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Simulated effects of herb competition on planted *Quercus faginea* seedlings in Mediterranean abandoned cropland

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Abstract. We tested simulated effects of herb competition on the performance of planted seedlings of *Quercus faginea* subsp. *faginea* in Mediterranean abandoned cropland. We produced three types of environment with respect to herb competition: absence of competition (AC), below-ground competition (BGC), and total competition (TC). We assessed the performance of *Q. faginea* seedlings in each treatment in five ways: 1) seedling mortality, 2) leaf length and total plant leaf area, 3) water potential, 4) total biomass and biomass allocation, and 5) non-structural carbohydrate storage in different plant organs. We also measured 6) soil moisture at different depths and 7) biomass production of herbs. The TC treatment reduced water availability more than the BGC treatment, in agreement with the most pronounced water stress in seedlings under TC conditions. BGC and TC treatments showed a high and similar seedling mortality, which was one order of magnitude higher than that in the AC treatment. Competition treatments affected glucose concentration in both shoots and roots, and followed the rank TC > BGC > AC. *Q. faginea* seedlings might compensate a lower water availability through glucose accumulation in leaves to reduce the osmotic potential. There was a maximum starch concentration in the BGC treatment that hints that a moderate resource limitation would limit tissue growth but not carbon assimilation. We conclude that the negative effects of herbs on *Q. faginea* seedlings are mostly a result of competition for water, and that this competition is noticeable since the earliest stages of the establishment. Complete weed removal is a technique that would strongly improve seedling survivorship.

Key-words: Ecophysiological effects; Herb competition; Mediterranean cropland; *Quercus faginea;* Soil moisture.

Introduction

Various social, economical and technological changes have resulted in the abandonment of extensive areas of former cropland in developed countries during the last few years (FAO 1998). This phenomenon has created considerable quantities of “empty” spaces in some regions of these countries. These spaces can be left to undergo natural secondary succession (Debussche et al. 1996), or they can be planted with native shrubs and trees to reduce soil erosion, increase biological diversity and create carbon sinks (Vieira et al. 1994; Whisenant et al. 1995; Bakker et al. 1998). However, the environmental conditions of these areas largely differ from those of the sites where natural regeneration of shrubs and trees occurs. Radiation input, soil evaporation, thermal variation, and weed seed banks are much larger in recently open fields than in shrublands or forests, thus hindering the establishment of woody seedlings (Rey Benayas 1998; Aronson et al. 1998; Rey Benayas et al. 2002). These constraints require an appropriate management to guaranty the success of revegetation projects.

In herbaceous dominated patches and ecosystems, such as recently abandoned croplands, tree establishment is influenced by the ability of woody seedlings to survive and grow in direct competition with herbaceous vegetation (Brown et al. 1998). Numerous studies have demonstrated that herb competition reduces survival and growth of different woody species, either planted or naturally established (Gordon et al. 1989; Morris et al. 1993; Owens et al. 1995; Geyer & Long 1998; Holl 1998; Lemieux & Delisle 1998; Davis et al. 1999). Herbs compete with woody species for both below-ground resources (water and nutrients) and above-ground resources (light) (James 1999). Herbaceous plants allocate a larger proportion of biomass to productive tissues as compared with woody seedlings, which results in a larger growth rate (Hunt &

Cornelissen 1997). Therefore, herbs may deplete both below- and above-ground resources much quicker than woody seedlings do during their peak of growth. Acclimation to cope with water and nutrient shortage takes place mainly through an increase in the root:shoot ratio (Joffre et al. 1999 & 2001) and a decrease of the exposed leaf area (Sala et al. 1994; Castro-Díez et al. 1997; Rambal & Leterme 1987; Villar-Salvador 2000; Valladares & Pugnaire 1999). On the contrary, acclimation to low light occurs through the reverse trends (Valladares & Pearcy 1998; Balaguer et al. 2001). Thus, it is apparently impossible to respond to both shortages efficiently (Zavala et al. 2000; Valladares 2001). However, herbs may improve soil properties e.g by transferring carbon from the atmosphere to the soil (Morris et al. 1993).

We assessed the performance of planted *Quercus faginea* subsp. *faginea* seedlings under simulated conditions of different levels of herb competition in abandoned cropland in a Mediterranean region. This species is a major structural component of the native plant communities in many mesic forests in Mediterranean environments. Herb competition is usually mitigated with herbicides, a practice that also eliminates the potential benefits of herbs to the soil. We ask whether the elimination of only above-ground competition could be an effective practice to reduce herb damage on extensive plantations of tree seedlings.

Water has been shown to be an important limiting factor during the establishment of tree seedlings (Canham et al. 1996; Kavanagh and Zaerr 1997; Rousset and Lepart 2000). Our hypothesis is that herb clipping might enhance seedling performance in two ways. First, by reducing herb leaf area, transpiration will decrease and so will do herb water absorption, increasing soil water availability to the seedlings. Secondly, by reducing the radiation shortage that tall herbs impose to tree seedlings, these will be more efficient to acclimate to water shortage by changing their biomass allocation pattern. To test these hypotheses, one-year old *Q. faginea* seedlings were planted under three simulated levels of herb competition: 1) no herb competition, 2) below-ground competition, where herbs were periodically clipped to a maximum height of 8 cm, and 3) full competition. Soil moisture was monitored along the growing season, and the performance of the seedlings was assessed by measuring their mortality and several growth and physiological traits. If seedlings under the clipped herb treatment perform satisfactorily as compared to the total competition treatment, extensive clipping may be an environmentally-friendly technique to be considered as an alternative to herbicides in afforestation projects.

Methods

Study species and site

Quercus faginea subsp. *faginea* is a deciduous oak tree up to 20 m tall which occurs in neutral to calcareous soils of North-western Africa and the Iberian Peninsula ranging between 500 and 1900 m in elevation. On average, *Q. faginea* forests can be found in localities of mean annual precipitation over 500 mm, although the species also grows in drier sites, where topographic and soil properties enhance water accumulation.

The study was conducted in the Juan Carlos I Botanical Garden located in Alcalá de Henares University, central Spain (Longitude 40º35´ N, Latitude 3º25´ W). In the area, the mean annual temperature is 13.5 ºC and the annual precipitation averages 450 mm, with a pronounced summer drought. Total precipitation during the experiment (February to June, 2000) was 179.5 mm, and temperature averaged 14.6 ºC.

The experimental design

Sixty one-year old *Q. faginea* seedlings were individually planted in early February 2000 in polyethylene containers of 40-cm diameter and 80-cm depth filled with the local haploxeralf typic soil according to the Soil Taxonomy System (USDA 1995). Texture characteristics are the following: coarse sand = 5.4%, fine sand = 39.3%, silt = 37.6%, and clay = 17.8% (soil texture class is clayly loam, Bienes & Nieves 2000). The most superficial soil layer (4-5 cm) was rejected to avoid the natural weed seed bank. The seedlings were planted with 20-cm depth plugs. All containers were left outside and exposed to full sunshine. We added 3 l of water per container right after plantation to eliminate soil cavities.

The experiment consisted in three treatments, each with 20 replicates of planted *Q. faginea* seedlings: i) absence of herb competition (AC); ii) below-ground competition from herbs (BGC); and iii) total competition from herbs (TC). The herbaceous community was simulated by sowing a seed mixture that consisted in 15 g of *Lolium rigidum* seeds and 5 g of *Medicago sativa* seeds per container in Mid February. The seed mixture we used guarantees an strong competition effect and a similar herb water extraction in all containers (Kollmann & Reiner 1996; Peñuelas et al. 1996). The seed mixture was not added to the AC treatment. Right after sowing, we added 1 l of water per container to foster seed germination, and another liter of water per container was added one week later. Besides the irrigation right after planting and sowing, we added ¾, 4, ½, and 3 l of water per container at different times during the experiment to avoid excessive soil desiccation in the containers and support plant growth. In the BGC treatment, herbs were periodically clipped since the beginning of April six times, with an average periodicity of two weeks, in order to maintain them below 8 cm above ground, a lower height than the average height of the terminal buds of the *Q. faginea* seedlings when they were planted. For the TC treatment, herbs were left to grow freely.

Measurements

We examined the performance of *Q. faginea* seedlings in the different treatments in five ways: 1) seedling mortality, 2) leaf length and total leaf area, 3) water potential, 4) total biomass and biomass allocation to roots, stems and leaves, and 5) non-structural carbohydrate storage in roots and shoots. We also measured 6) soil moisture at different depths and 7) biomass production of herbs.

The monitoring period extended from mid February through late June when seedlings were harvested. The first leaves were unfolded at mid March in the AC treatment, and they were delayed in the competition treatments.

Seedling shoot mortality was assessed at the beginning of the dry season (mid May) and after a few weeks of the summer drought (mid June). We deemed a seedling as dead if all their aerial shoots were clearly dry, though we are aware that some of these seedlings might be capable of resprouting later under less stressful conditions. Leaf length was measured in all leaves ≥ 5 mm in all seedlings at the beginning of April, before the summer drought. For semi-destructive measurement (3) and destructive measurements (2), (4) and (5), five randomly selected alive seedlings per treatment were sacrificed at mid June. Before the sacrifice, pre-dawn and mid-day leaf water potential were measured using a Scholander´s chamber. Then the seedlings were taken to the laboratory and were fractioned into the following parts: leaves, stems, and roots. The total fresh leaf area was measured with a delta-T leaf area meter. Roots were gently washed and the three plant fractions were kept in an oven at 80 ºC for 48 h before weighing. The roots were also incinerated at 550 ºC and the ash weight was subtracted to eliminate the weight of mineral residuals. Then, we measured total biomass and the proportion of biomass allocated to leaves, stems, and roots.

Glucose and starch concentration in root and shoots (pooled stems and leaves) was also determined. We could not differentiate stem and leaf tissues because leaf samples were too small to assess carbohydrate concentration. Plant material was collected in the field at dawn and transported to the laboratory in a refrigerated box. There it was oven-dried at 60 ºC for three days and then ground with a Culatti mill through a 0.5 mm-mesh screen. Monosaccharides and disaccharides were extracted with hot ethanol. Approximately 7 ml of 95% ethanol were added to 50 g of the sample in a Pyrex tube and warmed to 80 ºC for 90 minutes, shaking periodically. Then the extracts were separated by centrifugation and the residue re-extracted. The ethanol was removed from the extract by evaporation. The rest of the non-structural carbohydrates contained in the residue (oligosaccharides and starch) were broken to monosaccharides through an enzimatic procedure. Six ml of acetate buffer (pH = 4.5) containing 5.6 units α-amilase and 0.4 of amylo-glucosidase were added to the dry residue and left at 45 ºC for 24 hours. The liquid extract containing the sugars was then separated by centrifugation. The monosaccharide content of both extracts was colorimetrically assessed using the DuBois et al. (1956) method. The dry extract resulting after ethanol evaporation was dissolved on 2 ml of acetate buffer. Two aliquots of both solutions (from the ethanol and the enzimatic extractions) were dissolved in distilled water to a final volume of 1 ml. Then 1 ml of 5% phenol and 5 ml of concentrated sulfuric acid were added to each tube. In presence of the acid, phenol reacts with the monosaccharides producing a colored product whose absorbance at 483 nm is proportional to the sugar concentration.

Soil moisture was measured four times (mid March, twice in May and mid June) at 15, 30, and 45 cm depth using the TRIME-method, an specially designed TDR technique (IMKO, Micromodultechnik company). Clipping was performed on the twenty BGC containers every ca. two weeks since the beginning of April, up to a total of six clippings. The clipped herb biomass was dried at 80º C and weighed to estimate the accumulated aerial herb production.

Data analysis

Because a major difficulty in experiments with young plants is the variability in plant size, we first tested if there were differences among treatments in seedling height and stem diameter right after plantation took place. The ANOVA indicated that both measurements were not different among treatments ($F_{2,57} = 1.297$, $p = 0.29$ and $F_{2,57} = 0.926$, $p = 0.4$, respectively). The initial size of the seedlings was the following: height (cm) = 21.22±11.36 SD, and stem diameter (mm) = 6.04±12.36 SD. In order to obtain a reference value of the initial seedling weight, 10 non-planted seedlings were weighed prior to the experiment and they averaged 8.4 g ±1.07 SD.

Statistical analyses were based upon χ^2 to test the effects of treatments on seedling mortality, and ANOVA and Kruskall-Wallis to test the effects of treatments on the rest of the above mentioned measures, including a repeated measure ANOVA for testing differences in soil moisture. We also correlated the amount of accumulated herb biomass production with both the soil moisture at different depths and with the average profile moisture for the BGC treatment.

Results

Soil moisture

A repeated-measure analysis of variance indicated significant effects of the competition treatment, soil depth, and time on the soil moisture (Table 1). Soil moisture progressively decreased along the growing period, and this decrease was more pronounced in the presence of herbs (Fig. 1). The differences in soil moisture between the BGC and TC treatments were usually smaller than those found between the AC and BGC treatments, these differences decreasing with depth across the soil profile (Fig. 1).

The relationship between the accumulated amount of herb biomass production and the average moisture across the soil profile in the BGC treatment at the end of the experiment (Pearson´s r=-0.58, P=0.03, n=20) suggests that herb production reduced water availability to *Q. faginea* seedlings. This reduction was most pronounced at 45-cm depth (Pearson´s r=-0.64, P=0.01, n=20) and least at 15-cm depth (Pearson´s r=-0.4, P=0.1, n=20).

Seedling mortality

The results of the two mortality counts indicated significant effects of competition treatments. Right after the start of the dry season, all seedlings in the control treatment were alive, while 7 out of 20 seedlings presented their aerial parts dry in both the BGC and TC treatments (χ^2=22.9, P=0.001, df=5). At that time herb clipping had been practiced four times in the BGC treatment. At the end of the experiment, all seedlings but one in the AC treatment were alive, while 13 out of 15 seedlings died in the BGC and TC treatments (χ^2=26.7, P=0.0001, df=5).

Growth, biomass partitioning, and physiological traits

One of the earliest observations in our experiment was that the new leaves of the seedlings in the AC treatment were significantly larger than those under competition from herbs (mean leaf length at early April in AC was 18.7 mm ±9.22 SD, and it averaged 15.38 mm ±7.27 SD in the competition treatments; $F_{1, 37}$=5.9, P=0.01). At that time clipping had not been performed yet in the BGC treatment because herbs did not attain 8 cm in height; thus, this observation was an effect of below-ground competition. The differences in average total plant leaf area at the end of the experiment were not significant (Table 2a; Kruskal-Wallis K=2.14, p=0.34).

Pre-dawn and mid-day water potential were different among competition treatments. Seedlings in the TC treatment were more water-stressed than those in the BGC or AC treatments according to post-hoc tests (Fig. 2a and b).

Total seedling biomass was not different among treatments (Table 2b; $F_{2,12}$=0.74, p=0.5). Dry matter of survivors at the end of the experiment averaged 8.48±2.53 g, and it represented an increment of 0.08 g as compared to the reference value at the beginning of the experiment (see *Data Analysis*). The proportion of biomass allocated to leaves, stems, and roots among treatments resulted in marginal differences ($F_{2,12}$=3.1, p=0.08) only in biomass allocated to leaves, and it followed the rank TC < BGC < AC (Table 2c). The allocation to stems and roots resulted in non-significant differences among treatments (Table 2d and e, $F_{2,12}$=2.53, P=0.11 and $F_{2,12}$=1.62, P=0.24, respectively).

Competition treatments significantly affected the glucose concentration in both shoots and roots, following the rank TC > AGC > AC in both plant compartments (Fig. 3a and b). Differences in starch concentration among treatments did not appear for shoots (Table 2f, Kruskall-Wallis K=2.14, p=0.34) and marginally appeared for roots (Table 2g, $F_{2,12}$=2.72, P=0.106), and in both cases it tended to be larger for the BGC treatment.

Discussion

We found significant differences among treatments related to soil conditions and seedling performance evaluated as mortality, growth, and physiological responses. Overall, our data indicate that, for the conditions of our experiment, which are representative of fertile and recently abandoned cropland in Mediterranean environments, herbs strongly compete with *Q. faginea* seedlings. Nevertheless, plant interactions are dynamic relationships and positive and negative interactions act simultaneously, the outcome depending on abiotic conditions (Berkowitz et al. 1995; Holzapfel & Mahall 1999, Pugnaire & Luque 2001). Actually, other studies have shown facilitation or neutral processes of herbs in the recruitment of woody species in environments under more severe abiotic conditions (e.g. less water availability and higher radiation inputs) and less herb density (Rejmanek & Leps 1996; Brown & Archer 1999; Paez & Marco 2000).

Soil moisture

Herbs reduced soil moisture, mainly in the TC treatment. In addition, the amount of herb biomass produced in the BGC treatment was negatively correlated with soil moisture. These patterns suggest that a larger amount of standing crop transpired more water and hence provoked the reduction in soil moisture. This moisture reduction increased along the growth period, when shortage of water and temperatures are higher. The profile of soil moisture indicates that increased transpiration from herbs outweighed the reduction of evaporation from soils due to shading by herbs (Rey Benayas et al. 2002).

Differences in soil moisture between the BGC and TC treatments were very small one month after the beginning of the experiment, when much of the soil water might have been invested in germination of herb seeds and their immediate growth (López-Pintor et al. 2000; Rebollo et al. 2001), and at the end of it, when soil water was already so low that provoked a severe herb and seedling mortality (Fig. 1). This desiccation effect has been widely observed in numerous studies on the influence of herb competition on the establishment of woody seedlings (Knoop & Walker 1985; Zutter et al. 1986; Gordon et al. 1989; Kolb & Robberecht 1996; Harrington 1991). Henkin et al. (1998) also found that soil water depletion during the spring-summer transition period left very little water availability in the rooting zone of the herbaceous vegetation to sustain the demands of woody seedlings throughout the summer.

Seedling response to the competition environment

The pattern of soil moisture in the competition treatments may explain in part the differences in water potential found in *Q. faginea* seedlings (Fig. 3 a and b). Both the pre-dawn and mid-day water potential of the seedlings subjected to the AC and BGC treatments were substantially higher that those of the seedlings in the TC treatment, where water availability was the lowest. This means that the clipping treatment ameliorated the water stress of the seedlings.

However, the BGC and TC treatments did not differ in seedling mortality. In other words, the elimination of aerial competition from herbs did not translate into more survival of planted *Q. faginea* seedlings at the beginning of the dry season. Similarly, Brown et al. (1998) imposed different levels of grass clipping intensity (no clipping, clipped to 5 cm and clipped to 25 cm) and did not find any effect on shrub seedling survival. In our case it is more likely that competition is mostly for water since the plantation substrate is not infertile. Anderson et al. (2001) found that competition for water was a key mechanism in oak-understory interactions. Henkin et al. (1998) suggested that the success of woody seedling establishment mainly reflected the accessibility of water below the rooting zone of the herbaceous vegetation. Rey Benayas et al. (2002) obtained the same result for planted *Retama sphaerocarpa* seedlings in the same type of habitat than the one studied here. However, these authors found a positive effect of weed clipping on seedling survival in early autumn. The subterranean parts of both plant species easily resprout when their aerial biomass is removed and conditions are not extremely severe. Hill et al. (1995) found that the duration of competition was more important than the initial intensity of competition in determining tree establishment. Some differences between the BGC and TC treatments might have appeared in a longer experiment if seedling roots in the BGC treatment were vigorous enough to sprout. Other studies in different parts of the world have highlighted the importance of weed clipping and herbicide treatments for the success of afforestation practices (Raza 1993; Flemming & Wood 1996; Peñuelas et al. 1996; Holl 1998; Imo & Timmer 1998 and 1999).

The early observation of reduced leaf length in the BGC and TC treatments was an effect of below-ground competition. We also found consistencies in the competition treatment ranking for total plant leaf area and biomass allocated to leaves. Both the lower size of the new leaves and the lower proportion of biomass allocated to leaves are mechanisms to reduce transpiration. One would expect an inverse relationship between biomass allocated to leaves and roots that may constitute further evidence of the trade-off in the development of plant tissues aimed at capturing different limiting resources (Tilman 1998; Lewis & Tanner 2000; Zavala et al. 2000; Valladares 2001). However, neither the differences in total plant leaf area nor biomass allocated to roots between competition treatments were significant, may be due to the short duration of our experiment or because *Q. faginea* has a low response to water stress at the root level as it has been observed for *Q. ilex* (Villar per. com.). Sack & Grubb (2002) found that watering frequency, i.e. drought intensity, did not significantly alter biomass allocation across three irradiance treatments in seedlings of four Mediterranean species. They claim that "*such orthogonal impacts of deep shade and drought on seedling growth and biomass allocation indicate a large potential for niche differentiation at combinations of irradiance and water supply for species of forest seedlings*".

The pattern of glucose concentration is in agreement with the patterns of soil moisture and water potential (Fig. 3 a and b). The accumulation of monosaccharids in leaf vacuoles during water-stress periods may contribute in some plant species to decrease their leaf osmotic potential, enhancing water extraction from dry soils (Gebre et al.

1994; Épron & Dreyer 1996; Clifford et al. 1998). Thus, the observed increase in shoot glucose concentration in the BGC and TC treatments may reflect that *Q. faginea* seedlings compensate a lower water availability with osmotic adjustment.

The allocation of carbohydrates to starch is expected to be enhanced by environmental limitations to tissue growth (Bloom et al. 1985; Herms & Mattson 1992) such as resource depletion by herb competition. All seedlings exhibited about three times more starch concentrations in roots as compared with their shoots (Table 2d). The smaller differences in starch concentration among treatments as compared to the glucose content have two explanations. First, it may be due to the slower response of starch biosynthesis to stress, so that more than one growing season is necessary to find divergence among treatments. And secondly, a fraction of the original starch concentration may have been excised into glucose as competition intensity increases (Épron & Dreyer 1996). The maximum starch concentration in the BGC treatment can be explained as follows. The most favorable environment (AC) would have favored the allocation of current assimilation to present growth, while a moderate resource limitation (BGC treatment) would limit tissue growth, but not carbon assimilation, the excess of carbon being invested in carbon-rich compounds such as starch (Herms & Mattson 1992). On the other hand, the strong above- and below-ground resource limitation imposed by the TC treatment severely limits carbon assimilation through both water and light shortages, so that plants cannot accumulate starch.

Conclusions and implications for plantation management

We conclude that the negative effects of herbs in the establishment of *Q. faginea* are primarily a result of competition for water, as indicated by the soil water availability and the same seedling mortality in the BGC and TC treatments. This competition effect is noticeable since the earliest stages of the establishment, right after planting, as pointed out by the smaller leaves of the seedlings under below-ground competition. Some remarkable responses in seedlings under below-ground competition conditions are a water potential similar to that of the seedlings grown in absence of herb competition, an increase in glucose concentration that may favor water extraction from soils, and an accumulation of starch that may provide them a reserve for facing future harsh conditions. However, in our experiment these features did not translate into fewer dead seedlings in the BGC treatment as compared to the TC one. These apparently dead seedlings may resprout in the following favorable growth period, in agreement with the observations of Rey Benayas (1998) for *Q. ilex* seedlings.

For management of *Q. faginea* plantations in abandoned Mediterranean cropland, we conclude that it is necessary that the introduced seedlings of this species take advantage of a low competition environment from herbs during the favorable period before the dry season (Paez & Marco 2000). In response to our question, clipping of weeds around the seedlings is not a technique that improves seedling survivorship in the short term (first growth season), and herbicide application before weed proliferation would provide better results. Consequently, further research is necessary to analyze the trade-off between the pursued environmental benefit (seedling establishment) and the potential risk of soil and water pollution, and alternatives such as weed hoeing must be tested.

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Table 1. Results of a repeated-measure analysis of variance used to test the effects of the herb treatment, soil depth, and time on soil moisture.

Effect	df Effect	df Error	F	p-level
Herb competition	2	60	127.4	0.0001
Soil depth	2	60	13.2	0.0001
Time	3	180	133.7	0.0001
Herb competition*soil depth	4	60	2.2	0.08
Herb competition*time	6	180	58.8	0.0001
Soil depth*time	6	180	3.1	0.006
Herb competition*soil depth*time	12	180	3.9	0.0001

Table 2. Values (mean±SD) in the three competition treatments of a) Average total leaf area; b) Total seedling biomass; c-e) Proportion of biomass allocated to leaves, stems, and roots, respectively; f-g) Starch concentration for shoots and roots, respectively. Differences for these values among treatments are never different at $P<0.05$.

	Absence of competition	Below-ground competition	Total competition
a) Average total leaf area (cm^2)	65.33±52.47	44.72±19,32	23.0±28.55
b) Total seedling biomass (g)	9.48±2.76	8.47±2.05	7.49±2.86
c) Proportion of biomass allocated to leaves	8.11±3.62	6.72±2.33	3.62±2.65
d) Proportion of biomass allocated to stems	10.06±2.54	16.12±5.33	13.4±4.44
e) Proportion of biomass allocated to roots	81.83±5.45	77.16±5.35	82.99±5.44
f) Starch concentration for shoots (mg/g)	59.79±6.04	61.23±25.75	51.74±9.29
g) Starch concentration for roots (mg/g)	174.06±54.36	223.52±48.4	147.71±53.65

FIGURE LEGENDS

Figure 1. Variation of soil moisture with herb treatment, soil depth, and time. Symbols for treatment are the following: open squares = absence of competition; filled circles= below-ground competition; filled triangles = total competition. Time notation is the following: t1 = March 15th, t2 = May 5th, t3 = May 22nd, and t4 = June 29th. Note that every point in the graph is the average of 20 measurements.

Figure 2. Variation of (A) pre-dawn and (B) mid-day water potential with herb treatment. Pre-dawn comparisons between treatments are based on Mann-Whitney´s U post-hoc test: (nominal P-value<0.05). Mid-day comparisons between treatments are based on Tukey´s post-hoc test (nominal P-value<0.05).

Figure 3.- Variation of glucose concentration in (A) shoots and (B) roots with herb treatment. Comparisons between treatments are based on Mann-Whitney´s U post-hoc test (nominal P-value<0.045).

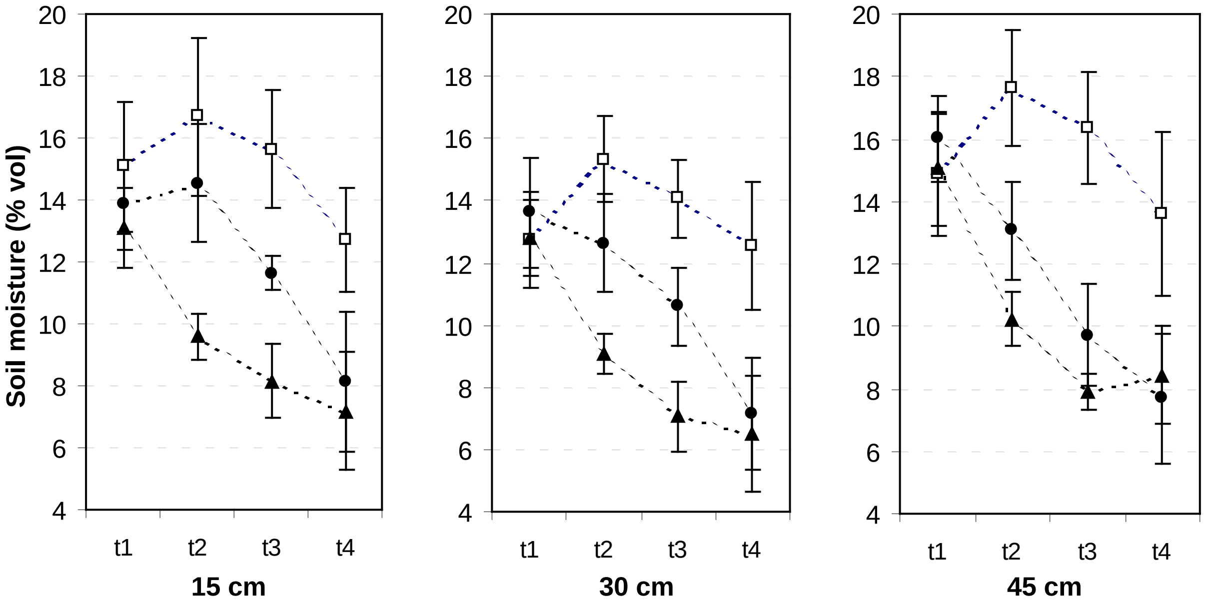


Figure 1

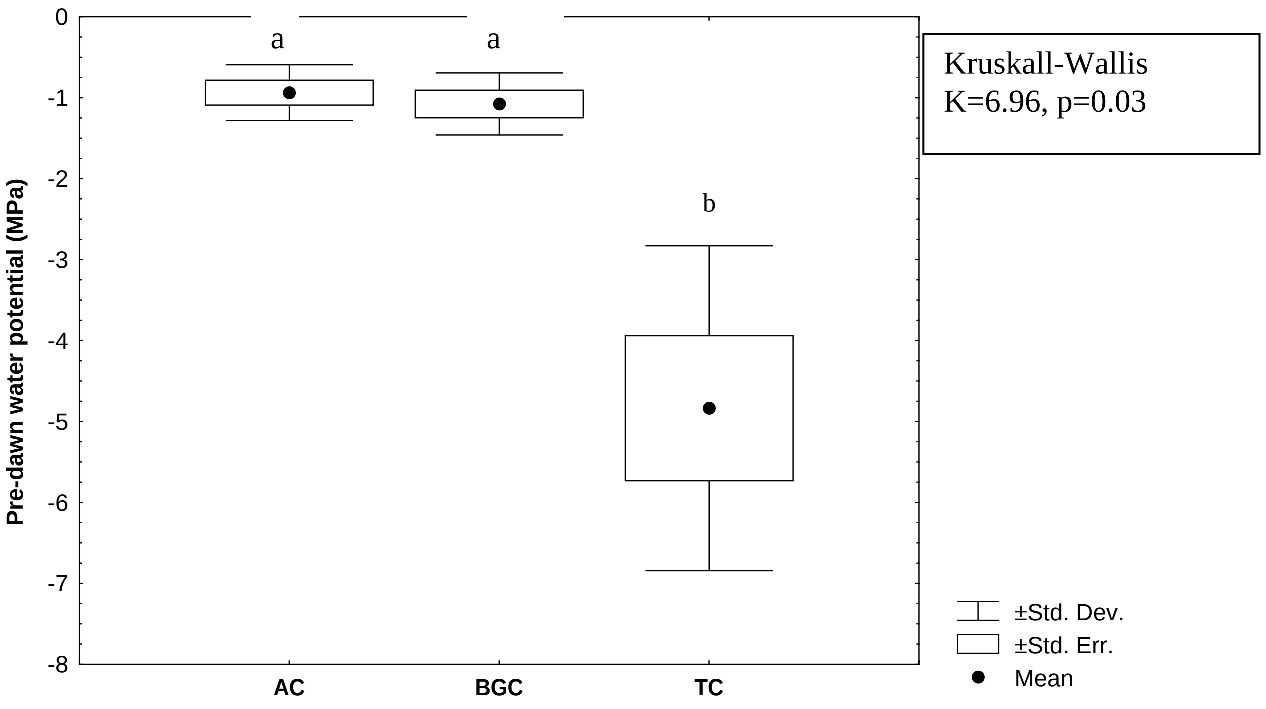


Figure 2A

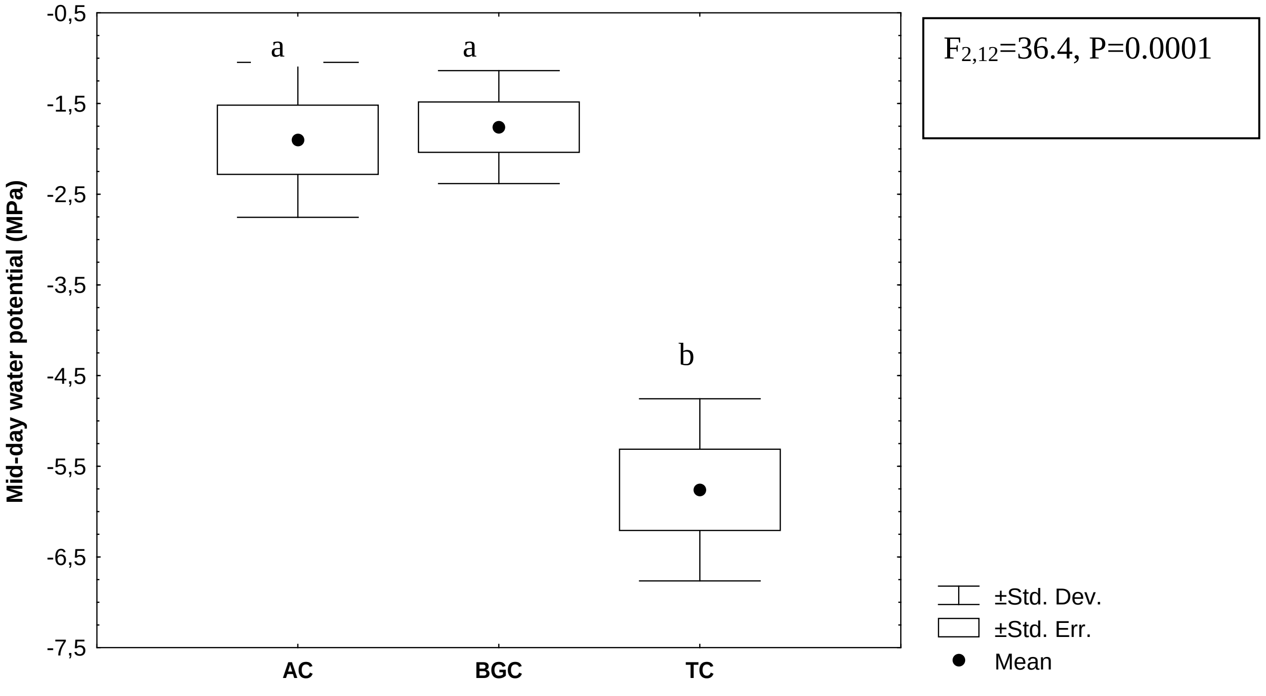
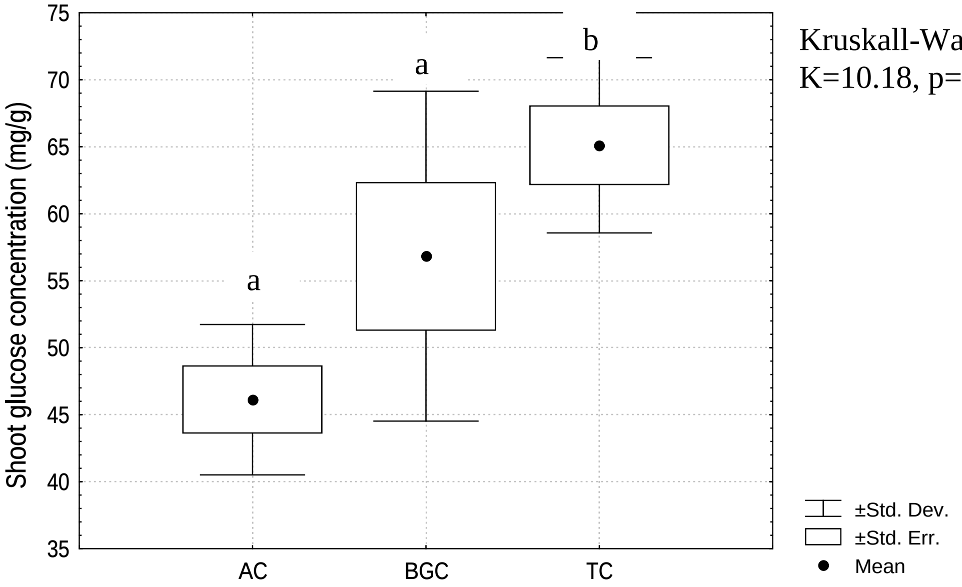
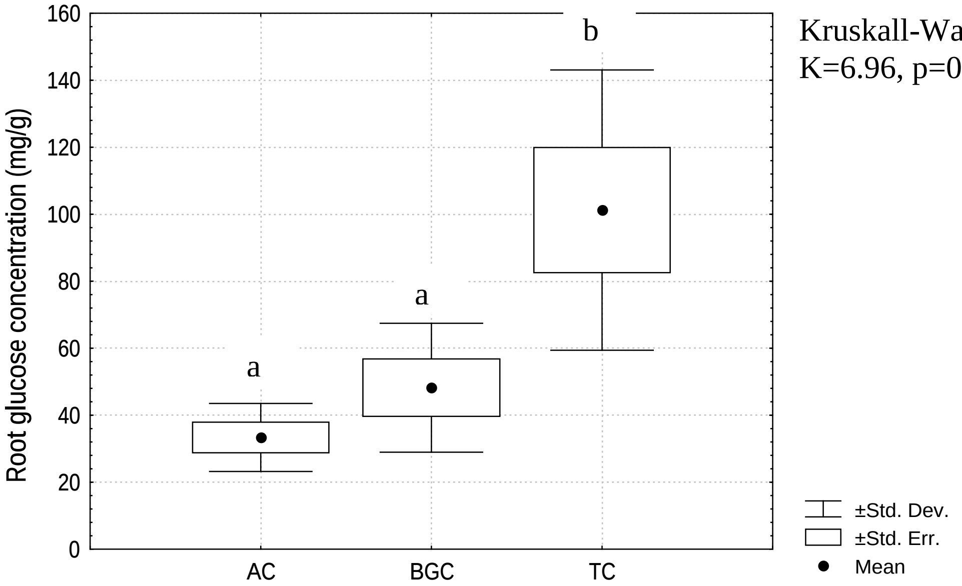


Figure 2B



Kruskall-Wallis
K=10.18, p=0.006

Figure 3A



Kruskall-Wallis
K=6.96, p=0.03

Figure 3B