peat had dropped to merely 10%, well below the permanent wilting point designated for this particular type of peat (Fig. 3). Permanent wilting point is, however, dependent not only on the soil type but also plant species (Or et al. 2011). Thus here, it is possible that the soil water potential was still higher (i.e., less negative) than the water potential of Scots pine seedlings at –1554 kPa. On the other hand, wilting was already apparent in old and new needles by the time their photochemical efficiency dropped. Therefore, our results with Scots pine appear to demonstrate that needle wilting does not lead to an immediate reduction in F_v/F_m. In any case, our results coincide with the findings of several previous studies on *Pinus* species (Binder et al. 1996, Otronen & Rosenlund 2001, Fangyuan & Guy 2004) in that drought stress has to be severe before a sustained collapse in F_v/F_m is detectable. In their study, Otronen & Rosenlund (2001) found the differences between the F_v/F_m ratios of Scots pine seedlings grown at five different soil water content levels ranging from 10–80% to be insignificant. In other pine species, Binder et al. (1996) demonstrated a drop in F_v/F_m only after severe drought in jack pine (*Pinus banksiana* Lamb.), while no indication of water stress in the F_v/F_m ratio was evident in Masson pine (*Pinus massoniana* Lamb.) seedlings (Fangyuan & Guy 2004). However, Mena-Petite et al. (2000) did observe a clear decline in F_v/F_m in drought-stressed Monterey pine (*Pinus radiata* D. Don) seedlings. The sustained change in F_v/F_m we observed does nevertheless indicate that the photochemical apparatus had become damaged (Maxwell & Johnson 2000, Mena-Petite et al. 2000).

Although Otronen & Rosenlund (2001) found no differences in F_v/F_m of new needles between drought-stressed and control seedlings, they nonetheless noted that water stress was unevenly distributed amongst the different parts of the seedling from which new needles were sampled, i.e., top versus bottom of current leader shoot versus lateral shoots of topmost whorl.

As Bukhov & Carpentier (2004) and Bigras (2005) have pointed out, the required minimum water content in leaves to ensure functioning of the photosynthetic apparatus depends on the plant species**.** Scots pine's strategy of early stomatal closure limits water stress (Picon-Cochard et al. 2006), and in our study as well it apparently had an important role in postponing the inevitable. In doing so, it also reduces the risk of xylem embolism (Cochard 1992). Stomatal closure results in lower transpiration, respiration, as well as net carbon assimilation (Panek 2004, Zweifel et al. 2005, Bréda et al. 2006, Matyssek et al. 2006, Zweifel et al. 2007, Sterck et al. 2008). In any case, our results show that the integrity of PSII in Scots pine is not easily compromised, and this would likely aid post-stress recovery in the event that soil water availability would once again improve.

Polyamines

Peat water content in the drought treatment had decreased to the permanent wilting point by the second time polyamine samples were taken (Aug. 27th) (Figs. 3 & 4). This lower limit of available water coincided with higher free putrescine concentrations in drought-stressed roots and new needles (Fig. 6a, g) as well as higher spermine levels in new needles (Fig. 6i), whereas in the old needles putrescine and spermine concentrations were similar in both treatments at the second sampling time (Fig. 6d, f). Higher polyamine levels in transgenic pine have been reported to be associated with increased drought tolerance (Tang et al. 2007). The fact that F_v/F_m was higher in the new than old needles of drought-stressed seedlings when the permanent wilting point was reached implies that higher putrescine and spermine concentrations increased their drought tolerance by keeping F_v/F_m at a normal level. Serafini-Fracassini et al. (2010) reported in their paper that spermine prevents the decay of chloroplast photosystems in lettuce (*Lactuca sativa* L.) suggesting that higher spermine levels in the new needles in this study may have protected the photosynthetic machinery so as to sustain a higher F_v/F_m ratio in the new needles.

Polyamines have been implicated in the regulation of stomatal closure by activating the biosynthesis of signalling molecules (Yamasaki et al. 2006, Alcázar et al. 2010). Spermine-deficient rockcress (*Arabidopsis*) mutants are unable to close stomata properly indicating a protective role of spermine against drought stress (Yamaguchi et al. 2007).

Free spermidine concentrations were higher in the roots of the control than in the drought treatment throughout the experiment (Fig. 6b). It is well documented that mycorrhizal association increases spermidine concentrations in the roots of Scots pine seedlings (Niemi et al. 2006, Sarjala et al. 2010) and mature trees (Sarjala & Kaunisto 2000). Therefore, higher spermidine levels in the roots of the well-watered seedlings were probably due to the significantly higher proportion of mycorrhizal root tips than in the drought-stressed seedlings.

Although the free putrescine level in the drought-stressed new needles was higher than in the control at the second sampling time, it decreased dramatically below the control (Fig. 6g) when the water content of the peat **(**Fig. 4) had dropped considerably beneath the wilting point into the zone of unavailable water (Fig. 3). A similar decrease in the putrescine level was also observed in the old needles (Fig. 6d), which is suggestive of severe limitation in polyamine synthesis in the photosynthesizing tissues under extreme drought. This was accompanied by a decrease in F_v/F_m ratio, first detected in the old needles (Sept. 3rd) and later also in the new needles (Sept. 26th) (Figs. 4 and 5).

Shoot and root traits

Reduced shoot and root growth is a commonly observed response to drought amongst pine seedlings (Kaufmann 1968, Rikala & Puttonen 1988, Torreano & Morris 1998, Otronen & Rosenlund 2001, Sword Sayer et al. 2005) and our study is no exception. In this study, the number of ectomycorrhizal root tips was also significantly lower in the drought-stressed seedlings than in control ones at the end of the experiment. Since fine roots and associated mycorrhizae are the first to be in contact with desiccating soil, they are also highly vulnerable to drought compared to other plant parts (Konôpka et al. 2005). From the forest management perspective, we may thus conclude that minimizing restrictions on root growth and development is key to establishing Scots pine stands.

Indeed, prolonged drought typically results in reduced root growth (i.e., fine root biomass) of forest trees **(**Torreano & Morris 1998, Joslin et al. 2000, Cudlin et al. 2007), although mild drought may actually increase it (Becker et al. 1987). In the meta-analysis performed by Cudlin et al. (2007), drought did not however restrict fractional colonization of ectomycorrhizae, which contrasts with our results wherein the proportion of colonized root tips in drought-stressed Scots pine seedlings was only half that of the control (40% vs. 80%, respectively). Cudlin et al. (2007) attributed the non-effect to the influence of drought on the total number of root tips, i.e., less tips present but the proportion of colonized tips remained unchanged. On the other hand, ectomycorrhizal species composition has been shown to influence the resistance of Scots pine to water stress (Kipfer et al. 2012). Even though Scots pine is resilient to drought and adapted to grow in a wide range of environments (Kozlowski et al. 1991), poor water availability clearly hinders growth of both roots and shoots, finally leading to death. For example, Scots pine forest decline due to drought has already been a reality for some time in the Alps (e.g., Rebetez & Dobbertin 2004).

Cudlin et al. (2007) noted a significantly greater negative impact of drought on tree roots and ectomycorrhizae in the field than in laboratory experiments in their meta-analysis in part due to the simultaneous influence of multiple environmental factors. This gives us reason to believe that the negative effects of drought on the roots of Scots pine seedlings could be even more severe than what we observed here. Recently, mounding has been reported to reduce peat decomposition likely in part due to the disruption of the microbial community (Pearson et al. 2011). According to the present study, belowground carbon allocation to the root system and fungal association decreases under dry conditions, which may be linked to further decrease microbial activity in the soil. Exposing the deeper, decomposed, less microbially active peat as is done in mounding may also have consequences for the natural ectomycorrhizal community (Harvey et al. 1981, Hashimoto & Hyakumachi 1998, Jones et al. 2002*)*. Though Scots pine seedlings are systematically inoculated with mycorrhizae in nurseries nowadays (Tammi et al. 2001), if the inoculated species are unable to adapt to field conditions in the long run e.g., due to drought, and/or the natural community is displaced by the soil preparation maneuver, then seedling survival may be compromised. There is also some evidence that competition between nursery and native, forest-adapted ectomycorrhizal fungi may restrict colonization by native fungi and even replace them, and this could pose a threat to forest productivity (Jones et al. 2002).

The insignificant effect of drought on the root to shoot ratio was primarily due to the reduced allocation of carbon not only to roots but also shoots caused by drought. These trends are congruent with those observed by Torreano & Morris (1998) for drought-stressed loblolly pine (*Pinus taeda* L.) seedlings. The drought-induced inhibition of root and shoot growth of newly planted Scots pine seedlings to the degree as that seen in our study would undoubtedly have a serious impact on future forest productivity.

Limitations and implications

Our study mimicked a scenario, which can materialize in field conditions when a peat mound (in our experiment specifically in the form of a block) is subjected to an extended period of drought after planting. In particular, *Carex* peat has been implicated in unsuccessful regeneration via natural and artificial seeding of mounds in peatland forest regeneration areas (Saarinen 1997, 2005). Although such peat is effective at retaining water as our study demonstrated, drought of sufficient duration will eventually lead to substrate desiccation starting with the surface layers, which consequently repel water. In order for the dried peat to become rewetted, abundant, long-lasting rainfall is required (Saarinen 2005). Due to the deeper location of their root system within a mound, however, planted containerized pine seedlings are typically less susceptible to drought than those germinated from seed in (*Carex*) peat mounds. The bulk density of the *Carex* peat used here was higher than on average for Finnish peats (Päivänen 1973). Bulk density has been shown to correlate with the stage of peat decay (Päivänen 1969). The degree to which the peat has decomposed inevitably influences its water retention capacity. The soil water content equating with the permanent wilting point in our *Carex* peat was higher than that modeled by Weiss et al. (1998), but once again, their peat was not as dense as ours. Admittedly, the bulk density of our peat may be an overestimate due to the small sample size used to determine water retention. Only four of the 50 peat blocks were included in this determination, thus we may not have captured all the variation actually occurring between blocks. Furthermore, lifting and hauling the fresh peat manually in blocks from the peatland site was an utterly laborious task. Hence, it was next to humanly impossible to guarantee the “identicalness” of the blocks when the enslaved lifters were under tremendous physical and mental strain.

An overestimation of water retention due to insufficient sample size could explain why new needle F_v/F_m did not markedly drop until at 10% soil water content (Fig. 5) despite the permanent wilting point having already been reached at 28% soil water content according to the retention graph (Fig. 3). In addition, the Moisture Meter used to regularly measure the water content of the peat blocks has a margin of error of 4%, thus the specific peat water contents initiating changes in, e.g., F_v/F_m are only suggestive. In any case, our purpose was not to define the absolute limits of available water, rather to illuminate how Scots pine seedlings respond as peat soil dries. Based on the observations of this study, the ill effects of drought on Scots pine seedlings would presumably be best minimized by applying a mounding technique, which inverts the peat mass on the excavated spot rather than beside it. Such an inverted mound is lower, less exposed to drying, and likely allows for better capillary movement of water from below—critical during drought periods—compared to an excavated tall heap of peat set atop the intact, vegetated peatland surface (with raw humus) as in ditch mounding. However, field experimentation is paramount to confirm the wisdom behind this speculation.

Conclusions

Our study demonstrated the negative effects of prolonged drought on year-old Scots pine seedlings grown in authentic, highly decomposed *Sphagnum-Carex* peat. Drought clearly suppressed root and shoot growth as well as fractional colonization of ectomycorrhizal fungi. Drought stress affected F_v/F_m first in the old needles of Scots pine when the soil water content had sunk to the permanent wilting point at just below 30%, while the new needles proved to tolerate extreme drought longer with a sustained decline finally occurring at 10% peat water content. The maintenance of rather high photochemical efficiency despite severe drought stress would seem to indicate a potential for seedling recovery if water availability in the peat substrate improved. Responses seen in polyamine concentrations supported the findings that new needles are preferred in protecting the different parts of the seedlings against drought stress. Nonetheless, the extreme severity of soil drying necessary in our study to actually inflict death is demonstrative of Scots pine’s high tolerance to water stress at least in the seedling stage. These results are of value when planning reforestation with Scots pine on boreal forestry-drained peatlands especially if the climate becomes progressively drier.

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Tiivistelmä: Kasvualustan kuivumisen vaikutukset rahkasaraturpeeseen istutettujen männyntaimien ensikehitykseen

Ilmastonmuutoksen seurauksena kuivuus saattaa lisääntyä boreaalisissa metsissä, jolloin paljaisiin turvemättäisiin istutetut taimet voivat altistua entistä enemmän kasvualustan kuivumisesta johtuville haittavaikutuksille. Männyntaimien (*Pinus sylvestris* L.) kuivuudenkestävyydellä on siten tärkeä merkitys metsänuudistamisen onnistumisessa mäntyvaltaisilla turvekankailla Suomessa. Tässä tutkimuksessa tarkasteltiin yksivuotiaiden männyntaimien vastetta vähitellen kehittyvälle kuivuusstressille fysiologisten, metabolisten ja morfologisten ominaisuuksien avulla pitkälle maatuneessa rahkasaraturpeessa. Kuivuus heikensi selvästi taimien juurten ja versojen kasvua kuten myös mykorritsallisten juurenkärkien määrää. Fotosynteesin tehokkuus (F_v/F_m) laski yksivuotiaissa neulasissa vasta turpeen kosteuspitoisuuden laskiessa 30 %:iin tilavuudesta, ja uusissa neulasissa se alkoi laskea vasta turpeen kosteuden ollessa 10 % tilavuudesta. Polyamiinianalyysin perusteella uudet neulaset ja hienojuuret ovat edellisvuoden neulasiin ja hienojuuriin nähden suojatuimpia kuivuusstressiä vastaan. Ankarasta kuivuusstressistä huolimatta uusien neulasten fotosynteesin tehokkuus pysyi verraten korkealla tasolla, vaikka kasvu heikentyi. Tämän voidaan katsoa kuvaavan taimen hyvää kykyä toipua kuivuuden aiheuttamasta stressistä, jos veden saatavuus turpeessa paranee.

Avainsanat: männyntaimet, *Pinus sylvestris*, kuivuus, rahkasaraturve, fotosynteesin tehokkuus (F_v/F_m), mykorritsat, polyamiinit, juurten ja versojen kasvu

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