

# Vitality of bog pine and colonising Norway spruce along environmental gradients within a bog

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## SUMMARY

Bog pine is an endangered species in Europe as drainage of bogs permits colonisation by Norway spruce, resulting in severe bog pine habitat loss in marginal bog forests, and a habitat shift towards the bog centre where growing conditions are extreme. Thus, we investigated the physiological causes that limit bog pine regeneration at the bog margins and growth in the centre. We measured needle nitrogen concentration, chlorophyll content, photosynthetic capacity and the morphological traits of bog pine and spruce along transects from the centre to the margin of a bog in the Black Forest, Germany. Needle nitrogen and chlorophyll contents in the bog pine increased from the centre to the margin. However, photosynthesis was independent of chlorophyll content indicating that other factors, such as light rather than nutrients, may limit regeneration of bog pine. Vitality of bog pine was highest at the edge of the bog centre. This zone appears to be a compromise between nutrient limitation and shallow water levels on the one hand, and light limitation caused by spruce on the other. Therefore, in order to conserve bog pine, it is necessary to maintain wet and open bog forests that cannot be colonised by spruce.

**KEY WORDS:** bog woodland, competition, drainage, *Picea abies*, *Pinus rotundata*, vitality

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## INTRODUCTION

Bogs are unique ecosystems that require very specific abiotic conditions and need exceptionally long time-spans to develop. Although species poor, they are exclusive habitats for specialised species (Leuschner & Ellenberg 2017). However, bogs are threatened ecosystems in many parts of the world (Linderholm & Leine 2004, Lachance *et al.* 2016) and most European countries have lost more than 90 % of active mire areas due to human activities, such as drainage, peat cutting and agricultural use (Succow & Joosten 2001).

Trees are rare in the central parts of raised bogs because of extreme environmental conditions. Shallow water tables, poor nutrient availability and acidic soils exclude most tree species from bogs. However, bog pine (*Pinus rotundata* Link or *Pinus mugo* subsp. *rotundata*) is more tolerant of these specific conditions. It occurs mainly around the open parts of a bog and reaches its limits only in the central and wettest parts (von Sengbusch 2013). It is an endangered species with a decreasing population trend (Farjon 2013) and is endemic to central Europe and restricted to bogs as it is not able to compete with other tree species under more favourable environments (Leuschner & Ellenberg 2017). Seedlings of bog pine require a high light availability

for establishment and, thus, the species does not regenerate when it is shaded by other trees (Schmid *et al.* 1995).

The drainage of bogs generally permits colonisation by other tree species and understorey vegetation from surrounding forests, resulting in severe habitat loss for bog pine and other species characteristic of bogs, and the vegetation shifts from open peatland vegetation to forest plant communities (Parish *et al.* 2008, Kollmann & Rasmussen 2012). For instance, Norway spruce (*Picea abies* L.) and dwarf shrubs such as *Vaccinium myrtillus* L. colonise the central parts of the bog where they shade understorey vegetation and, consequently, suppress regeneration of bog pine. Thus, a dieback of bog pine and a habitat shift from marginal bog forest towards the wetter parts near the centre has taken place in many drained bogs in southern Germany (Schmid *et al.* 1995, von Sengbusch 2004, 2006 and 2015), Switzerland (Freléhoux *et al.* 2003) and the Czech Republic (Unar *et al.* 2012).

Furthermore, drainage of bogs also affects the growth form of bog pine. Deeper water levels cause increased nutrient availability due to higher peat decomposition rates and, in turn, lead to increased growth of bog pine (von Sengbusch 2006). Therefore, trees at the bog margin are taller and have a higher height: diameter ratio than those at the

centre. Regeneration does not take place at the margins due to shading by old bog pines and colonising spruce. Consequently, bog pine may disappear from these areas and will be replaced by spruce. With more shallow water levels towards the centre of the bog, bog pine becomes smaller with a lower height: diameter ratio. It still regenerates in these parts because open *Sphagnum* lawns provide more suitable conditions for germination of bog pine, and other competitors are absent (Freléchoux *et al.* 2000, von Sengbusch 2015). However, although light availability in the central parts of the bog is sufficient to allow for bog pine regeneration, bog pine survival could be seriously affected by waterlogging, anaerobic conditions and frost damage (Mach *et al.* 2009).

The observed shift of bog pine towards the more open, central parts of the bog, as well as perceived morphological differences, are potential consequences of multiple gradients formed by abiotic and biotic factors from the bog margin to the centre. The main ecological gradients that control vegetation distribution in bogs are the increasingly shallow water levels found nearer the bog centre, and, consequently, highly anaerobic conditions and decreasing nutrient availability. Furthermore, soil acidity and light availability increase towards the bog centre (Malmer 1986, Wheeler & Proctor 2000). High solar radiation in open bog areas also increases the possibility for chlorophyll bleaching during winter. Since photosynthetic activity is paused in winter, radiation energy cannot be utilised and may damage chlorophyll and membrane lipids, which delays the reactivation of the photosynthetic apparatus in the spring (Larcher 2003). All these factors increasingly limit the growth of bog pine nearer the bog centre. On the other hand, the cover of trees and shrubs decreases towards the bog centre because competitors, such as spruce or dwarf shrubs are even more limited by the extreme conditions in the bog. Thus, competitive pressure decreases towards the bog centre (von Sengbusch 2004).

Several studies have investigated the reasons for the lack of bog pine regeneration at the bog margin and why it is replaced by Norway spruce. Most concluded that shading by a denser canopy inhibits germination and the growth of bog pine seedlings (e.g. Schmid *et al.* 1995). However, physiological studies that provide a mechanistic explanation for this phenomenon are still lacking. Therefore, we attempt to fill this gap by investigating how needle chlorophyll content, nitrogen concentration, photosynthetic capacity and morphological traits, as measures of the vitality of bog pine and Norway spruce, change along gradients from the centre to the

margin of a bog in early and late spring. Furthermore, we try to identify whether there is a zone between the two opposing gradients where bog pine is most vibrant. This should help identify the zone that needs to be prioritised for conservation in order to provide a habitat for the species in the future.

We tested the hypotheses that (I) needle nitrogen concentration, chlorophyll content and photosynthetic capacity increase towards the bog margins; (II) chlorophyll content and photosynthesis increase during spring and are more pronounced in bog pine than in Norway spruce because of chlorophyll bleaching during winter in the bog centre; and (III) morphological traits indicate increased growth potential of bog pine towards the bog margins.

## METHODS

### Study site

The study was conducted in the western part of the ‘Hinterzartener Moor’, a bog in the southern Black Forest close to the town of Hinterzarten (47° 54' 28" N, 08° 06' 30" E; 880 m a.s.l., Figure 1). Mean annual temperature is 6.9 °C and mean annual precipitation is 1334 mm (www.worldclim.org). The bog developed after terrestrialisation of a lake, which was formed by the Feldberg glacier during the ‘Würm’ glacial period.

The western part of the bog can be considered as a quaking bog with floating peat above an almost 300 m water lens (Lang 2005). The open central part consists of a mosaic of hummocks, hollows and pools. The vegetation comprises bog species, such as *Eriophorum vaginatum* L., *Andromeda polifolia* L. and *Vaccinium oxycoccus* L.; species that are indicative of the influence of mineral water in the bottoms of the hollows and pools, such as *Eriophorum angustifolium* Honck. and *Carex lasiocarpa* Ehrh., and *Sphagnum* lawns. Furthermore, the water level was shallow (mean water level during the measurement period was 15 cm below the hollow surface,) and signs of decomposing peat were rare. Towards the bog margin, the water level decreased to 26 cm below the surface, while the decomposition level of the peat increased, and the vegetation changed to a closed forest formed by old bog pines and Norway spruce with an understorey of *Vaccinium myrtillus* and *Vaccinium uliginosum* L.

Peat cutting did not influence the western part of the bog, but the water supply was blocked by the construction of nearby railway tracks in the late 19<sup>th</sup> century, which caused drainage and the subsequent establishment of Norway spruce.

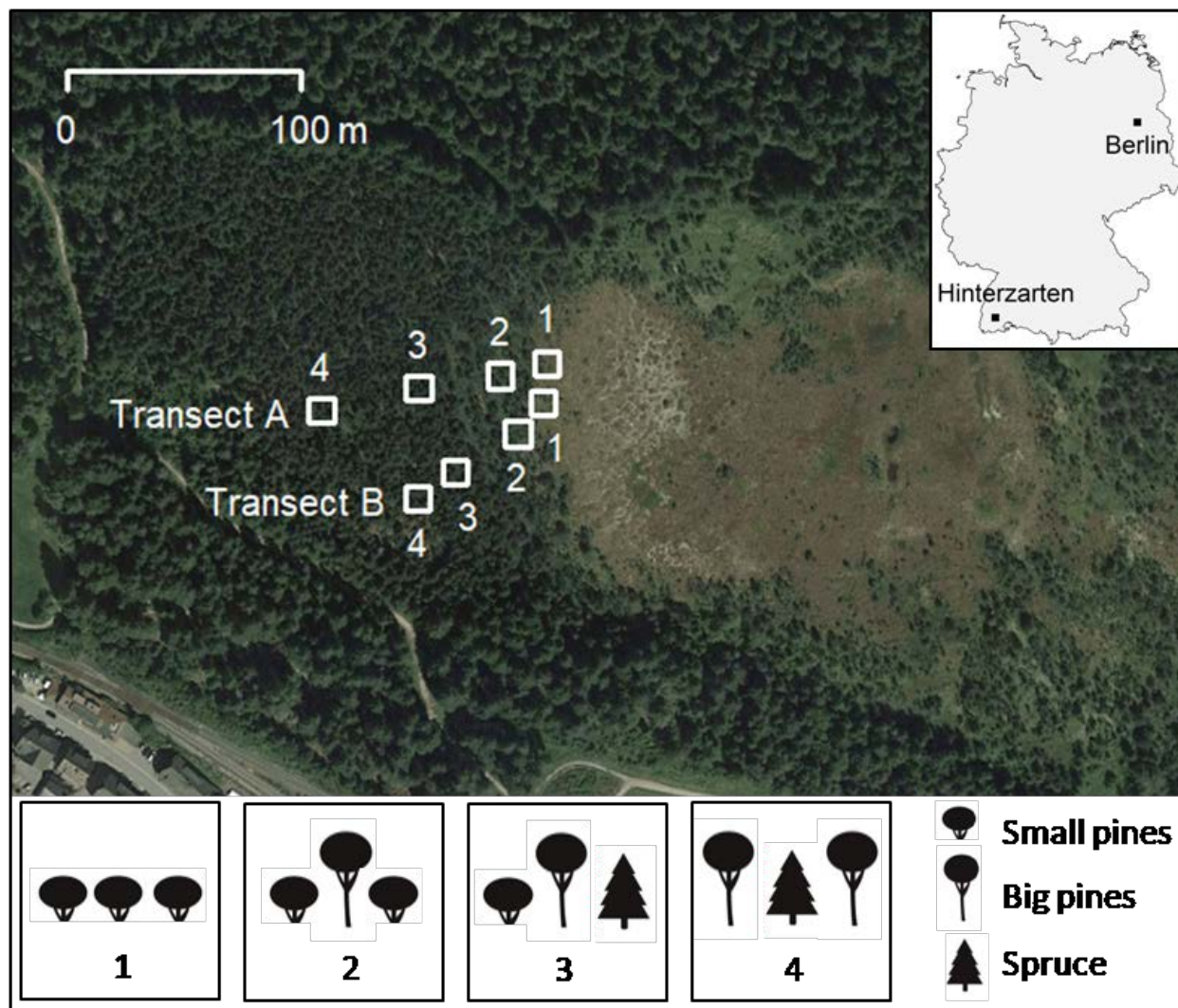


Figure 1. Western part of the ‘Hinterzarter Moor’, with the two transects from open centre of the bog (Position 1) to the bog margin (Position 4) and groups of trees present at the different plot positions shown. The railway tracks that caused drainage of the bog are visible in the lower left corner of the picture. Maps: R-packages ‘mapdata’ (Becker *et al.* 2016) and ‘RgoogleMaps’ (Loecher & Ropkins 2015).

### Sampling design

Two transects were established along the gradient from the open central part to the margin of the bog. Each transect contained four plots (60–100 m<sup>2</sup> in area). The plot positions represented the different conditions and the changing vegetation between the centre and margin of the bog. The innermost plots (Position 1) lay in the central part and were characterised by typical bog vegetation with small scattered bog pines. Larger and continuously regenerating bog pines occurred in the plots at the edge of the open bog (Position 2). Plots at the succession border of Norway spruce (Position 3) contained large bog pine trees and a few small, old bog pines. Bog pine regeneration or spruce saplings were not observed at this position. Plots at the bog margin (Position 4) were characterised by well-established spruce and old bog

pines that had reached their maximum height.

Three groups of trees were sampled: small bog pines (1–4 m in height), large bog pines (5–14 m) and small Norway spruce (1–2 m). In each plot (one per position and transect = 8 plots), three individuals were sampled per group. Due to the changing vegetation observed along the two transects, not all groups were present in each plot (Figure 1).

The first cycle of measurements took place between 17 and 23 Apr 2014. Air temperature at this time was below -10 °C during the night and up to 20 °C during the day. Measurements were repeated between 13 and 15 May 2014 when the minimum night air temperature was -1 °C. Branches with southern or south western exposure were sampled and the needles of the youngest needle cohort were used for the measurements.

### Chlorophyll content

The chlorophyll content ( $\text{mg m}^{-2}$ ) of the bog pine and Norway spruce needles was measured with a Chlorophyll Content Meter CCM 300 (Opti-Sciences, Hudson, USA). The chlorophyll content of the small trees was measured in situ on three branches per tree. For the taller pines, three branches per tree were cut at a height of approximately 12 m. Chlorophyll content was measured within 15 minutes of cutting.

### Gas exchange and nitrogen concentrations

For gas exchange measurements, one branch per tree was sampled; the cut end was immediately put into water and taken to the laboratory. The following day, we measured the maximum photosynthetic capacity ( $A_{\text{max}}$ ) at a photon flux density of  $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$  using an infrared gas analyser (GFS 3000, WALZ, Effeltrich, Germany). The cuvette temperature was set to  $20^\circ\text{C}$ , the relative humidity to 50 % and the carbon dioxide ( $\text{CO}_2$ ) concentration to 390 ppm. The needles were allowed to adjust to these conditions for at least 10 mins before measurements, and light availability and temperature outside the cuvette were kept close to cuvette conditions.

Subsequently, the respective needles were oven-dried at  $60^\circ\text{C}$  for at least 72 h. They were cut into small pieces and 20 mg of each sample were analysed for nitrogen concentration using an elemental analyser (Vario EL Cube, ElementarAnalysesysteme GmbH, Hanau, Germany).

### Morphological traits

To compare the physiological and morphological traits of the small pines, we measured the number of needle cohorts, the length of the needle cohorts, the length of the needles and the total needle mass of bog pines at Positions 1, 2 and 3 following the sampling design described above for the physiological measurements. To estimate total needle mass, we counted the number of branches per tree, and weighed the oven-dried needles from one branch (only at Positions 2 and 3).

### Statistical analyses

All statistical analyses were performed with the software R (R version 3.2.3, R Core Team 2015). A significance level of  $P < 0.05$  was used for all analyses. and results at a significance level of  $0.05 < P < 0.1$  were indicated as trends.

The effect of species (bog pine or spruce), the position of the plot (as a factor) and the measurement period (April or May) on nitrogen concentrations, chlorophyll content, photosynthetic capacity and morphological traits was tested for the shrub layer

(small bog pine and Norway spruce) and trees (large bog pines) separately. To account for the two different transects and the repeated measurements, we used linear mixed models (lme4 package, Bates *et al.* 2015) that included tree and transect as random variables and all main effects as fixed. Both random variables proved to be non-significant and so we proceeded with the linear models. The linear models initially included all possible interactions between factors and were stepwise simplified until the final models included only significant variables. For post-hoc comparisons of the means, pairwise t-tests with Bonferroni-correction were used. The relationship between nitrogen concentration or chlorophyll content and the photosynthetic capacity of the bog pines was tested with linear regression.

## RESULTS

### Nitrogen concentrations

Nitrogen concentrations in the small and large pine needles did not change between the April and May sampling dates but were lower in the centre of the bog than farther outside (small pines:  $P = 0.045$ , large pines:  $P < 0.001$ ). Furthermore, plot position and measurement period had no effect on nitrogen concentration in the spruce needles (Figure 2, Table 1).

### Chlorophyll content

The chlorophyll content of the bog pine needles increased from the bog centre to the bog margin (small and large pines:  $P < 0.001$ ). Moreover, small pines at Positions 1 ( $P = 0.0023$ ) and 2 ( $P < 0.001$ ) contained more chlorophyll in May than in April (Figure 3, Table 1). The bog pines in the inner part were still bleached after loss of chlorophyll during the previous winter and yellow needles were evident in April (Figure A1 in Appendix). Chlorophyll content and nitrogen concentration of the pines were positively correlated and the correlation was stronger in April ( $r^2 = 0.68$ ,  $P < 0.001$ ) than in May ( $r^2 = 0.22$ ,  $P = 0.043$ ) (Figure 4).

Neither the position of the plot nor the measurement period had a significant effect on the chlorophyll content of the spruce (Figure 3, Table 1) and no correlation between chlorophyll content and nitrogen concentration was found for spruce (data not shown).

### Photosynthetic capacity

The photosynthetic capacity of the bog pine and spruce was not affected by the plot position but  $A_{\text{max}}$  in the small bog pines increased from  $0.004 \mu\text{mol g}^{-1} \text{s}^{-1}$  in April to  $0.019 \mu\text{mol g}^{-1} \text{s}^{-1}$  in May

( $P < 0.001$ ).  $A_{max}$  in Norway spruce did not increase between the two measurement periods. However, the photosynthetic capacity of spruce in April tended to be higher than in the small bog pines ( $P = 0.060$ ). Photosynthesis in the large pines was constantly low along the two transects, and over time (Figure 5, Table 1). The photosynthetic capacity of both species was neither correlated with nitrogen concentration nor with chlorophyll content (Figure 4).

**Morphology**

The plot position significantly affected the number of needle cohorts ( $P = 0.0071$ ), the length of the needle cohorts ( $P < 0.001$ ), the length of the needles ( $P = 0.0046$ ) and the needle mass ( $P < 0.001$ ) in the small bog pines. The individuals at Position 2 had the most needle cohorts, the longest needle age cohorts, the longest needles and the highest needle mass (Figure 6, Table 2).

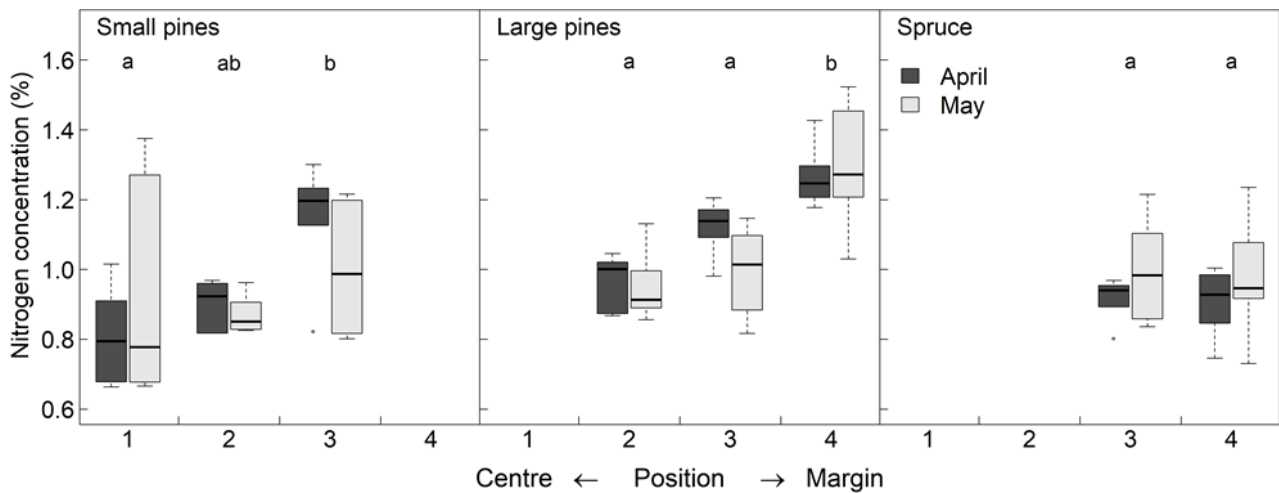


Figure 2. Nitrogen concentrations in *Pinus rotundata* (small and large pines) and *Picea abies* (spruce) needles in April and May 2014. No significant differences between the April and May measurement periods were found. Different letters indicate significant differences between the positions along the two transects.

Table 1. Summary of ANOVA-results for the linear models used to test the effects of plot position, measurement period and species composition on nitrogen concentration, chlorophyll content and photosynthetic capacity of bog pine and Norway spruce. Separate models were run for the shrub layer (small pines and spruce) and the tree layer (large pines). Df = degrees of freedom

Response (Df)	Factor	Df <sup>a</sup>	F-value	P-value
<b>Shrub layer (small pines and spruces)</b>				
N concentration (56)	Plot position	3	2.9	0.045
Chlorophyll content (53)	Species	1	17.0	<0.001
	Plot position	3	72.5	<0.001
	Measurement period	1	63.1	<0.001
	Species: Measurement period	1	3.8	0.057
Photosynthesis (56)	Measurement period	1	40.5	<0.001
	Species	1	2.7	0.100
	Species: Measurement period	2	4.4	0.040
<b>Tree layer (large pines)</b>				
Chlorophyll content (33)	Plot position	2	19.2	<0.001
Nitrogen concentration (33)	Plot position	2	24.1	<0.001

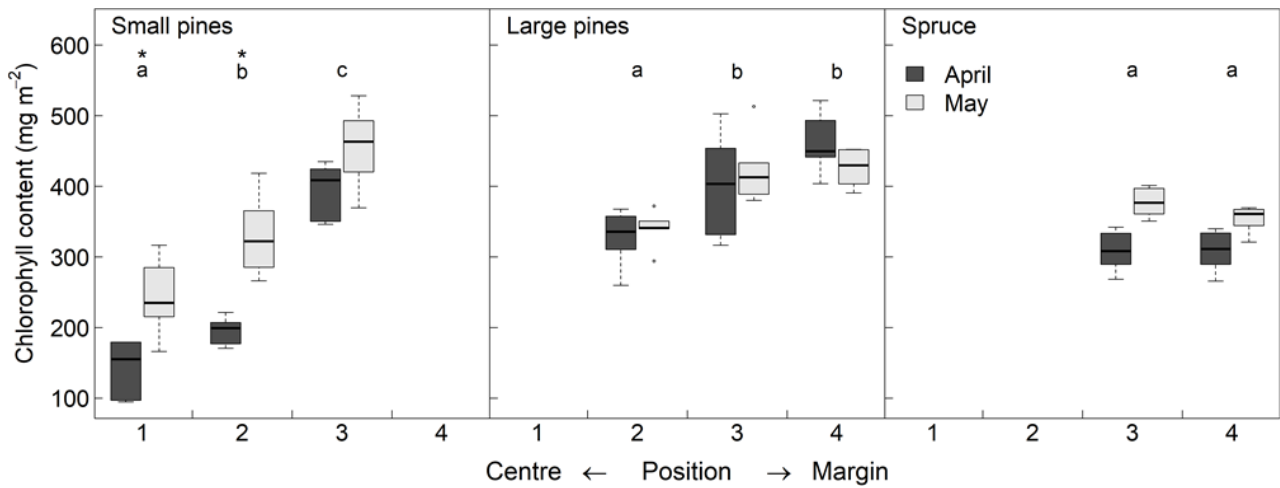


Figure 3. Chlorophyll content in *Pinus rotundata* (Small and Large pines) and *Picea abies* (Spruce) needles in April and May 2014. Asterisks indicate significant differences between the April and May measurement periods. Different letters indicate significant differences between the positions along the two transects.

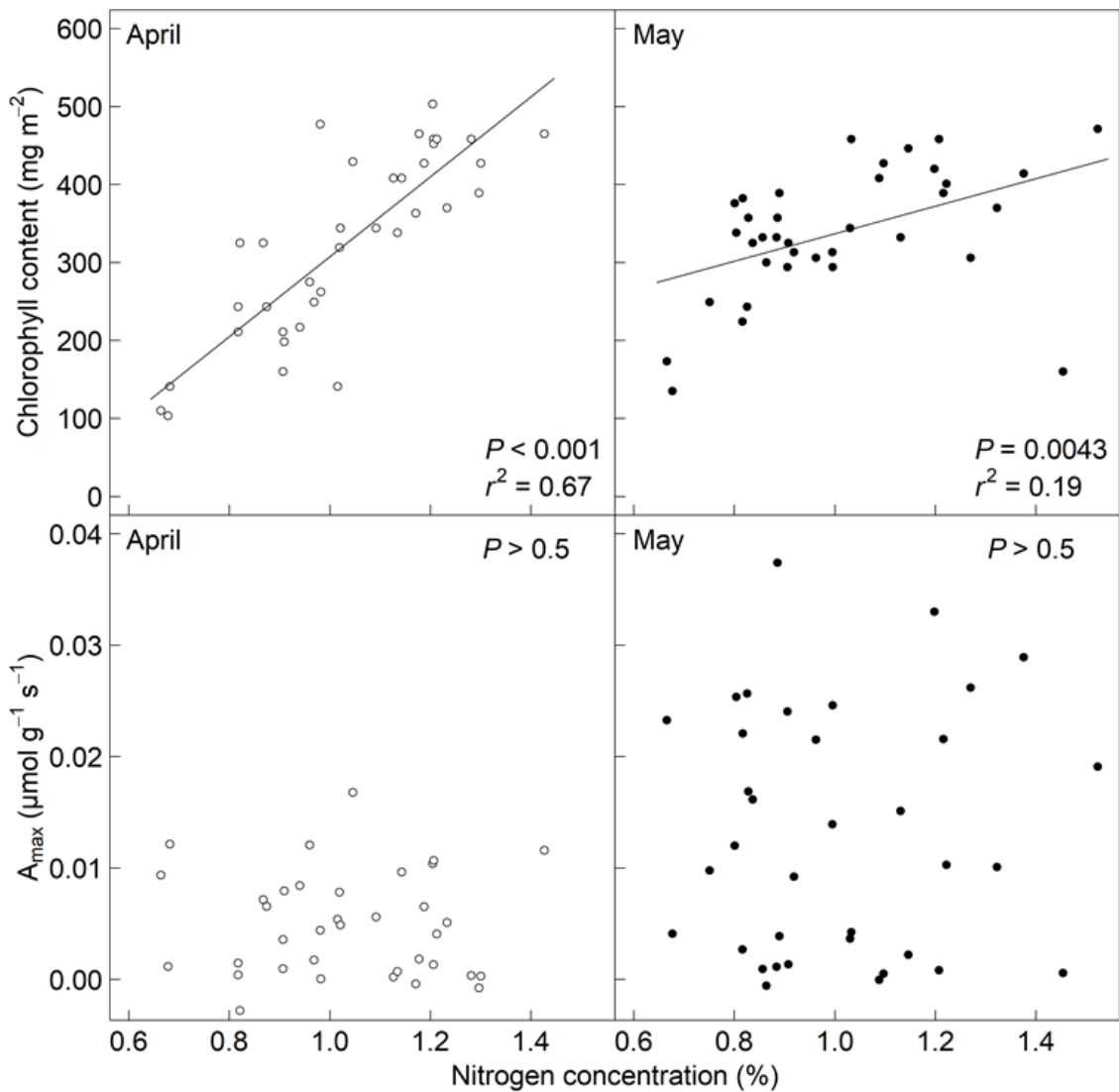


Figure 4. Relationships between chlorophyll content and nitrogen concentration, and between photosynthetic capacity and nitrogen concentration in *Pinus rotundata* in April and May 2014.

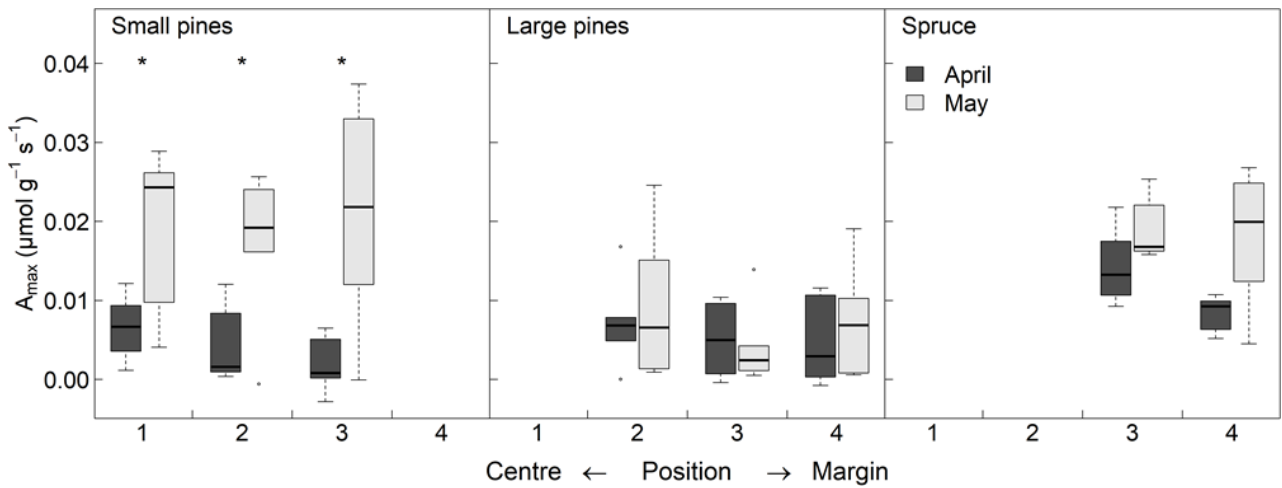


Figure 5. Maximum photosynthetic capacity ( $A_{max}$ ) in *Pinus rotundata* (Small and Large pines) and *Picea abies* (Spruce) in April and May 2014. Asterisks indicate significant differences between the April and May measurement periods. No significant differences were observed between the positions along the two transects.

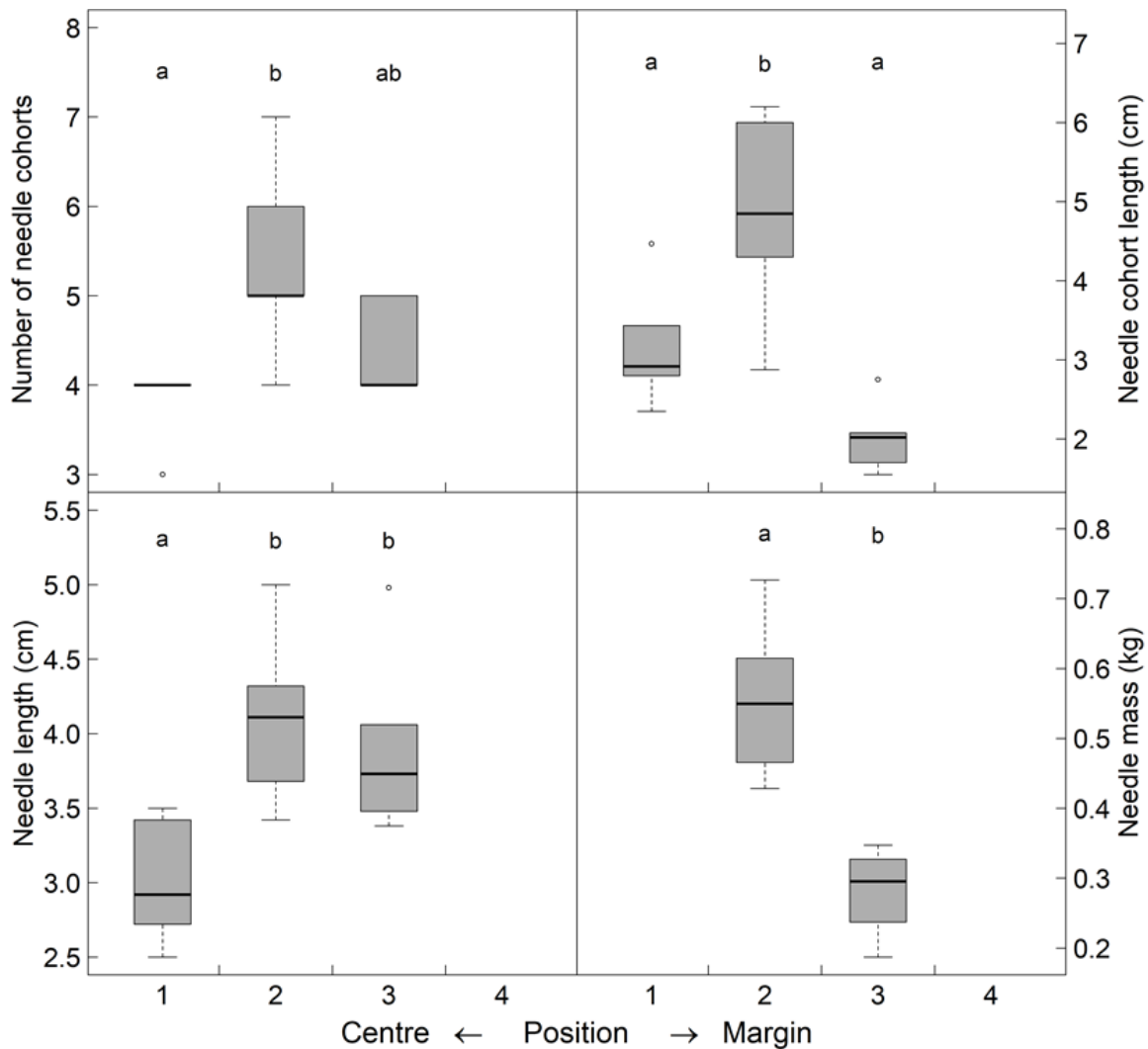


Figure 6. Number of needle cohorts, needle cohort length, needle length and total needle mass of small bog pines. Different letters indicate significant differences between the positions along the transects.

Table 2. Summary of ANOVA-results for linear models to test the effect of plot position on morphological traits of bog pine and Norway spruce. Df = degrees of freedom.

Response (Df <sup>a</sup> )	Factor	Df <sup>a</sup>	F-value	P-value
Number of needle cohorts (15)	Plot position	2	7.0	0.0071
Length of needle cohorts (15)	Plot position	2	16.7	<0.0001
Length of needles (15)	Plot position	2	7.8	0.0046
Needle mass (10)	Plot position	2	29.6	<0.0001

## DISCUSSION

Several ecological gradients are evident from the margin to the centre of a bog: the nutrient content of the peat (decreases), soil acidity (increases) and water level (increases). Furthermore, the abundance and canopy cover of trees and shrubs decreases, which leads to increasing light availability towards the bog centre (Malmer 1986, Bridgham *et al.* 1996). According to our results, the interaction between these opposing gradients affects physiology and morphology and, thus, the vitality of the bog pines.

### Effects of changing site conditions along the transects

The deeper water levels found near bog margins result in higher mineralisation rates and, thus, increased nutrient availability (Bridgham *et al.* 1996). For example, von Sengbusch (2006) observed higher ammonium availability in drained bog forests compared to active raised bogs. These findings may explain the increase in nitrogen concentrations in the pine needles, which were observed in our study from the bog centre towards the margin. While nitrogen concentrations in the spruce needles did not increase, the higher peat decomposition at the margin may still favour Norway spruce colonisation. Nevertheless, nitrogen concentrations in both species growing in the 'Hinterzartener Moor' are low compared to concentrations measured outside the bog. Mean nitrogen concentrations in spruce needles in Europe range between 1.54–1.72 % (Bauer *et al.* 1997, Oleksyn *et al.* 1998), whereas we measured concentrations of about 0.95 % (mean across positions and measurement dates), thereby indicating that the invading spruce were strongly nitrogen limited. Thus, low nutrient availability in the central part of the bog may restrict spruce from further colonisation. Furthermore, since mean nitrogen concentrations were 0.87 % in the bog centre and 1.28 % at the bog margin, all bog pines may suffer from nitrogen limitation, which is assumed to occur

at concentrations below 1.6 % (Bücking 1985).

As expected, the chlorophyll content in the pine needles also increased towards the bog margin. In general, leaf nitrogen, chlorophyll content and photosynthesis are strongly related, as nitrogen is the main component of photosynthetic proteins (Field & Mooney 1986). Thus, we also expected an increase in photosynthesis concomitant with increasing leaf nitrogen and chlorophyll content although surprisingly, higher chlorophyll content did not result in higher photosynthetic capacity. Despite the low amount of nitrogen and chlorophyll, the photosynthetic capacity of the bog pines growing in the centre of the bog was comparable to the pines growing at the margin.

Thus, light (rather than nutrients) may be more important for bog pines to maintain relatively high photosynthetic rates. The importance of light for seedling establishment of bog pine, and its low demands in terms of nutrients and rooting space, has also been proposed by others (e.g. Schmid *et al.* 1995, von Sengbusch 2015) and is supported by our results. Accordingly, the independence of photosynthesis from leaf nitrogen concentrations suggests that the outermost small pines may be light limited because of shading by the taller pine and spruce trees (Figure A2). It is a well-known phenomenon that the maximum photosynthetic capacity of shade-adapted leaves is lower than sun-adapted leaves (Boardman 1977, Givnish 1988). Furthermore, bog pine is very light-demanding (Schmid *et al.* 1995) and its regeneration is completely suppressed in areas where spruce is already established. In addition, shading improves the growing conditions for algae and fungi and, indeed, the needles of pines growing closer to the bog margin were covered in algae and fungi (Figure A3). Consequently, gas exchange through stomata may be blocked, which may further restrict photosynthesis. In general, the photosynthetic capacity of the large pines was very low, which could also be a result of shading, algae and fungi cover. Furthermore, the photosynthetic capacity of trees



often decreases with height and age (Bond 2000) because of hydraulic limitations, which also cause lower stomatal conductance and decreased CO<sub>2</sub> uptake (Ryan & Yoder 1997). Thus, our results may indicate that the large bog pines located at the bog margins have reached their maximum height and may die back eventually. Since regeneration of bog pine does not occur in these areas, this would result in a replacement of bog pine forests by spruce forests.

Morphological traits reflect the limitation of bog pine growth from two aspects: light limitation and competition at the bog margin, and nutrient limitation, shallow water levels and other stresses in the bog centre. Contrary to our hypothesis, growth of bog pine (based on different morphological traits) did not increase with increasing nitrogen availability and needle chlorophyll content along the two transects from the centre to the margin, but was at an optimum between the bog centre and the bog margin. This might be due to the lack of observed correlation between chlorophyll content and photosynthesis capacity in our study. However, while photosynthesis in the pine needles was similar at Positions 1 and 2 (corresponding to the centre and close-to-the-centre position, respectively), the bog pines at Position 2 were more vibrant (i.e. had more and longer needles), thereby suggesting that growth of bog pines in the centre was not limited by carbon assimilation. Moreover, stressors, such as chlorophyll bleaching (Figure A1), shallow water tables and snow damage may negatively affect the growth of bog pine. In addition, temperature is often lower in the open centre of bogs than in the bog forests, and night frosts may also occur during the summer, which may further limit growth of bog pine. In general, the growth of trees under specific environmental constraints, for instance temperature or nutrient limitation, may be restricted before carbon limitation would occur (Körner 2003, Palacio *et al.* 2014). For example, a similar response has been observed in trees at the alpine tree line (Wieser 2007, Körner 2012): although species growing either in alpine habitats or in valleys show the same photosynthetic capacity, the trees at the tree line are usually smaller and less productive. Thus, comparable to bog pines in the bog centre (where only small pines occurred), trees at the tree line are normally not able to exceed shrub size (Wieser 2007, Körner 2012). Consequently, maintenance costs, such as respiration, frost protection or regrowth after damage, may be higher in the bog centre and, thus, less assimilated carbon can be invested in growth.

### Effects of seasonality

As expected, chlorophyll content and photosynthetic

capacity in the bog pine increased between April and May but nitrogen concentration in the needles did not change. This may indicate photo-inhibition and destruction of chlorophyll caused by high solar radiation in the open bog centre. Another possibility could be that pines had adapted to lower energy demand during winter by reducing chlorophyll content and increasing carotenoids as a protection against excess radiation (Linder 1972). Since the reduction of chlorophyll content in the pines in April was strongest in the bog centre, high solar radiation in winter may have damaged the photosynthetic apparatus and, consequently, limited photosynthesis of bog pines in the open areas early in the growing season. However, photosynthesis in the small pines at the bog margin was also low in April and increased in May, although significant increases in chlorophyll content or in the signs of bleaching (yellow needles) were not observed. Hence, bog pines may still be in winter dormancy during April, regardless of reduced chlorophyll content and chlorophyll bleaching. In contrast, neither the chlorophyll content nor the photosynthetic capacity in spruce increased between April and May. Thus, spruce may recover earlier from winter depression than bog pine (von Sengbusch 2004).

In this study, we show that bog pine is affected by two opposing gradients, which limit its growth at the margin and at the centre of the bog. Despite the advantages for spruce in a bog forest (shade tolerance and a longer growing season), it reaches its ecological limits farther away from the bog centre because of shallow water tables and low nutrient availability. Thus, the transition zone from open bog to bog forest seems to be a compromise for bog pine between a lack of nutrients and a shallow water table on the one hand, and competition of Norway spruce and dwarf shrubs on the other. Since conditions are not as severe as in the centre, bog pine was most vibrant in this part of the bog. Here, nutrient supply was still adequate for bog pine, and light availability was sufficient for continuous regeneration. It follows that nitrogen and, therefore, chlorophyll content in the needles might not be the most important factors determining the vitality of bog pine but that the combined effects of stressors, such as competition for light, infestation of algae and fungi and snow damage also play an important role in determining the growth of bog pines.

Our results confirm that from a physiological perspective it is necessary to maintain wet and open bog areas for the conservation of bog pine. These areas are unsuitable for spruce but still provide favourable conditions for the growth of bog pine. Several measures are currently in practice to achieve

this objective and include avoidance of further drainage, renaturation of previously drained bogs, or the removal of spruce trees. Overall, the maintenance of shallow water levels is critical to the conservation of bogs and the species that are associated with them.

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## REFERENCES

- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Bauer, G., Schulze, E.D. & Mund, M. (1997) Nutrient contents and concentrations in relation to growth of *Picea abies* and *Fagus sylvatica* along a European transect. *Tree Physiology*, 17, 777–786.
- Becker, R.A., Wilks, A.R., Brownrigg, R., Minka, T.P. & Deckmyn, A. (2016) maps: Draw geographical maps. R package version 3.1.1. Online at: <https://cran.r-project.org/web/packages/maps/maps.pdf>, accessed 14 Jan 2019.
- Boardman, N.K. (1977) Comparative photosynthesis of sun and shade plants. *Annual Review of Plant Physiology*, 28, 355–377.
- Bond, B.J. (2000) Age-related changes in photosynthesis of woody plants. *Trends in Plant Science*, 5, 349–353.
- Bridgham, S.D., Pastor, J., Janssens, J.A., Chapin, C. & Malterer, T.J. (1996) Multiple limiting gradients in peatlands. A call for a new paradigm. *Wetlands*, 16, 45–65.
- Bücking, W. (1985) Ökologisch-chemische Untersuchungen im Bannwald “Waldmoor-Torfstich” (Ecological-chemical studies in the protected forest “Waldmoor-Torfstich”). In: *Der Bannwald “Waldmoor-Torfstich”. “Waldschutzgebiete”*, Mitteilungen der Forstlichen Versuchs- und Forschungsanstalt Baden-Württemberg 3, Freiburg, Germany, 223–259 (in German).
- Farjon, A. (2013) *Pinus mugo* subsp. *rotundata*. The IUCN Red List of Threatened Species 2013: e.T18153856A18153859.
- Field, C. & Mooney, H.A. (1986) The photosynthesis - nitrogen relationship in wild plants. In: Givnish, T.J. (ed.) *Responses of Plants to Multiple Stresses*, Cambridge University Press, 25–55.
- Freléchoux, F., Buttler, A., Schweingruber, F.H. & Gobat, J.M. (2000) Stand structure, invasion, and growth dynamics of bog pine (*Pinus uncinata* var. *rotundata*) in relation to peat cutting and drainage in the Jura Mountains, Switzerland. *Canadian Journal of Forest Research*, 30, 1114–1126.
- Freléchoux, F., Buttler, A., Gillet, F., Gobat, J.M. & Schweingruber, F.H. (2003) Succession from bog pine (*Pinus uncinata* var. *rotundata*) to Norway spruce (*Picea abies*) stands in relation to anthropic factors in Les Saignolis bog, Jura Mountains, Switzerland. *Annals of Forest Science*, 60, 347–356.
- Givnish, T.J. (1988) Adaption to sun and shade: A whole-plant perspective. *Australian Journal of Plant Physiology*, 15, 63–92.
- Kollmann, J. & Rasmussen, K.K. (2012) Succession of a degraded bog in NE Denmark over 164 years: monitoring one of the earliest restoration experiments. *Tuexenia*, 32, 67–85.
- Körner, C. (2003) Carbon limitation in trees. *Journal of Ecology*, 91, 4–17.
- Körner, C. (2012) *Alpine Treelines*. First edition, Springer, Basel, Switzerland, 220 pp.
- Lachance, D., Lavoie, C. & Desrochers, A. (2016) The impact of peatland afforestation on plant and bird diversity in southeastern Québec. *Écoscience*, 12, 161–171.
- Lang, G. (2005) *Seen und Moore des Schwarzwaldes (Lakes and Mires of the Black Forest)*. Andrias16, Staatliches Museum für Naturkunde Karlsruhe (SMNK), 160 pp. (in German).
- Larcher, W. (2003) *Physiological Plant Ecology - Ecophysiology and Stress Physiology of Functional Groups*. Fourth edition, Springer, Berlin Heidelberg, 514 pp.
- Leuschner, C. & Ellenberg, H. (2017) *Ecology of Central European Non-Forest Vegetation: Coastal to Alpine, Natural to Man-Made Habitats*. First edition, Vegetation Ecology of Central Europe II, Springer, International Publishing, Switzerland, 1093 pp.
- Linder, S. (1972) Seasonal variation of pigments in needles. A study of Scots pine and Norway spruce under different nursery conditions. *Studia Forestalia Suecica*, 100, 1–37.
- Linderholm, H.W. & Leine, M. (2004) An assessment of twentieth century tree-cover changes on a southern Swedish peatland combining dendrochronology and aerial photograph analysis. *Wetlands*, 24, 357–363.
- Loecher, M. & Ropkins, K. (2015) RgoogleMaps and loa: Unleashing R graphics power on map tiles. *Journal of Statistical Software*, 63, 1–18.
- Mach, J., Lanta, V. & Bastl, M. (2009) The effect of

- mining and vegetation scarification on the survival and establishment of *Pinus rotundata* Link. and *P. sylvestris* L. in contrasting peat bog habitats. *Polish Journal of Ecology*, 57, 239–250.
- Malmer, N. (1986) Vegetational gradients in relation to environmental conditions in northwestern European mires. *Canadian Journal of Botany*, 64, 375–383.
- Oleksyn, J., Modrzyński, J., Tjoelker, M.G., Zytkowski, R., Reich, P.B. & Karolewski, P. (1998) Growth and physiology of *Picea abies* populations from elevational transects. Common garden evidence for altitudinal ecotypes and cold adaptation. *Functional Ecology*, 12, 573–590.
- Palacio, S., Hoch, G., Sala, A., Körner, C. & Millard, P. (2014) Does carbon storage limit tree growth? *New Phytologist*, 201, 1096–1100.
- Parish, F., Sirin, A., Charman, D., Joosten, H., Minayeva, T., Silvius, M. & Stringer, L. (2008) *Assessment on Peatlands, Biodiversity and Climate Change, Main Report*. Global Environment Centre and Wetlands International. 179 pp.
- R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ryan, M.G. & Yoder, B.J. (1997) Hydraulic limits to tree height and tree growth. *BioScience*, 47, 235–242.
- Schmid, J., Bogenrieder, A. & Schweingruber, F.H. (1995) Verjüngung und Wachstum von Moorkiefern (*Pinus rotundata* LINK) und Fichten (*Picea abies* [L.] H. Karsten) in Mooren des südöstlichen Schwarzwaldes (Süddeutschland) (Regeneration and growth of bog pines (*Pinus rotundata* LINK) and Norway spruce (*Picea abies* [L.] H. Karsten) in bogs in the southeastern Black Forest (Southern Germany). *Mitteilungen der Eidgenössischen Forschungsanstalt für Wald, Schnee und Landschaft*, 70, 175–233 (in German).
- Succow, M. & Joosten, H. (2001) *Landschaftsökologische Moorkunde (Landscape Ecological Peatland Science)*, Second edition, E. Schweitzerbart, Stuttgart, Germany, 622 pp (in German).
- Unar, P., Janik, D., Soucek, J., Vrska, T., Adam, D., Kral, K. & Hort, L. (2012) The *Pinus rotundata* LINK bog forests on mined peat bogs - is the conservation of undisturbed edge an effective tool for its protection? *Polish Journal of Ecology*, 60, 707–715.
- von Sengbusch, P. (2004) Untersuchungen zur Ökologie von *Pinus rotundata* LINK (Moorkiefer) im Südschwarzwald (*Study of the Ecology of Pinus rotundata LINK (Bog Pine) in the Southern Black Forest*). *Dissertationes Botanicae* 388, J. Cramer Verlag, Stuttgart, Germany, 148 pp. (in German).
- von Sengbusch, P. (2006) *Ein multivariates Monitoring-Verfahren zur Bewertung der Gefährdung von Bergkiefern-Mooren im Schwarzwald (A Multivariate Monitoring Procedure to Assess Threats to Pine Bogs in the Black Forest)*. *Dissertationes Botanicae* 400, J. Cramer Verlag, Stuttgart, Germany, 139 pp. (in German).
- von Sengbusch, P. (2015) Probleme bei der Ansprache von Moorwald-Lebensraumtypen im Schwarzwald (Problems with the classification of peatlands in the Black Forest). In: Vischer-Leopold, M., Ellwanger, G., Ssymank, A., Ullrich, K. & Paulsch, C. (eds.) *Natura 2000 und Management in Moorgebieten (Natura 2000 and Management in Peatlands)*, Naturschutz und Biologische Vielfalt 140, Bundesamt für Naturschutz (BfN), Münster, 155–174 (in German). Online at: [www.buchweltshop.de/bfn](http://www.buchweltshop.de/bfn)
- von Sengbusch, P., Limberger-Andris, S., Peter, H.M. & Lutz, P. (2013) *Moore. Urwüchsige Inseln in der Kulturlandschaft (Peatlands. Natural Islands in the Cultivated Landscape)*. Naturpark Südschwarzwald und Schwarzwaldverein, Freiburg, Germany, 16 pp. (in German).
- Wheeler, B.D. & Proctor, M.C.F. (2000) Ecological gradients, subdivisions and terminology of north-west European mires. *Journal of Ecology*, 88, 187–203.
- Wieser, G. (2007) Limitation by an insufficient carbon assimilation and allocation. In: Wieser, G. & Tausz, M. (eds.) *Trees at their Upper Limit. Treelife Limitation at the Alpine Timberline*. *Plant Ecophysiology* 5, Springer, Dordrecht, The Netherlands, 79–129.

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## Appendix



Figure A1. Yellow needles of a bog pine growing in the centre of the ‘Hinterzartener Moor’ in April 2014.

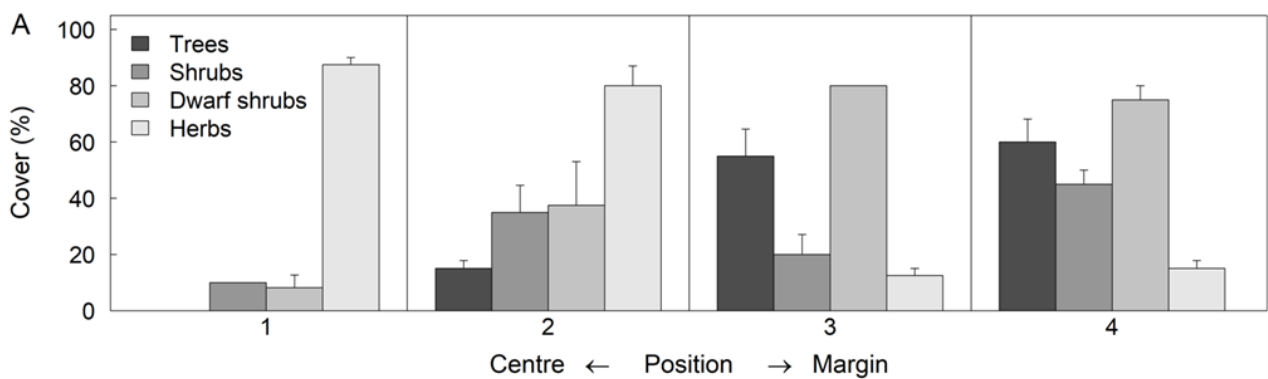


Figure A2. Percentage cover of tree, shrub, dwarf shrub and herb layer at Positions 1–4 along the two transects from the centre to the margin of the bog.



Figure A3. Bog pine needles covered with algae and fungi collected in the ‘Hinterzartener Moor’ in April 2014.