

## Indirect effects of litter on woody seedlings subject to herb competition

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We tested the hypothesis that litter indirectly enhances the establishment of woody seedlings in oldfields, because litter reduces the intensity of herb competition. We counted and measured the woody seedlings growing in experimental plots with different amounts of litter of *Solidago sp.*, or leaves of *Quercus alba*, and in plots with the dominant herb removed. We also conducted a factorial experiment in a greenhouse to test the effect of water availability, litter, and competition on the growth of seedlings of *Ailanthus altissima*. The results showed a strong negative effect of herb competition and a positive indirect effect of litter on woody seedling establishment. Litter had only a marginal effect on the number of seedlings established in the field. The removal of the dominant herb increased woody seedling size. Dense oak leaf litter reduced the cover of herbs and increased the size of the woody seedlings. In the greenhouse, litter reduced the density and biomass of herbs, thus improving the growth of the woody seedlings by reducing competition. We found evidence of a possible complex interaction, in which the presence of trees that produce the litter affect the competition between herbs and woody seedlings from a distance.

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The rejection of Clement's (1916) superorganismic view of succession (Pickett et al. 1987, Walker and Chapin 1987) led many researchers to overlook the importance of the environmental changes produced by plants as a successional force (but see Roberts 1987). Litter accumulation may produce rapid changes in the microenvironment and may strongly affect successional communities (Grime 1979, see Facelli and Pickett 1991a, for a review). Most studies on the effect of litter on successional dynamics have focused on the herbaceous components of the community (e.g., Goldberg and Werner 1983, Monk and Gabrielson 1985, Carson and Peterson 1990, Facelli and Pickett 1991b). The effect of litter on the colonization of oldfields by trees, arguably an important turning point in many successions, deserves special attention. The empirical evidence available is scant and mostly circumstantial. Litter may affect woody

seedlings through allelopathy (Rice 1979), shading, or mechanical impedance (Barrett 1931, Grime 1979, Borchet et al. 1989). Field observations suggest that litter may affect the distributions of woody seedlings (Keever 1973, Collins and Good 1987).

In addition to the direct effects mediated by changes in the abiotic environment (Facelli and Pickett 1991a), litter may affect plant communities through indirect effects, by altering the patterns of interspecific interactions (Sydes and Grime 1981, Facelli and Pickett 1991a). Grime (1979) suggested that litter coming from forest borders into oldfields could enhance woody seedling establishment because of the negative effect of litter on herbs (see also Sydes and Grime 1981). This may constitute a complex indirect interaction, in which the trees that produce the litter affect the competition between herbs and woody seedlings from a distance. Fur-

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thermore, accumulated litter depends on past events affecting litter production, movement, and destruction (Facelli and Pickett 1991a).

In a previous work (Facelli and Pickett 1991b) we found that litter substantially reduced the density and biomass of herbs in a 1-year oldfield at the William L. Hutcheson Memorial Forest Center (HMF), East Millstone, New Jersey, USA. Therefore, this system seems to be appropriate to test the hypothesis that the negative effect of litter on herbs may indirectly improve woody seedling establishment by reducing competitive inhibition (Grime 1979, Sydes and Grime 1981). Here we report results from a field experiment designed to answer the following questions: 1) How do different types and amounts of litter affect tree seedling establishment early in succession? and 2) How do herb competition and seed availability affect the establishment of woody seedlings? We also report results of a greenhouse experiment designed to assess the effects of the presence of litter and of different water availability on the interaction between woody seedlings and herbs.

## Materials and methods

### Field experiment

The field experiment was carried out at HMF, East Millstone, New Jersey, USA (40°30'N, 74°34'W). HMF is located in the New Jersey Piedmont. The climate is subcontinental, with 1120 mm of precipitation evenly distributed throughout the year. Mean annual temperature is 17.3°C, with monthly temperature ranging from 0.0°C in January, to 24°C in July (United States Weather Bureau 1959). The soil is a well drained silty loam, derived from the Triassic red shales of the Brunswick Formation, and corresponds to the Penn Silt Loam series (USDA 1976). The season in which we carried out the experiment (spring-summer 1988) was conspicuous for the extreme high temperatures and dryness, especially during the first part of the experiment (early June to mid July).

The composition of the litter mat in oldfields at HMF varies with the age of the plot, and with the distance to a forest edge (Facelli and Carson 1991). Floral stalks of dicots (mainly *Erigeron annuus* (nomenclature follows Gleason and Cronquist 1963) in 1- to 2-yr oldfields, or *Solidago* spp. in older fields) form the predominant component of litter. Patches with heavy accumulation of oak leaves are frequent close to forest edges (Facelli and Carson 1991). When disturbed in late spring, the fields are colonized by a few summer annual species, forming a community with strong dominance of *Setaria faberii* with *Panicum dichotomiflorum*, and *Solanum carolinense* as subdominants. *Erigeron* spp. and *Aster* spp. seedlings are established in late summer or early fall (Facelli and Pickett 1991b).

The experimental site had been under agriculture

until 1985, when it was left fallow. On 3 June 1988 the area was rototilled to a depth of 15 cm, and on 7 June the experimental plots were established. The experiment used a randomized complete block design, with eight treatments replicated once in each of ten blocks. Each plot was 1 × 0.6 m in size, and was surrounded by 1 m buffer strips. We had five treatments with litter and three without litter (controls). Two of the treatments had litter of a dicot (*Solidago canadensis*, goldenrod) added at 200 or 400 g m<sup>-2</sup> (respectively D1 and D2). The other three litter treatments had oak leaf litter added at 50, 100, and 200 g m<sup>-2</sup> (respectively L1, L2 and L3). Those amounts of litter are within the ranges observed to occur in oldfields at HMF (Facelli and Carson 1991). We collected the litter used in all the experiments from successional sites at HMF. The litter was collected from the forest floor in early spring. It was sorted, air dried, cleaned of extraneous materials, and weighed in aliquots to be used in the experiments.

In the five litter treatments we added 25 seeds of *Rhus glabra* and 25 of *Acer rubrum* before adding the litter. Both species are dispersed into young, open oldfields by birds and wind respectively. Seeds of *R. glabra* were locally collected in the fall and, after cold winter storage (4°C), they were treated with sulfuric acid as recommended by USDA (1974). Seeds of *A. rubrum* were collected in the spring just before starting the experiment. Germination assessed in laboratory was 63% for *R. glabra* (after treatment), and 41% for *A. rubrum*. We added the same amount of seeds to an otherwise unmanipulated control treatment (CL), and to a control treatment in which we reduced competition by removing the dominant herb (*Setaria faberii*) (CC). In the third control we did not add any seeds (CS). Thus, the three treatments without litter controlled for the effects of litter (CL), competition (CC), and seed addition (CS), and allowed planned pairwise comparisons (Day and Quinn 1989).

On 7 July and 26 August 1988 we estimated herb cover in all the plots. This non-destructive assessment allowed us to characterize the herb community in the different treatments, and to roughly estimate the intensity of competition. Starting on 14 June, and every two wk thereafter, we counted all the woody seedlings emerging in the plots, and marked them using color-coded toothpicks. To account for the effect of the litter on the visibility of the developing seedlings, we considered a seedling "emerged" when the cotyledons were fully open and exposed to sunlight. On 26 August and 24 September we measured the height of the woody seedlings to the apex, and estimated the area occupied by each seedling as the horizontal projection of the diamond defined by the longest dimension of the crown, and its perpendicular.

We analyzed accumulated tree establishment by Repeated Measurements ANOVA (SAS 1982) of the square root of the number of seedlings per plot plus one. Because the final density data were unsuitable for

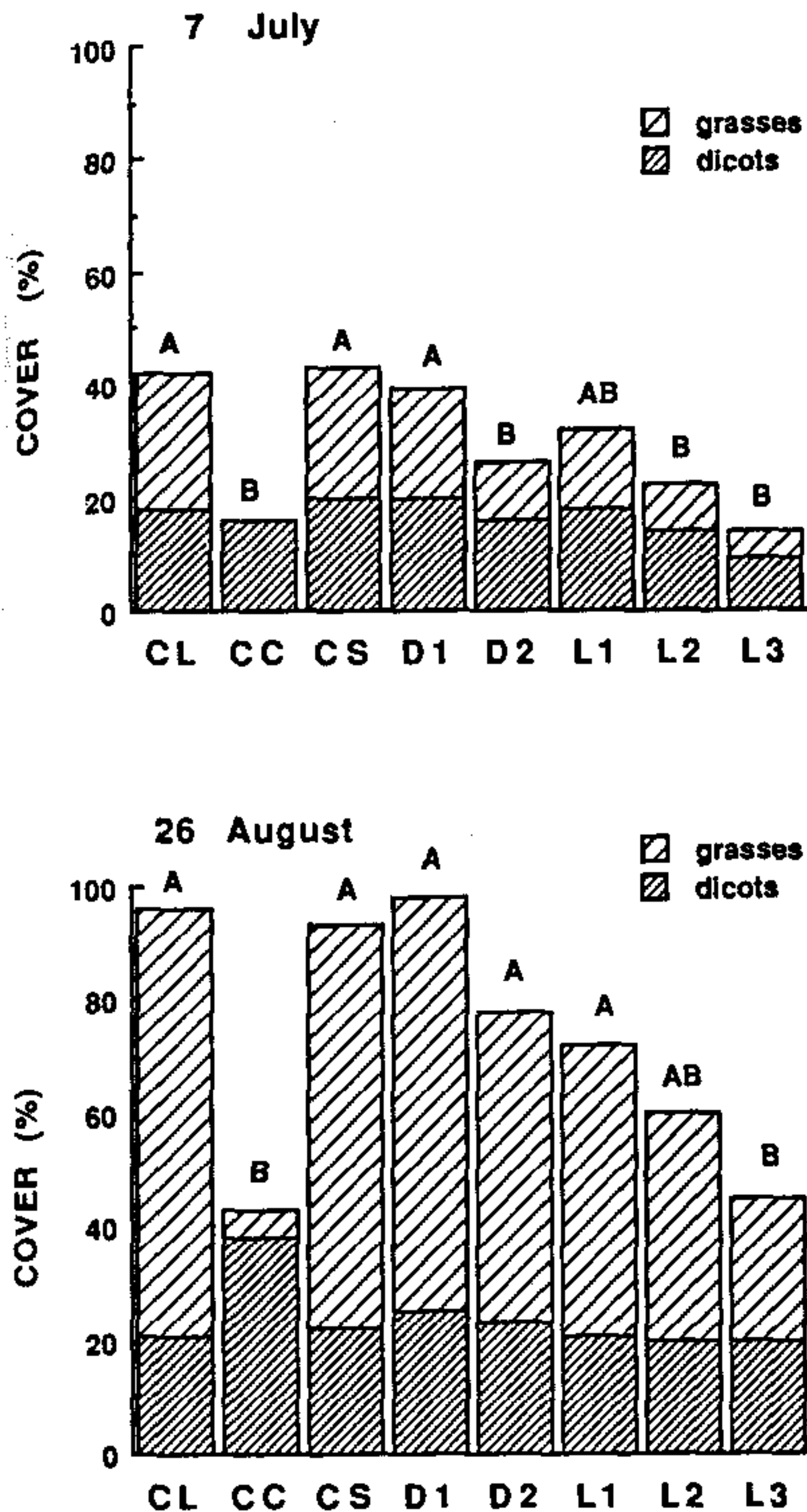


Fig. 1. Estimated percent cover of herbaceous dicots and grasses on 17 July and 26 August in field plots with litter of goldenrod (D1 and D2), oak leaf litter (L1, L2 and L3), with the dominant species removed (CC), or without manipulation of the growing community (CL, CS). In all treatments except CS, seeds of woody species were added. Bars marked with the same letters as in CL indicates that effect of the treatment on total herb cover was not significant ( $p > 0.05$ ).

parametric analyses, we analyzed the final densities by Wilcoxon's signed rank test (SAS 1982), testing all treatments against the control for litter (CL). We tested the effect of the treatments on seedling size by Multivariate Analyses of Variances (MANOVA) using Wilks' criterion to estimate the  $F$  value (SAS 1982). To increase normality in the distribution of the variables we used the logarithm of height and the square root of area in the analyses. When MANOVA showed a significant effect of treatments ( $p < 0.01$ ), we performed Analysis of Variance and Least Significant Difference (LSD)

pairwise comparison test ( $p < 0.01$ ), comparing each treatment to CL for each variable at each date.

### Greenhouse experiment

The greenhouse experiment started on 20 May 1989. We used 750 cm<sup>3</sup> plastic pots filled with standard gardening mixture (75% mineral soil, 25% compost). We placed ten seeds of *Ailanthus altissima* per pot. *Ailanthus altissima* was chosen as the target species for three main reasons: 1) we found it volunteering in the field experiment, reaching higher densities than the added species, 2) it is one of the first trees to successfully colonize the oldfield we were working in, and 3) its fast growth rates makes it suitable for competition experiments. On top of the gardening mix we added 5 g of top soil from our experimental site containing the propagules in the soil seed bank, to mimic the natural plant community. We used a factorial design with three factors (litter, competition, and watering frequency) at two levels. Each of the eight possible factor combination was replicated in 10 pots randomly distributed in a ten by eight grid on the greenhouse bench. In each of the pots in the litter treatments (L), we added 5 g of leaf litter of white oak (*Quercus alba*) collected from the ground in early spring. In the treatments with competition (C), all the germinating herbs were allowed to grow, while in the plots without competition they were removed with forceps as soon as they emerged, taking care to minimize the disturbance of the soil and litter. The pots were watered to saturation every 5 d in the treatment of high water availability (W) or every 10 d in the remaining pots (considered the control level). Plants in the pots with lower water availability showed symptoms of water deficits only late in the experiment.

The emergence of tree seedlings was recorded every two d, each seedling was identified by a color-coded toothpick. On 1 June the number of seedlings per pot was reduced to four, and on 19 June to two, to minimize intraspecific competition. Each time, the randomly picked seedlings were clipped at the soil surface with special care not to disturb the litter layer. No emergence occurred after 1 June, and no natural mortality occurred. When *S. faberii* started to flower (7 July) we harvested the remaining woody seedlings and the herbs. On the first two harvest dates we measured total height, length of the hypocotyl, leaf area, and dry weight of the leaves and stem. On the final sampling we also assessed the number of expanded leaves, and the weight of the roots of the woody seedlings, and the density of grasses and dicots, and total herb biomass per pot (the biomass of dicots was negligible).

The effect of the main factors and their interactions on woody seedling emergence was analyzed by Repeated Measurement Anova (SAS 1982). We analyzed all the seedling size and morphology variables by a Multivariate Analysis of Variance (MANOVA) for each

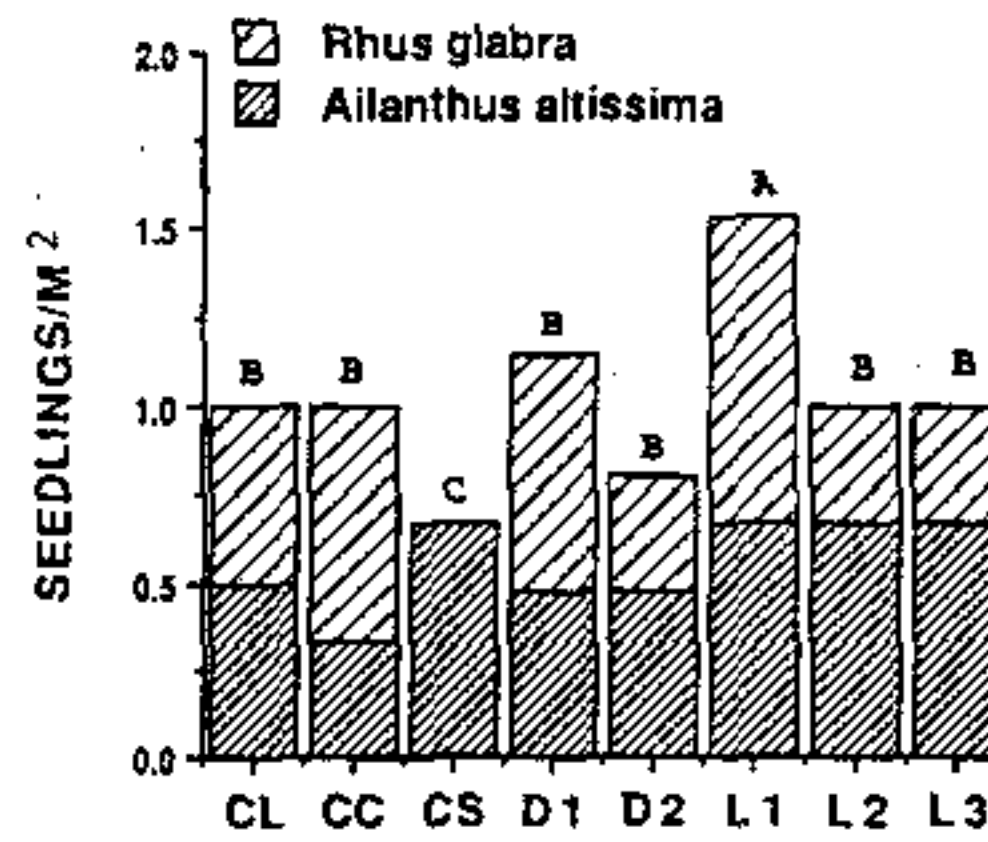
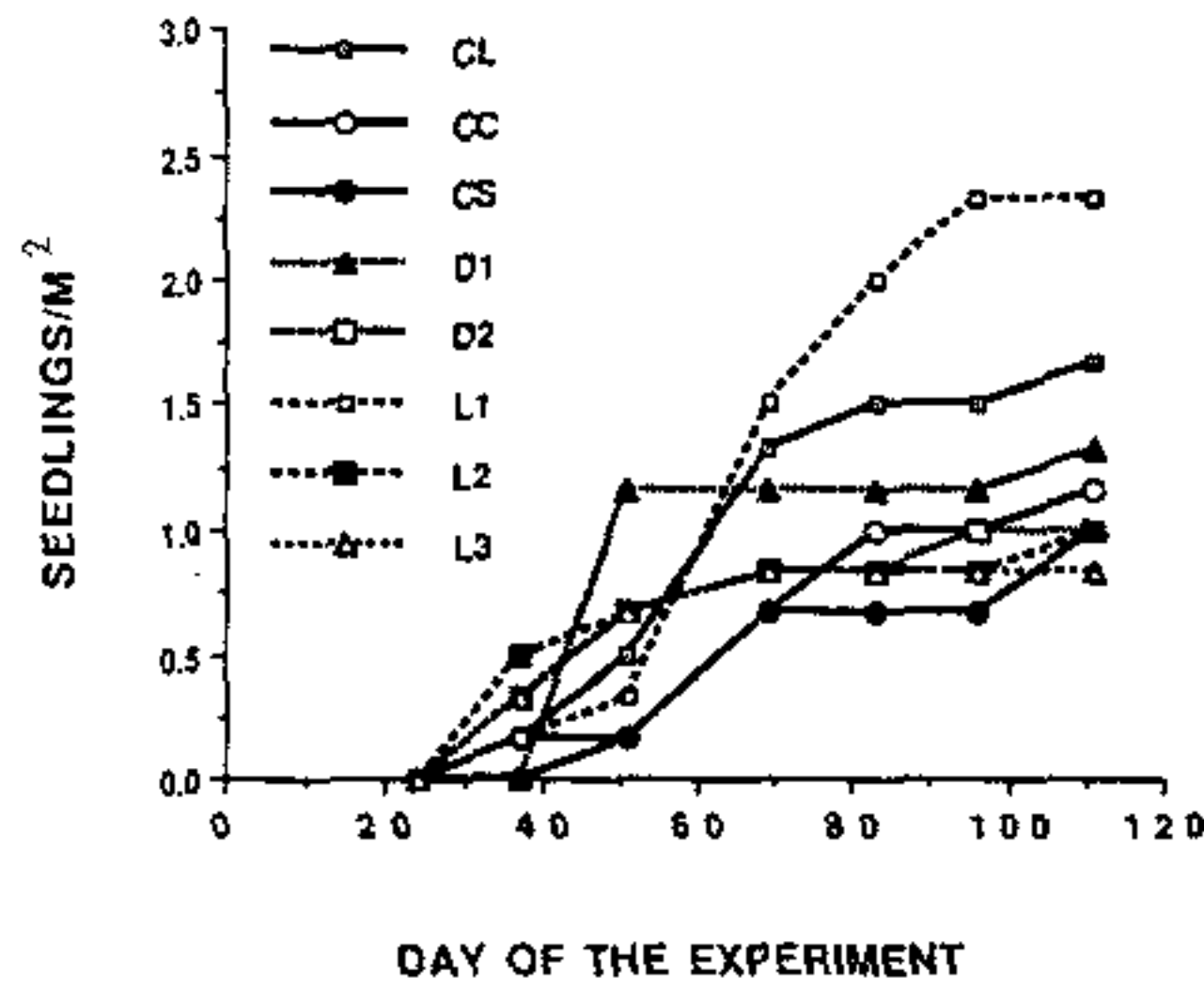


Fig. 2. Accumulated woody seedling establishment from 15 June to 24 September 1988 (left) in the field experiment, and densities of seedlings of *Rhus glabra* and *Ailanthus altissima* on 24 September (right). Bars marked with the same letter as in CL indicates that the effect of the treatment was not significant ( $p > 0.05$ ).

date, estimating  $F$  by Wilks' criterion (SAS 1982). When MANOVA indicated significant effect ( $p < 0.01$ ), we performed the corresponding ANOVA for the main effects and the interactions. Given the large number of comparisons performed, we corrected the calculated  $p$  values by Bonferroni's correction, and declared significant those differences with  $p < 0.01$  after the correction.

We also analyzed the shoot Relative Growth Rates ( $RGR$ ) and the shoot Net Assimilation Rates ( $NAR$ ) of the woody seedlings for the intervals 1 June-19 June, and 19 June-7 July, using the formulae in Harper (1977: 310-311):

$$RGR = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1}$$

and

$$NAR = \frac{W_2 - W_1}{T_2 - t_1} \times \frac{\log_e L_2 - \log_e L_1}{L_2 - L_1}$$

where  $W$  is the aerial biomass, and  $L$  the leaf area of the

woody seedlings at times  $t_1$  and  $t_2$ . To calculate the  $RGR$  and  $NAR$  for each pot, individuals harvested in that pot at two successive dates were paired at random.

## Results

### Field experiment

The removal of the dominant herb (*S. faberii*) reduced the total cover of herbs (Fig. 1) at 7 July and 26 August; only on the last date did a slight but significant ( $p < 0.05$ ) increase in the cover of the dicots (mostly *Solanum carolinense*) give evidence of competitive release (Fig. 1). Goldenrod litter reduced the cover of herbs only initially and in the highest amount ( $p < 0.05$ ; Fig. 1). Oak leaf litter strongly reduced herb cover in the two highest doses ( $p < 0.01$ ). Litter had no effect on dicots (Fig. 1). Thus, the addition of oak litter in higher doses (L3) had an effect somewhat similar to the control for competition (CC), although the removal of the dominant species probably reduced competition more than litter addition, because of the high competitive ability of *S. faberii*.

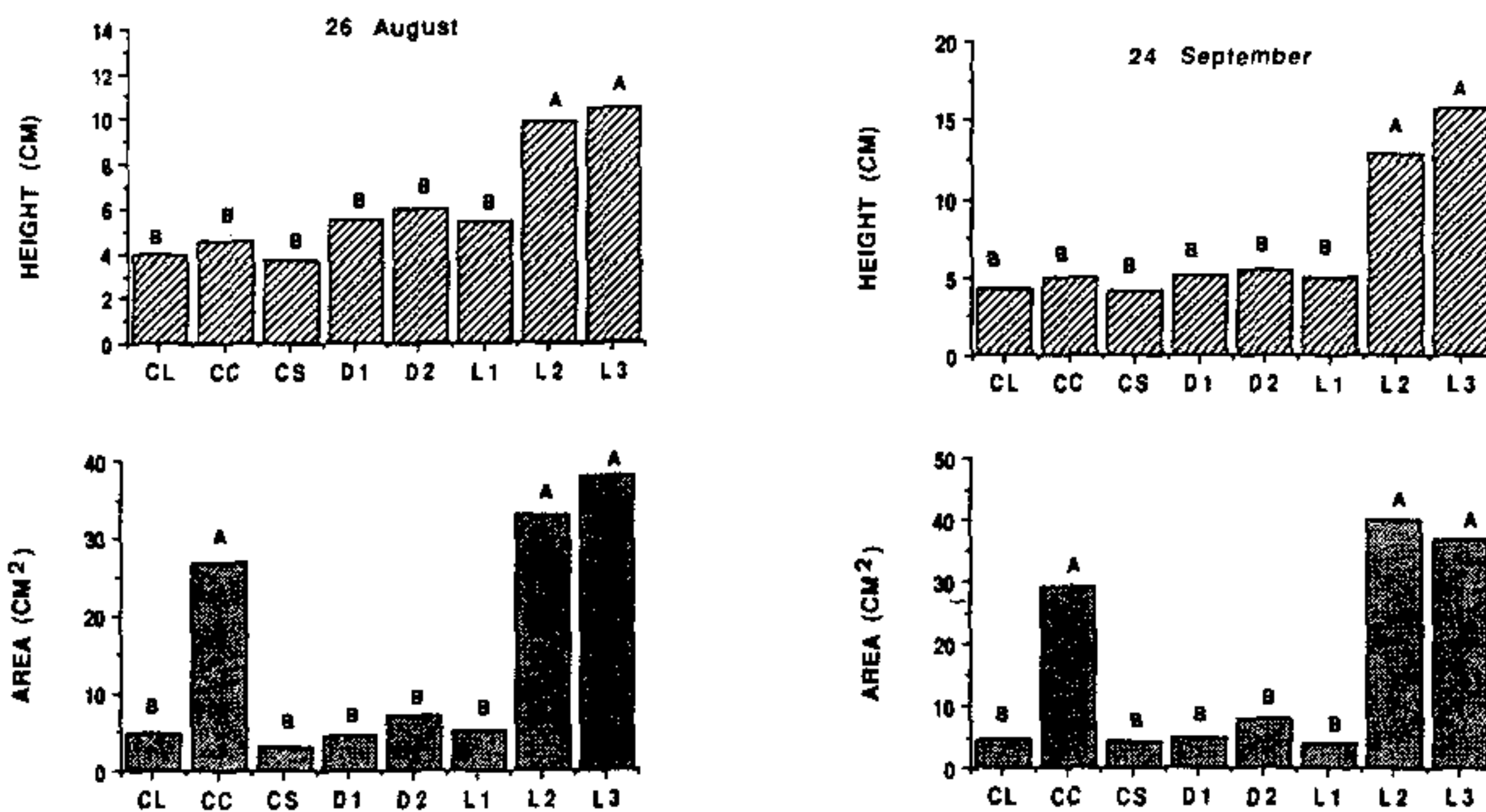
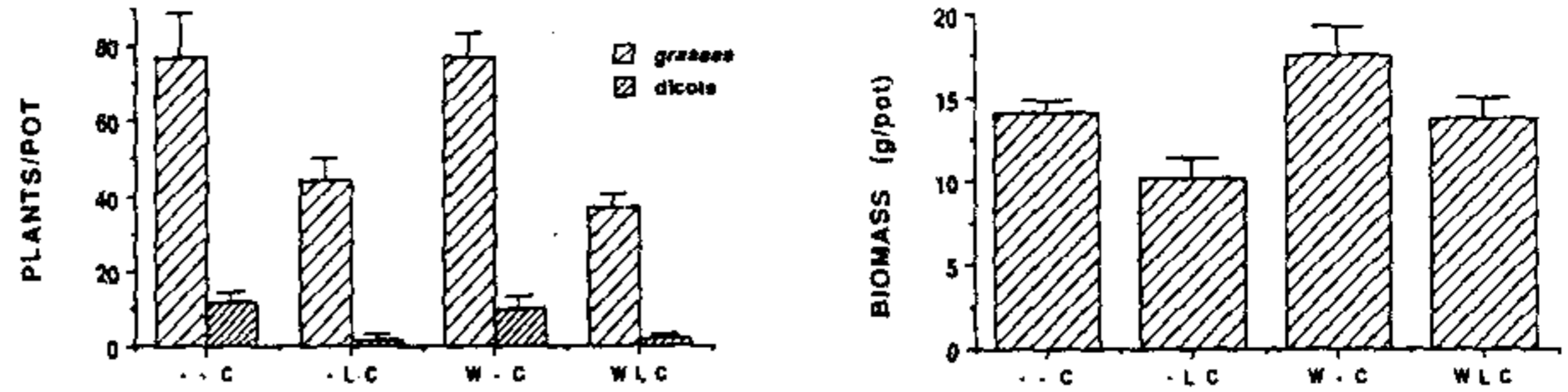


Fig. 3. Mean height (upper) and crown area (lower) of individual woody seedlings on 26 August (left) and 24 September 1988 (right) in the field experiment (treatment denomination as in Fig. 1). Bars marked with the same letter as in CL indicates that the treatment effect was not significant ( $p > 0.1$ ).

Fig. 4. Density and biomass of herbs growing in pots in the greenhouse factorial experiment with different combinations of litter (L), water (W), and herb competition (C). Only treatments with competition are included (see text for details).



The establishment of woody seedlings was sparse, especially during the first part of the experiment (Fig. 2), due to the intense drought affecting the area. Most of the establishment occurred by the end of July, after some rains alleviated the severe drought. No seedlings of *A. rubrum* were observed, and many seeds were found dead (dry) soon after starting the experiment. *Acer rubrum* is very sensitive to desiccation (USDA 1974) and was probably affected by the high temperatures and drought. Only seedlings of *R. glabra* and *A. altissima* were recorded in the plots (Fig 2). The seeds of volunteering *Ailanthus* probably came from the forest edge 30 m E of the plots.

The Repeated ANOVA of seedling emergence showed significant effects of time, and of time  $\times$  treatment interaction ( $p < 0.01$ ), but the effect of treatment was only marginal ( $p < 0.06$ ) (Fig. 2). The smaller amount of oak litter (L1) increased the final density of seedlings ( $p < 0.05$ ).

The treatments had significant ( $p < 0.01$ ) effects on the size of the seedlings at the two dates. Oak leaf litter at the highest densities (L2 and L3) significantly increased the height of the seedlings on both 26 August and 24 September (Fig. 3). L2, L3 and the removal of the dominant (CC) increased ( $p < 0.01$ ) the crown size of the seedlings at both dates (Fig. 3).

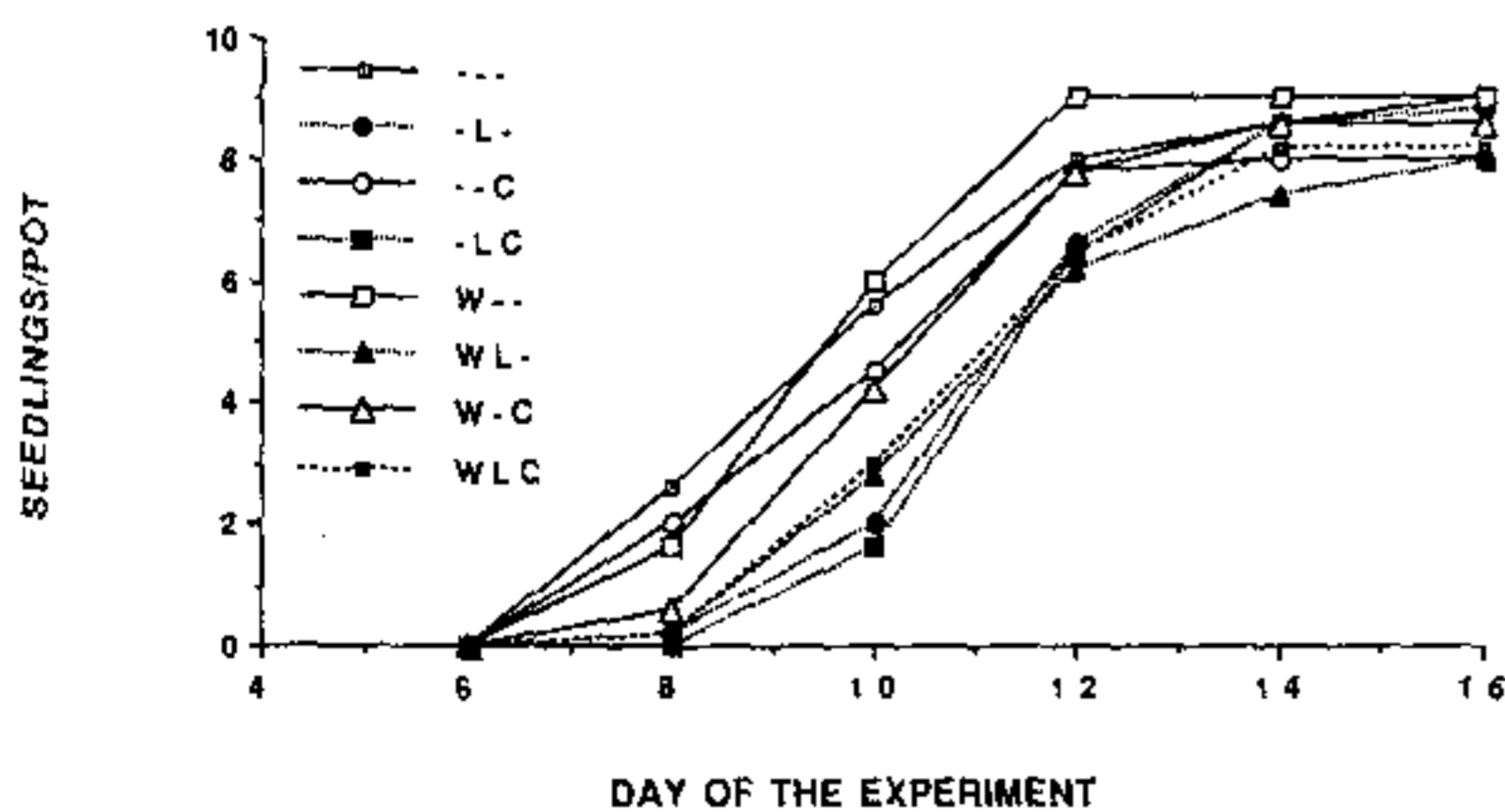


Fig. 5. Density of woody seedlings established in pots in the greenhouse factorial experiment with different combinations of litter, water, and herb competition. The asterisks show the dates when the effect of litter was significant ( $p < 0.01$ ). See Table 1 for further details on the Repeated Measurement ANOVA.

### Greenhouse experiment

The herbs established in the pots resembled closely the herb community in the field (cf. Facelli and Pickett 1991b). *Setaria faberii* was dominant (ca. 75% of density, and 95% of biomass), accompanied by a few *S. glauca*, *Panicum dichotomiflorum* and some seedlings of the dicots *Draba verna*, *Amaranthus* spp., and *Erigeron annuus*. Litter reduced the density of both grasses and dicots ( $p < 0.01$ ; Fig. 4); there was no significant effect of the water treatment on density ( $p > 0.44$ ). The effect of litter on herb biomass was less strong than on herb density (Fig. 4). More frequent water addition increased herb biomass ( $p < 0.01$ ; Fig. 4).

None of the treatments affected the final number of seedlings of *A. altissima* per pot ( $p > 0.45$ ; Fig. 5). However, the Repeated Measurement ANOVA (Table 1) showed that, in addition to a significant time effect ( $p < 0.01$ ), there was a significant time  $\times$  treatment interaction ( $p < 0.01$ ) because litter delayed the emergence of seedlings by nearly 2 d (Fig. 5).

Litter, competition, and their interaction had significant effects on the woody seedling size and morphology on all three dates (Table 2). Water availability had a significant effect only on the last harvest (Table 2). The relative importance of different effects on different variables changes over time (Table 3). On 1 June, when the seedlings were 8 to 12 d old, most of the variance was due to the effect of litter and competition. On 19 June and 7 July, the effect of litter was relatively less important, while the effect of competition, and the interaction between litter and competition became more important (Table 3).

Table 1. Repeated Measurements Analysis of the density of *A. altissima* in the factorial greenhouse experiment. F calculated by Wilks' criterion. (T: Time, L: Litter, W: Water, C: Competition).

Effect	DF	F	P
T	4	353.40	<0.0001
T $\times$ L	4	15.02	<0.0001
T $\times$ W	4	0.34	0.8502
T $\times$ C	4	0.43	0.7834
T $\times$ L $\times$ W	4	2.16	0.0983
T $\times$ L $\times$ C	4	0.12	0.9755
T $\times$ W $\times$ C	4	1.12	0.3521
T $\times$ L $\times$ W $\times$ C	4	0.73	0.5707

Table 2. Alpha probabilities for F calculated by Wilks' criterion in MANOVAs (df = 8 for the numerator and = 65 for the denominator) for the main effects and interaction for the three dates in the greenhouse experiment. See text and Table 3 for the descriptions of the variables measured at each date.

Effect	Date		
	1 June	19 June	7 July
Water	0.0147	0.0489	0.0004
Litter	0.0001	0.0001	0.0001
Competition	0.0001	0.0001	0.0001
W × L	0.0906	0.0608	0.0356
W × C	0.6055	0.2692	0.2283
L × C	0.0001	0.0005	0.0009
W × L × C	0.8385	0.7147	0.5290

The most persistent effect of litter was the increase in the length of the hypocotyl (Table 3). Consequently with that increase, litter initially increased the weight of

the stem and the total height, and reduced the weight of the leaves and the leaf area in the first sampling (Fig. 6). The weight/length relationship of the stem was also reduced ( $p < 0.01$ ) by the addition of litter. This pattern reflects changes in the partitioning of seed reserves and photosynthates, since litter did not affect the total seedling biomass ( $p > 0.25$ ). Even though the seedlings of both herbs and trees were less than 12 days old, and no shading was evident in the plots, the effect of competition was already significant (Tables 2, 3). Competition increased the length of the hypocotyl, decreased the height above the hypocotyl, and reduced the weight of the leaves (Fig. 6) but did not affect total biomass ( $p > 0.20$ ), also suggesting changes in reserve and photosynthate partitioning.

In the second sampling, litter had no effect on the height above the hypocotyl, though the negative effect of litter on weight of the stem was still detectable (Fig. 7). The negative effect of competition was far

Table 3. Summary of the results of ANOVAs on the main effects and their interactions on size and morphology of *A. altissima* seedlings at the three sampling dates in the greenhouse experiment. [\*\*: significant effect,  $p < 0.01$  after Bonferroni's correction by number of comparisons; NS: not significant.]. Complete statistical results are available from the authors upon request.

1 June

Variable	Effect						
	W	L	C	W×L	W×C	L×C	W×L×C
Length of hypocotyl	NS	**	**	NS	NS	**	NS
Height above hypocotyl	NS	NS	**	NS	NS	NS	NS
Leaf area	NS	**	NS	NS	NS	NS	NS
Weight of leaves	NS	**	**	NS	NS	NS	NS
Weight of stem	NS	**	NS	NS	NS	NS	NS

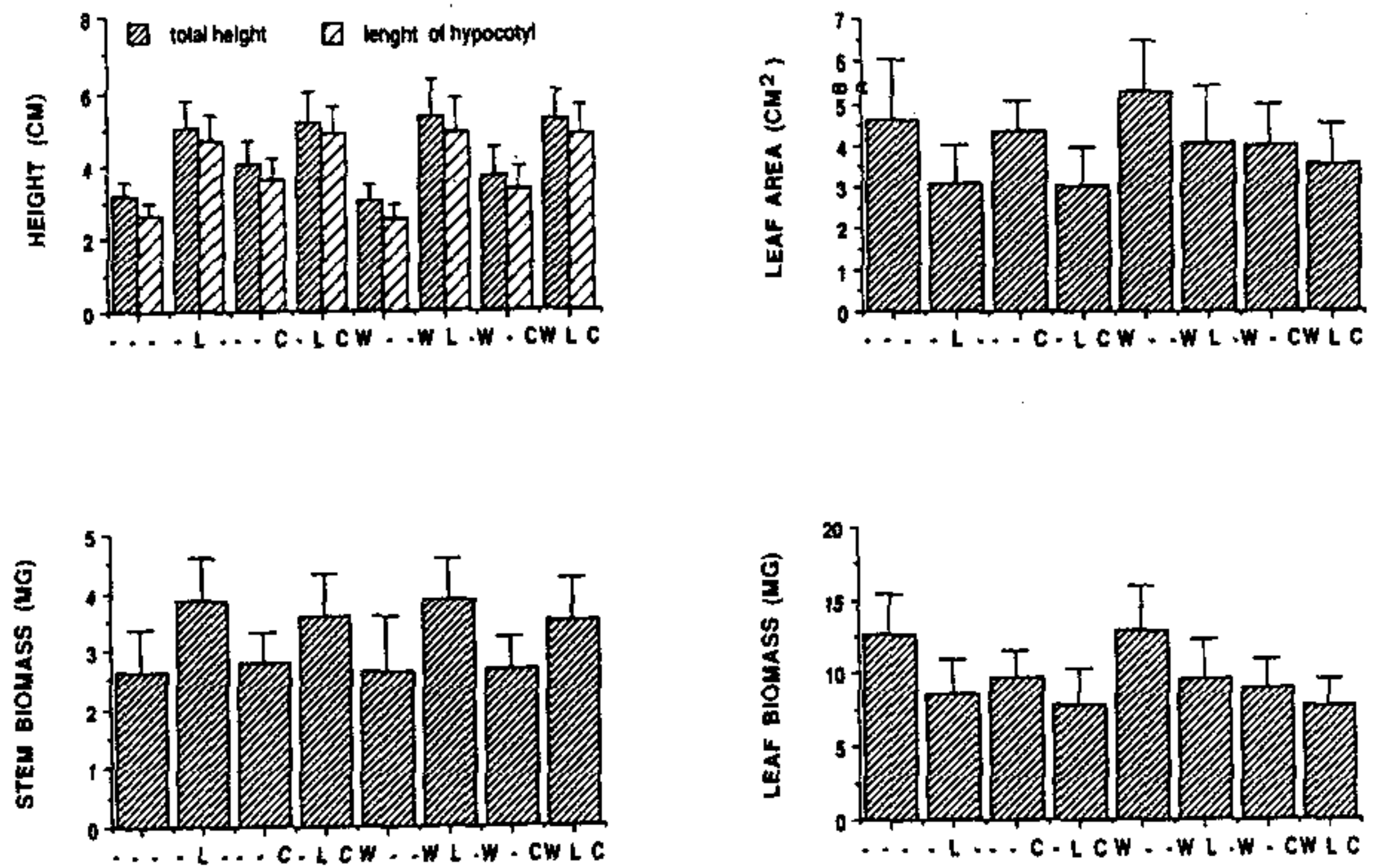
19 June

Variable	Effect						
	W	L	C	W×L	W×C	L×C	W×L×C
Length of hypocotyl	NS	**	**	NS	NS	**	NS
Height above hypocotyl	NS	NS	**	NS	NS	NS	NS
Leaf area	NS	NS	**	NS	NS	**	NS
Weight of leaves	NS	NS	**	NS	NS	**	NS
Weight of stem	NS	**	**	**	NS	**	NS

7 July

Variable	Effect						
	W	L	C	W×L	W×C	L×C	W×L×C
Length of hypocotyl	NS	**	**	NS	NS	**	NS
Height above hypocotyl	NS	NS	**	NS	NS	**	NS
Leaf area	NS	NS	**	NS	NS	**	NS
Number of leaves	**	NS	**	NS	NS	**	NS
Weight of leaves	NS	NS	**	NS	NS	**	NS
Weight of stem	NS	NS	**	NS	NS	**	NS
Weight of roots	NS	NS	**	NS	NS	**	NS

Fig. 6. Mean length of the hypocotyl and total height (a), leaf area (b), and dry weight of leaves (c), and stem (d) of seedlings of *A. altissima* at 1 June in different combinations of litter (L), water (W), and herb competition (C) in the greenhouse factorial experiment. Bars above the columns represent one Standard Deviation. See Tables 2 and 3 for statistical analyses.



more important than that of litter on weight of stem, leaf area, and weight of leaves (Fig. 7). By that time, the interaction litter  $\times$  competition also became more important (Table 3), because litter reduced the negative effects of competition on weight of stem, leaf area, and weight of leaves of the tree seedlings (Fig. 7).

The effect of water was significant only in the last harvest (Table 2), when increased water availability reduced the number of differentiated leaves, but did not affect leaf area (Table 3). In this sampling, competition also resulted in a reduction of the growth of the woody seedlings. It reduced the height, the leaf area, the number of differentiated leaves, and the weight of roots, stem, and leaves (Fig. 8). Concurrently, the interaction

between litter and competition was still more marked. The correlation of the aboveground biomass of herbs to the biomass of the seedlings was not significant ( $r = -0.233$ ,  $p > 0.15$ ). However, biomass of the seedlings was significantly correlated to the density of the herbs ( $r = -0.478$ ,  $p < 0.01$ ). Both the Relative Growth Rate (RGR) and the Net Assimilation Rate (NAR) for the first period were reduced by competition ( $p < 0.01$ ), but the presence of litter reduced the negative effect of competition ( $p < 0.01$ ) (Fig. 9). During the second period RGR and NAR were again reduced by competition ( $p < 0.01$ ), but the interaction between litter and competition had no effect on either RGR or NAR ( $p > 0.75$ ) (Fig. 9).

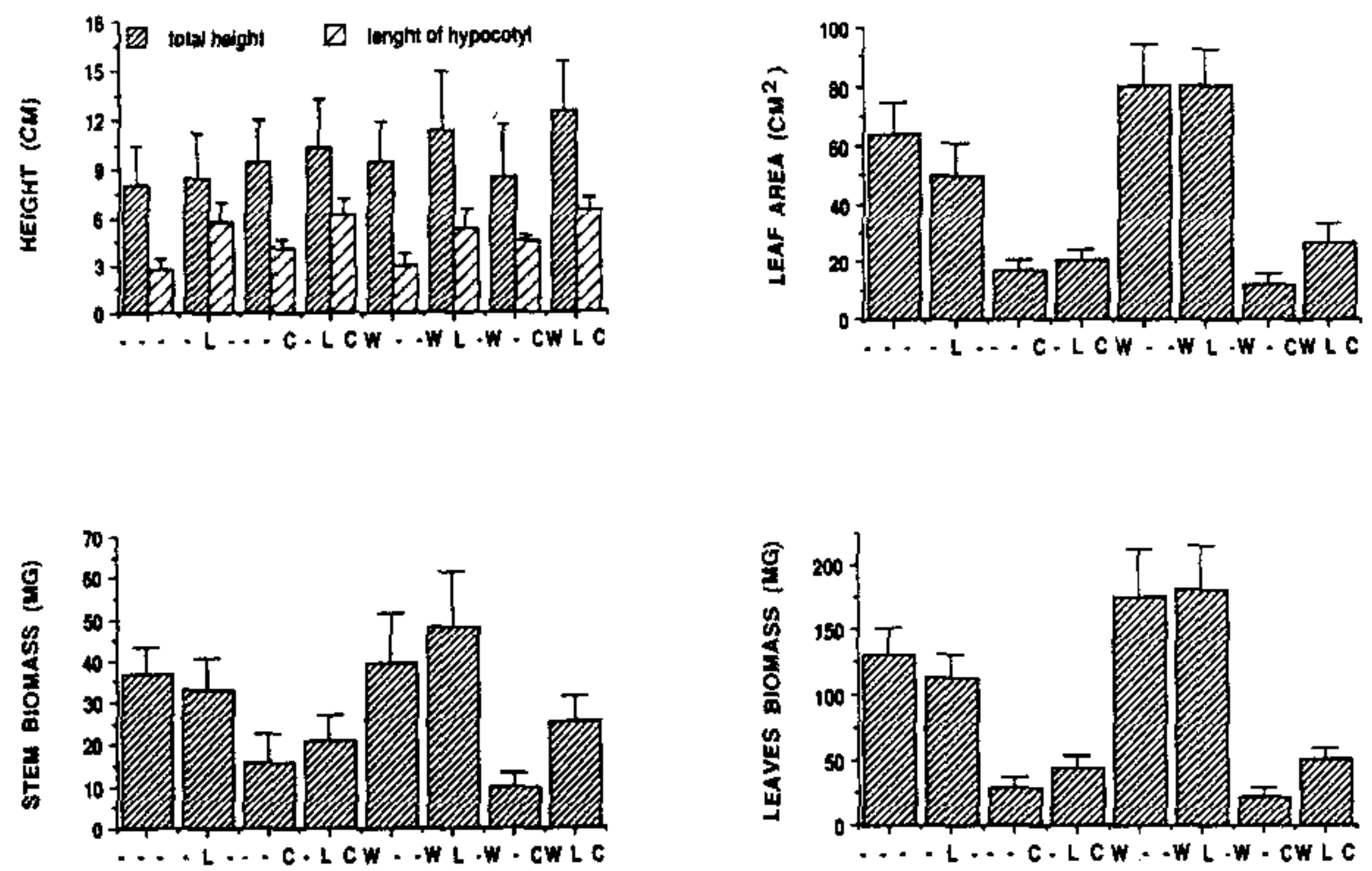


Fig. 7. Mean length of the hypocotyl and total height (a), leaf area (b), dry weight of leaves (c), and stem (d) of seedlings of *A. altissima* at 19 June, in different combinations of litter (L), water (W), and herb competition (C) in the greenhouse factorial experiment. Bars above the columns represent one Standard Deviation. See Tables 2 and 3 for statistical analyses.

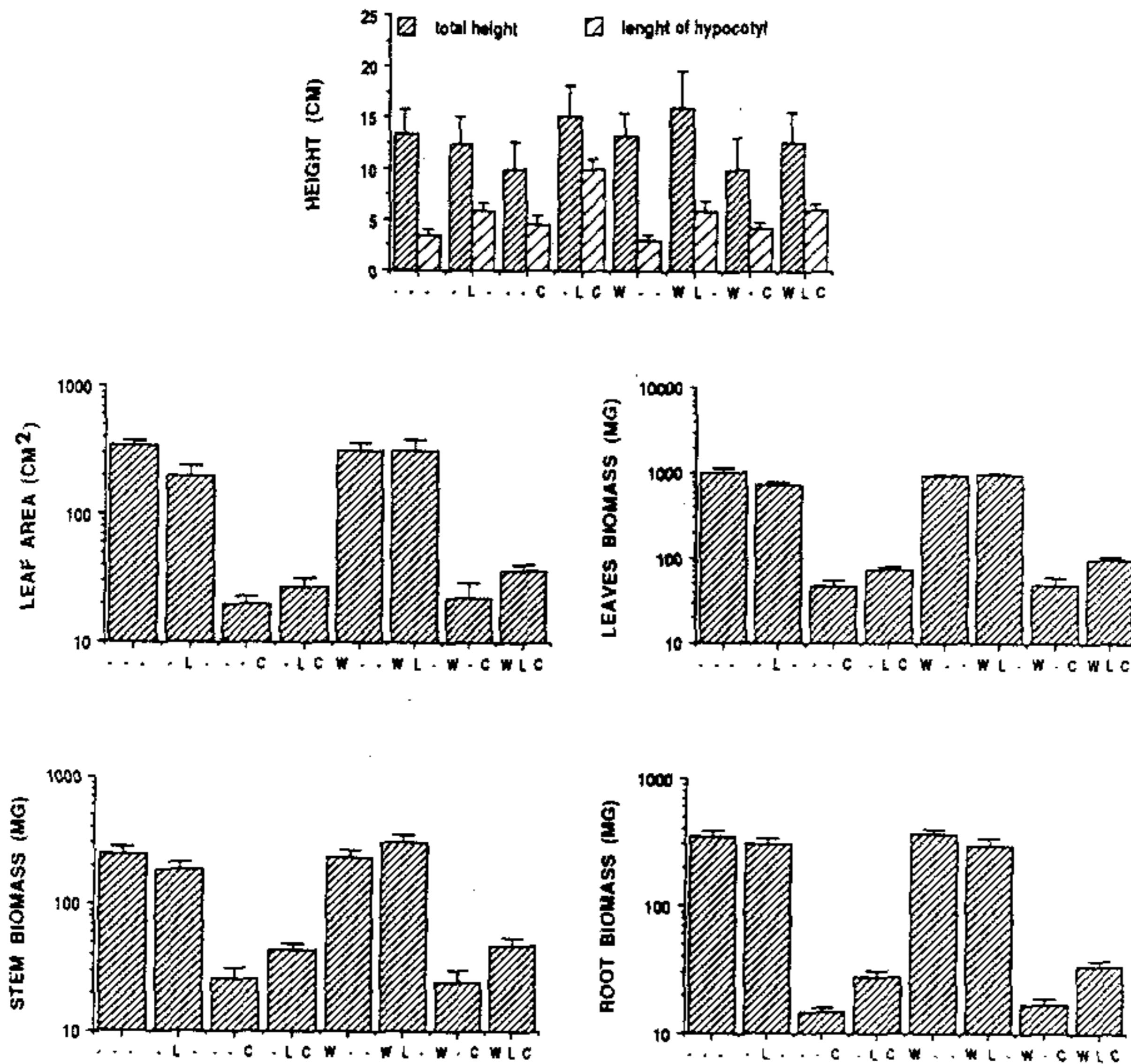


Fig. 8. Mean length of the hypocotyl and total height (a), leaf area (b), and dry weight of roots (c), leaves (d), and stem (e) of seedlings of *A. altissima* at 7 July, in different combinations of litter (L), water (W), and herb competition (C) in the greenhouse factorial experiment. Notice logarithmic scales in b, c, d, and e. Bars above the columns represent one Standard Deviation. See Tables 2 and 3 for statistical analyses.

## Discussion

Our results support the hypothesis that the presence of litter may enhance the growth of woody seedlings in oldfields, because litter reduces the negative effect of competition by herbs. Both the field and the greenhouse additions of oak leaf litter enhanced the growth of woody seedlings subject to competition by herbs.

The effects produced in the field by intermediate and high levels of oak leaf litter (L2 and L3) were similar to that produced by the removal of the dominant competitor, though litter also had a direct effect on seedling morphology. The increased height of the seedlings produced by both L2 and L3 was probably due to the effect of litter on hypocotyl elongation, as verified in the

greenhouse experiment. Goldenrod litter had no significant effect on seedling establishment even at the highest level, suggesting that the litter of the dominant species in the oldfields does not have any important effect on woody seedling establishment.

The effect of the shallow cover of oak litter (L1) on woody seedling establishment in the field may be due to extreme dryness during that particular summer. Litter has been observed to increase germination and establishment under water-limiting conditions (e.g., Fowler 1986, Facelli and Pickett 1991a). The lack of positive effects of higher amounts of oak litter could be due to negative effects of litter (i.e., shading, mechanical impedance to seedling emergence) compensating for improved water conditions. We expected a negative effect

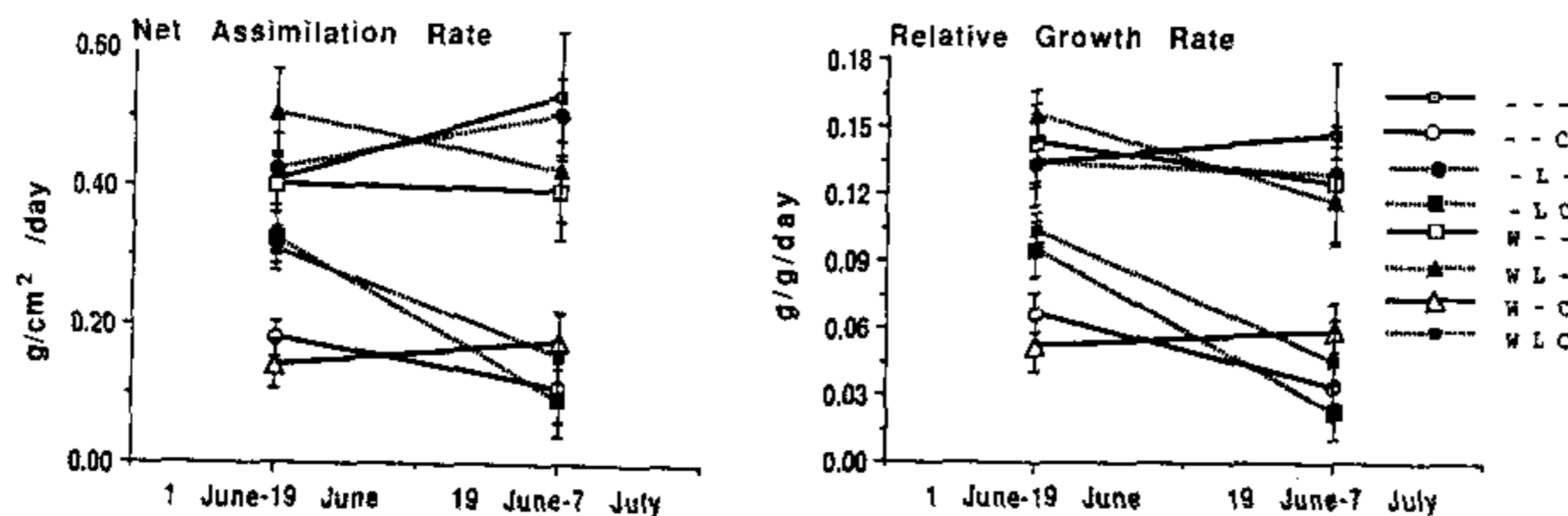


Fig. 9. Relative Growth Rates (RGR) and Net Assimilation Rates (NAR) of seedlings of *A. altissima* at 7 July, in different combination of litter, water, and herb competition in the greenhouse factorial experiment. Bars represent one Standard Deviation.



of litter on the germination of *R. glabra* because it is known to be limited by light deprivation and enhanced by temperature fluctuation (Lovell 1964). The peculiarities of the year of the field study, and the scant establishment hinder any generalization. It must be noted that we restricted our experiments to seeds placed beneath the litter. Previous studies (Fowler 1986, Hamrick and Lee 1987) showed that germination of seeds placed on top or within the litter mat may be severely limited.

The field study also suggested that seed availability may limit more intensely the establishment of some woody species (i.e., *R. glabra*) than of others (*A. altissima*), which may be related to different mechanisms of dispersal (McDonnell and Stiles 1983). The role of seed availability on woody invasion in oldfields has seldom been experimentally investigated (Pickett et al. 1987, Walker and Chapin 1987), and this study can only provide weak evidence.

Several traits of the natural system were successfully replicated in the greenhouse, though water limitation was certainly less severe than that in the field even in normal years. The effect of litter on the herbs was similar to that observed in the field (Facelli and Pickett 1991b). The absence of any effect of water availability on woody seedling growth may be explained by the positive effect of more frequent watering on herb biomass, which increased competitive pressure from herbs.

We did not find any consistent negative effect of litter on woody seedling establishment, which contrast with other reported results (see reviews in Rice 1979 and Facelli and Pickett 1991a). The slight delay in emergence produced by litter may be simply explained by the physical effect of litter, which increases the effective depth of burial of the seeds. Associated with that effect was the increase in hypocotyl length, and in total height. Although these effects on seedling morphology and biomass partitioning were strong at the first harvest, most differences disappeared as interspecific interactions became more important. It is still possible that initial differences in the partitioning of the seed reserves during germination could eventually affect the fate of the seedlings under natural conditions.

The greenhouse experiment confirmed most of the results from the field experiment, showing that competition by herbs was the main factor affecting woody seedling growth. The effect of competition was noticeable even when seedlings were still very small, and no overlap of the aerial part of the plants was visible (Facelli, pers. obs.). Since the effect seems to reflect developmental rather than growth changes, early effect of competition may be due to early detection of neighbors (Ballaré et al. 1990).

The main mechanism of the indirect effect of litter on competition was likely through the negative effect of litter on the dominant herb, which releases the woody seedlings from competition. The results of the growth analysis suggest that most of the indirect effect of litter on competition was exerted during the first half of the

experiment. The effect of the interaction litter  $\times$  competition on *RGR* and *NAR* at the beginning of the experiment suggests that the competition by herbs was limited by the number of herbs established in each plot. Increased individual herb biomass later in the experiment probably compensated for the lower densities (Facelli and Pickett 1991b) and increased the intensity of the competition. However, the transient relief from competition allowed those seedlings to reach a larger biomass and leaf area at the end of the experiment than the other seedlings under competition. Thus, litter opens a temporary "competition-free window". Woody seedlings may or may not profit from this opportunity, depending whether their establishment is fast enough to take advantage of the window before plastic responses of the herbs close it later in the growing season. Recent studies showed that initial advantages may determine the outcome of above-ground competition, but not that of below-ground competition (Wilson 1988). The final outcome of those complex relationships may depend on the prevalent competitive mechanism, which is likely to be species and environment dependent. Obviously, factors not present in the greenhouse, such as herbivory (Myer and McCarthy 1989), pathogens (Sydes and Grime 1981, Augspurger 1983), and environmental variation (Chesson 1986) may also have a sizable effect under field conditions.

Our experimental results confirm the importance of litter as a factor affecting community structure through both direct and indirect effects. A pertinent question here is whether our results are peculiar to the studied species, or whether litter may be a factor that controls the competitive outcome between herbs and woody seedlings under other conditions. We predict that the indirect effect of litter will be important when: 1) the tree population is not limited by dispersal or physical stress, 2) interspecific competition is more important than other biotic interactions in the regulation of the establishment and growth of the tree population, 3) the establishment of the herbs is more severely affected by litter than that of the tree population, and 4) the plasticity of the herbs is not fast enough to rapidly compensate for the lower density by increasing their individual size (cf. Facelli and Pickett 1991b). These conditions may apply to the colonization of early successional sites (i.e., dominated by short-lived species, highly dependent on germination) by "weedy" trees, like the species we studied. In fields dominated by perennial species, relatively insensitive to the presence of litter (Carson and Peterson 1990), and/or when the invading species is tolerant to competition or limited by other factors (Myer and McCarthy 1989), the effect of litter on competition may not be significant.

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