The effect of competition from different weed species on the growth of *Betula pendula* seedlings

Ian Willoughby, David V. Clay, Fiona L. Dixon, and Geoff W. Morgan

Abstract: The identification of less competitive weed species and infestation rates might allow weeding operations to be better targeted, help conserve local plant biodiversity, and facilitate reductions in the amount of herbicide used to achieve woodland regeneration. Therefore, the effect of competition from pure stands of *Cirsium vulgare* (Savi) Ten., *Epilobium ciliatum* Raf., *Holcus lanatus* L., *Poa annua* L., and *Persicaria maculosa* Gray on *Betula pendula* Roth was investigated over 2 years. All weed species reduced tree growth significantly compared with weed-free plots, but there were no significant differences among species. When *Lolium perenne* L., *Rumex obtusifolius* L., and *Cirsium vulgare* were established at four densities in plots containing newly planted *B. pendula* over a 1-year period, all weed species reduced tree growth, but *Lolium perenne* was the most competitive. Weed density had no significant effect, indicating that even sparse weed growth can have a major impact on tree performance. None of the treatments affected *B. pendula* survival. These results confirm the inhibitory effects of a range of weed species on tree growth, but not survival, and the capacity of *B. pendula* to recover in the second year after planting from an initial check in growth. Percent cover was a good explanatory variable for models developed to describe the effects of weeds on tree growth, and preliminary competition indices for the different species are presented.

Résumé : L'identification d'espèces de mauvaise herbe moins compétitives ayant des taux d'infestation moindres pourrait permettre de mieux cibler les opérations de désherbage, de contribuer à conserver la biodiversité végétale locale et de faciliter la réduction des quantités d'herbicide utilisé pour régénérer les terres forestières. L'effet de la compétition dans des peuplements purs de *Cirsium vulgare* (Savi) Ten., *Epilobium ciliatum* Raf. *Holcus lanatus* L., *Poa annua* L. et *Persicaria maculosa* Gray sur *Betula pendula* Roth a donc été étudié pendant deux ans. Toutes les espèces de mauvaise herbe ont significativement réduit la croissance des arbres comparativement aux parcelles sans mauvaises herbes, mais il n'y avait pas de différence significative entre les espèces. Lorsque *Lolium perenne* L., *Rumex obtusifolius* L. et *Cirsium vulgare* étaient établis selon quatre densités dans des parcelles contenant des individus de *B. pendula* nouvellement plantés, toutes les espèces de mauvaise herbe ont réduit la croissance des arbres au cours d'une période d'un an, mais *Lolium perenne* était l'espèce la plus compétitive. La densité des mauvaises herbes n'a eu aucun effet significatif, ce qui indique que même la croissance d'un couvert épars de mauvaises herbes peut avoir un impact majeur sur la performance des arbres. Aucun des traitements n'a affecté la survie de *B. pendula*. Ces résultats confirment les effets inhibiteurs d'une gamme d'espèces de mauvaise herbe sur la croissance des arbres, sans affecter leur survie, et la capacité de *B. pendula* de récupérer d'une perte de croissance initiale au cours de la deuxième année après la plantation. Le pourcentage de couverture était une bonne variable explicative dans les modèles mis au point pour décrire les effets des mauvaises herbes sur la croissance des arbres et des indices préliminaires de compétition sont présentés pour les différentes espèces.

[Traduit par la Rédaction]

Introduction

The effect of weed competition in severely limiting the growth of newly planted trees in the United Kingdom is well established (Davies 1985, 1987; Mason et al. 1993). Acceptable levels of tree growth can usually be achieved in most British situations by maintaining a minimum weed-free area of 1.0 m^2 around each tree for 3–5 years after planting (Davies 1987). Although this is a relatively straightforward principle, implementation can require appreciable inputs of herbicides (Willoughby and Dewar 1995; Willoughby and Clay 1996) at a time when there is pressure to reduce pesticide use and maintain biodiversity (Willoughby et al. 2004). An alternative to practising total control of all species within weed-free areas around trees might be to identify threshold densities of particular weed species, below which any reductions in tree growth and survival are considered acceptable.

Problem weed species both obtain and retain finite resources of water and nutrients, and utilize light and space equally or more effectively than crop species. Therefore, the

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relative competitiveness of a weed species is linked to its potential growth rate, size, morphology, and efficiency in acquiring and utilizing finite resources in a specific microsite compared with crop species. In addition to above- or below-ground competition being dependent on plants occupying the same locations in space, it also requires those species to coexist temporally (Balandier et al. 2006). The greatest problems are caused by weeds, such as grasses, that grow throughout the season when trees are also active (Davies 1987) and by species that are dominant during those months or years that are particularly critical to tree establishment (Wagner 2000; Adams et al. 2003). In the United Kingdom, these tend to be grass and herbaceous species that rapidly colonize and establish on planting sites and then compete in particular for water and nutrients (Willoughby et al. 2004). These effects can be compounded by the fact that reduced root growth potential of newly planted trees during the process of establishment may put them at a competitive disadvantage with weed species (Jinks and Kerr 1999). Proximity of weed vegetation to the crop tree through time has also been shown to be critical when competition for light is the dominant factor (Richardson et al. 1999). Therefore, variation in weed species growth rate, size, rooting depth, and utilization efficiency of water and nutrients may result in differences in competitive ability relative to establishing trees, which could be exploited to allow managers to avoid unnecessary control treatments and, hence, reduce herbicide inputs and conserve biodiversity.

Unfortunately, there is little information on the comparative effects of different weed species on tree growth in the United Kingdom, although work has taken place in other cropping systems. For example, in developing data for guiding decisions on herbicide treatment in crops of *Triticum aestivum* L. (wheat), Wilson and Wright (1990) found that species such as *Galium aparine* L. (cleaver) and *Avena fatua* L. (wild oat) were very competitive, whereas low-growing and early senescing species such as *Lamium purpureum* L. (red dead nettle) and *Viola arvensis* Murray (field pansy) had little effect even at high densities. Weed-control density thresholds to guide decisions on herbicide treatments have been developed in many arable crops based on weed density or weed cover of individual species (Froud-Williams 2002), but it is recognised that such values are site and year dependent (Ingle et al. 1997; Blair et al. 1999).

For tree species in the United Kingdom, Willoughby (1999) found no significant differences in the degree of growth suppression of newly planted *Fraxinus excelsior* L. (ash) or *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) from competition with *Brassica oleracea* L. (kale) or a mixture of *Galium saxatile* L. (heath bedstraw) and *Prunella vulgaris* L. (selfheal). However, with *Fraxinus excelsior*, a mixture of *Prunella vulgaris* and *Plantago lancelota* L. (ribwort plantain) was more competitive than these other species mixtures. Davies (1987) suggests that grasses and *Trifolium* spp. (clover) can be particularly competitive, the former possibly because of their long season of active growth. Harmer (1996) found differences between the competitive effect of different grass species, with *Deschampsia flexuosa* (L.) Trin. (wavy hair grass) having a greater impact on the growth of tree seedlings than *Poa trivialis* L. (rough meadow grass).

There is some evidence from other countries of the effect of different weed species on tree growth. For example, herbaceous weeds have been reported as being more competitive immediately after establishment, with taller woody species becoming greater competitors later on, as they become larger and better established, and as herbaceous species are suppressed by the tree canopy (Richardson et al. 1996; Bell et al. 2000; Wagner 2000). At low weed densities, Bell et al. (2000) found only small differences in competitiveness between grass, broadleaved herbaceous, and woody species during the first year after planting, but herbaceous species became more competitive after 3 years. Balandier et al. (2006) have proposed a conceptual competition model suggesting that competing plants could be grouped by growth forms and that, of these groups, grasses are often the most competitive in general, followed by dense sprouting trees, dense sprouting shrubs, and then dense small shrubs, herbaceous species, and ferns. However, Balandier et al. (2006) also noted that such a ranking will vary through time and that there will also be exceptions within each grouping.

Two experiments were set up to obtain preliminary information on the comparative competitive effect of different weed species on tree growth in British conditions. These investigated the effect of five different weed species each sown at only one density and a further three weed species established at four different initial densities on the growth of young trees. Weed species were typical of those found on afforestation sites in the lowlands of the United Kingdom, and *Betula pendula* Roth (silver birch) was chosen as an example of a potentially fast-growing tree species, increasingly utilized for new native woodland creation and restoration, which is reported to be sensitive to weed competition (Atkinson 1992).

Materials and methods

General

Both experiments were sited on land at Failand, near Bristol, United Kingdom (51°27′N, 02°41′W), which receives an annual average of 853 mm of rainfall, has 1883 growing degree-days (above 4 °C), and has an annual average soil moisture deficit of 156 mm (data from Pyatt et al. 2001). Soil type according to Mackney et al. (1983) is a typical brown earth, Newbiggin Association, with a pH of 5.8 and an organic matter content of 3.3%. Soil samples for textural and nutrient analysis were taken on 11 September 2003 from two positions on each of the weed-free plots on each experiment. Sample cores (15 cm deep × 2.5 cm diameter) were pooled, mixed, and subsampled for analysis using methodology detailed in MAFF (1986) (Table 1). Rainfall was recorded on site from the 9 June 2003 through to 31 August 2003 using rain gauges. Other rainfall data were obtained from nearby (within 3 km) United Kingdom Meteorological Office recording sites (Table 2).

Experiment 1

The site was fully cultivated using an agricultural plough in early March just prior to planting, leaving a weed-free site. On 27 March 2002, 1-year-old *B. pendula* planting stock, 30–40 cm tall, was planted at a spacing of 0.5 m be-

Table 1. Soil analysis data from competition experiments (sampled 11 September 2003).

Property	Experiment 1	Experiment 2
pH	5.7	6.0
Organic matter (%)	3.2	3.3
Nitrogen (total) (mg/kg)	1650	1710
Phosphorus (ppm)	18	41
Potassium (ppm)	129	138
Magnesium (ppm)	105	121
Sand (%)	36.3	35.1
Silt (%)	48.3	48.7
Clay (%)	15.4	16.2
Texture	Sandy silt loam	Sandy silt loam

Table 2. Total monthly rainfall (mm) from March to September in 2002 and 2003.

Month	2002	2003
March (15–31)	34.9	0
April*	49.7	41.9
May	98.4	88.2
June	70.7	30.1
July	86.6	99.2
August	39.3	18.2
Total (15 March – 31 August)	379.6	277.6

*All newly planted plots were irrigated in April in both years; irrigation figures were not included in the total.

tween trees, in a line down the centre of 2 m × 3.5 m plots. There were four trees in each plot, which were irrigated once, immediately after planting, until the soil was saturated. On 4 April, 1936 seeds/m^2 of *Chenopodium album* L. (fat hen), 1010 seeds/m^2 of *Cirsium vulgare* (Savi) Ten. (spear thistle), 3836 seeds/m^2 of *Epilobium ciliatum* Raf. (American willow herb), 1143 seeds/m^2 of *Holcus lanatus* L. (Yorkshire fog grass), and 4382 seeds/m^2 of *Poa annua* L. (annual meadow grass) were surface sown and rolled in. Seed numbers were calculated on the basis of suppliers germination test data to give target densities of 100, 400, 2500, 400, and 2500 plants/m^2 for the five species, respectively, estimated as densities that for each species would give an even cover of competing vegetation from an early stage in the growing season. There were six weed treatments (including a weed-free control) and four replicates of each treatment. Plots were irrigated through application of 20–30 mm of water via sprinklers one or two times a week throughout April only to encourage even weed germination and initial survival of the trees. Plots were hand weeded throughout the growing season to maintain weed-free controls and pure species plots.

Three of the weed species treatments (*Cirsium vulgare*, *Epilobium ciliatum*, and *Holcus lanatus*) were maintained throughout the following year (2003). The *Poa annua* died out during the winter of 2002, and a natural population of weeds were left to develop; the main species were *Epilobium ciliatum*, *Cardamine hirsuta* L. (hairy bittercress), *Sonchus oleraceus* L. (smooth sow thistle), and latterly, *Plantago major* L. (greater plantain). Plots sown with *Chenopodium album* that failed to germinate and had been invaded by a dense natural population of *Persicaria maculosa* Gray (redshank) in 2002 were cleared that winter, and subsequently, the plots were kept weed free throughout 2003.

Tree height and basal stem diameter were measured in April, July, and September 2002 and November 2003. Weed growth was measured by laying out two 30 cm × 30 cm (0.09 m^2) quadrats at random in each plot in July and September 2002, recording plant numbers, and after harvesting at ground level, shoot fresh mass. The harvested vegetation was subsequently oven-dried to a constant mass to give shoot dry mass. Visual estimates of green weed cover were estimated to the nearest 1% if <15% in total and to the nearest 5% if ≥15%, for each half of each plot, then averaged for analysis.

Experiment 2

This experiment used an additive competition design (Froud-Williams 2002) with a constant density of trees and varying densities of weed species. Four replicates of thirteen treatments consisting of three weed species sown at four densities plus a weed-free control (except for *Rumex obtusifolius* L. (broadleaved dock); see below) were laid out in a randomized complete block design, giving 52 plots in total. The site was fully cultivated using an agricultural plough in early March prior to planting, leaving a weed-free site. On 26 and 27 March 2003, four 1-year-old *B. pendula* trees 35–50 cm tall were planted down the centre of each 2 m × 3.5 m plot at 50 cm spacing between trees and thoroughly watered. Immediately after planting, *Cirsium vulgare* seed was surface sown at 80, 320, 1280, and 5120 seeds/m^2, with germination anticipated at 20% to give equivalent plant numbers to other species. Seed was pressed lightly into the surface with a rake head but left uncovered. *Lolium perenne* L. (perennial rye grass) seedlings were planted at densities of 16, 64, 256, or 1024 plants/m^2. *Rumex obtusifolius* was planted at 16, 64, or 256 plants/m^2, but because of the lack of plants the highest density was only approximately 500 plants/m^2 and only planted on two replicates. *Lolium perenne* and *Rumex obtusifolius* seedlings were grown in plugs, with a height and spread of approximately 5 cm at time of planting. All plots were irrigated to field capacity immediately after planting and then irrigated with applications of 20–30 mm of water via sprinklers one or two times a week throughout April only to encourage even weed germination and initial survival of the weeds and trees. Plots were hand weeded throughout the growing season to maintain weed-free controls and pure species plots.

Many *Rumex obtusifolius* plants suffered insect attack, firstly with *Aphis rumicis* Linn. (black fly) and then repeatedly through the season with *Gastrophysa viridula* Degeer (dock beetle). Plots were sprayed on four dates with chlorpyriphos (Dursban) to control these insect pests.

Tree height and basal stem diameter were measured in March and November 2003. Above ground dry mass of *B. pendula* was measured by destructively harvesting the trees in December 2003. Weed growth was measured at four dates using the same methodology as experiment 1.

Analysis

The effect of species (experiment 1) and species density (experiment 2) treatments on tree growth were tested by

Table 3. Weed cover, density, and dry mass in July and September 2002, experiment 1.

	30 July 2002				19 September 2002		
Weed species	Canopy height (cm)	Cover (%)	Dry mass (g/m^2)	Plants/m^2	Cover (%)	Dry mass (g/m^2)	Plants/m^2
Cirsium vulgare	12.5	57.5	124	79	70.0	419	76
Epilobium ciliatum	30.8	62.5	97	419	73.8	294	350
Holcus lanatus	17.6	69.4	111	164	76.3	244	128
Poa annua	6.1	58.7	56	437	41.3	103	369
Persicaria maculosa	51.1	53.1	480	919	52.0	292	1064

Table 4. Effect of weed competition on growth of *Betula pendula* during the first year after planting, experiment 1.

	3 April 2002		19 September 2002 (end of first growing season)		
	Initial stem diameter (mm)	Initial height (cm)	Diameter increment (mm)	Height increment (cm)	Survival (%)*
Cirsium vulgare	3.0	29.9	2.9	22.2	100
Epilobium ciliatum	3.1	33.0	2.9	22.7	93.8
Holcus lanatus	3.1	33.4	2.8	22.2	100
Poa annua	3.1	34.3	3.9	31.2	100
Persicaria maculosa	3.2	34.8	3.1	37.3	100
No weeds	2.9	33.1	8.4	62.7	100
SED (df = 15)	—	—	0.91	7.44	—
LSD ($p \le 0.05$)	—	—	1.93	15.86	—

*Survival was not significantly different from 100% (Fisher's exact test, $p > 0.05$). SED, standard error of differences of means; LSD, least significant difference.

analysis of variance using Genstat (Genstat 1993), and standard errors of differences of means were generated. The assumptions underlying the analysis of variance of the absence of heteroscedasticity and approximate normality were validated by graphical methods. A least significant difference test was then carried out, again using Genstat. Fisher's exact test was used to analyse tree survival (Genstat 1993), as few plots suffered mortality and because there was generally a low number of dead trees on those that did; hence, analysis using a more elaborate parametric modelling approach, such as generalized linear modelling, was inappropriate. Relationships between tree growth and the explanatory weed species variables of percent cover, density, and fresh and dry mass, were examined by fitting rectangular hyperbola models using the regression facilities in Genstat. Estimated values for the two missing replicates in experiment 2 were calculated using the iterative approach employed by Genstat (Genstat 1993). In addition, indicative relative competition indices were calculated (Davis et al. 1998).

Results

Experiment 1

Chenopodium album failed to germinate, and a dense natural population of polygonaceous weed species, predominately *Persicaria maculosa*, was allowed to grow. The remaining species were slow to germinate and establish, but they had all produced appreciable levels of ground cover by July (Table 3); this was despite actual density being considerably less than planned, at approximately 20, 17, 40, and 18% of the target densities for *Cirsium vulgare*, *Epilobium ciliatum*, *Holcus lanatus*, and *Poa annua*, respectively. The natural population of *Persicaria maculosa* reached the highest density.

Compared with the control, all treatments caused significant reductions in tree growth in the first year, but there were no significant differences among species (Table 4). There were no significant effects of species on tree survival. Regression analysis showed that, irrespective of species, weed cover in July provided a better explanation for reduction in height or stem diameter increment than weed fresh or dry mass (Table 5). Within the observed (nonzero) range of values for weed cover, there was evidence of a slope, i.e., a significant relationship between cover and tree growth. Using a common value for the weed-free endpoint, Figure 1 shows the best-fit model which accounts for 76.2% of variation in *B. pendula* stem diameter increment, where

$$\text{Annual diameter increment} = \frac{8.336}{1 + 0.027\,69 \times \text{average percent vegetation cover in July}}$$

Table 5. Coefficients of determination (R^2) for model terms fitted to explain growth of *Betula pendula*, experiment 1.

Response variable	Fitted term	R^2	P
Height increment	July % weed cover	61.1	<0.001
Height increment	July weed plants/m^2	0	0.40
Height increment	July fresh mass weeds	0.2	0.28
Height increment	July dry mass weeds	14.6	0.02
Height increment	September % weed cover	58.3	<0.001
Height increment	September weed plants/m^2	0	0.58
Height increment	September fresh mass weeds	41.4	<0.01
Height increment	September dry mass weeds	44.2	<0.01
Diameter increment	July % weed cover	76.2	<0.001
Diameter increment	July weed plants/m^2	29.6	0.02
Diameter increment	July fresh mass weeds	21.6	0.02
Diameter increment	July dry mass weeds	57.3	<0.001
Diameter increment	September % weed cover	73.3	<0.001
Diameter increment	September weed plants/m^2	29.5	0.02
Diameter increment	September fresh mass weeds	56.1	<0.01
Diameter increment	September dry mass weeds	64.8	<0.001

Fig. 1. The effect of weed cover in July 2002 on annual diameter increment of *Betula pendula* in experiment 1.

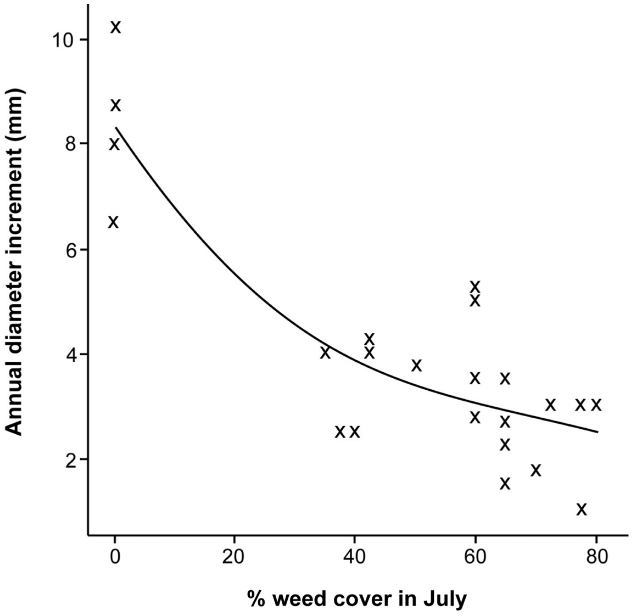


Fig. 2. The effect of weed cover in July 2002 on annual height increment of *Betula pendula* in experiment 1.

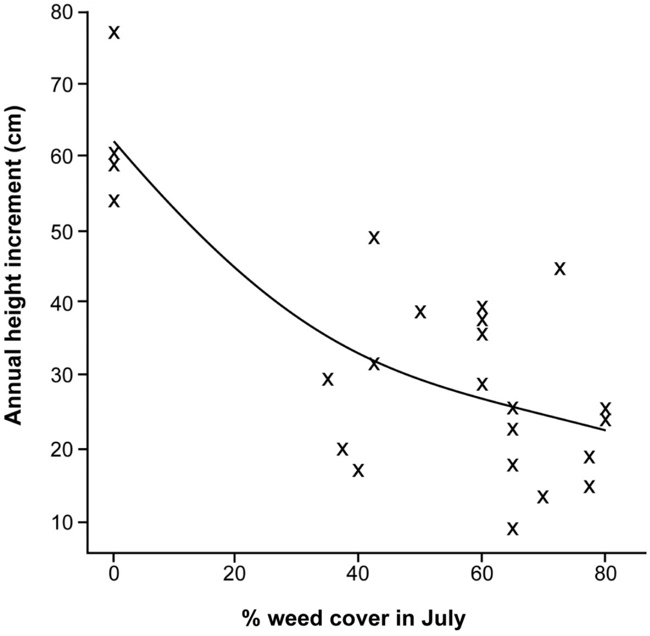


Figure 2 gives the best fit model which accounts for 61.1% of variation in *B. pendula* height increment where

$$\text{Annual height increment} = \frac{62.20}{1 + 0.020\,704 \times \text{average percent vegetation cover in July}}$$

By the end of the second year, there were clear differences in the relative competitiveness of the different species treatments (Table 6). *Cirsium vulgare* and *Holcus lanatus* were the most competitive, reducing growth significantly compared with *Epilobium ciliatum* and the natural weed population. Trees in the plots that had previously contained *Persicaria maculosa* but had been cleared in the spring and kept weed free made considerable growth. Although overall

Table 6. Effect of weed competition on growth of *Betula pendula* measured at the end of the second growing season (21 November 2003) after planting, experiment 1.

Weed treatments (second year)	Stem diameter increment (mm)	Height increment (cm)	Survival (%)*
Cirsium vulgare	4.3	74.3	100
Epilobium ciliatum	12.7	100.1	93.8
Holcus lanatus	5.0	54.4	100
Natural population	13.9	99.4	100
No weeds (year 2)	20.1	125.4	100
No weeds (years 1 + 2)	24.8	144.5	100
SED (df = 14)	2.44	12.86	—
LSD ($p \leq 0.05$)	5.24	27.58	—

Note: See Table 4 for abbreviations.

*Survival was not significantly different from 100% (Fisher's exact test, $p > 0.05$).

size was less than in the control treatment (weed free over 2 years), second-year increments for these two treatments were not significantly different.

Experiment 2

Despite a very dry April, all weed species survived with the addition of irrigation, but their growth was delayed; this was particularly true for *Cirsium vulgare*, where seedlings did not begin to emerge until late April and only began to form a dense ground cover after the end of May.

Assessments of weed cover and plant numbers (Table 7) showed the highest densities generally gave the greatest cover, particularly early in the growing season. In the case of *Cirsium vulgare*, although there were fewer plants at the higher density than other species, there was little difference in ground cover, and little difference in dry mass per square metre between *Cirsium vulgare* and *Lolium perenne*. *Rumex obtusifolius* was always the least bulky species, probably as a result of insect damage. Aboveground dry mass did not vary significantly between the lowest and highest densities, although individual weed plants were considerably larger in the lower density plots.

All three weed treatments significantly reduced tree growth by at least 60% compared with the weed-free control (Table 8). *Lolium perenne* appeared to be the most competitive species, reducing height and diameter increments significantly more than the other two species, but there was very little difference between the effect of *Cirsium vulgare* and *Rumex obtusifolius*. Although there were indications that tree growth was reduced more by the higher weed densities, this effect was not statistically significant (Table 9). There were no significant effects on survival.

Regression analysis showed that, as in experiment 1, weed cover in July provided a better explanation for reduction in height or stem diameter increment than weed fresh or dry mass (Table 10). When attempting to fit a model to these data, there was clearly a significant difference in growth of trees in zero weed cover, compared with those grown amongst weeds, but there was no firm evidence of a slope, i.e., no significant density effect, within the observed (non-zero) range of values for weed cover. However, it was assumed that logically there must be a smooth relationship between cover and growth rather than an abrupt transition between no effects and significant effect, and so a rectangular hyperbola was fitted jointly to all three species with a common value for the weed free end point; this had been shown to be a good model for experiment 1. The best explanatory variable was found to be percent vegetation cover for individual species in July. Figure 3 gives the best fit model which accounts for 77.3% of the variation in *B. pendula* diameter increment where

$$\text{Annual diameter increment} = \frac{14.67}{1 + 0.0149 \times \text{percent } \textit{Rumex obtusifolius} \text{ cover in July}} - 2.42$$

$$\text{Annual diameter increment} = \frac{14.67}{1 + 0.0282 \times \text{percent } \textit{Lolium perenne} \text{ cover in July}} - 2.42$$

$$\text{Annual diameter increment} = \frac{14.67}{1 + 0.0156 \times \text{percent } \textit{Cirsium vulgare} \text{ cover in July}} - 2.42$$

Figure 4 gives the best fit model, which accounts for 74.6% of the variation in *B. pendula* height increment, where

$$\text{Annual height increment} = \frac{942}{1 + 0.0131 \times \text{percent } \textit{Rumex obtusifolius} \text{ cover in July}} - 135$$

$$\text{Annual height increment} = \frac{942}{1 + 0.0332 \times \text{percent } \textit{Lolium perenne} \text{ cover in July}} - 135$$

Table 7. Weed numbers, cover, and foliage mass in year of planting, experiment 2.

	23 June 2003	24 July 2003					8 Aug 2003	11 September 2003				
Initial density	Weed cover (%)	Plants/m^2	Weed cover (%)	Fresh mass (g/m^2)	Dry mass (g/m^2)	Dry mass (g/plant)	Weed cover (%)	Plants/m^2	Weed cover (%)	Fresh mass (g/m^2)	Dry mass (g/m^2)	Dry mass (g/plant)
Lolium perenne												
16 plants/m^2	35.0	12.5	64.4	710	235	18.8	58.8	13.8	61.9	802	303	22.0
64 plants/m^2	52.5	51.4	73.1	849	281	5.5	68.8	49.3	77.5	756	283	5.7
256 plants/m^2	83.8	223.6	93.1	1046	349	1.6	88.8	197.2	95.6	970	363	1.8
1024 plants/m^2	88.8	530.5	95.0	833	276	0.5	91.3	608.3	95.0	948	355	0.6
Rumex obtusifolius												
16 plants/m^2	35.0	16.7	69.4	1027	211	12.6	65.0	14.2	66.9	691	153	10.8
64 plants/m^2	67.5	54.9	83.1	750	154	2.8	75.6	54.4	76.9	637	142	2.6
256 plants/m^2	90.0	222.2	93.1	923	189	0.9	70.6	190.3	75.6	833	186	1.0
500 plants/m^2*	90.0	425.0	93.7	839	172	0.4	85.0	388.9	88.8	764	170	0.4
Cirsium vulgare												
3 g/m^2	13.5	7.6	59.4	1505	196	25.8	63.8	11.7	71.9	2344	315	26.9
13 g/m^2	38.8	27.1	75.0	2429	334	12.3	75.0	27.1	81.9	2332	282	10.4
51 g/m^2	61.3	100.0	88.1	2351	306	3.1	85.0	72.2	86.9	2312	280	3.9
205 g/m^2	82.5	244.4	96.3	2358	307	1.3	96.3	200.7	93.8	2747	332	1.7
No weeds	0	0	0	0	0	0	0	0	0	0	0	0
Mean density												
Lolium perenne		204.3	81.4	85.9	285	—	76.9	216.9	82.5	868	326	
Rumex obtusifolius		179.0	85.5	914	188	—	75.0	162.2	77.9	805	176	
Cirsium vulgare		94.7	79.7	2159	285	—	80.0	77.8	83.6	2432	302	

*Estimated values used for missing plots.

Table 8. Effect of weed competition on growth of *Betula pendula* in the year of planting, all densities combined, experiment 2.

	31 March 2003		21 November 2003 (end of growing season)			10 December 2003	
Weed species	Initial height (cm)	Initial diameter (mm)	Height increment (cm)	Diameter increment (mm)	Survival (%)*	Fresh mass (g/plot)	Dry mass (g/plot)
Lolium perenne	42.0	3.8	11.6	2.1	98.4	37	19.8
Rumex obtusifolius	40.1	3.8	30.4	4.1	100	99	53.0
Cirsium vulgare	40.4	3.6	33.2	4.2	98.4	94	50.1
No weeds	44.4	3.9	79.2	12.25	100	657	349.9
SED (df = 34)	—	—	4.22	0.57	—	41.35	22.04
LSD ($p \leq 0.05$)	—	—	8.58	1.16	—	84.04	44.80

Note: See Table 4 for abbreviations.

*Survival was not significantly different from 100% (Fisher's exact test, $p > 0.05$).

Table 9. Effect of weed species and density on growth of *Betula pendula* in the year of planting, experiment 2.

	31 March 2003		21 November 2003 (end of growing season)			10 December 2003	
Initial density	Initial height (cm)	Initial diameter (mm)	Height increment (cm)	Diameter increment (mm)	Survival (%)*	Fresh mass (g/plot)	Dry mass (g/plot)
Lolium perenne							
16 plants/m^2	40.2	3.6	15.1	3.1	100	48	25.8
64 plants/m^2	40.1	3.8	10.7	1.9	100	32	16.9
256 plants/m^2	44.7	3.9	8.5	1.8	93.8	32	17.1
1024 plants/m^2	43.0	3.8	12.0	1.8	100	37	19.5
Rumex obtusifolius							
16 plants/m^2	40.5	3.8	43.4	5.9	100	140	74.5
64 plants/m^2	41.1	3.9	22.5	2.9	100	60	31.8
256 plants/m^2	38.0	3.8	26.4	3.8	100	91	48.7
500 plants/m^{2†}	40.8	3.7	29.2	3.8	100	107	56.9
Cirsium vulgare							
3 g/m^2	37.9	3.6	41.6	5.0	100	139	74.1
13 g/m^2	39.9	3.8	32.8	4.4	93.8	84	45.7
51 g/m^2	40.5	3.6	29.7	4.1	100	80	42.9
205 g/m^2	43.2	3.4	28.7	3.3	100	71	37.6
No weeds	44.4	3.9	79.2	12.25	100	657	349.9
SED (df = 34)	—	—	8.44	1.13	—	82.7	44.07
LSD ($p \leq 0.05$)	—	—	17.15	2.30	—	168.1	89.57

Note: See Table 4 for abbreviations.

*Survival was not significantly different from 100% (Fisher's exact test, $p > 0.05$).

†Estimated values used for missing plots.

$$\text{Annual height increment} = \frac{942}{1 + 0.0125 \times \text{percent } \textit{Cirsium vulgare} \text{ cover in July}} - 2.42$$

Table 11 shows indicative relative competition indices for both experiments. These give an index ranging from 1 to –1, where positive numbers indicate the presence of competitive vegetation, negative values indicate augmentation of tree growth by the vegetation, and zero indicates no effect of the vegetation (Davis et al. 1998). The indices summarize the effects found in both experiments, indicating *Holcus lanatus*, *Cirsium vulgare*, and *Lolium perenne* were the most competitive species tested.

Discussion

Model terms

Competition can result in the development of weed biomass at the expense of crop biomass (Froud-Williams 2002), suggesting weed plant mass might provide a suitable experimental measure for weed vigour. However, different species of similar size may differ in their efficiency of acquisition of water and nutrient resources and, therefore, in their effects

Table 10. Coefficients of determination (R^2) for model terms fitted to explain growth of *Betula pendula*, experiment 2.

Response variable	Fitted term	R^2	P
Height increment	July % weed cover	74.6	<0.001
Height increment	July weed plants/m^2	65.0	<0.001
Height increment	July fresh mass weeds	71.1	<0.001
Height increment	July dry mass weeds	71.2	<0.001
Height increment	August % weed cover	71.7	<0.001
Height increment	September % weed cover	73.6	<0.001
Height increment	September weed plants/m^2	69.2	<0.001
Height increment	September fresh mass weeds	67.3	<0.001
Height increment	September dry mass weeds	69.5	<0.001
Diameter increment	July % weed cover	77.3	<0.001
Diameter increment	July weed plants/m^2	71.1	<0.001
Diameter increment	July fresh mass weeds	72.8	<0.001
Diameter increment	July dry mass weeds	72.8	<0.001
Diameter increment	August % weed cover	75.9	<0.001
Diameter increment	September % weed cover	77.4	<0.001
Diameter increment	September weed plants/m^2	73.6	<0.001
Diameter increment	September fresh mass weeds	72.7	<0.001
Diameter increment	September dry mass weeds	73.8	<0.001

Fig. 3. The effect of weed cover in July 2003 on annual diameter increment of *Betula pendula* in experiment 2.

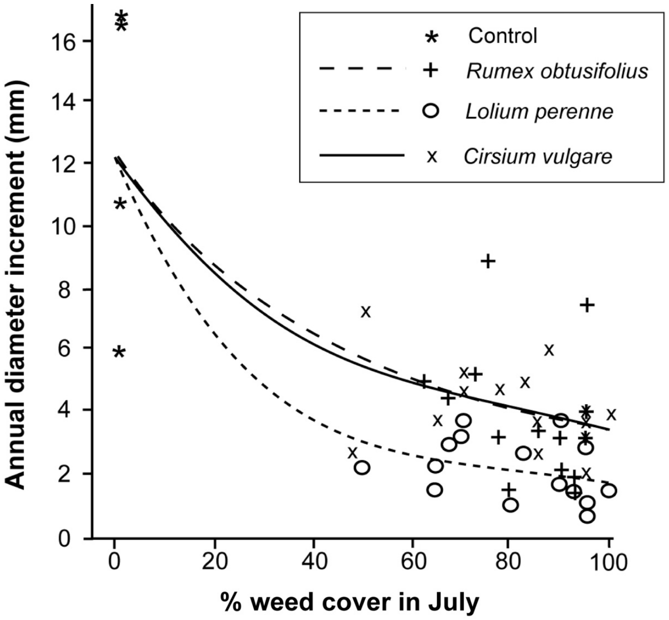
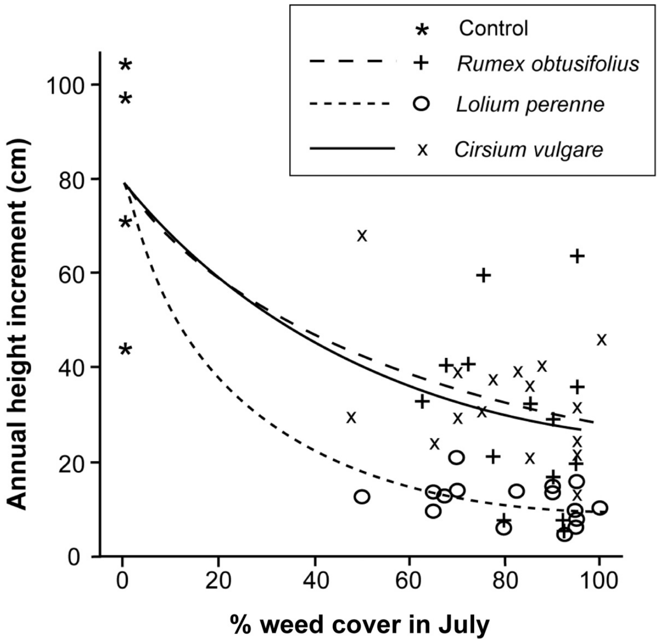


Fig. 4. The effect of weed cover in July 2003 on annual height increment of *Betula pendula* in experiment 2.



on tree growth (Goldberg 1996). Density or leaf area index (leaf area per unit area of ground) have frequently been used to quantify weed vigour or competitiveness (Froud-Williams 2002; Davies 1987), but more simply assessed visual estimates of cover have also been found to be acceptable indicators of plant competitiveness in studies of the effects of herbaceous species on conifers (Bell et al. 2000; Wagner and Radosevich 1998). Hytönen and Jylhä (2005) identified a linear relationship between increasing levels of vegetation cover and reductions in growth of *B. pendula* on abandoned farmland in Finland. With woody weed species, weed height and position relative to the crop trees can be more relevant particularly where competition for light is the dominant factor (Richardson et al. 1999).

Of the factors assessed when modelling the competitive effects of the weed species in our work, percent weed cover provided the best explanatory variable for variation in tree height and diameter increment. Assessments of weed species density, fresh mass, and dry mass were also made, because it was thought they might prove a better measure of weed vigour and, hence, the effects of substitution of weed biomass for crop biomass. The fact that density in particular did not provide as good a fit in the model as cover was unexpected.

Table 11. Indicative relative competition indices (RCI) based on basal diameter increment.

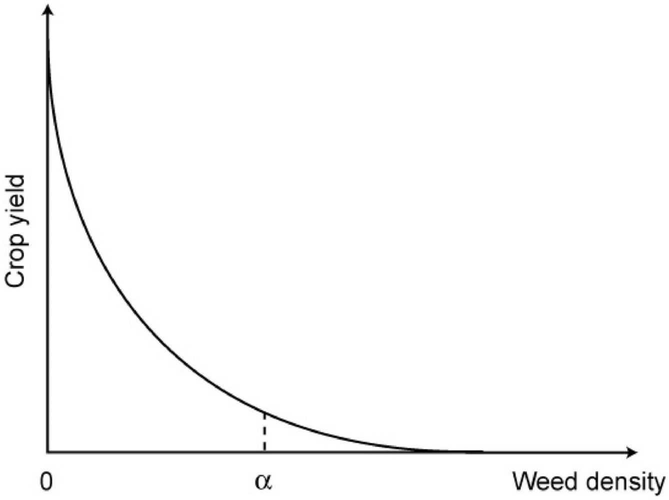
	Experiment 1		Experiment 2
Species	2002	2003	2003
Epilobium ciliatum	0.65	0.49	—
Holcus lanatus	0.67	0.80	—
Poa annua	0.54	0.44	—
Persicaria maculosa	0.63	(0.05)*	—
Cirsium vulgare	0.65	0.83	0.66†
Lolium perenne	—	—	0.83†
Rumex obtusifolius		—	0.67†

Note: RCI = (weed-free *Betula pendula* diameter increment – weedy diameter increment)/weed-free diameter increment. Higher RCI values indicate that the species is more competitve.

*Weed-free in 2003.

†Mean of four densities.

Fig. 5. Hypothetical curvilinear relationship depicting the effect of increasing weed density on crop yield (adapted from Zimdahl 1999).



However, if we assume a classical approximately curvilinear relationship between density and yield, then it may be that the densities we tested were all above point α as identified on Fig. 5, i.e., beyond the level at which the greatest density-dependent changes had already taken place. Hence, density may have provided a better explanation for the effects of competition on tree growth if lower initial weed densities had been examined. Additional experimentation with lower weed densities is also required to improve on the accuracy of initial models presented here. If competition is most critical when it occurs early on in the growing season as suggested by authors such as Davies (1987), then assessments made earlier in the year may also help to refine the models.

Nature of the competitive effects

Betula pendula establishes most effectively in bare soil, free of competing vegetation. Seedlings are relatively shallow rooted and intolerant of both drought and shade; in addition, low levels of nitrogen can result in chlorosis and reductions in growth (Atkinson 1992). Hence, for the lowland former agricultural site used in our experiments, it is likely that either light, soil moisture, or nutrients were the limiting resources. On freely draining soils in lowland Britain, summer soil moisture deficits are usually regarded as the major resource limitation leading to reduced tree growth (Davies 1987). Mean monthly rainfall at this experiment site is known to be around 71 mm. In the first experiment, this value was largely met or exceeded from May to July, whereas there was considerably less rain in June and August in the second experiment (Table 2). Plots were irrigated in April in both years. In spite of these differences in precipitation, competition from *Cirsium vulgare,* the species present in both years, was similar and severe. This suggests that, on this typical lowland site with an average soil moisture deficit of 156 mm per annum, where weed competition occurs, a limitation in the moisture resource is likely to reduce tree growth, even in normal rainfall conditions.

Competition for other resources may also have limited tree growth. Soil analysis (Table 1) suggest nutrient levels would not be limiting for more demanding agricultural or horticultural crops (MAFF 1994), and such a site would not normally require fertilization for tree growth. Foliar nutrient levels were not assessed. Although there were no obvious signs of deficiency symptoms, the trees may have been subject to competition for both moisture and nutrients, because the ability of trees to take up available nutrients would have decreased as the top layers of soil started to dry out (Davies 1987; Coll et al. 2004).

Competition for light was unlikely to be a major factor in this work in the year of planting since, with the exception of *Persicaria maculosa* plots, tree shoots were generally well above the weed canopy (Tables 3 and 4). In the second year of experiment 1, *Cirsium vulgare* shoots rapidly extended and heavily shaded tree shoots for much of the growing season. Diameter growth of *B. pendula* was severely suppressed, although effects were not significantly greater than that of *Holcus lanatus*, which did not shade the trees. Height increment was not suppressed to the same degree. Height:diameter ratios for *B. pendula* within the *Cirsium vulgare* plots doubled from year 1 to year 2 but remained broadly unchanged for the weed-free plots. This suggests that trees may have been concentrating limited resources on height growth in response to shading or physical competition for growing space, an effect also found in other studies on similar sites (Willoughby and McDonald 1999). The results from our experiments suggest that, in lowland Britain, competition for moisture will probably form the dominant influence on tree growth in most cases; however, competition for light can also play a part, particularly with taller growing weed species and slow to establish tree species.

Effects of the weeds on tree growth

In the first year of Experiment 1, there were clear differences in the rate of establishment and growth pattern of the five weed species, with *Persicaria maculosa* for example having greater biomass, cover, and plant numbers earlier in the season because of earlier germination. Despite these differences, all weed species gave similar reductions in height and diameter increment of *B. pendula*. However, irrigation in April and plentiful rainfall in early summer 2002 (Table 2) may have reduced the competitive effect of dense stands of

Persicaria maculosa. In the second year after planting, tree height and diameter increment was significantly reduced in *Cirsium vulgare* and *Holcus lanatus* plots compared with *Epilobium ciliatum* or with a natural population of annual weeds on the previous years *Poa annua* plots. The lack of irrigation, slightly lower annual rainfall, better establishment of perennial species, and the fact that all weed treatments gave a virtually unbroken cover of vegetation from early in the growing season may have contributed to the difference in effect between the first and second years. Perhaps most significantly, weed biomass on *Cirsium vulgare* and *Holcus lanatus* plots was much greater than on the other treatments; the *Cirsium vulgare* reached a height of 1.5–2.0 m before flowering in summer and overtopping the trees, and *Holcus lanatus* formed a uniformly dense cover. However, the lack of more detailed measurements of second-year weed cover or density limit the conclusions that can be drawn from this initial experiment.

In experiment 2, *Lolium perenne* reduced tree growth more than the other species, which corresponds with the general grouping based on growth form suggested by Balandier et al. (2006), although percent ground cover and biomass were no greater than *Cirsium vulgare*. Measures of leaf area index or investigations into root morphology may have shown greater differences in the species. Comparison with experiment 1 suggests that, for grasses, this species may be more competitive than the others investigated, since comparable populations and ground cover of *Holcua lanatus* and *Poa annua* had less effect in year 1, albeit in a wetter growing season. Clay and Dixon (1997) also found dwarf *Lolium perenne* to be very competitive in newly planted short-rotation coppice. For *Cirsium vulgare*, effects were very similar to those in the first year of experiment 1.

Mortimer (1990) estimates seed banks of up to 1 000 000 seeds/m^2 may exist on arable and grassland sites in the United Kingdom, and up to 10% of this seed might go on to form viable weed seedlings. This suggests that the densities of weeds used in experiment 1 were well within the potential populations at equivalent newly planted former arable sites in lowland Britain; the highest densities in experiment 1 in fact resulting from the naturally occurring population of *Persicaria maculosa.* Where different densities of weeds were planted in experiment 2, there were no significant differences in their effect on tree growth. The minimum density used (16 plants/m^2) for the species planted as plugs or the lowest rate of *Cirsium vulgare* grown from seed was appreciably lower than that present in experiment 1. Plugs were used to ensure survival and good weed cover in May and June to simulate situations of competition early in the season. At the lowest densities, weed cover was 35% or less in late June but still resulted in considerable growth reduction at the end of the year. There was, however, evidence of compensatory weed growth with individual weed plants at lower densities growing much larger than those established at higher densities. Hence, even at lower densities, total biomass by the end of the growing season did not vary greatly. Compensatory growth responses such as this are characteristic of many weed species (Milthorpe and Moorby 1979).

Consequences for weed management

If the results of our two experiments are typical, very low populations of some weed species would appear to reduce growth; subject to the site manager objectives, this suggests the need to control all individuals of the species tested around young trees. In a comparable study on the effects of grass, broadleaved herbaceous, and woody species on newly planted conifer seedlings in Canada, Bell et al. (2000) used a maximum of 8 plants/m^2 and bigger propagules, but these had little or no effect on tree growth in the first year and generally less than 50% reduction after 3 years. Considerable differences in competitive effect may occur according to site and weather (Froud-Williams 2002). In *Triticum aestivum* in England, the densities of three species of annual weeds reducing yield by 5% were found to vary by a factor of 10 to 200 depending on site or year (Ingle et al. 1997), with variation in time of emergence of weeds being a major factor. These findings confirm the need to carry out experimentation at lower weed densities, on different sites, and in different years, to refine any model of the effect of different weed densities on tree growth in British conditions.

There appear to be few studies in the international literature specifically addressing the effects of individual weed species on the growth of *B. pendula*. However, Harmer and Robertson (2003) using seed sown in controlled conditions in a nursery, and Hytönen and Jylhä (2005), working with trees planted on farmland, determined that a variety of weed species reduced growth and, to a lesser extent, survival of *B. pendula*. This latter work concluded that, although long-term seedling growth could be reduced by relatively low levels of vegetation cover in the year of planting, significant mortality only occurred with subsequent, higher levels of weed cover. Hytönen and Jylhä (2005) recommended that intensive soil preparation and weed control was necessary to achieve successful establishment on abandoned farmland in Finland. In the United Kingdom, conventional best practice is to maintain a minimum area of 1 m^2 around each tree free of competing vegetation for at least 3–5 years after planting, regardless of the specific tree or weed species present, to achieve an acceptable level of survival and early growth (Davies 1987). However, despite severe reductions in growth over the 2 years our experiments were run, competition from weeds had no significant effect on tree survival, although some initial irrigation to encourage tree and weed survival did take place. In addition, *B. pendula* growth increment in the first experiment appeared to largely recover when weed-free conditions were imposed at the start of the second year. This suggests that there may be scope to identify a critical period of weed competition (Wagner 2000) for trees in UK conditions, both across and, potentially, within seasons. This might make it possible to adopt a lower intensity of weed control to achieve an acceptable minimum level of tree survival, where growth maximization for timber production is not the primary aim.

The relative competition indices calculated (Table 11) indicated *Holcus lanatus*, *Cirsium vulgare*, and *Lolium perenne* were the most competitive species tested. The use of indices such as these is conceptually attractive, because they could provide a straightforward method of grouping species and providing guidance on relative weed competitiveness to managers. However, the indices presented as a result of this work can only be indicative, brcause one-time measurements give a static snapshot of competitiveness to be more widely applicable, effects on different sites, with different tree species and over several years, would need to be made (Burton 1993). In addition, an increase in biomass of competing weed vegetation may not necessarily result in predictable reduction in the availability of resources to neighbouring trees in sites with different levels of underlying resource (Goldberg 1996; Davis et al. 1998). To have a wider application, future studies need to determine the effect of increasing weed abundance of a particular species or group of species, and relate this to net resource supply and subsequent effects on tree growth. Other factors that may influence relative response to weed competition in practice, but which were not tested in this work, were the effect of initial tree nutrient status, initial tree size at planting, and the growth pattern of different tree species through the growing season (e.g., South et al. 1993; Balandier et al. 2006).

These experiments have confirmed the value of initial weed control when establishing *B. pendula* and provided useful information on the relative competitiveness of different weed species in UK conditions. The technique of growing weed species as plugs proved to be more practical in achieving a prescribed plant density than sowing seed. More work is needed using lower initial weed densities, earlier assessment dates, a variety of sites, different tree species, and weed control timings before it is safe to recommend threshold control levels for a particular weed species at different stages of tree establishment. Characterization of the limiting resources and the effects of different weed species or groups of species both on the availability of those resources and on subsequent tree growth is also required.

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