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zOriginal article

Influence of herbaceous competitors on early growth in direct seeded *Fagus sylvatica* L. and *Quercus robur* L.

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Abstract – Compared to planting of bare-rooted seedlings, direct seeding of broadleaves for afforestation of farmland has the potential of becoming an effective low-cost alternative. In an experiment carried out in an abandoned field in the southernmost part of Sweden, four treatments including herbicide; herbicide in combination with fertilization; mowing and undisturbed control were applied. Growth and the development of direct seeded beech (*Fagus sylvatica* L.) and oak (*Quercus robur* L.) were monitored over three years and interpreted according to resources availability. Herbaceous competitors clearly decreased growth in seedlings. Mowing treatment had no effect on seedling growth and development when compared to the undisturbed control treatment. Soil and leaf water potentials indicated that herbaceous vegetation competed with the seedlings mainly for soil water. Moreover, fertilization in combination with herbicide treatment had no additional effect on growth or leaf nitrogen levels. The results indicate that seeded beech and oak are equally sensitive to herbaceous competition although oak was more deeply rooted than beech.

afforestation / sowing / weed competition / rooting depth / soil water

Résumé – Influence de concurrents herbacés sur la croissance précoce du *Fagus sylvatica* L. et du *Quercus robur* L. semés directement. Comparé à la plantation à racines nues, l'ensemencement direct de feuillus pour le boisement de terres a le potentiel de devenir une alternative efficace peu coûteuse. Dans une expérience menée sur un champ abandonné dans l'extrême sud de la Suède, quatre traitements comprenant l'herbicide, l'herbicide combiné à la fertilisation, le fauchage et le contrôle non dérangé ont été appliqués. La croissance et le développement de hêtres (*Fagus sylvatica* L.) et de chênes (*Quercus robur* L.) semés directement ont été suivis pendant trois ans et interprétés selon la disponibilité des ressources. Les concurrents herbacés ont clairement affaibli la croissance des jeunes plants. Le traitement du fauchage n'a pas eu d'effet sur la croissance et le développement des plants si on le compare au traitement par contrôle non dérangé. Les potentiels de l'eau du sol et des feuilles ont indiqué que la végétation herbacée était en compétition avec les plants, surtout au niveau de l'eau du sol. En outre, la fertilisation combinée avec un traitement herbicide n'a pas eu d'effet supplémentaire sur la croissance ou les niveaux d'azote des feuilles. Les résultats indiquent que les hêtres et les chênes semés sont également sensibles à la compétition herbacée même si les chênes ont été plus profondément enracinés que les hêtres.

boisement / ensemencement / compétition des mauvaises herbes / profondeur d'enracinement / eau du sol

1. INTRODUCTION

European temperate broadleaved forests used to cover much larger areas than they do today and for several reasons, restoration of these forests is believed to be a step toward sustainable forestry [16, 34]. One type of restoration activity is afforestation of abandoned farmland. Here, planting of bare-rooted seedlings is the common practice. It is an expensive method and the development of less costly alternatives is needed [25]. Direct seeding is an old method that has attracted new attention in the last few years [1, 20, 23, 30, 39]. The cost is one-half or less compared with the cost of conventional planting [5]. The periodical large crops may result in even lower prices. Consequently, direct seeding has the potential of reaching high stem density at low costs, resulting in a large population to be used to select future timber trees. Moreover, when the main afforestation objective is to provide wildlife habitat, direct seeding might be a low cost alternative where natural invasion of woody species are greater and more diverse compared to sites that are planted [36].

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Broadleaved tree species are preferably cultivated on better soils, since a high growth rate is necessary for these species for future profitability. However, on those sites natural vegetation (herbaceous, bush and tree species) also invades and grows rapidly. When not managed, the natural vegetation often severely reduces tree seedling establishment and growth [9, 19, 33]. Low seedling growth also prolongs the period when seedlings are most sensitive to destructive agents such as voles [26]. Thus, it has been concluded that vegetation control is essential for successful afforestation using direct seeding [25, 39].

Plant species respond differently to stress, which influences their ability to compete with the natural vegetation [21]. Although vegetation control is essential when using direct seeding, total control over several years is normally not an option in practical forestry. Therefore, it may be of interest to know if certain tree species are better competitors than others. Beech is believed to have high tolerance of shade and low tolerance of drought, whereas oak is believed to have low tolerance of shade and high tolerance of drought [11]. This characterization is based on performance of older saplings under shaded and dry conditions. However, seedlings may differ from saplings in performance [13]. Moreover, during natural regeneration oak is regarded as a good competitor and regenerates well in grasslands compared to beech, which is considered to need conditions with less competing ground vegetation [29]. However, only rarely have beech and oak been cultivated side by side for a comparison of the effects of competition on growth and morphology [37].

Numerous studies have been done with seedlings to investigate the competition with herbaceous vegetation and to highlight which growth factors limit growth in the process [28]. The relative importance of different growth factors varies among vegetation zones and sites and among tree species. The boreal forest is characterized by low productivity, primarily resulting from a short growing season and low temperature and soil nutrient availability [35]. The present study was carried out in the southernmost part of Sweden, in the temperate zone. With a longer growing season and higher temperature (and thus also mineralisation rates) in more productive habitats in the temperate zones of Europe and North America, water may limit plant growth [22]. However, scientists disagree on the subject [14].

Our previous research has demonstrated the importance of vegetation control for improved growth in small oak seedlings in a clear-cut and shelterwood [24]. This paper reports on the interference from herbaceous species on the establishment and early growth in beech (*Fagus sylvatica* L.) and oak (*Quercus robur* L.) seedlings established from seeds. The specific objectives of this study were (i) to examine whether any growth reduction caused by the presence of herbaceous vegetation was mainly a result of limiting water, nutrients or light and (ii) to evaluate if oak seedlings compete better with herbaceous species than beech seedlings.

2. MATERIALS AND METHODS

2.1. Experimental site and design

The experiment was set up in an abandoned field at the Swedish University of Agricultural Sciences at Alnarp (55° 40’ N/13° 10’ E, 15 m a.s.l.). The soil texture was sandy loam and the site was flat. The average annual temperature (climatic station located 10 km southwest of Alnarp) was 8.1 °C and the average annual precipitation was 518 mm during the experimental period [2].

A randomized block design with four blocks and four treatments with sub-plots (split-plot) was used in the experiment. The site was free from herbaceous competitors at the start of the experiment in May 1995 due to repeated harrowing. The size of the treatment plots were 8 × 19 m with 2–4 m buffer zones around each plot. The treatments were: herbicide treatment (H), herbicide treatment in combination with fertilization (HF), mowing of herbaceous competitors (M) and an undisturbed control (C). Thus, the size of each block was approx. 20 × 42 m. Three of the blocks were laid out close to each other and the fourth block were located approx. 35 m from the others. The herbicide treatment consisted of three regular applications of glyphosate (0.29 g active ingredient per m^2) during each growing season in combination with manual weeding near the seedlings. In addition, propyzamide (0.12 g active ingredient per m^2) was applied on one occasion to the H and HF treatments in the middle of December 1995 and 1996 to facilitate control of herbaceous competitors the following growing season. Fertilization in HF treatment, 10 g m^{-2} NPK 11:5:18 along with magnesium and micronutrients (5 mm pellets, Hydro Agri AB, Sweden), was regularly applied four times during each growing season. To assure that the nutrients penetrated the soil, fertilization was done in combination with irrigation in the HF treatment (about 10 mm each time) during drought periods in 1995 and 1996. Mowing was carried out three times each growing season with a clearing saw. Mowing was carried out manually close to the seedlings, to assure that the leaves of the seedlings were never shaded. The experimental area was fenced against hare and large herbivores.

Within each treatment plot, acorns and beech-nuts were seeded in species-separated rows (sub-plots) in April 1995 and 1996. In 1995, each row consisted of 19 seeding spots and in 1996 of 30 seeding spots. In each seeding spot, three acorns and four beech-nuts were seeded, respectively. Acorns were seeded at a depth of 5 cm in the soil, and beech-nuts at a depth of 2 cm. Newly emerged beech seedlings were protected from various predators by polyethylene tubes (25 cm in length with a diameter of 11 cm) during the epicotyl development. The tubes were pressed down to 5 cm in the soil. After one month the tubes were removed. In October of both 1995 and 1996, all planting spots were thinned to assure that only one seedling was growing in each spot. The distance between seeding spots seeded in 1995 was 50 cm. When seeding was carried out in 1996, the distance was 25 cm. The distance between rows varied from 1.25 m to 3.75 m.

Different seed sources were used. In 1995, *Fagus sylvatica* L. (Maramures, Romania, collected in 1994) and *Quercus robur* L. (Vestfold, Norway, collected in 1994) were used. In 1996, *Fagus sylvatica* L. (Gråsten, Denmark, collected in 1995) and *Quercus robur* L. (Scherpenzeel, The Netherlands, collected in 1995) were used. Seeds were obtained from the Tree Improvement Station, Humlebæk in Denmark. Acorns were stored in a cooler at –2 °C with a water content of 43% until transport and planting. Beech-nuts were stored at –3 °C with a water content of 8.7% and vernalized at 4 °C for 10 weeks with a water content of 33%.

2.2. Measurements

Soil water potential (ψ_S) at 10, 20 and 50 cm soil depth was measured in June, July, August and September each growing season with gypsum blocks (5201 Soil moisture Blocks, Soil moisture Equipment Corp., CA, USA) in one point in each treatment in all four blocks during the 1995, 1996 and 1997 growing seasons.

Light intensity (Photosynthetic photon flux density, PPFD) was measured at seedling level and above herbaceous competitors (0.3 m and 1.5 m) in the middle of July in 1995 and in August 1996 and 1997 on ten locations per treatment and block (LI-190SA, LI-COR Inc. Lincoln, Neb). On each occasion the sky was clear and the measurements were made between 11.00 h and 13.00 h.

At the end of each growing season, the root collar diameter of each living seedling in the experiment was measured. In addition, one apical bud at the top of the foliage of four seedlings per treatment and block were marked with colour at the beginning of the growing season in 1997. Then, the number of leaves on the resulting shoot was counted regularly in 1997.

In early October 1995, four seedlings and in 1996, three seedlings from each treatment, block, species and planting year were carefully dug up. The excavation was done from the same side of each treatment in 1995 and 1996 and the last seedlings in each row were excavated. In early October 1997, a sample of four seedlings from each treatment, block, species and planting year were sampled for above-ground biomass determination. However, in some treatments no living seedlings were found, something which resulted in missing values. After sampling, the seedlings were washed in running water and the dry mass of seedling roots, stem and leaves were determined after drying at 70 °C for 48 h. Before root excavation in 1995, an excavator (Hydrema 805) had prepared 0.75 m deep ditches in order to simplify manual root excavation. The rooting depth was determined using a ruler. Following measurements, the soil was restored to its former state using the same excavator. In 1996, the ditches were 1.5 m deep. Excavation was done from the same side of each treatment in 1995 and 1996. In 1996, sampling of seedlings was done at least 1 m from the excavation spots in 1995.

To determine the seedling leaf area a sub-sample of up to 10 leaves per sampled seedling was photocopied, dried at 70 °C for 48 h in order to establish the dry mass. Leaf area was measured on photocopies with a computer image system (Image access, Micro Macro Bildanalys AB, Sweden).

The diurnal pattern of leaf water potential (ψ_L) was measured in the middle of August 1995 and 1996 using a pressure chamber [32]. On each occasion, approx. every 2 h, two randomly selected seedlings in the H and C treatments from each of two blocks were used and leaves from the top of the foliage were sampled. Only two treatments were used, since the measurements are time-consuming. Between sampling and measurement, approx. 20 min, the leaves were stored in darkness, in tubes with 100% RH and at a temperature of ± 0 °C.

From seedlings sampled in early October 1995, 1996 and 1997, up to 10 leaves per seedling were sampled for an analysis of the nitrogen concentration. Leaves were oven-dried at 70 °C for 48 h and ground to a fine powder in a mill. Before analysis, samples from the same block, treatment, species and planting year were pooled. The nitrogen concentration was determined using an elemental analyzer (Carlo Erba NA 1500, Carlo Erba Strumentazione, Italy).

2.3. Calculations

The leaf area per seedling was calculated using the total leaf dry mass per seedling and the ratio leaf dry mass to leaf area of the sub-sample. In order to account for size-related variations, the mean relative growth rate in diameter (R_D, year^{-1}) was calculated for the 1996 and 1997 growing seasons. R_D was calculated using the formula:

$$R_D = (\ln (D_2) - \ln (D_1))/ (t_2 - t_1) \quad (1)$$

where D_1 and D_2 denote root collar diameter at the end of the previous growing season and at the beginning of October in the current growing season and $t_2 - t_1$ is one year. The general linear model (GLM) procedure for analysis of variance was used to perform statistical tests on seedling growth variables (SAS Institute Inc., Cary, NC, USA). For R_D and rooting depth, comparisons between species were made using a split-plot design. Otherwise, one-way ANOVA was used and means were compared using Tukey's multiple range test after calculating plot averages. Data were analysed separately for each planting year. In the comparisons, $p < 0.05$ was considered as significant.

Table I. Monthly precipitation (mm) and average air temperature (°C) during the 1995, 1996 and 1997 growing seasons at Malmö climatic station located 10 km southwest of the experiment ([2], 1995–1997).

Month	1995	1996	1997	30-year-mean
		Precipitation		
May	45	151	71	44
June	77	22	67	54
July	31	54	60	63
August	17	37	10	62
September	79	64	23	62
		Air temperature		
May	11.1	9.4	10.1	11.2
June	14.9	14.5	15.7	15.2
July	19.0	15.6	18.0	16.6
August	19.8	18.3	20.8	16.3
September	14.1	11.2	14.3	12.8

3. RESULTS

3.1. Environmental conditions

Compared to the 30-year mean, precipitation was high in May 1996 and low in July and August 1995, June and August 1996 and in August and September 1997 (Tab. I). The mean air temperature was high in July 1995 and in August all years.

No low value of ψ_S was recorded in June or September during the three growing seasons (Tab. II). In the H and HF treatments, only short periods of low ψ_S were recorded in the top 10 cm of the soil during July and August. In the C and M treatments, low ψ_S were recorded in August in 1995, 1996 and 1997. During the periods with low ψ_S values, ψ_S decreased towards the soil surface.

The PPFD at seedling level (0.3 m) was similar in the H, HF and M treatments during all years and corresponded to about 82–100% of full light (PPFD at 1.5 m) (Fig. 1). In the C treatment, the light intensity corresponded to approx. 69%, 52% and 60% in 1995, 1996 and 1997, respectively.

3.2. Growth in beech and oak seedlings

By the end of the first growing season following direct seeding in 1995 and 1996, there were no differences between treatments concerning seedling shoot dry mass (Figs. 2A–B and 2G–H). By the end of the 1997 growing season, the herbaceous competitors in the C and M treatments had reduced the shoot dry mass in both beech and oak seedlings (Figs. 2E–F and 2I–J). However, this was not statistically significant in all cases. Three years following seeding of acorns, the shoot dry mass was 17 times higher in the HF compared to the M treatment (Fig. 2F). There was no difference in shoot growth in the HF compared to the H treatment, and no difference in shoot growth in the M compared to the C treatment. The development of leaf area followed about the same trends (Fig. 2).

Table II. Mean soil water potentials (ψ_S, MPa) in four treatments and three soil depths (10, 20 and 50 cm soil depth) in 1995, 1996 and 1997 from June to September. Herbicide (H); herbicide and fertilization (HF); undisturbed control (C) and mowing of vegetation (M). For description of treatments, see text. Mean ± SE.

		1995				1996				1997			
	(cm)	June	July	Aug.	Sept.	June	July	Aug.	Sept.	June	July	Aug.	Sept.
H	10	–0.03 ± 0.0	–0.17 ± 0.1	–0.26 ± 0.1	–0.03 ± 0.0	–0.02 ± 0.0	–0.03 ± 0.0	–1.04 ± 0.3	–0.02 ± 0.0	–0.06 ± 0.0	–0.05 ± 0.0	–0.93 ± 0.4	–0.07 ± 0.0
	20	–0.03 ± 0.0	–0.04 ± 0.0	–0.07 ± 0.0	–0.02 ± 0.0	–0.03 ± 0.0	–0.03 ± 0.0	–0.16 ± 0.1	–0.04 ± 0.0	–0.04 ± 0.0	–0.03 ± 0.0	–0.34 ± 0.2	–0.12 ± 0.1
	50	–0.03 ± 0.0	–0.03 ± 0.0	–0.03 ± 0.0	–0.03 ± 0.0	–0.03 ± 0.0	–0.04 ± 0.0	–0.05 ± 0.0	–0.03 ± 0.0	–0.03 ± 0.0	–0.03 ± 0.0	–0.03 ± 0.0	–0.11 ± 0.1
HF	10	–0.02 ± 0.0	–0.76 ± 0.6	–0.30 ± 0.1	–0.03 ± 0.0	–0.03 ± 0.0	–0.04 ± 0.0	–1.66 ± 0.6	–0.66 ± 0.6	–0.06 ± 0.0	–0.05 ± 0.0	–0.29 ± 0.1	–0.03 ± 0.0
	20	–0.03 ± 0.0	–0.03 ± 0.0	–0.05 ± 0.0	–0.01 ± 0.0	–0.03 ± 0.0	–0.02 ± 0.0	–0.33 ± 0.2	–0.03 ± 0.0	–0.03 ± 0.0	–0.02 ± 0.0	–0.09 ± 0.0	–0.05 ± 0.0
	50	–0.03 ± 0.0	–0.02 ± 0.0	–0.02 ± 0.0	–0.03 ± 0.0	–0.03 ± 0.0	–0.03 ± 0.0	–0.04 ± 0.0	–0.03 ± 0.0	–0.03 ± 0.0	–0.03 ± 0.0	–0.02 ± 0.0	–0.03 ± 0.0
C	10	–0.03 ± 0.0	–1.42 ± 0.5	–2.55 ± 0.0	–0.03 ± 0.0	–0.05 ± 0.0	–0.45 ± 0.4	–2.23 ± 0.3	–0.03 ± 0.0	–1.22 ± 0.5	–0.10 ± 0.1	–0.65 ± 0.4	–0.04 ± 0.0
	20	–0.03 ± 0.0	–0.77 ± 0.6	–1.67 ± 0.5	–0.02 ± 0.0	–0.03 ± 0.0	–0.28 ± 0.2	–1.68 ± 0.5	–0.03 ± 0.0	–0.14 ± 0.0	–0.09 ± 0.1	–0.23 ± 0.1	–0.14 ± 0.1
	50	–0.03 ± 0.0	–0.04 ± 0.0	–0.72 ± 0.6	–0.15 ± 0.1	–0.03 ± 0.0	–0.17 ± 0.1	–0.74 ± 0.6	–0.05 ± 0.0	–0.03 ± 0.0	–0.08 ± 0.0	–0.37 ± 0.1	–0.24 ± 0.1
M	10	–0.02 ± 0.0	–0.89 ± 0.6	–2.34 ± 0.2	–0.03 ± 0.0	–0.05 ± 0.0	–0.05 ± 0.0	–2.55 ± 0.0	–0.04 ± 0.0	–1.85 ± 0.4	–0.27 ± 0.1	–1.23 ± 0.6	–0.08 ± 0.0
	20	–0.03 ± 0.0	–0.34 ± 0.3	–1.04 ± 0.5	–0.02 ± 0.0	–0.03 ± 0.0	–0.05 ± 0.0	–1.80 ± 0.4	–0.03 ± 0.0	–1.02 ± 0.5	–0.19 ± 0.1	–0.47 ± 0.2	–0.16 ± 0.0
	50	–0.03 ± 0.0	–0.03 ± 0.0	–0.35 ± 0.3	–0.08 ± 0.0	–0.03 ± 0.0	–0.03 ± 0.0	–0.66 ± 0.6	–0.06 ± 0.0	–0.04 ± 0.0	–0.07 ± 0.0	–0.22 ± 0.1	–0.14 ± 0.0

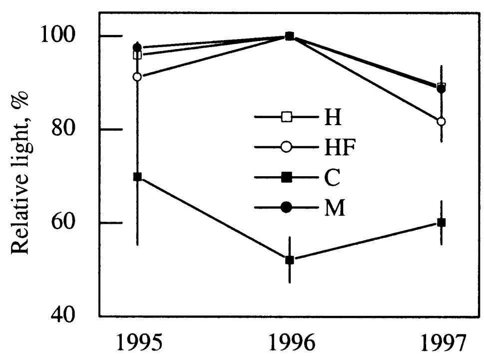

Figure 1. Relative light level (PPFD at seedling level at 0.3 m above ground / PPFD above vegetation at 1.5 m) in four treatments in three years. For a description of treatments see Table II and text. Mean ± SE.

During the 1997 growing season, the first flush in beech and oak seedlings had about the same number of leaves in all treatments (Tab. III). The number of leaves on subsequent flushes, and the proportion of seedlings that produced more than one flush, was reduced in the C and M treatments compared to the H and HF treatments. More oak seedlings than beech produced more than one flush, and oak also produced more leaves on subsequent flushes than beech.

In the 1997 growing season, there was no statistical significant difference in relative growth rate in diameter (R_D) between beech and oak ($p = 0.0537$) following seeding in 1995 (Fig. 3A). However, oak had higher R_D than beech following seeding in 1996 ($p < 0.05$) (Fig. 3B). R_D was lower in the C and M treatments compared to the H and HF treatments, except for beech following seeding in 1995. There was no difference in R_D in the HF compared to the H treatment, and no difference in R_D in the M compared to the C treatment.

Oak was more deeply rooted than beech both in 1995 and 1996 following seeding in 1995 ($p < 0.001$) (Fig. 4A–D). The same was found in 1996 following seeding in 1996 ($p < 0.0001$) (Fig. 4E–F). When the mean rooting depth was plotted against the mean seedling dry mass, no effect from herbaceous competitors was found on rooting depth. Although there was a trend towards deeper rooting depth in the H and HF treatments in all cases except for beech in 1995 (Fig. 4A), this was only significant for oak in 1996 following seeding in 1996 (Fig. 4F). Deep roots were observed to follow soil cracks or older root channels. Beech and oak had about the same number of deep roots, about one in the first growing season and about two in the second season (data not shown).

3.3. Leaf water potential and nitrogen

Predawn ψ_L (04.00 h) remained above –0.3 MPa in both species in the H and C treatments (Fig. 5), except for oak in the C treatment seeded in 1996 (Fig. 5F). ψ_L decreased during the midday hours (10.00–16.00 h). Then, ψ_L increased in both species and treatments with the highest rate in the H treatment. ψ_L showed similar development in both species. For both species, there were higher leaf-nitrogen concentrations in the H and HF treatments compared to the other treatments, except in 1997 for seedlings established following seeding in 1995 (Fig. 6). In general, oak had higher leaf-nitrogen concentrations than beech.

Table III. Mean number of leaves in the first and following flushes in beech and oak seedlings in four treatments in 1997. Herbicide (H); herbicide and fertilization (HF); undisturbed control (C) and mowing of vegetation (M). Means within columns and planting years followed by different letters are significantly different ($p < 0.05$). The proportion of seedlings that produced more than one flush are also given.

Treatment	Beech			Oak		
	No. leaves 1 flush	No. leaves 2–3 flush		No. leaves 1 flush	No. leaves 2–3 flush	
Seedlings planted in 1995						
H	7 a	18 a	60%	9 a	27 a	100%
HF	7 a	11 a	70%	10 a	22 ab	90%
C	7 a	6 a	38%	8 a	7 ab	33%
M	5 a	3 a	50%	6 a	1 b	17%
Seedlings planted in 1996						
H	6 a	8 a	47%	7 a	26 a	100%
HF	6 a	6 ab	40%	7 a	23 ab	100%
C	5 a	0 b	0%	7 a	2 ab	22%
M	4 a	0 b	6%	5 a	0 b	8%

4. DISCUSSION

The performance of seeded beech and oak seedlings was clearly affected by the competition from herbaceous vegetation. Two and three years following direct seeding, the shoot dry weight and leaf area had decreased to a similar extent in the treatments with vegetation. This is in line with several other studies [9, 15]. However, the treatment's effect on seedling growth was not obvious until the second year after seeding. This has also been found in studies on the effect of competition, fertilization and shading on the growth of seeded beech, oak and other broadleaved species [6, 7, 18]. A possible explanation is that the seeds had sufficient resources to support the early phases of seedling emergence, something which has been indicated for oak by Brookes et al. [4]. In addition, due to the small size of the seedlings in the first year, the demand for light, nutrients and water was small and the competition from the herbaceous vegetation less than in following years.

Field experiments and experiments under controlled conditions have shown that biomass in beech and oak seedlings increases with increasing light if no other growth factor is limited [6, 7, 38]. In the present study, there was no effect on growth in seedlings when mowing of herbaceous competitors was carried out compared to untreated control, although the treatment increased the incoming radiation. Most likely, light is not the primary resource for competition between herbaceous vegetation and seedlings for both species. Similar results have been found by Davies [9].

When the beech and oak seedlings were surrounded by competing ground vegetation, the N content of the seedling leaves decreased. This may indicate a competition for nutrients, but it could also be explained by the decline in available water, which may impair nutrient uptake [31]. In this experiment, measurements of ψ_S showed that soil drought occurred at all soil depths in August where herbaceous vegetation was present. Moreover, during these periods, low values of ψ_L indicated a competition for water. Re-equilibration of ψ_L with the predawn ψ_L required more time in the undisturbed control treatment, where the water supply was limited [33]. However, predawn ψ_L was generally the same in the control and herbicide treatments and parts of the root systems had consequently access to water. Furthermore, fertilization in combination with herbicide treatment did not have any positive effect on seedling growth compared to herbicide treatment only, indicating a shortage of water also in treatments without herbaceous vegetation, or that nutrients were not limiting. Similar results have been found by others [9, 10, 27].

The number of leaves formed in the spring flush was rather similar in both species in all treatments, probably due to the fact that water was not yet in short supply. However, the number of leaves in the first flush is also dependent on the growth conditions of the previous year and the data is not easily interpreted. Later in the growing season the water availability decreased due to low precipitation and growth of the vegetation and consequently increased the demand for water. This was seen in the reduced leaf number formed in the second and third flush, in both beech and oak seedlings. The competition for water later in the growing season may explain why beech and oak sometimes show only one growth flush per year. Borchert [3] states that the decline in the number of flushes in one season probably depends on low water uptake, restricted either by water availability or by reduced root growth. However, in addition to water, nutrients may also influence the number of flushes and the number of leaves formed in the second and third flushes. In oak, low N availability resulted in fewer flushes and buds in the later flushes [17]. This indicates that the leaf production may also be affected by the competition for nutrients. In the present study, however, a shortage of soil water probably affected nutrient uptake as mentioned earlier.

In general, the N content in oak leaves was higher than in beech, something which may indicate that beech has smaller demands regarding nutrient availability in the soil. The high N content in oak leaves may also explain why oak seedlings showed a trend towards higher relative growth rate compared to beech. Similar results have been found where the seedling

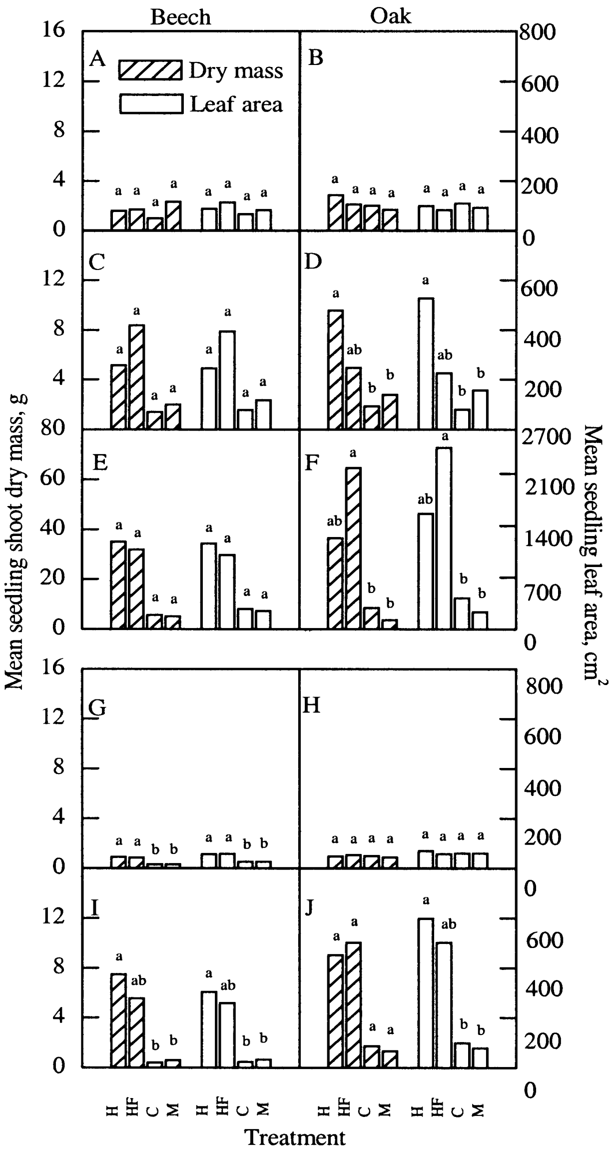

Figure 2. Mean shoot dry mass (g, leaves + stem, left axes) and seedling leaf area (cm^2, right axes) in beech and oak seedlings in four treatments and three years. Seedlings planted in 1995 (A–B year 1995, C–D year 1996, E–F year 1997) and in 1996 (G–H year 1996, I–J year 1997). Columns within box and seedling components with different letters are significantly different ($p < 0.05$). Note different axes scale in boxes E and F. For a description of treatments see Table II and text.

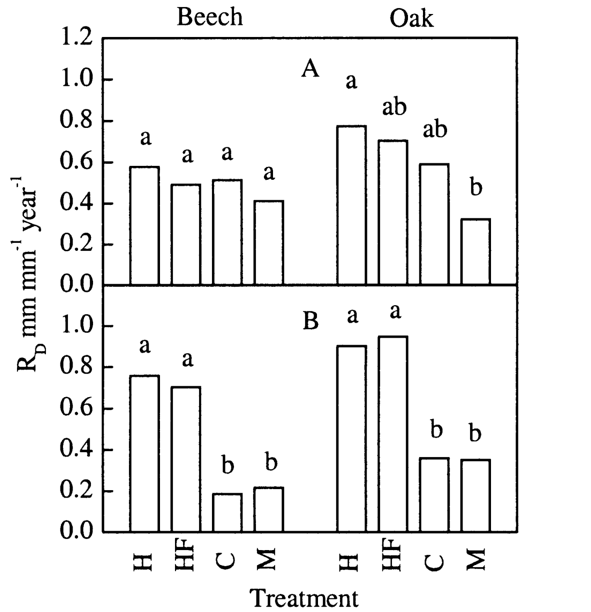

Figure 3. Mean relative growth rate in diameter (R_D mm mm^{-1} $year^{-1}$) in beech and oak seedlings in 1997 following direct seeding in 1995 (A) and in 1996 (B). Treatment means within box and species followed by different letters are significantly different ($p < 0.05$).

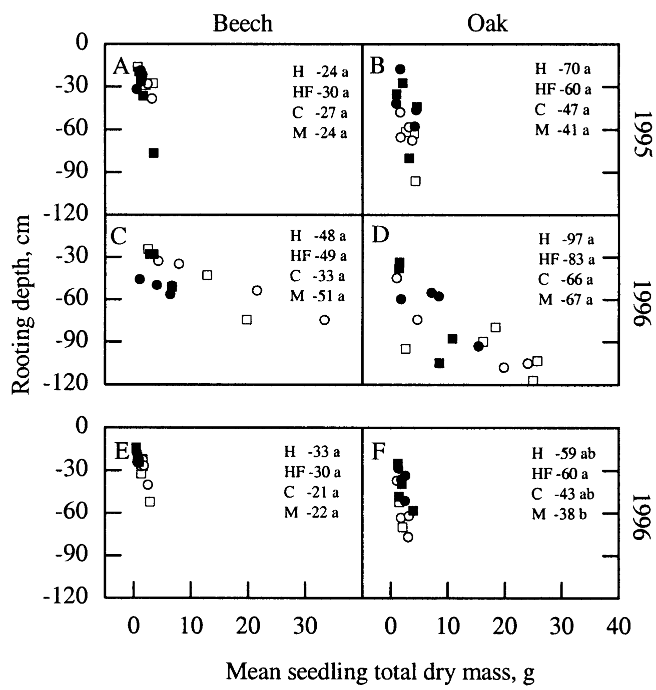

Figure 4. Mean rooting depth (negative values) of beech and oak seedlings in 1995 and 1996 plotted against mean seedling dry mass in the H (□), HF (O), C (■) and M treatments (●). Seedlings from direct seeding in 1995 (A–D) and in 1996 (E–F). Treatment means within box followed by different letters are significantly different ($p < 0.05$).

dry mass increase compared with unit leaf area was greater in oak than in beech [38].

Beech and oak seedlings following direct seeding showed a similar decrease in growth due to competing ground vegetation. This indicates that in our conditions beech and oak were equally sensitive to competition and is in contrast to findings by Newbold and Goldsmith [29]. The fact that naturally regenerated oak seedlings more frequently will be established in the open can not be ascribed to a better competition ability from oak seed-

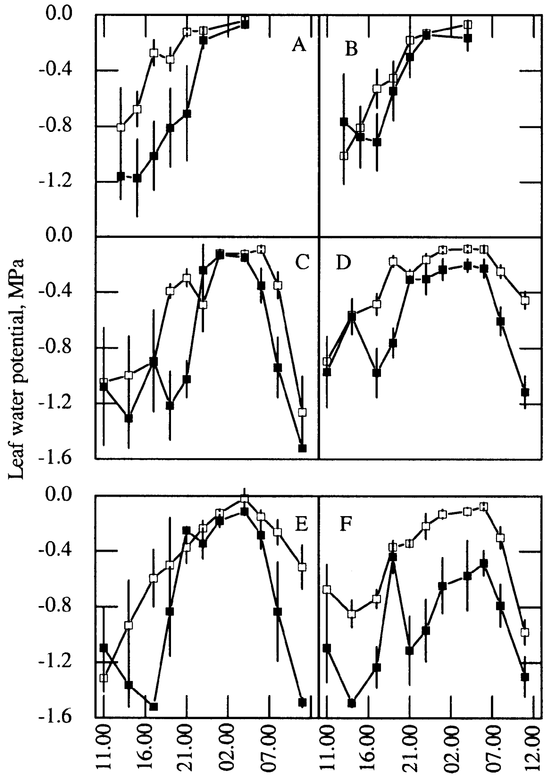

Figure 5. Mean leaf water potential (ψ_S, MPa) in beech and oak seedlings in the H (□) and C treatments (■) measured in the middle of August 1995 (A–B) and 1996 (C–F). Seedlings planted in 1995 (A–D) and 1996 (E–F). Mean ± SE.

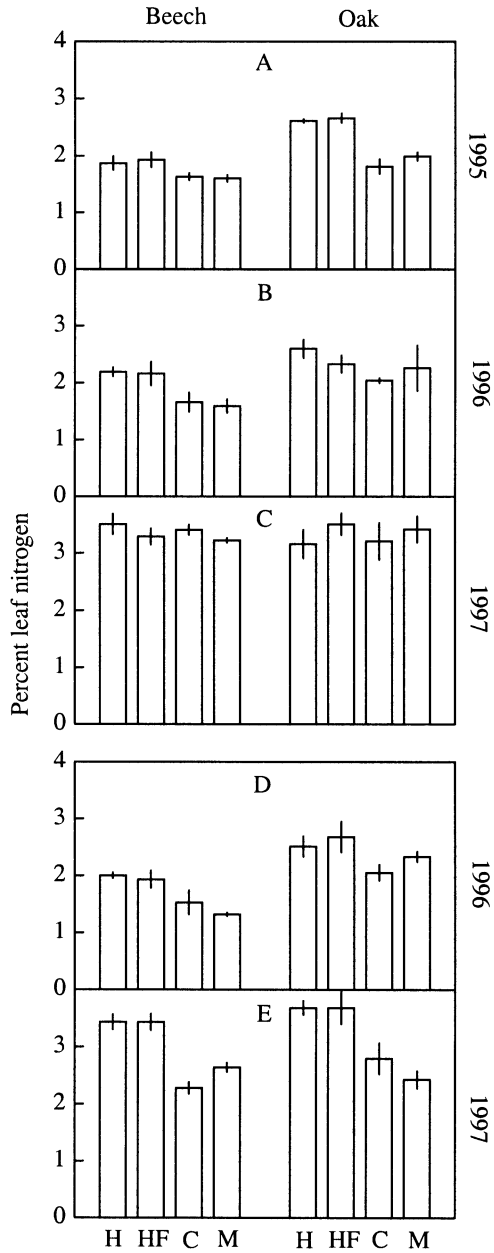

Figure 6. Mean percent leaf nitrogen (N_{leaf}, g g^{-1} × 100) in beech and oak seeded in 1995 (A–C) and in 1996 (D–E) in four treatments and during three years. For a description of treatments see Table II and text. Mean ± SE.

lings, compared to beech. It is a well-known fact that dispersal of acorns may occur over long distances [12]. Perhaps these characteristics are more important than the ability to compete with herbaceous vegetation in our effort to explain the difference in occurrence in the field between beech and oak. From these results and the fact that this study has established that oak is more deeply rooted than beech, it can be concluded that a deep root system is not necessarily a way to avoid competition from herbaceous vegetation. However, it is known that the survival of some species in arid systems depends completely on the ability in deep roots to tap water from permanent water tables [8]. Thus, during long periods and more severe soil droughts, the deep root systems of oak seedlings may be a way to promote seedling survival.

This study presents several management implications to the afforestation of farmland using direct seeding of beech and oak. Firstly, there was no effect of competition from herbaceous vegetation on seedling growth during the first year. In addition, competition was not strong in the beginning of the growing seasons. Thus, the forest manager may choose the most optimal time to apply vegetation control. However, although growth effects from competition were not apparent in the first year, limitations in below-ground resources during the first year probably affect the growth of seedlings in the second year. Secondly, mowing was not effective as a tool for vegetation control since competition did not occur for light, only for belowground resources. Furthermore, in fields and ecosystems in the temperate zone dominated by herbaceous vegetation, competition for water between seedlings and herbaceous vegetation during the first years following seeding is more important than for nitrogen. However, during wet years competition for nutrients might be equally important and the effect on seedling growth and morphology is similar. Fertilization only or in combination with vegetation control does not seem to be effective in order to improve seedling growth, but it depends also on soil fertility. In addition, under the conditions prevailing in the experiment, oak and beech responded in similar ways to herbaceous competition. This may limit the forest manager, since it is not possible to select a better competitor for stand establishment. However, in very dry years oak would probably be less sensitive to competition than beech. Finally, other factors than the ability to compete with vegetation probably explain differences in natural occurrence between beech and oak in open field environments.

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