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ORIGINAL PAPER

How long can young Scots pine seedlings survive waterlogging?

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Abstract The aim of this study was to clarify the capability of Scots pine seeds (*Pinus sylvestris* L.) of different origins to germinate and survive under waterlogging conditions. Seeds were used from one Spanish and three UK sources. All experiments were carried out in the glasshouse and under the optimum conditions for Scots pine seed to germinate and establish. A technique using inner and outer pots was used to produce four depths of waterlogging below the soil surface. Seed mass and viability were examined prior to use in the experiments. Waterlogging reduced germination, but an increase in time between sowing and waterlogging of up to 3 weeks and a watertable >4 cm below the surface greatly improved germination and seedling growth. Once established, seedling survival was remarkably tolerant of waterlogging, and seedlings survived 25 months even with the watertable at the soil surface. Seeds collected from trees on a floating bog in the English Midlands were least affected by waterlogging, but the variation among seed sources was small compared to the effects of the timing, depth and duration of waterlogging. Management implications are discussed.

Keywords *Pinus sylvestris* · Waterlogging · Seedling · Germination

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Introduction

In wetland ecosystems, waterlogging is one of the main environmental factors that affect tree seed germination and early seedling establishment (Kozlowski and Pallardy 2002). It is, however, difficult to control the level and duration of waterlogging in the field, and very few studies have investigated the effects of continuous and periodic waterlogging on germination, survival and growth (Megonigal and Day 1992).

In flooded areas, germination of woody plants is prevented or postponed by oxygen depletion and carbon dioxide accumulation (Kozlowski and Pallardy 2002), and fluctuations in flooding level determine seedling survival (Kozlowski 1997; McVean 1961), particularly in young seedlings (Brink 1954). The build-up of anaerobic organisms causes denitrification and decomposition of organic matter (Kozlowski and Pallardy 2002). In seedlings that survive, flooding causes premature leaf senescence and abscission, suppresses leaf formation and expansion of leaves and internodes, and induces shoot dieback (Kozlowski 1997). Flooding can decrease the rate of photosynthesis, lower the concentration of ATP and decreasing the absorption of macronutrients (Kozlowski 1997; Crawford 2008). Root formation and growth is often affected more than the shoots (Kozlowski and Pallardy 2002), decreasing the root/shoot ratio (Kozlowski 1997).

Several studies have shown a mixed response of *Pinus* species to waterlogging. Hunt (1951) was surprised by the limited mortality and reduction in shoot growth in flooded seedlings of *Pinus taeda*, *P. echinata* and *P. rigida*. By contrast, Sena Gomes and Kozlowski (1980) found that flooding of seedlings of *Pinus halepensis* from 10 to 70 days arrested secondary needle formation and decreased shoot dry weight. Only about half the needles remained by the end of the experiment compared to unflooded seedlings. Moreover, flooding has been seen to halve total leaf dry weight in *P. banksiana* and *P. resinosa* as a result of leaf shedding (Tang and Kozlowski 1983).

Compared to many *Pinus* species, however, Scots pine (*Pinus sylvestris* L.) appears well adapted to wet conditions, at least in the early seedling stages. It grows successfully on a wide range of soils from freely drained gravels (Steven and Carlisle 1959) to heaths and deep peat. It has also spread widely on sites prone to waterlogging (Brown et al. 1966). Armstrong and Read (1972) found that Scots pine seedlings can convey oxygen from shoot to root parts through cortical intercellular spaces. However, there are suggestions that Scots pine invades wetlands only during periods of drought and as such is not resistant to waterlogging as seed or seedlings (McHaffie et al. 2002; Rodwell 1991).

The aim of this study is to clarify the effects of different depths and timing of waterlogging on *Pinus sylvestris* seed germination and early stages of seedling establishment in the glasshouse. Several seeds sources of Scots pine are used to make the results more widely representative.

Materials and methods

Source of seeds

Four different seed sources were used in this study of which three were commercially provided. Two of these sources were from Scotland representing the main UK native range [a Scottish plantation at Cambridge (SP), 57°17′N, 3°48′W, elev. 252 m a.s.l., and a Scottish native woodland at Glenbeg (SN), 57°19′N, 3°38′W, elev. 330 m]. One source represented a continental source [Sierra de Guadarrama, Spain (ES), 40°40′N, 4°09′W, elev. 1,329 m], while the fourth was self-collected seeds from a waterlogged peatland source in central England [Wybunbury Moss, Cheshire (WM) 53°02′N, 2°25′W, 71 m].

Mass, viability and germination of seed

The average mass of 50 groups of 100 seeds was measured for all 4 seed sources. Germination tests in Petri dishes and using triphenyl tetrazolium chloride (TTC) were used to verify the seed viability of all seed (Lakon 1949). All experiments were carried out in a glasshouse: mean 18 °C, 16 h daily photoperiod. Commercial peat moss was used as a substrate and rainwater was used for watering.

Experiment 1: depth and timing of waterlogging

Germination and establishment was followed after different time periods of normal watering before being subjected to waterlogging at different depths below the soil surface. Seeds used were from the three UK sources: Scottish Native woodland, Scottish Plantation and Wybunbury Moss. For each seed source, three groups of pots were used. Each group had 16 pots divided into 4 waterlogging depths (with 4 replicates, arranged in a Latin square): a control (unwaterlogged and watered normally) and three waterlogged depths with water 6.6, 4.0 and 0 cm below the surface. This was controlled by using outer pots with holes on all sides at the appropriate depths except the control which had holes in the bottom; waterlogging levels were maintained by keeping the outer pot topped up with water (Fig. 1). Each pot was sown with 20 seeds. The three

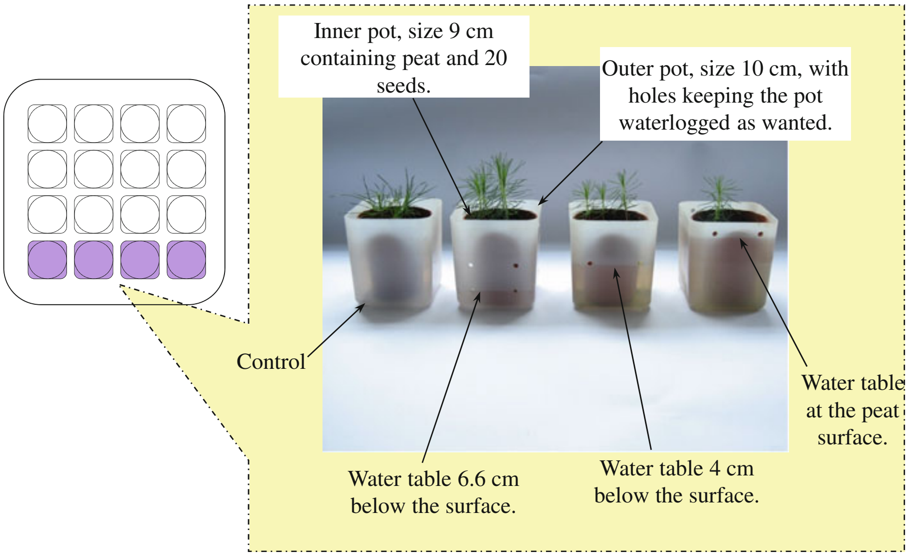

Fig. 1 Experimental design in the glasshouse. Four replicates of four different waterlogging depths form a Latin Square ($n = 16$)

groups of pots were watered normally, without waterlogging, after seeds were sown for 1, 3 and 5 weeks, respectively, before applying 6 weeks of the appropriate waterlogging depth. Germination and survival were followed. Length and dry mass of shoot and root were measured at the conclusion and root/shoot ratios calculated.

Experiment 2: duration of waterlogging

The objective was to see whether seedlings could survive long-term waterlogging. The experiment was set up as in Experiment 1 but using only 3 weeks of normal conditions followed by waterlogging for 25 months, at which point seedlings were beginning to die. Seeds from the two seed sources from Scotland and that from Spain were used. Seedling emergence and mortality were monitored. The bottom needles of many seedlings turned red during the experiment and the vitality of three needles per pot was verified using a 1 % solution of 2,3,4-triphenyl tetrazolium chloride (Lakon 1949). Soil pH of all pots was measured after 4 and 5 months.

Statistical analysis

One-way ANOVA was used followed by Tukey's post hoc paired comparisons between means to test for differences in seedlings characteristics among seed origin and timing and depth of waterlogging. Two- and three-way ANOVAs were used to test for interactions between seed origin, and the timing, depth and duration of waterlogging. Minitab® v.16 was used for the analyses.

Results

Mass, viability and germination of seed

The average mass of 100 seeds from Scottish Native woodland (SN), Scottish Plantation (SP), Spain (ES) and Wybunbury Moss (WM) were 0.625 ± 0.0031, 0.542 ± 0.0042, 1.229 ± 0.0113 and 0.443 ± 0.0098 g, respectively. Seed viability using TTC was, for the same seed sources, 82 ± 0.7, 71 ± 0.9, 40 ± 1.0 and 77 ± 0.5 %, respectively. In Petri dish tests of seed germination, SN seeds similarly showed higher germination percentage over all other seed sources. ES seeds, which had the highest mass, again showed the poorest germination percentage of 40 ± 1.0 %. Germination percentage from WM seeds was 64 ± 5.2 % ($n = 10$).

Experiment 1: depth and timing of waterlogging

Germination and seedling success

In all three seed sources, germination was significantly lower when normal watering was just 1 week long compared to 3 and 5 weeks (SN: $F_{2,47} = 11.41$; $P < 0.01$; SP: $F_{2,47} = 17.24$; $P < 0.01$; WM: $F_{2,47} = 10.73$; $P < 0.01$; Fig. 2). Depth of waterlogging was most critical following just 1 week of normal watering (Fig. 2). For SN seed, germination was significantly higher in the waterlogging treatments than the control ($F_{3,15} = 11.67$; $P < 0.01$), and for WM seed germination was highest in the control and least flooded pots ($F_{3,15} = 5.79$; $P < 0.01$). For the WM

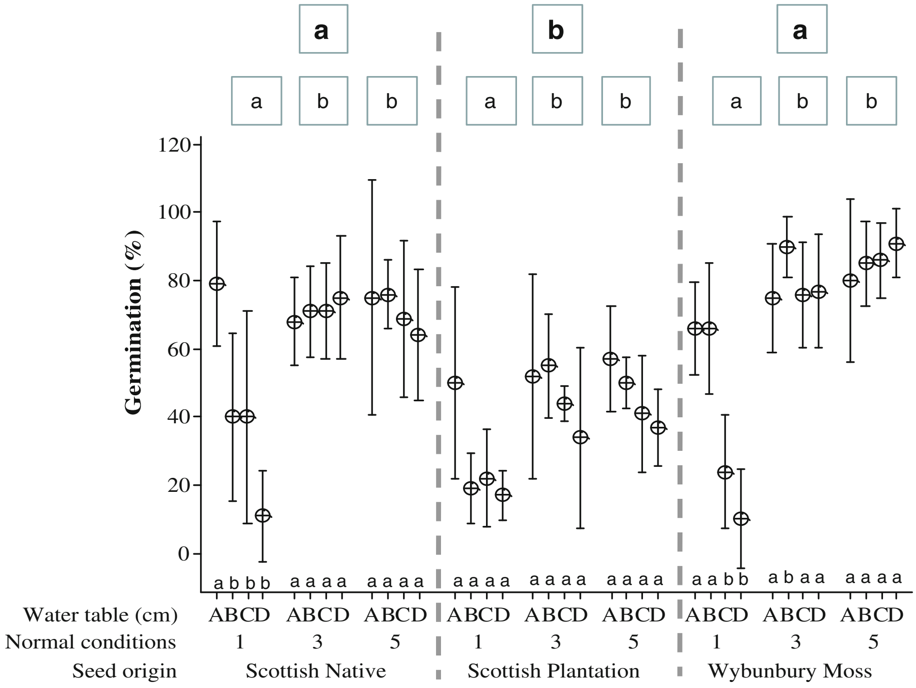

Fig. 2 Differences in germination percentage in short-term experiment between different depths to the watertable (below the surface in cm; A = control, $B = 6.6$, $C = 4.0$ and $D = 0$), different timing (1, 3 and 5 weeks of normal conditions before 6 weeks under waterlogging stress) and different origin of seeds used in the experiment. Data are means and 95 % confidence interval ($n = 16$ in each treatment). Within treatments or seed origin characteristics that do not share a *letter* are significantly different

seed, germination was significantly higher in the 3 weeks treatment with 6.6 cm flooding compared to the other treatments ($F_{3,15} = 6.28$; $P < 0.01$) at 90 ± 4.1 % (Fig. 2).

Shoot length was also significantly lower with just 1 week of normal watering (SN: $F_{2,47} = 12.01$; $P < 0.001$; SP: $F_{2,47} = 50.30$; $P < 0.01$; WM: $F_{2,47} = 57.16$; $P < 0.05$; Fig. 3). Waterlogging depth had no significant impact on shoot length; the highest shoot length was in 3 weeks normal, flooding 6.6 cm below the surface at 60.76 ± 0.528 mm (Fig. 3). Shoot dry mass was also affected by the length of normal watering (Fig. 4), increasing significantly the longer the normal period (SN: $F_{2,47} = 140.25$; $P < 0.01$; SP: $F_{2,47} = 115.08$; $P < 0.01$; WM: $F_{2,47} = 140.94$; $P < 0.01$). Waterlogging affected shoot dry mass only with 5 weeks of normal watering, and in both SP and WM seed, it was lowest in the controls compared to the three waterlogging treatments (SP: $F_{3,15} = 4.20$; $P < 0.01$; WM: $F_{3,15} = 7.55$; $P < 0.01$).

Roots were generally longer with increased time of normal watering, particularly in WM ($F_{2,47} = 129.44$; $P < 0.01$) (Fig. 5). Waterlogging closer to the surface tended to reduce root length. Often the control and lowest waterlogging were significantly different from the two highest degrees of waterlogging (SN, 1 week: $F_{3,15} = 9.96$; $P < 0.01$; WM, 1 week: $F_{3,15} = 12.02$; $P < 0.01$; WM, 3 weeks: $F_{3,15} = 51.98$; $P < 0.01$; WM, 5 weeks: $F_{3,15} = 7.74$; $P < 0.01$). In three other cases, the control was significantly longer than any of the waterlogging treatments (SN, 5 weeks: $F_{3,15} = 52.13$; $P < 0.01$; SP, 3 weeks: $F_{3,15} = 7.57$; $P < 0.01$; SP, 5 weeks: $F_{3,15} = 42.03$; $P < 0.01$). The longest mean root length was from SN seed: 166 ± 10.7 mm. Root dry mass was also higher with a longer period before waterlogging (SN: $F_{2,47} = 10.62$; $P < 0.001$; SP: $F_{2,47} = 10.73$; $P < 0.01$; WM: $F_{2,47} = 144.90$; $P < 0.01$; Fig. 6). For SN seed, roots had significantly more mass in the control and least in the waterlogged treatments ($F_{3,15} = 6.20$; $P < 0.01$; $F_{3,15} = 10.99$; $P < 0.01$; $F_{3,15} = 24.23$; $P < 0.01$ for 1, 3 and 5 weeks, respectively). This was also found in SP seed in the 5 weeks normal watering treatment ($F_{3,15} = 7.17$; $P < 0.01$). A similar pattern occurred in WM seed in the 3 and 5 weeks treatments where the control and least waterlogged treatment had the highest masses ($F_{3,15} = 41.83$; $P < 0.01$, $F_{3,15} = 4.72$; $P < 0.01$, respectively) (Fig. 6).

Timing of flooding had little effect on root/shoot ratios (Fig. 7). Increased waterlogging appeared to decrease the root/shoot ratio and, in three cases, the control was higher than the waterlogging treatments (SN, 1 week: $F_{3,15} = 9.18$; $P < 0.01$; SN, 5 weeks: $F_{3,15} = 33.69$; $P < 0.01$; WM, 3 weeks: $F_{3,15} = 5.62$; $P < 0.01$) (Fig. 7).

Differences between Scots pine seed origin in response to the waterlogging

There were significant differences between seed from the Scottish Plantation (SP) and the two other seed sources in germination ($F_{2,143} = 19.48$; $P < 0.01$; Fig. 2), root length ($F_{2,143} = 16.39$; $P < 0.01$; Fig. 5) and root/shoot ratio ($F_{2,143} = 8.88$; $P < 0.01$; Fig. 7). Seedlings from WM and SN seed differed only in shoot length (Fig. 3) and root and shoot dry mass (Figs. 4, 6).

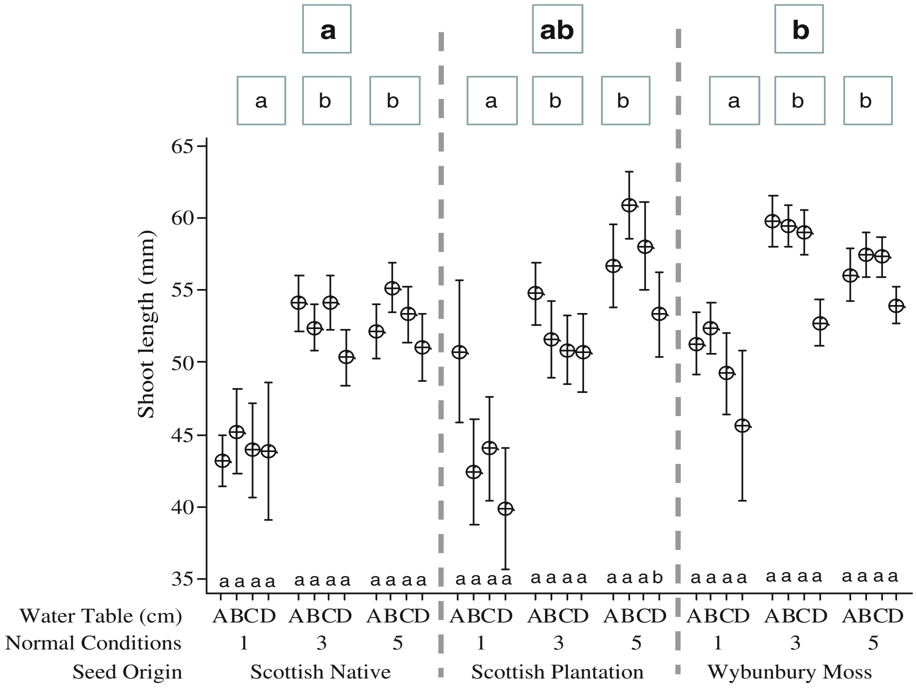

Fig. 3 Differences in shoot length in a short-term experiment (depth to the watertable, timing of waterlogging and seed origin as in Fig. 2). Data are means and 95 % confidence interval ($n = 16$ in each treatment). Within treatments or seed origin characteristics that do not share a *letter* are significantly different

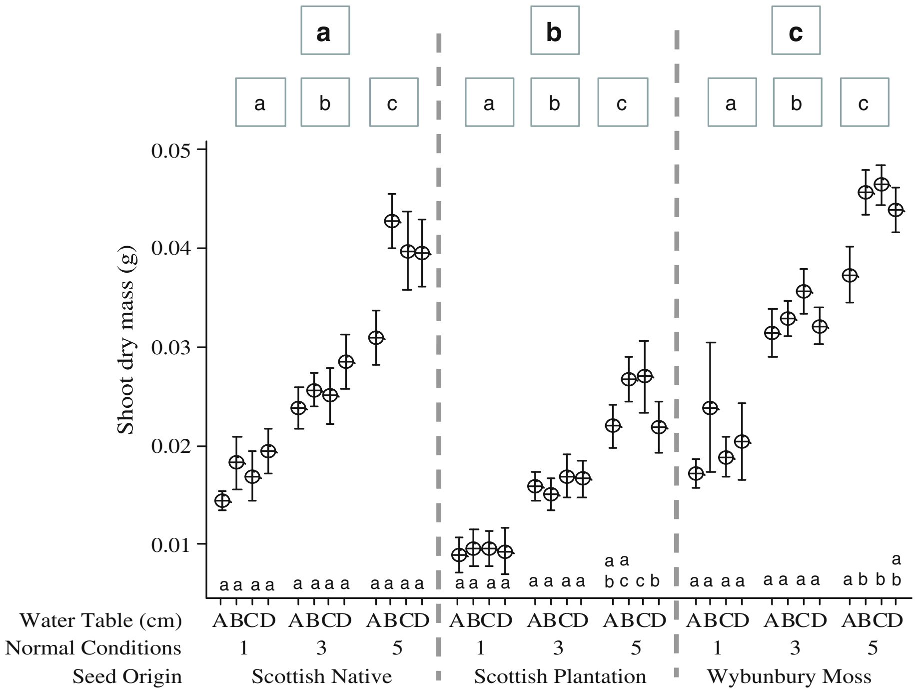

Fig. 4 Differences in shoot dry mass in a short-term experiment (depth to the watertable, timing of waterlogging and seed origin as in Fig. 2). Data are means and 95 % confidence interval ($n = 16$ in each treatment). Within treatments or seed origin characteristics that do not share a letter are significantly different

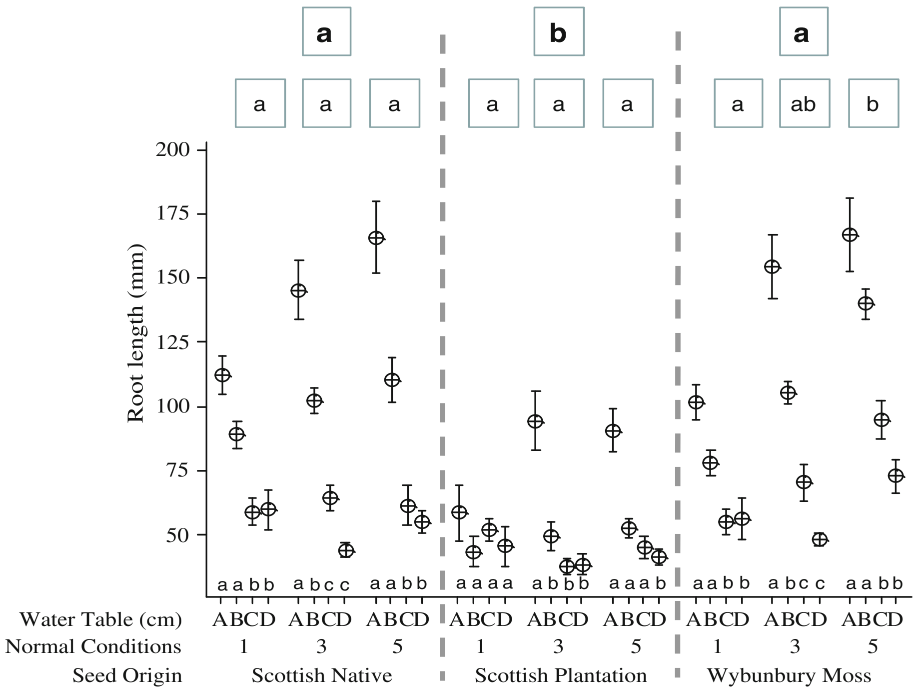

Fig. 5 Differences in root length in a short-term experiment (depth to the watertable, timing of waterlogging and seed origin as in Fig. 2). Data are means and 95 % confidence interval ($n = 16$ in each treatment). Within treatments or seed origin characteristics that do not share a letter are significantly different

Interactions between seed origin, waterlogging timing and depth

A three-way ANOVA showed significant differences in germination between seed origin, time before waterlogging and waterlogging depth. WM seeds gave the highest germination percentage followed by SN then SP ($F_{2,143} = 44.75$; $P < 0.001$). Germination was significantly higher in the 3 and 5 weeks normal watering treatment than in the 1 week treatment ($F_{2,143} = 66.16$; $P < 0.001$). In the 1 week treatment, there were significant differences in germination between waterlogging depths: higher waterlogging depth, lower germination. The control and waterlogging 6.6 cm below the surface gave the highest germination followed by 4.0 and 0 cm below the surface ($F_{3,143} = 10.94$; $P < 0.001$). No significant differences in germination for positional effect within the Latin square were found for any times before flooding for any seed source. Also, in

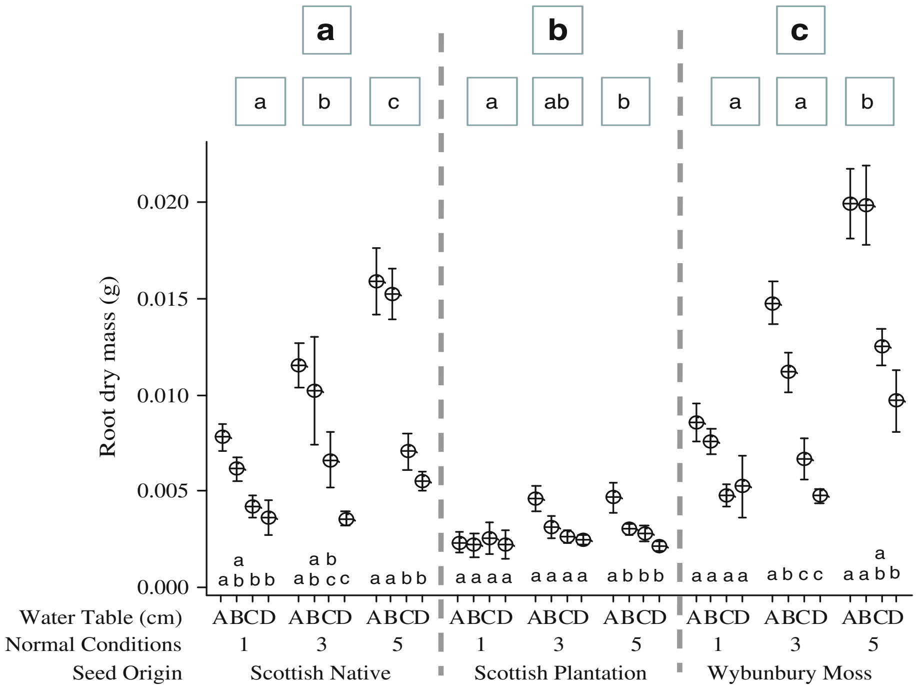

Fig. 6 Differences in root dry mass in a short-term experiment (depth to the watertable, timing of waterlogging and seed origin as in Fig. 2). Data are means and 95 % confidence interval ($n = 16$ in each treatment). Within treatments or seed origin characteristics that do not share a letter are significantly different

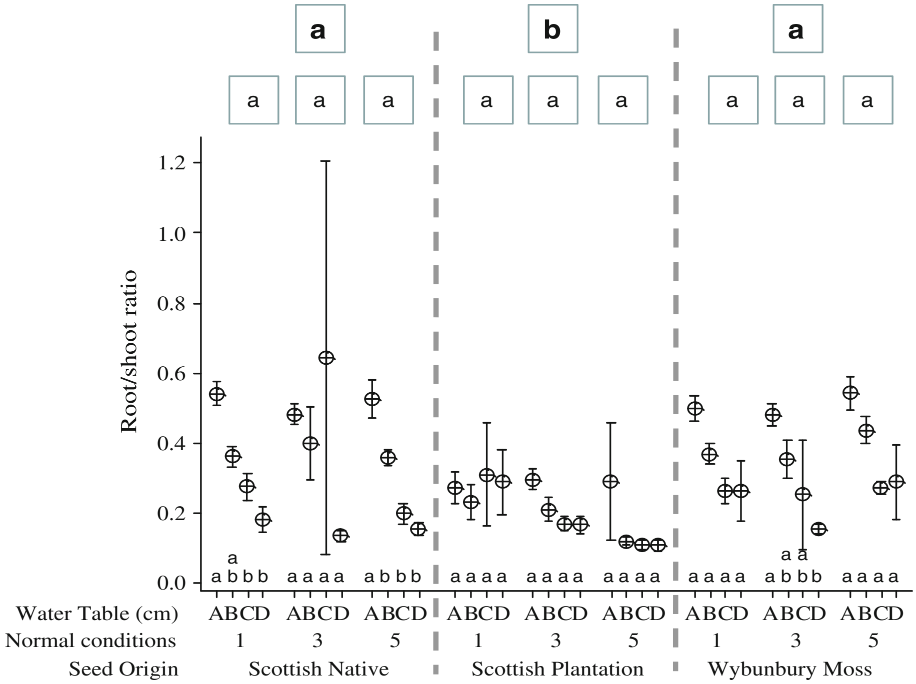

Fig. 7 Differences in root/shoot ratio in a short-term experiment (depth to the watertable, timing of waterlogging and seed origin as in Fig. 2). Data are means and 95 % confidence interval ($n = 16$ in each treatment). Within treatments or seed origin characteristics that do not share a letter are significantly different

germination, there was a significant interaction between timing of waterlogging and waterlogging depth ($F_{6,143} = 2.39$; $P < 0.05$) and an interaction between seed origin, timing and waterlogging depth ($F_{12,143} = 2.61$; $P < 0.05$). Over the three seed sources, the waterlogging depths of 0 and 4.0 cm below the surface with 1 week delay were significantly different in germination from all other waterlogging depths in the 3 and 5 weeks delay. However, Scots pine seeds over a high watertable since the first week of sowing decreased in germination. Furthermore, seeds from Wybunbury (WM) were better able to germinate under high levels of waterlogging even in early stages.

There were significant interactions between seed source and waterlogging timing, and between seed source and waterlogging depth in all characteristics examined except shoot length between seed source and waterlogging.

In root length, a combination of the three factors (origin, timing and waterlogging) played a significant role in the

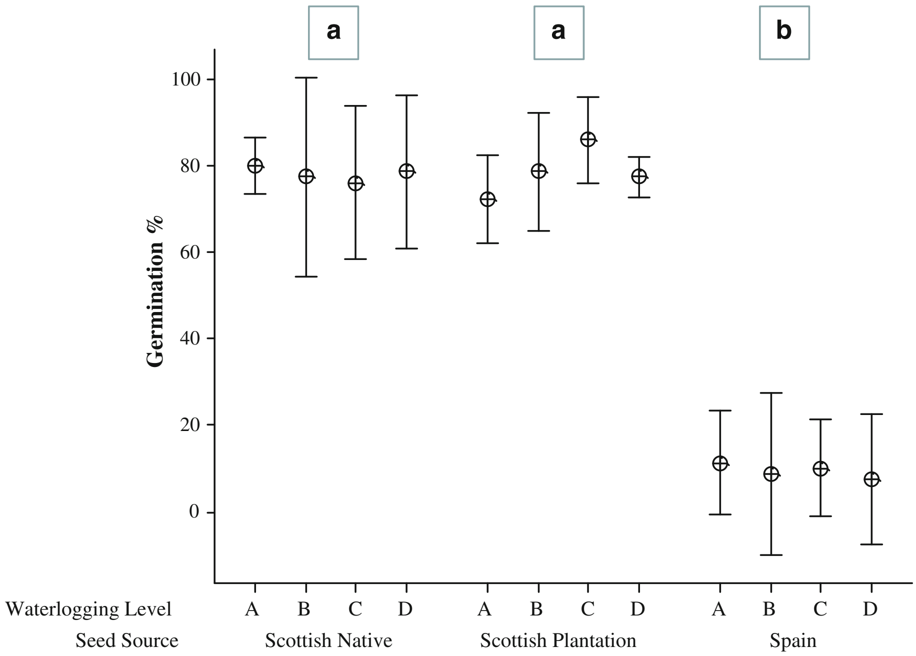

Fig. 8 Seedling germination percentages in the three seed sources examined and different depths of waterlogging below the surface. Data are means and 95 % confidence interval ($n = 48$). Waterlogging depths: $A =$ control, $B = 6.6$ cm, $C = 4$ cm and $D = 0$ cm below the surface. Seed origins that do not share a *letter* are significantly different

response of seedlings with those from Wybunbury (WM) under different depths of waterlogging having longer roots than obtained by the two other seed sources. Seedlings from Wybunbury and with a delay of 3 and 5 weeks before waterlogging gave the longest roots (Fig. 5). WM and SN seedlings that had 5 weeks delay had significantly longer roots than all other blocks of seed source and delay.

Experiment 2: duration of waterlogging

Seeds from the Scottish Native woodland (SN), Scottish Plantation (SP) and Spain (ES) were used in this experiment. Scottish seeds had the highest germination percentage with a maximum of 83 % in SP seed, 82 % in SN, and was significantly higher than the <12 % germination of ES seed ($F_{2,47} = 394.75$; $P < 0.001$; Fig. 8). Seed viability tests in the laboratory showed the same sequence of result, although viability of Spanish seed reached 39 %. There were no significant differences in germination response to waterlogging depth in any of the seed sources. This was expected since most germination was completed within the 3 weeks of normal watering prior to waterlogging. Also, the same two-way ANOVA showed no significant differences in germination between waterlogging depths or positional effect within the Latin square.

Seedling mortality was monitored during the experiment for 25 months. Neither Scottish seed sources showed mortality in the unwaterlogged control and 6.6 cm water-table depth, and an average of about one dead seedling per pot in the two other depths of waterlogging. Spanish seeds showed even less mortality. A two-way ANOVA showed significant differences in mortality between seed sources ($F_{2,47} = 3.68$; $P < 0.05$). Throughout the experiment, there were significant differences between depth of waterlogging in mortality, the control depth being significantly lower in mortality than in the most waterlogged pots ($F_{3,47} = 3.55$; $P < 0.05$). Interactions between waterlogging depth and seed source were not significant, indicating the similarity in response to waterlogging between seedlings from different sources.

A change in needle colour from green to red was noticed after 10 months flooding across the treatments. At this point, seedlings with more than 50 % red needles were counted. Only 53 ± 1.9 % of Spanish seedlings had changed colour and was significantly lower than Scottish Native and Plantation which had 71 ± 4.1 and 77 ± 3.8 %, respectively ($F_{2,47} = 27.01$; $P < 0.05$). Generally, the controls had less change in needle colour which ranged between 46 and 54 % in the three seed sources, and was significantly less than the waterlogged treatments across seed sources ($F_{3,47} = 16.70$; $P < 0.05$). Soil pH measurements ranged between 3.75 and 5, almost the optimum range for Scots pine.

Discussion

Seed from Wybunbury Moss (WM) was the lightest seed of the three regions, which matches previous work showing that wetland tree species tend to produce large crops of low density seed (Streng et al. 1989). However, it is known that trees under such stress channel a great proportion of their energy into seed production (Thomas 2000). The various tests confirmed that the Scots pine seeds used had little or no dormancy (Castro et al. 2005). WM and Scottish Native woodland (SN) seedlings were strongly affected by the length of time prior to flooding in terms of shoot length and biomass, and root length in WM seedlings. However, WM seedlings showed high sensitivity to flooding depth.

Seed origin, delay in applying the waterlogging stress and waterlogging depth all individually had a clear affect on seed germination and seedling growth. Interactions between seed source and timing showed that seeds from Wybunbury had a greater ability to germinate and grow if they had more time of normal conditions and less waterlogging stress. However, their performance was significantly better than the two other sources, even though there were less significant interactions with the SN seeds. Armstrong and Read (1972) have suggested that seed origin might play a crucial role in response to waterlogging. The Scots pine at Wybunbury Moss is of unknown origin, being planted in the 1880s (Poore and Walker 1959). It is possible that they originate from a native Scottish source.

Less than 10 % of Scots pine seeds germinated in completely waterlogged soil when they had just 1 week of unflooded conditions. This is likely due to the anaerobic conditions (Mary and McLeod 1986). In comparison, seed given normal watering for 5 weeks before waterlogging showed up to 80 % germination. So although germination is greatly affected by waterlogging, a non-flooded period in which the watertable is below the surface will allow high germination. The waterlogging noticeably affected shoot performance. One week of normal conditions, which exposes the majority of seedlings to waterlogging while barely or not at all out of the seed case, produced much shorter seedlings but particularly reduced their mass. Conversely, a longer waterlogging-free period, allowing the seedlings to grow in optimal conditions, produced seedlings with much higher mass. Observations suggest that this extra mass is not primarily grown before waterlogging, but that larger seedlings grow faster when subsequently waterlogged. Interestingly, once waterlogged, the height of the watertable had little effect on subsequent shoot growth.

A similar pattern to shoot growth was seen in roots: the longer the dry period, the greater length and mass of the roots. However, whereas the shoots were little affected by the degree of waterlogging, roots were considerably shorter and lower in mass with waterlogging closer to the soil surface. This was particularly prominent when the watertable was <4 cm below the surface, even in seedlings that had 5 weeks of normal conditions before waterlogging. This is expected, as waterlogging is known to inhibit the production of new roots and also to cause deterioration of the original root system (Sena Gomes and Kozlowski 1980; Kozlowski and Pallardy 2002). In *Pinus densiflora* seedlings, waterlogging decreased the rate of dry mass increment of roots (Yamamoto and Kozlowski 1987).

After 25 months of waterlogging, seedling mortality was only 2 % where the watertable was 4 and 6.6 cm below the surface, and even when complete waterlogged for the whole time, mortality was still <3 %. Continuous flooding under optimum growing conditions for 25 months, without allowing normal dormancy periods, is clearly artificial, but makes the results more conservative since dormancy normally improves flooding tolerance. Here, we have seedlings surviving for more than 2 years when they were at maximum vulnerability the entire time. This response to waterlogging may be attributed to the accelerated production of flood-induced ethylene (Reid and Bradford 1984). Ethylene is known in *Pinus halepensis* to induce increased bark thickness, lead to proportionally more xylem rays, enlarged ray cells, resin ducts and phloem parenchyma cells, and therefore increase shoot biomass (Yamamoto and Kozlowski 1987; Yamamoto et al. 1987). Intercellular spaces are known to occur in the cortex of *Pinus sylvestris* seedlings providing a pathway for oxygen diffusion (Armstrong and Read 1972).

The change in needle colour spotted after several months of growing is a common feature in bog plants, but the causal reasons are difficult to identify, though factors like ectomycorrhizal infection, temperature, soil pH, competition, lack of nutrients and light have been postulated as probable causes (Nilsson et al. 2000; Castro et al. 2004; Erefur et al. 2011). Ectomycorrhizal infection was unlikely to be the cause of colour change here; similarly, neither disease (such as the currently prevalent *Dothistroma septosporum*) nor temperature was the probable cause. In the field, synthesis of chlorophyll can be affected by temperature; no synthesis of chlorophyll takes place at temperatures below −2 °C (Linder 1972). However, *Pinus contorta* trees growing on bogs suffered considerably from yellowing, die-back and needle-drop, but were rarely killed (Brink 1954). The most probable reasons for this change in colour is some direct affect of waterlogging. Further work is needed to clarify this point. SN seeds responded in a similar manner to WM seeds, and both were very quite different from SP seed.

In conclusion, it is clear that the response of Scots pine seed and seedlings to waterlogging varies depending upon the source of the seed but that this variation is comparatively small compared to the large effects produced by the depth, timing and duration of waterlogging. Germination of Scots pine is reduced by waterlogging, but a dry period, with the watertable >4 cm below the surface, will allow significant germination to occur. Subsequent growth is stronger given the longest dry period possible, and the lowest watertable below the surface. But once established, it is likely that survival will be very high. Suitable conditions for establishment are obviously dependent upon weather patterns, but are also strongly dependent on the surface topography of the bog (Mukassabi et al., in preparation). From these results, it is clear that, if a management objective is to prevent Scots pine establishment on a bog (as it is in many UK peatlands), then it is necessary to concentrate on preventing seedlings establishing, perhaps by controlling water levels, rather than hoping that they will die once established. There is, of course, a need to study the long-term effects of waterlogging on Scots pine seedlings.

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References

Armstrong W, Read DJ (1972) Some observations on oxygen transport in conifer seedlings. New Phytol 71:55–62

Brink VC (1954) Survival of plants under flood in the lower Fraser river valley, British Columbia. Ecology 35:94–95

Brown AHF, Carlisle A, White EJ (1966) Some aspects of the nutrition of Scots pine on peat. Physiol For 39:78–87

Castro J, Zamora R, Hódar JA, Gómez JM (2004) Seedling establishment of a boreal tree species (*Pinus sylvestris*) at its southernmost distribution limit: consequences of being in a marginal Mediterranean habitat. J Ecol 92:266–277

Castro J, Zamora R, Hódar JA, Gómez JM (2005) Ecology of seed germination of *Pinus sylvestris* L. at its southern Mediterranean distribution range. Investig Agraria: Sistemasy Recursos Forestales 14:143–152

Crawford RMM (2008) Plants at the margin ecological limits and climate change. Cambridge University Press, Cambridge

Erefur C, Bergsten U, Lundmark T, de Chantal M (2011) Establishment of planted Norway spruce and Scots pine seedlings: effects of light environment, fertilisation, and orientation and distance with respect to shelter trees. New For 41:263–276

Hunt FM (1951) Effect of flooded soil on growth of pine seedlings. Plant Physiol 26:363–368

Kozlowski TT (1997) Responses of woody plants to flooding and salinity. Tree Physiol Monogr 1:1–29

Kozlowski TT, Pallardy S (2002) Acclimation and adaptive responses of woody plants to environmental stresses. Bot Rev 68:270–334

Lakon G (1949) The topographical tetrazolium method for determining the germination capacity of the seed. Plant Physiol 24:389–394

Linder S (1972) Seasonal variation of pigments in needles. A study of Scots pine and Norway spruce seedlings grown under different nursery conditions. Stud For Suec 100:1–37

Mary AT, McLeod KW (1986) Responses of *Pinus clausa*, *Pinus serotina* and *Pinus taeda* seedlings to anaerobic solution culture I. Changes in growth and root morphology. Physiol Plant 68:523–531

McHaffie H, Legg CJ, Worrell R, Cowie N, Amphlett A (2002) Scots pine growing on forested mires in Abernethy Forest, Strathspey, Scotland. Bot J Scot 54:209–219

McVean DN (1961) Experiments on the direct sowing of Scots pine. Empire For Rev 40:217–227

Megonigal JP, Day FP (1992) Effects of flooding on root and shoot production of Bald cypress in large experimental enclosures. Ecology 73:1182–1193

Nilsson MC, Zackrisson O, Sterner O, Wallstedt A (2000) Characterisation of the differential interference effects of two boreal dwarf shrub species. Oecologia 123:122–128

Poore MED, Walker D (1959) Wybunbury Moss, Cheshire. Mem Proc Manch Lit Philos Soc 101:72–95

Reid DM, Bradford KJ (1984) Effects of flooding on hormone relations. In: Kozlowski TT (ed) Flooding and plant growth. Academic, Orlando, pp 195–219

Rodwell JS (1991) British plant communities, mires and heaths, vol 2. Cambridge University Press, Cambridge

Sena Gomes AR, Kozlowski TT (1980) Responses of *Pinus halepensis* seedlings to flooding. Can J For Res 10:308–311

Steven HM, Carlisle A (1959) The native pinewoods of Scotland. Oliver & Boyd, Edinburgh

Streng DR, Glitzenstein JS, Harcombe PA (1989) Woody seedling dynamics in an east Texas floodplain forest. Ecol Monogr 59:177–204

Tang ZC, Kozlowski TT (1983) Responses of *Pinus banksiana* and *Pinus resinosa* seedlings to flooding. Can J For Res 13:633–639

Thomas PA (2000) Trees: their natural history. Cambridge University Press, Cambridge

Yamamoto F, Kozlowski TT (1987) Effects of flooding, tilting of stems, and ethrel application on growth, stem anatomy and ethylene production of *Pinus densiflora* seedlings. J Exp Bot 38:293–310

Yamamoto F, Kozlowski TT, Wolter KE (1987) Effect of flooding on growth, stem anatomy, and ethylene production of *Pinus halepensis* seedlings. Can J For Res 17:69–79