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Original article

Growth and morphology of pedunculate oak (*Quercus robur* L) and beech (*Fagus sylvatica* L) seedlings in relation to shading and drought

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Summary – The effects of three intensities of shading in combination with drought on the growth and morphology of pedunculate oak and beech seedlings were studied in a pot experiment. The two species responded similarly to shading, but had different reactions to drought. Shading reduced growth, increased partitioning to stem and branches, increased leaf area and reduced partitioning to fine roots. Drought reduced growth, decreased partitioning to leaves and increased partitioning to fine root biomass. In beech, drought increased the diameter of fine roots; the increased partitioning to these roots did not increase fine root length. In oak, drought combined with high light resulted in less partitioning to stem and branches and increased partitioning to coarse roots.

growth / morphology / shading / drought / biomass partitioning / specific leaf area / specific root length

Résumé – Croissance et morphologie de plants de chêne pédonculé (*Quercus robur* L) et de hêtre (*Fagus sylvatica* L) en relation avec l'ombrage et le dessèchement. Les effets d'ombrage à différents degrés – en combinaison avec un traitement de dessèchement – sur la croissance et la morphologie de plants de chêne pédonculé et de hêtre ont été étudiés en conditions expérimentales. La réaction du chêne et du hêtre s'est trouvée identique à l'ombrage mais elle était différente quant au dessèchement. L'ombrage réduit la croissance mais il augmente l'allocation de matière sèche à la tige et aux branches, de même qu'au feuillage mais il la réduit pour les racines d'une diamètre de < 2 mm. Le dessèchement réduit la croisssance et l'allocation de matière sèche à la biomasse foliacée mais il l'augmente pour la biomasse des racines fines. Dans les plants de hêtre, le dessèchement accroît le diamètre des racines fines ; cependant l'allocation de matière sèche augmentée n'accroît pas la longueur des racines fines. Pour le chêne, le dessèchement en combinaison avec lumière pleine aboutit à moins d'allocation au tige et aux branches mais plus au racines d'un diamètre de > 2 mm.

croissance / morphologie / ombrage / dessèchement / allocation de biomasse / feuillage / épaisseur de racines

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INTRODUCTION

Spontaneous regeneration of broad-leaved tree species in Scots pine (*Pinus sylvestris* L) plantations on poor sandy soils is a common phenomenon in northwestern Europe (Fanta, 1982; Lust, 1987). Current silvicultural practice is to take advantage of this spontaneous regeneration in order to develop mixed stands (Kuper, 1994; Preuhsler et al, 1994). Of the spontaneously regenerated broad-leaved tree species, pedunculate oak (*Quercus robur* L) and beech (*Fagus sylvatica* L) are especially valuable for further stand development. Their seeds are dispersed into pine plantations predominantly by blue jays (*Garrulus glandarius* L) and small rodents (*Apodemus sylvaticus* L and *Clethrionomys glareolus* Schreber). The probability that acorns and beechnuts will develop into saplings depends on the degree of herbivory and on the seedlings' ability to grow under low resource availability (Fanta, 1982).

Pedunculate oak and beech differ in their tolerance of limited availabilty of light and moisture. Pedunculate oak has a low tolerance of shade and a high tolerance of drought; beech has a high tolerance of shade and a low tolerance of drought (Ellenberg, 1988). This general ecological characterization is primarily based on the performance of older saplings under shaded and dry conditions. However, seedlings may differ from saplings in shade and drought tolerance (Grubb, 1977). Tolerance of shade and drought can be attributed to ecophysiological and morphological adjustments (Kozlowski, 1982; Givnish, 1988). Ecophysiological studies of pedunculate oak and beech in relation to shading and drought have generally focused on photosynthetic capacity (Stickan and Zhang, 1992) and plant–water relations (Epron and Dreyer, 1993; Vivin et al, 1993). Morphological plasticity has been studied primarily in leaves and roots (Osonubi and Davies, 1981; Eschrich et al, 1989). However, shading and drought affect biomass distribution within plants (Ledig, 1981), and thus plant morphology in general. This morphological plasticity might be an important feature of shade and drought tolerance.

To investigate the options for spontaneous regeneration in Scots pine stands as describe earlier, seedling response to shading and drought was studied experimentally for both species, and seedling size and morphology were analysed. The experiment was set up to ascertain: i) the difference between seedlings of pedunculate oak and beech in their response to shading and drought, and ii) the implications of this difference for the ability of seedlings to tolerate shading and drought in Scots pine plantations.

MATERIALS AND METHODS

In 1993 an experiment was conducted using seedlings grown in large pots (5 000 cm^3) placed under three plastic rain shelters. Two of these shelters were covered with green nets that intercepted 35 and 65% of the incoming radiation. The plastic roofings gave an additional reduction in incoming radiation. Repeated measurements around noon on three sunny days in July showed that the average incoming photosynthetic active radiation (PAR) in these treatments were, respectively, 510 to 580, 340 to 360 and 180 to 210 μmol m^{-2} s^{-1}. These shading treatments corresponded to 60, 39 and 22% of the PAR measured outside the shelters. They will be referred to as the high light, intermediate light and low light treatments, respectively.

The pots were filled with a mixture of 20% clay, 20% fine sand and 60% wheathered peat (pH-H_2O 4.0–4.5, no additional fertilizer, average bulk density of 0.42 g cm^{-3}). At the beginning of the experiment the pots were watered to field capacity. During the experiment the pots were watered at weekly intervals. Care was taken to water the deeper soil by pouring water into narrow vertical holes in the soil. The exact amount of water supplied depended on the assigned moisture treatment and the measured moisture content. Changes in soil moisture were monitored by sampling weekly. This involved taking small soil samples at a depth of 10 to 25 cm and determining the moisture content gravimetrically. The results are given in figure 1. There were two moisture treatments: one in which the mean soil moisture content in the driest period was between 70 and 80% by weight (referred to as moist) and one in which

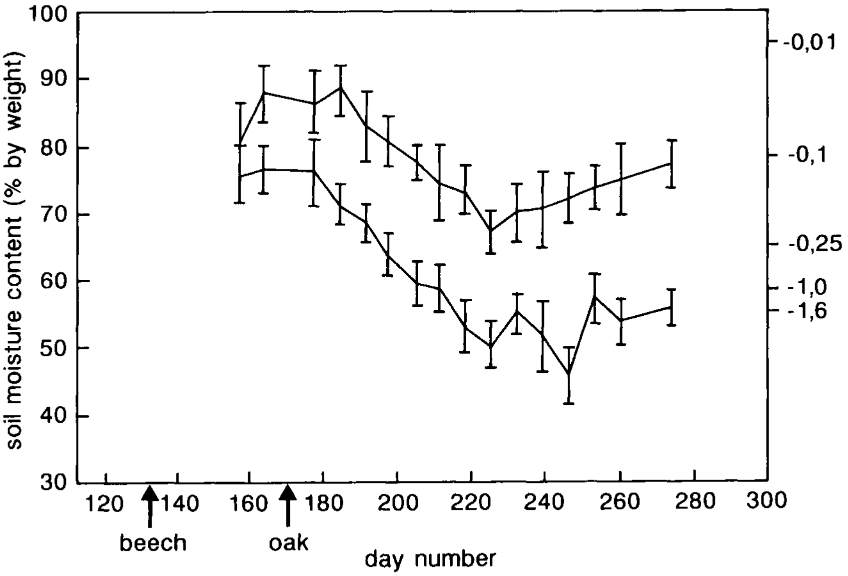

Fig 1. Soil moisture conditions during the experiment. X-axis: day (number) since 1 January; left Y-axis: soil moisture content in percentage (%) of total weight; right Y-axis: soil matric potential; 95% confidence limits are indicated by vertical bars. Arrows mark the day of emergences of the third seedling (mean, light and moisture treatments pooled).

the mean soil moisture content was below 60% (referred to as dry). An analysis of variance for the dry treatment showed that from day 208 on, soil moisture content was significantly lower (*Fprob* < 0.001) under high light conditions (49.9%) than under intermediate (56.2%) and low light conditions (53.7%). Soil moisture content did not differ between species. Ten weeks after the start of the experiment the moisture retention characteristics of the soil were determined in six control pots. At a moisture content of 55%, matric potential was equal to –1.6 MPa, which is equivalent to wilting point. Field capacity (taken as a matric potential of –0.1 MPa) corresponded to a moisture content of 78%.

Per species three pots for each moisture treatment were placed under each shelter. During the experiment, pots in the same light treatment were randomly redistributed four times, to minimize any effects of spatial heterogeneity in light availability under the shelters.

In the last week of March a total of 54 seeds per pot were sown at a depth of 5 cm; seedling emergence was recorded weekly. The seedlings were thinned to five per pot: beech on day 170 (third week of June) and oak on day 185 (first week of July). Any seedlings that subsequently emerged were removed. The remaining oak seedlings had a height of 13.4 cm (se 2.4); the beech seedlings had a height of 12.6 cm (se 1.4). From May 29 onwards, the plants were sprayed every 10 days against oak mildew (*Microsphaera alphitoides* Griffon and Maubl) and beech aphids (*Phyllaphis fagi* L).

The plants were harvested during the first week of October. Each plant was measured and separated into leaves, stem and branches, coarse roots (diameter > 2 mm) and fine roots (diameter < 2 mm). Leaf area (one-sided) was determined using an LI-3100 area meter (LI-COR Inc, Lincoln, NE, USA). In order to determine dry weight, the leaves and fine roots were oven-dried for 24 h at 70 °C and the stem, branches and coarse roots were dried for 24 h at 90 °C. The data on leaf area and leaf dry weight were used to calculate specific leaf area (SLA, one-sided; in cm^2 g^{-1}).

Specific root length (SRL; in m g^{-1}) was determined for one seedling per pot, using a seedling with approximately the mean diameter at root collar. A sample of about one-third of the fine root fresh biomass was taken and root length was estimated using the grid intersection method (Tennant, 1975). Next, the dry weight of this sample was determined. The resulting value for SRL was used to calculate the fine root length of each of the plants in the same pot.

Differences in seedling morphology were analysed with an allometric model relating organ size (Y) to seedling dry weight (X). A linearized form of this model [1] was fitted for the five seedlings per pot, taking *a* as a species parameter and *k* as a pot parameter.

$$\ln(Y) = a + k * \ln(X) \qquad [1]$$

The ratio between organ size and total plant size immediately after seedling appearance is approximated by exp (*a*). This value is assumed to be independent of light and moisture availability. The effects of light and moisture availability on seedling morphology were expressed by the allometric coefficient *k*, representing differences between growth of an organ relative to growth of the total plant (Causton and Venus, 1981).

The experiment was analysed as a split-plot experiment (ANOVA; GENSTAT 5) with shelter–pot combination as a block in the analysis of biomass, height and SLA, and with shelter as a block in the analysis of biomass partitioning, leaf area, fine root length and SRL.

RESULTS

Growth

Seedling biomass and height are presented in figure 2. In all treatments the seedlings of pedunculate oak had a larger biomass than beech, but differences in height were not statistically significant. The larger biomass of oak must be attributed to its larger root biomass, as average shoot biomass did not differ between the two species. Beech seedlings emerged 5 weeks before oak seedlings (fig 1). The pedunculate oak seedlings were able to attain a larger size in a shorter period because of their larger seed biomass (mean seed dry weight without seed coat was 2.14 g for pedunculate oak but only 0.14 g for beech).

Both species responded similarly to shading and drought, with reduced seedling biomass and height. The reduction by drought was proportionally greater in the high light treatment than in the intermediate and low light treatments (fig 2). The response of the shoot biomass was similar to the response of height. Root biomass was only reduced by shading; drought had no statistically significant effect on it.

Biomass partitioning

The effects of the treatments on the parameter estimates for the fitted allometric models are given in tables I and II. Shading increased biomass partitioning to stems and branches at the expense of partitioning to fine roots, although the effect on partitioning to fine roots was only statistically significant in beech. Drought resulted in less partitioning to leaf biomass and increased partitioning to the fine root biomass. In pedunculate oak, but not in beech, drought in combination with high light led to reduced partitioning to stem and branches and enhanced partitioning to coarse roots.

Leaves and fine roots

Pedunculate oak and beech had a similar SLA (fig 3) and their leaf area was proportionally similar to seedling biomass (tables I and II). The effects of shading and drought on SLA and leaf area did not differ between both species. Shading increased SLA and leaf area; drought primarily resulted in a decrease in leaf area. Drought reduced SLA statistically significantly, but the effects were small.

Generally, compared with beech, pedunculate oak had thicker fine roots (fig 3) and a smaller proportion in fine root length in relation to seedling biomass (tables I and II). The SRL and fine root length of both species increased as available light decreased, although the effects of shade were only statistically significant in pedunculate oak. Under dry conditions the SRL of beech decreased, but fine root length was not affected. This implies that fine root length is maintained by the enhanced partitioning to fine

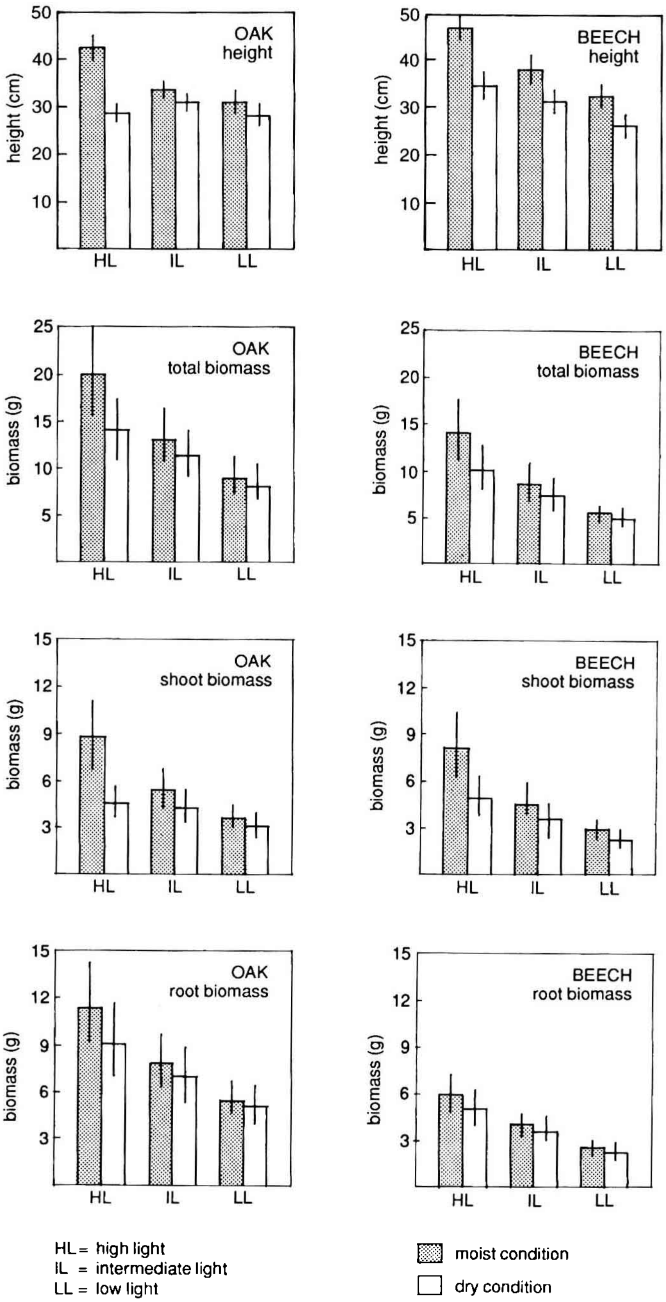

Fig 2. Height and biomass of oak and beech. Lines in the bars give the 95% confidence limits for the means.

Table I. Pedunculate oak: estimated values for the allometric constant a and the allometric coefficient k and least significant differences for treatment effects.

Treatment		*Leaf biomass* (– *1.221)*	*Stem/branch biomass* (– *2.354)*	*Coarse root biomass* (– *0.526)*	*Fine root biomass* (– *2.813)*	*Leaf area* *(3.941)*	*Fine root lenght* *(1.221)*
HL	M	0.912	1.248	0.918	1.164	0.864	0.934
	D	0.829	1.157	0.978	1.224	0.751	1.002
IL	M	0.906	1.224	0.943	1.124	0.928	1.167
	D	0.975	1.210	0.950	1.150	0.858	0.997
LL	M	0.874	1.286	0.952	1.034	0.948	1.017
	D	0.840	1.261	0.949	0.169	0.917	1.233
Least significant difference							
Light		ns	0.031	ns	ns	0.044	0.113
Moisture		0.020	0.024	0.018	0.067	0.034	ns
Interaction		ns	0.046	0.032	ns	ns	0.168

Estimates of a are shown in the column heading in parentheses. HL: high light; IL: intermediate light; LL: low light; M: moist; D: dry; ns: not significant.

Table II. Beech estimated values for the allometric constant a and the allometric coefficient k and least significant differences for treatment effects.

Treatment		*Leaf biomass* (– *1.427)*	*Stem/branch biomass* (– *1.599)*	*Coarse root biomass* (– *0.989)*	*Fine root biomass* (– *1.687)*	*Leaf area* *(3.941)*	*Fine root lenght* *(2.674)*
HL	M	1.008	1.180	0.957	0.809	0.862	0.701
	D	0.974	1.125	0.952	0.917	0.817	0.613
IL	M	1.017	1.164	0.957	0.792	0.921	0.871
	D	0.953	1.141	0.981	0.851	0.840	0.720
LL	M	1.018	1.213	0.945	0.710	1.020	0.855
	D	0.917	1.211	0.990	0.772	0.897	0.770
Least significant difference							
Light		ns	0.040	ns	0.085	0.057	ns
Moisture		0.020	ns	ns	0.066	0.045	ns
Interaction		ns	ns	ns	ns	ns	ns

Estimates of a are shown in the column heading in parentheses. HL: high light; IL: intermediate light; LL: low light; M: moist; D: dry; ns: not significant.

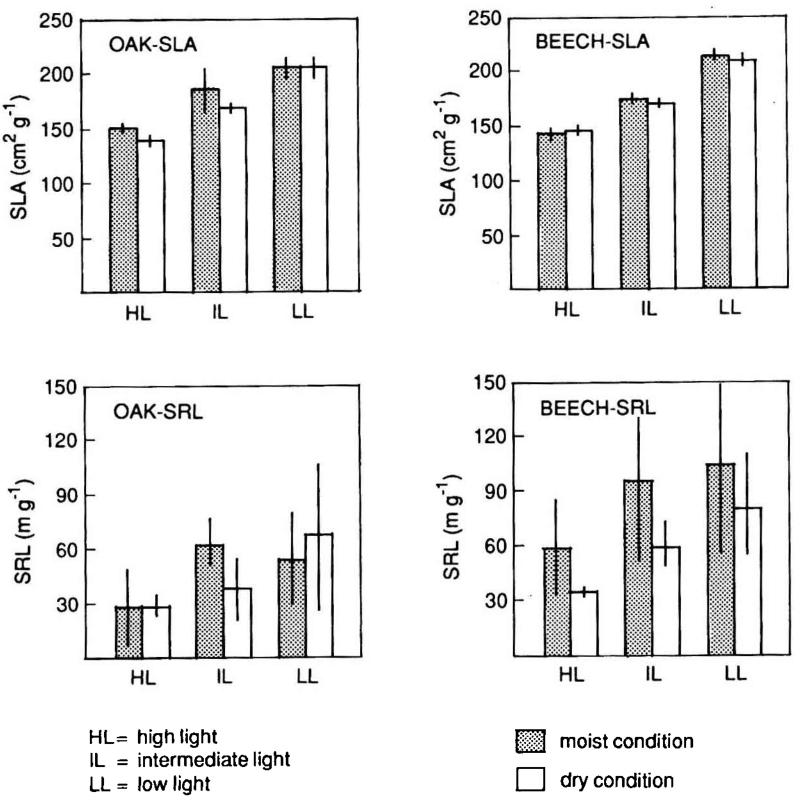

Fig 3. Specific leaf area (SLA) and specific fine root length (SRL) of oak and beech. Lines in the bars give the 95% confidence limits for the means.

root biomass. Drought had no clear effect on the SRL and fine root length of pedunculate oak: at intermediate light, SRL increased and fine root length decreased; at low light, SRL decreased and fine root length increased.

DISCUSSION AND CONCLUSION

In this experiment oak and beech seedlings growing under high light and moist conditions were larger than in comparable experiments (Madsen, 1994; Ziegenhagen and Kausch, 1995). Despite the absence of fertilization and the high peat content of the substrate, growth was not limited by nutrient availability. Moreover, at the end of the experiment no evidence of root hypoxia under moist conditions was found.

Shading

The light conditions in the experiment ranged from those found under an open canopy of Scots pine (high light, LAI ≈ 1 m^2m^{-2}) to those found under a closed canopy of Scots pine (low light, LAI ≈ 3 m^2m^{-2}). The seedlings of pedunculate oak and beech responded similarly to the experimental shading, by reducing growth and thus seedling biomass. Shaded seedlings had a proportionally larger leaf area and stem plus branch biomass, and a smaller fine root biomass. The larger leaf area must be attributed to an increase in specific leaf area, because shading had no effect on partitioning to leaf biomass. These morphological adjustments reflect the priority for shoot growth over root growth, which is a common response of tree seedlings to shading (Grime, 1979; Kozlowski et al, 1991). The observed effect of shading on specific root length was unexpected; differences in specific root length are usually attributed to soil conditions (Fitter, 1985).

The effects of shading on growth and/or morphology were expected to differ between the shade-tolerant beech and the shade-intolerant pedunculate oak (Grime, 1979; Kozlowski et al, 1991). This was not the case, however. The similarity in species response leads to the conclusion that under experimental conditions as applied here, both species display a similar tolerance to shade. Possibly, differences in shade tolerance between both species become apparent at levels of light availability below those used in this study. Furthermore, differences in the effects of shading on seedling size and biomass distribution might first become evident in the sapling stage. When resources are limited, oak species can draw upon the large reserves of energy in their cotyledons for their first year of growth and development (Kolb et al, 1990).

These large reserves of energy might also buffer this shade-intolerant species against the effects of shading in its seedling stage. Older plants of pedunculate oak exhibit stronger reactions to low light (Ziegenhagen and Kausch, 1995). Morphological adjustments through a shift in biomass partitioning is a gradual process, which might result in a shade-specific habitus in older saplings. This adjustment can be interpreted as a strategy to maximize the net rate of energy capture (Givnish, 1988). In beech the ability to accommodate shading through morphological adjustment is associated with a relatively high investment in leafy exploitation shoots and low investment in exploration shoots (Dupré et al, 1986). This growth pattern seems to maximize light capture with a restricted investment in woody biomass. Comparable date for older pedunculate oak saplings are lacking.

Drought

The experimental drought mimicked a prolonged summer drought in which soil water availability is limited from mid-July onwards. Drought reduced the leaf area of both species by reducing the biomass partitioning to the leaves. Consequently, light interception and thus growth and seedling size were reduced. Drought reduces photosynthesis (Weber and Gates, 1990; Epron and Dreyer, 1993) and thus the efficiency of light conversion into biomass. However, on a yearly basis this effect is less important than the reduction in leaf area (Pereira et al, 1989). In both species root growth had priority over shoot growth, as can be seen from the high partitioning to fine roots and the absence of clear drought effects on root biomass.

In both species the response to drought differed between the high light treatment, and the intermediate and low light treatment, probably because of the observed lower soil moisture content and an enhanced transpiration at high irradiance (Kozlowski, 1982). The resulting intensified drought stress at high light produced a greater reduction in growth. The effect on seedling morphology was greater in pedunculate oak than in beech. This difference is related to a larger biomass partitioning to the root, primarily at the expense of the stem and branches. The additional investment in the root system while maintaining the capacity for light interception might explain why oak seedlings tolerate drought better than beech seedling. The proportionally large investment in roots under dry conditions is common for pedunculate oak (Osonubi and Davies, 1981) and reflects the tree's strategy to increase rooting depth under dry conditions. Plasticity in rooting depth is considered to be an important aspect of the drought tolerance of a species (Reader et al, 1993), as it enables plants to exploit deeper reserves of soil moisture to maintain high predawn potentials during drought (Hinckley et al, 1983; Abrams, 1990).

In this experiment the drought started in the second half of July and continued until the end of the experiment. Under natural conditions, the forest floor under the Scots pine stands in which blue jays and small rodents bury acorns and beechnuts may dry out earlier in the season (Clerkx and van Hees, 1993). Because of the ontogenetic priority in root growth of pedunculate oak (Jones, 1959), this species is better able to cope with an early summer drought than beech. The seedling roots of pedunculate oak will probably have penetrated the mineral soil by then, whereas the beech seedling roots are most likely still restricted to the litter and humus layer.

Seedling establishment

The results of this study indicate that the establishment and initial survival of pedunculate oak and beech seedlings in Scots pine stands is not restricted by light conditions. Pedunculate oak seedlings will be more successful than beech seedlings in their establishment and initial survival under dry conditions.

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REFERENCES

Abrams MD (1990) Adaptions and responses to drought in *Quercus* species of North America. *Tree Physiol* 7, 227-238

Causton DR, Venus JC (1981) *The Biometry of Plant Growth.* Arnold, London, UK, 307 p

Clerkx APPM, van Hees AFM (1993) Het vochtgehalte in de strooisellaag onder verschillende vegetaties in twee grove dennenopstanden. IBN rapport 40, Wageningen, the Netherlands

Dupré S, Thiébaut B, Teissier de Cros E (1986) Morphologie et architecture des jeunes hêtres (*Fagus sylvatica* L). Influence du milieu, variabilité génétique. *Ann Sci For* 43, 85-102

Ellenberg H (1988) *Vegetation Ecology of Central Europe.* Cambridge University Press, Cambridge, UK

Épron D, Dreyer E (1993) Photosynthesis of oak leaves under water stress: maintenance of high photochemical efficiency of photosynthesis II and occurrence of non-uniform CO_2 assimilation. *Tree Physiol* 13, 107-117

Eschrich E, Burchardt R, Essiamah S (1989) The induction of sun and shade leaves of the European beech (*Fagus sylvatica* L): anatomical studies. *Trees* 3, 1-10

Fanta J (1982) *Natuurlijke verjonging van het bos op droge zandgronden.* Rijksinstituut voor onderzoek in de bos- en landschapsbouw "De Dorschkamp", Rapport no 301, Wageningen, the Netherlands

Fitter AH (1985) Functional significance of root morpholgy and root system architecture. In: *Ecological Interactions in Soil* (D Atkinson, DJ Read, MB Usher, eds), Blackwell Scientific Publications, Oxford, UK, 87-105

Givnish TJ (1988) Adaption to sun and shade: a whole-plant perspective. *Austr J Plant Physiol* 15, 63-92

Grime JP (1979) *Plant Strategies and Vegetation Processes.* John Wiley & Sons, Chichester, UK, 222 p

Grubb PJ (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol Rev* 52, 107-145

Hinckley TM, Duhme F, Hinckley AR, Richter H (1983) Drought relations of shrub species: assessment of the mechanisms of drought resistance. *Oecologia* 59, 344-350

Jones EW (1959) Biological flora of the British Isles *Quercus* L. *J Ecol* 47, 169-222

Kolb TE, Steiner KC, McCormick LH, Bowersox TW (1990) Growth response of northern red-oak and yellow poplar seedlings to light, soil moisture and nutrients in relation to ecological strategy. *For Ecol Manage* 38, 65-78

Kozlowski TT (1982) Water supply and tree growth. I. Water deficits. *Forest Abst* 43, 57-95

Kozlowski TT, Kramer PJ, Pallardy SG (1991) *The Physiological Ecology of Woody Plants.* Academic Press, San Diego, CA, USA, 657 p

Kuper JH (1994) Sustainable development of Scots pine forests. PhD thesis, Agricultural University, Wageningen, the Netherlands

Ledig FT (1981) The influence of genotype and environment on dry matter distribution in plants. In: *Plant Research and Agroforestry* (PA Huxley, ed), Proc Consulative Meeting, International Council for Research in Agroforestry, Nairobi, 427-454

Lust N (1987) An analysis of a spontaneous ingrowth of deciduous trees in 70 year old stand of Scots pine. *Silva Gand* 52, 1-27

Madsen P (1994) Growth and survival of *Fagus sylvatica* seedlings in relation to light intensity and soil water content. *Scand J For Res* 9, 316-322

Osonubi O, Davies WJ (1981) Root growth and water relations of oak and birch seedlings. *Oecologia* 51, 343-350

Pereira JS, Linder S, Araújo MC, Pereira H, Ericsson T, Borralho N, Leal LC (1989) Optimization of biomass production in *Eucalyptus globulus* plantations: a case study. In: *Biomass Production by Fast-Growing Trees* (JS Pereira, J Lansberg, eds), Kluwer Academic Publishers, Dordrecht, the Netherlands, 101-121

Preuhsler T, Kühnel S, Bock L (1994) Zum Wachstum von Eichensaat unter Kieferschirm im Forstamt Nürnberg. *Forst Holz* 49, 123-128

Reader RJ, Jalili A, Grime JP, Spencer RE, Matthews N (1993) A comparative study of plasticity in seedling rooting depth in drying soil. *J Ecol* 81, 543-550

Stickan W, Zhang X (1992) Seasonal changes in CO_2 and H_2O gas exchange of young European beech (*Fagus sylvatica* L). *Trees* 6, 96-102

Tennant D (1975) A test of a modified line intersect method of estimating root length. *J Ecol* 63, 995-1001

Vivin P, Aussenac G, Levy G (1993) Differences in drought resistance among three deciduous oak species grown in large boxes. *Ann Sci For* 50, 221-233

Weber JA, Gates DM (1990) Gas exchange in *Quercus rubra* (northern red oak) during a drought: analysis of relations among photosynthesis, transpiration and leaf conductance. *Tree Physiol* 7, 215-225

Ziegenhagen B, Kausch W (1995) Productivity of young shaded oaks (*Quercus robur* L) as corresponding to shoot morphology and leaf anatomy. *For Ecol Manage* 72, 97-108