

The impact of ungulate browsing on black locust competitive abilities in a temperate oak forest

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Összefoglalás: Abstract: Invasive species such as black locust (*Robinia pseudoacacia*) cause several problems in conserving semi-natural forests in Europe. The selective browsing of ungulates can be a prominent regulating factor in the spread of black locusts. We set out a 4 year-long experiment in a fenced area of a Turkey oak (*Quercus cerris*) – sessile oak (*Quercus petraea*) forest in Hungary to 1) evaluate short-term responses of black locust saplings to simulated browsing; 2) identify the effects of browsing and soil conditions on the competition between black locust and oak saplings. We hypothesized that clipping treatments would reduce the growth and vitality of black locusts and indirectly enhance oak sapling development. Vegetation patches were designated to separate oak saplings with treated and intact black locust saplings, and without black locust. After the first round of treatments in September 2014, clipped black locusts compensated for height and shoot loss. The summer drought in 2015 reduced the survival of black locusts independently of the clipping and many saplings disappeared from previously occupied plots. In addition, the effects of the second clipping treatment in September 2015 have significantly slowed down, even hindering further growth of the clipped saplings. Soil nitrogen level was not higher in black locust plots, but low pH and significant soil compaction could be limiting factors for all saplings. Our results did not confirm any significant inhibitory effect of black locust on oak sapling development, but sessile oak had increased height growth compared to Turkey oak in black locust plots. It seems that browsing is only a secondary factor that influences the growth and competitiveness of black locusts since only repeated browsing after a heavy drought period could prevent black locust saplings from compensating for their losses.

Introduction

The concept of Potential Natural Vegetation (PNV) describes the expected state of mature vegetation in the absence of human intervention (Chiarucci et al. 2010). Different species of animals and plants interact with each other for a long time creating ideal conditions for living (Oliver et al. 1998, Silaeva et al. 2021, Åberg et al. 2003); however, several threats can

arise in this process. The spread of non-native species raises an increasing awareness of nature conservation issues in times of global climate change (Burgiel and Muir 2010). Among them, woody plant invasions are rapidly increasing in importance around the world containing 357 trees and 265 shrub species (Richardson and Rejmánek 2011). One of the biggest challenges in Europe is linked to the invasive black locust (*Robinia pseudoacacia*), since almost all countries, in which the tree species was successfully established, underwent a phase of large-scale cultivation and afforestation (Vítková et al. 2020). It occurs in forty-two European countries and is the most common broadleaved tree species on the continent, accounting for more than 200,000 ha in Hungary, Ukraine, Poland, Romania and Italy (Nicolescu et al. 2020); its proportion of the entire forested area is the highest in Hungary (Erdős 1999). Black locust has outstanding economic importance in those countries; however, they also pose a serious ecological threat to forest naturalness (Katona et al. 2013).

In its native range, the black locust is often a component of mature mesophytic forests; it makes up a majority of the stand during early stages but is short-lived and seldom matures to a sawtimber stand, thereby only forming a small part of the ultimate canopy layer (Huntley 1990). While in its exotic range, it can easily overgrow native major tree species such as oaks (*Quercus* spp.) or beech (*Fagus sylvatica*), and degrade forest habitats by its superior competitive abilities: fast growth, vegetative sprouting, nitrogen fixation, allelopathic effects (Benesperi 2012). Due to its ideal fiber/protein ratio, the shoots of black locust are valuable feed for ungulate herbivores; mostly preferred from late spring to early autumn based on the findings of Mátrai et al. (2004). Consequentially, ungulates can play a crucial role in regulating black locust invasion and their selective browsing can decelerate the penetration of this species into native forest habitats (Katona et al. 2013, Mátrai et al. 2004). However, our previous study revealed that their saplings tolerate ungulate browsing well (Fehér and Katona 2003), therefore black locusts can often escape from continuous herbivore pressure.

The impact of ungulate browsing on sapling development and forest regeneration induces a debate among different stakeholders, such as forest and game managers and nature conservationists (Graham et al. 2010). Besides ungulates and the pattern, intensity, timing, and recurrence of their browsing, the abiotic conditions, plant competition intensity and specific adaptiveness also determine plant responses (Kullberg and Welander 2003). The specific traits of black locust to resist ungulate herbivory have a great significance in the success of the species within its non-native range. All main plant anti-herbivore strategies (Belsky et al. 1993) are combined in black locusts, such as escape mechanisms by fast growth; physical defense by developing spines; and tolerance by compensating or overcompensating the loss caused by ungulate browsing. These diverse strategies are complemented by allelopathic traits (Nasir et al. 2005) and nitrogen fixation (Moshki and Lamersdorf 2011) making way for the considerable spread of black locusts in European temperate forests.

Moderate selective browsing (i.e., preference towards black locust, some shrub species and avoidance of oak) can have a profound beneficial impact on vegetation development and species composition of native oak forest understory (Katona et al. 2013), mitigating black locust penetration and spread in native forests. However, in other cases, a positive

correlation between the ungulate presence and invasion of non-native browse-tolerant woody plants was also reported (Shen et al. 2016). De-spite its increasing importance, black locust has not been studied in this context, yet.

Our aim in this short-term (4-year) study was to: 1) evaluate the short-term responses of black locust saplings to simulated browsing treatments; 2) identify the effects of simulated browsing and soil conditions on competition between black locust and oak saplings.

We hypothesized that 1) clipping treatments will reduce the growth and vitality of black locust saplings; 2) soil nitrogen levels will be higher near black locust saplings; 3) development of sessile oak (*Quercus petraea*) and Turkey oak (*Quercus cerris*) saplings will be reduced in proximity to black locust saplings; 4) oak sapling development will be higher in those plots where black locust saplings were affected by clipping treatments compared to plots where they were left intact.

Materials and methods

Study area

Field surveys took place in a 40-year-old even-aged Turkey oak-sessile oak forest (*Quercetum petraeae-cerris*) in the forest compartment 17/A of settlement Apc in Heves County, at the SW side of Mátra Mountains (North Hungarian Range Region, according to Csorba et al. 2018), Hungary (Figure 1 - 47°49'0.2" N; 19°42'59" E). Sessile oak and Turkey oak had the highest standing volume (43% and 33%, respectively), but black locust (13%) and northern red oak (*Quercus rubra* – 11%) were also important.

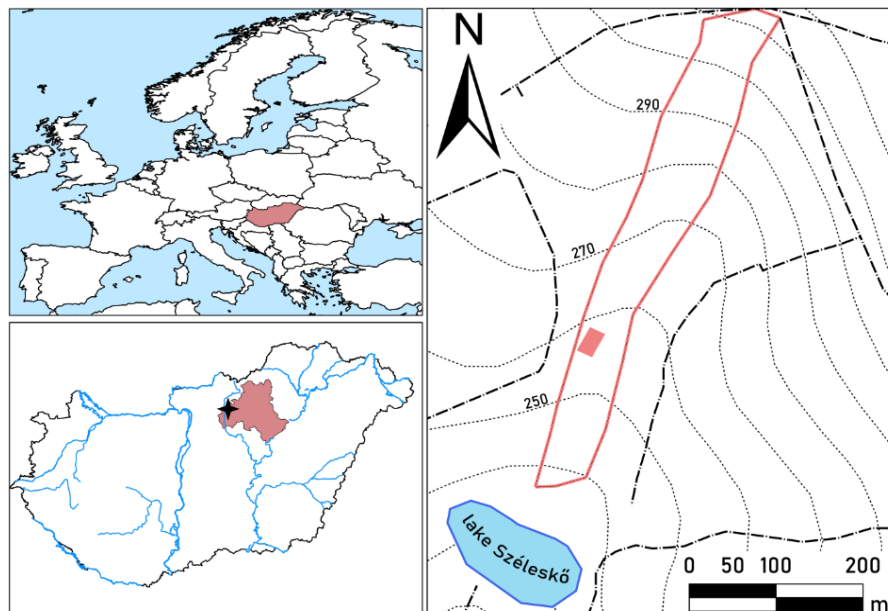


Figure 1. The location of the study site in Hungary is in Heves County (bottom left), and the enclosure is in the forest compartment 17/A (indicated with a red rectangle on the right)

1. ábra. A vizsgálati helyszín elhelyezkedése Heves megyében (balra lent) és a 17/A erdőrészletben (jobbra, a vadkizáró kerítés területe piros téglalappal jelölve)

The average stand height was 15 m and the average canopy closure exceeded 80%. Due to even-aged management, the forest structure was relatively simple. Field maple (*Acer campestre*) was the most common tree species in the understory. Saplings and young individuals of sycamore maple (*Acer pseudoplatanus*), Tatar maple (*Acer tataricum*), field elm (*Ulmus minor*), manna ash (*Fraxinus ornus*), European hornbeam (*Carpinus betulus*) and European wild pear (*Pyrus pyraster*) were sporadic. Shrubs including blackthorn (*Prunus spinosa*), hawthorns (*Crataegus monogyna* and *Crataegus laevigata*), bramble (*Rubus caesius* and *Rubus fruticosus*), common spindle (*Euonymus europaeus*), dog rose (*Rosa canina*) and wild privet (*Ligustrum vulgare*) formed a mixture with tree saplings. Black locusts occupied an increasing area in the understory at the western side of this 3.9 ha large stand and several nitrophilous herbs occurred in these patches such as black horehound (*Ballota nigra*), greater celandine (*Chelidonium majus*) or red dead-nettle (*Lamium purpureum*).

Lithomorphous and brown forest soils (Cambisols) are common in the area on andesite bedrock. However, the site-specific soil analysis (Fehér et al. 2014) found strong acidity, shallow humus layer, and deep E and B horizons; thereby the local soil type was rather Luvisol. The whole forest stand was situated on a steep slope (5–10°) facing E-SE. Ungulate species including red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), and mouflon (*Ovis musimon*) were common large game here; mouflon could be found often in high density due to favorable habitat conditions.

Simulated browsing

The advantage of simulated browsing over directly surveying browsed saplings is that the intensity, timing and frequency of browsing are known and fully controllable. We selected only intact and healthy saplings as subjects for our experiments. To exclude interfering effects of ungulate herbivory during simulated clipping experiments, a 460 m² large enclosure was built using a 1.8 m high, hinge joint high tensile steel fence around forest patches where both black locust and oak saplings (under 1 m in height) were prevalent under the mature stand which ensured regular seed and acorn production. The site was partitioned into 1 m² large sampling plots/quadrats to locate tree saplings properly during the study considering a 0.5 m wide edge effect of the fence at the boundaries (N = 413, approx. 30 m x 14 m effective size). Three types of vegetation patches were designated in the enclosure: 1) Treated Locust Plots (TLP): plots with clipped black locust saplings and unclipped oak saplings near-by; 58 black locust, 27 sessile oak and 30 Turkey oak saplings in 100 quadrats; 2) Control Locust Plots (CLP): plots with control (unclipped) black locust saplings and oak saplings nearby; 63 black locust, 52 sessile oak and 50 Turkey oak saplings in 126 quadrats; 3) Control Oak Plots (COP): plots where only oak saplings were found; 22 sessile oak and 41 Turkey oak saplings in 69 quadrats. Our main priority during the spatial arrangement of the patches was to ensure equal sample size for the clipped and non-clipped (control) black locust saplings; provide sufficient oak saplings for statistical inference in all patches

and harmonize these expectations with the real spatial distribution of the saplings. Furthermore, the plots of each vegetation patch were arranged by slope direction to compensate for the potential small-scale differences in soil attributes between the slope top and slope bottom, since preliminary results of soil core sampling showed different topsoil thicknesses between those locations (Fehér et al. 2014). Black locust and oak saplings were visually marked by vinyl tapes of various colors with unique codes on them to identify each sapling correctly.

Only black locust saplings were clipped. Their mean height was 51.1 ± 36 cm ranging from min. 12 cm to max. 168 cm in TLP before the treatments. Simulated browsing treatments were conducted twice: in September 2014 and 2015. The leader and 50% of lateral shoots (i.e., twigs) of all black locust saplings were clipped in the TLP plots. We aimed to simulate an intense and strong browsing disturbance by these treatments right after the most intensive seasonal growth stage of the saplings (reducing the possibility for compensatory growth). Stump sprouts were excluded from the study as investigated individuals. We registered the biometric data of treated black locust saplings and control saplings (black locust, sessile oak, and Turkey oak) in all vegetation patches seasonally: sapling height, basal diameter at ground level, shoot density, leaf density, spine density (for black locust) for 4 years (until August 2018). We used a tape measure for height measurement and a caliper for measuring basal diameter. The compound leaves of black locusts were counted instead of leaflets. Leaf density and spine density were reported relative to the actual shoot density, thereby expressed as a ratio of the number of leaves or spines divided by the total number of shoots. Seasonal mortality of black locust and oak saplings was also registered. We calculated the changes in the biometric data of each sapling between consecutive observations. The magnitude of these changes was interpreted as growth intensity (i.e., the amount of height-, shoot-, leaf-, spine gains or loss).

The growth intensity of black locust and oak saplings were compared by non-parametric tests among vegetation patches (Mann-Whitney U-test for two independent groups and Kruskal-Wallis test with Dunn's post hoc test for more than two independent groups) using GraphPad Prism ver. 6.01 after testing for normality with Shapiro-Wilk test. To reveal existing differences at the meaningful time points of the experiment (before-after clippings) we performed a Wilcoxon matched pairs test.

The full-time response of black locust saplings to clipping treatments and oak saplings to black locust presence was evaluated by using linear mixed models (LMM) in the case of height data, and generalized mixed models (GLMM) in the case of shoot, leaf and spine density data in R (R Development Core Team 2019) with the glmmTMB package (Brooks et al. 2017). We handled height as normally distributed data and the other biometric parameters as Poisson distributed data, using the shoot density as an offset term in the case of leaf and spine density. The sampling plots were integrated into the models as random effects and autoregressive temporal autocorrelation (AR1) was used due to repeated measures. Model selection was performed with ANOVA likelihood ratio test and diagnostics with the packages DHARMA (Hartig 2022) and performance (Lüdecke 2021). Sapling survival in the different patches was evaluated

by using the mixed effect Cox model (proportional hazards model) from the Coxme package (Therneau 2022) and reported in hazard ratio with its 95% confidence interval. A hazard ratio above 1 indicates a covariate that is positively associated with the event (mortality) probability, and thus negatively associated with the length of survival (Kassambara 2020).

Field soil test and laboratory analysis

We used a Pürckhauer-type core sampler for soil profile description (N = 13) and took soil samples from the upper 25 cm layer of the soil profile for laboratory analyses (N = 17) within the enclosure in autumn 2014. Laboratory analyses included measurements regarding the major nutrient (N, P, K) and organic matter content (humus and total organic carbon), soil pH, Arany-type plasticity index (KA) and hydrolytic acidity (y1) (Kátai 2013). We performed the Kruskal-Wallis test with Dunn's post hoc test on the measured data to find potential differences among the vegetation patches.

Results

Impact of simulated browsing on black locust saplings

The average biometrical values of black locust saplings in TLP and CLP did not differ from each other before the experiments, with one exception: the pretreatment shoot density was significantly higher (Mann-Whitney U-test: $U = 644$, $n_1 = 58$, $n_2 = 63$, $p < 0.001$) for control saplings (CLP: 5.37 ± 4.4) than saplings that were marked out for the later clip-ping in TLP (1.76 ± 1.5) (Figure 2).

No significant height difference was revealed between TLP and CLP saplings after the first treatment (after September 2014). Only the second clipping treatment in September 2015 reduced the height growth of clipped saplings compared to controls through November 2015 (TLP: -6 ± 6.7 cm vs. CLP: -0.6 ± 20.5 cm; $U = 506$, $n_1 = 39$, $n_2 = 48$, $p = 0.0002$).

The reduced growth of clipped saplings faded until March 2016 (TLP: -0.6 ± 5.8 cm vs. CLP: -1.7 ± 12 cm; $U = 581$, $n_1 = 35$, $n_2 = 44$, $p = 0.07$). However, a significant height growth reduction was found in the TLP saplings relative to the CLP ones when the full-time trend was analyzed with mixed modeling, and the estimated height growth loss was more than 20 cm in the treatment group (Table 1). Shoot development was also reduced after the second clipping treatment by November 2015 (TLP: -1.2 ± 1.9 ; Wilcoxon matched pairs test: $W = -302$, $p = 0.001$) and March 2016 (TLP: -0.5 ± 1.2 ;

$W = -137$, $p = 0.003$) compared to the previous time points. The cumulative loss of these periods was nearly equal to the amount that was compensated by TLP saplings in the first year of the experiment in August 2015 (TLP: 2.4 ± 3.4), but the majority of clipped saplings compensated for their losses again in May 2016 (Figure 2B).

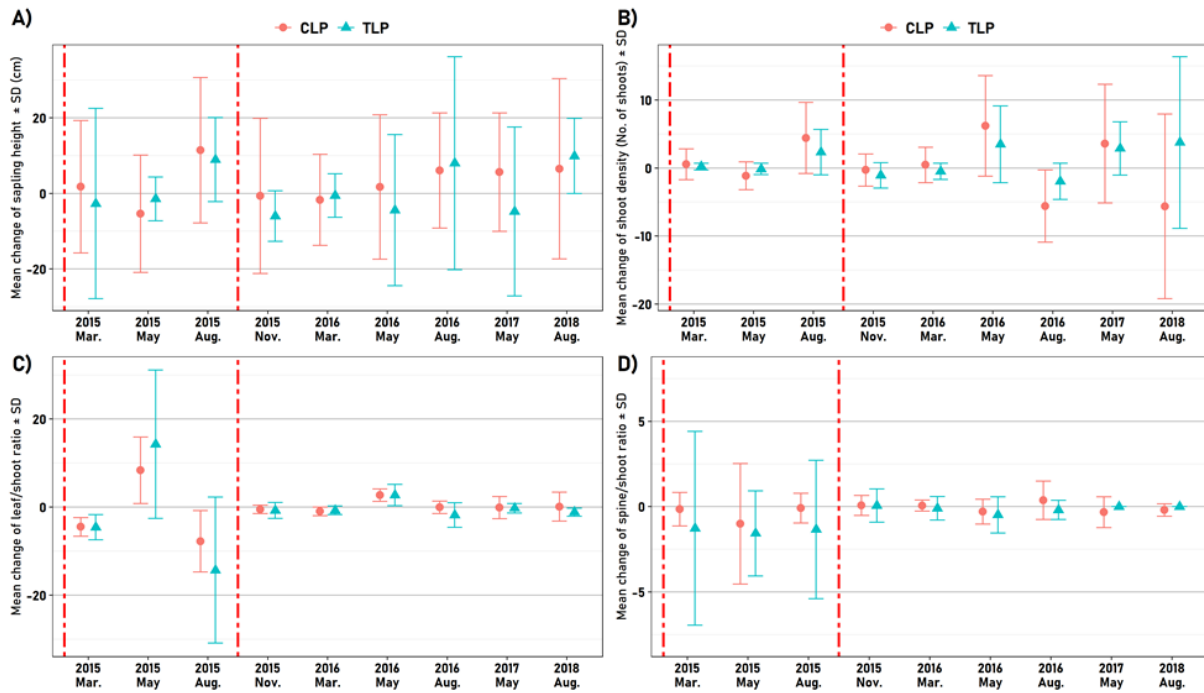


Figure 2. Average changes between consecutive time points in height (A), shoot density (B), leaf density (C) and spine density (D) of black locust saplings in different vegetation plots inside the enclosure. Red dashed lines indicate the time of simulated browsing. CLP: control saplings (n = 63) in control black locust plots, TLP: clip-ped saplings (n = 58) in treated black locust plots

2. ábra. Az akáccsemeték magasságának (A), hajtásszám (B), levélszám (C) és párhatóviszámának (D) átlagos változása a vizsgálat alatt, a vadkizárt területen kijelölt növényzeti foltokban. A piros szaggatott vonalak a szimulált vadragás kezelési idő-pontjait jelzik. CLP - kontroll akáccsemeték (n = 63), TLP - kezelt akáccsemeték (n = 58) a kezelt akác parcellákon

Table 1. Linear mixed model (for height data only) and generalized linear mixed model results of the black locust saplings. Control black locust plots (CLP) were used as a reference category when the effect of clipping was modeled. TLP: treated black locust plots

1. táblázat. Az akáccsemeték biometriai adataival végzett lineáris kevert modell (csak magassági adatokra) és általánosított lineáris kevert modell eredményei. A szimulált vadragás kezelés értékelésekor a kontroll csoportba tartozó csemetéket (CLP) használtuk referencia kategóriaként. TLP: kezelt akác parcellák

	fixed effects			random effects	autocorrelation (AR1)		
	coefficient	SE	z	variance (SD)	variance (SD)	correlation	
height	<i>intercept</i>	61.22***	4.97	12.3	<i>plot</i> 534.8 (23)	3.33 (1.82)	0.83
	<i>time</i>	1.71***	0.49	3.51			
	<i>plot (TLP)</i>	-25.74***	7.28	-3.54			
shoot density	<i>intercept</i>	1.67	45.2	0.04	<i>plot</i> 0.37 (0.6)	2044 (45.2)	0.9
	<i>time</i>	0.028	0.05	0.55			
	<i>plot (TLP)</i>	-0.95***	0.17	-5.6			
leaf density	<i>intercept</i>	3.11***	0.39	8.05	<i>plot</i> 0.5 (0.7)	0.27 (0.52)	0.3
	<i>time</i>	0.037	0.04	0.84			
	<i>plot (TLP)</i>	-1.03***	0.22	-4.75			

spine density	<i>intercept</i>	0.27	0.65	0.42	<i>plot</i>	5.3 (2.3)	0.21 (0.46)	0.77
	<i>time</i>	-0.01	0.05	-0.14				
	<i>plot (TLP)</i>	-1.43	0.71	-2.01				

*** $p < 0.001$

Significant shoot density reduction was registered in CLP saplings during summer 2016 (-5.6 ± 5.3), which was nearly 3 times higher than for TLP saplings (-1.9 ± 2.6) in this period ($U = 149$, $n_1 = 19$, $n_2 = 32$, $p = 0.017$). Despite the compensating effect of clipped saplings, overall shoot development was significantly lower in the TLP group (Table 1).

During the severe drought in the summer of 2015, a marked decrease in leaf density was registered in clipped and control saplings in August 2015 (Figure 2C). Mortality increased in both groups (Figure 3A). The rate of defoliation was two times higher in TLP than in CLP saplings in this period (TLP: -14.3 ± 16 vs. CLP: -7.7 ± 6.9), however, a significant difference was not confirmed ($U = 1081$, $n_1 = 39$, $n_2 = 48$, $p = 0.2$) due to the heterogeneous responses of TLP saplings (Figure 2C). This situation greatly affected the overall leaf production intensity in both groups (Table 2), and resulted in a significantly lower leaf density in clipped saplings (TLP) than in control ones during the study (Table 1).

Table 2. Overall differences in biometric data, and total mortality of black locust, sessile oak and Turkey oak saplings between the last and the first time point of the study. Saplings that died during the study were not included in the calculation.

2. táblázat. Az akác- és tölgycsemeték biometriai adatainak átlagos változása és mortalitása a vizsgálat kezdő és záró időpontja között. A változások az elpusztult csemeték nélkül kerültek kiszámításra.

		height (cm)	stem diame- ter (cm)	shoot den- sity (pcs)	leaf/shoot ratio	spine/shoot ratio	mortality (%)
black locust	TLP (N=58)	27 ±9	0.3 ±0.2	18.3 ±21	-6.7 ±7	-17.6 ±7	79
	CLP (N=63)	40.9 ±52	0.29 ±0.3	11.1 ±15	-1.8 ±3	-2.8 ±3	67
sessile oak	TLP (N=27)	17.7 ±10	0.11 ±0.1	3.5 ±4.5	0.13 ±1.8	–	7
	CLP (N=52)	16.1 ±10	0.05 ±0.1	1.7 ±1.8	-0.13 ±1.7	–	21
	COP (N=22)	15.2 ±12	0.1 ±0.1	3.3 ±4	-0.3 ±2.5	–	5
Turkey oak	TLP (N=30)	10.3 ±8	0.07 ±0.1	1.4 ±1.7	-1.1 ±3	–	10
	CLP (N=50)	19.2 ±11	0.12 ±0.1	2.9 ±3.6	-0.4 ±2	–	20
	COP (N=41)	9.7 ±7	0.07 ±0.1	1.4 ±2	-0.5 ±2	–	32

TLP: treated black locust plots, CLP: control black locust plots, COP: control oak plots.

TLP: kezelt akácparcellák, CLP: kontroll akácparcellák, COP: kontroll tölgyparcellák.

The clipped saplings did not develop more spines after the treatments (Figure 2D). On the contrary, spine density decreased both in TLP and CLP. The change in TLP was not significant in comparison to CLP saplings (Table 1) due to the high variance because the majority of saplings (70%) did not have any spines in either group.

Cumulative mortality rates reached a high level in both groups by August 2018: 79% of clipped saplings (46 out of 58 individuals in TLP) and 67% of control saplings (42 out of 63 individuals in CLP) were dead (Figure 3A). Due to similar trends, the mixed

effects Cox model has not proved any difference between treatment and control mortality rates (Table 3).

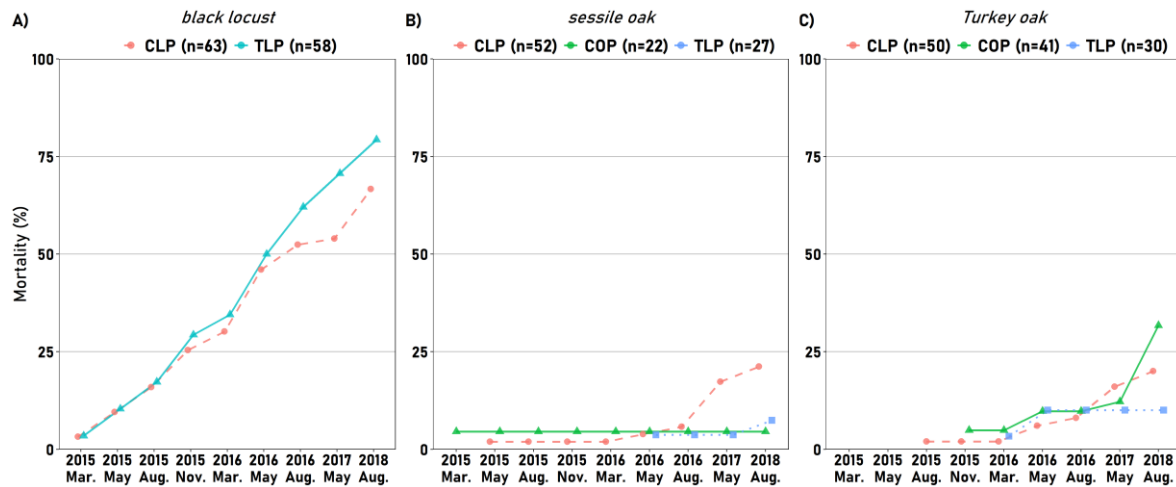


Figure 3. The cumulative mortality rate of black locust (A), sessile oak (B) and Turkey oak (C) saplings in different vegetation plots during the study. CLP – control black locust plots, COP – control oak plots, TLP – treated black locust plots

3. ábra. A fehér akác (A), a kocsánytalan tölgy (B) és a csertölgy (C) kumulált mortalitási aránya az egyes parcellákon a vizsgálat alatt. CLP – kontroll akác parcellák, COP – kontroll tölgyes parcellák, TLP – kezelt akác parcellák

Table 3. Mixed effects Cox regression results of black locust, sessile oak and Turkey oak saplings. Control black locust plots (CLP) were used as reference categories in the model

3. táblázat. A kevert Cox-regressziós modell eredményei akác, kocsánytalan tölgy és csertölgy csemeték esetében. A modellben a kontroll akác parcellákon (CLP) található csemeték adatait használtuk referencia kategóriaként

		HR	95% CI	z	p	random effect variance (plot)
black locust	plot (TLP)	1.27	0.99–1.63	1.88	0.06	0.69
sessile oak	plot (COP)	0.23	0.02–2.64	-1.2	0.23	5
oak	plot (TLP)	0.33	0.03–4	-0.89	0.38	
Turkey oak	plot (COP)	1.46	0.33–6.35	0.51	0.61	3.8
oak	plot (TLP)	0.51	0.09–2.72	-0.81	0.42	

HR: hazard ratio, CI: confidence interval, z: Wald statistic value, TLP: treated black locust plots, COP: control oak plots.

HR: kockázati arány, CI: konfidencia intervallum, z: Wald statisztika értéke, TLP – kezelt akácparcellák, COP – kontroll tölgyparcellák.

The response of oak saplings to black locust presence

The biometrical attributes of the two oak species were similar among CLP, TLP and COP at the beginning of the monitoring (sessile oak: Kruskal-Wallis test: $KW = 0.5\text{--}0.9$, $p = 0.6\text{--}0.8$; Turkey oak: $KW = 1.1\text{--}3.2$, $p = 0.2\text{--}0.6$; for different variables). Overall, oak species showed different growth intensities only in TLP (Figures 4A and 4D): sessile oak saplings had significantly more intensive growth than Turkey oak saplings ($U = 77$, $n_1 = 27$, $n_2 = 30$, $p = 0.02$).

The overall height change of Turkey oak saplings was significantly the highest in CLP ($KW = 11.85$, $p = 0.003$, Dunn test: $p < 0.01$), while sessile oak saplings had similar growth in every vegetation patch ($KW = 1.24$, $p = 0.54$, Table 2). Due to growth intensity fluctuations, the fitted GLMM model on the full-time trends of sapling height found no differences among vegetation plots at both oak species either (Table 4).

Sessile oak saplings had the lowest, while Turkey oaks had the highest intensity in shoot development among oaks in CLP (Table 2), but these differences were not significant in within-species comparisons among vegetation patches (sessile oak:

$KW = 1.51$, $p = 0.47$, Turkey oak: $KW = 1.49$, $p = 0.47$). Both oak species produced new shoots during the study (Table 4: see the significant time coefficient as a fixed effect). In the case of Turkey oak, the average trend of shoot density changes in COP was significantly lower than in CLP with a weak significance ($p < 0.03$, see Table 4).

Leaf density change was the most intensive in the first half of the growing season (until May) in the case of both oak species (Figure 4C and 4F). The heavy drought period in the summer of 2015 was not as damaging for oaks in either of the vegetation plots as it was for black locust saplings (Figure 2C). The amount of produced leaves was similar in all vegetation plots during the study for both oak species and stayed unaffected by neighboring black locust saplings (Table 4).

The total mortality rate of sessile oak was 14% (14 out of 101 individuals). Most saplings died in plots where black locust saplings were located (13 individuals – 93% of total mortality) especially in CLP (11 individuals – 78% of total mortality and 21% of individuals in this group). However, no fatality was registered in TLP until May 2016 at the earliest (Figure 3B). Mortality ceased in the absence of black locust (COP: only 1 oak sapling died – 7% of total mortality and 5% of the actual group). Differences were not significant among the vegetation plots (Table 3).

By August 2018, the total mortality rate of Turkey oak saplings reached 22% (26 out of 121 individuals). The first mortality occurred only after 1 year since studies began (Figure 3C). The same amount of saplings died in the occupied and non-occupied plots by black locust (TLP + CLP: 13 vs. COP: 13 individuals – 50% of total mortality). More saplings died in CLP (10 individuals – 20% in this group) than in TLP plots (3 individuals – 10% in this group). Fatalities started to occur at the latest in TLP (Figure 3C), but mortality was not significantly different among the vegetation plots (Table 3).

Soil attributes in different vegetation patches

Topsoil was highly compacted and laboratory tests confirmed a quite strong acidity (mean pH(H₂O): 4.3 ± 0.1) prevailing in all vegetation plots (N = 17); therefore soil characteristics affected the vegetation development uniformly in the fenced area. Moreover, the topsoil (A-horizon) was extremely shallow at some sampling points, especially in plots that were situated at the lowest part of the eastern-southeastern slope exposure (7.8 ± 7 cm for all samples). The eluvial (E) horizon (44 ± 33 cm), and the B-horizon (55 ± 27 cm) were much thicker than the topsoil in all vegetation plots. The core sampler reached the parent material (C-horizon) only once out of 13 occasions at a depth of 99 cm at the top of the slope.

Table 4. Linear mixed model (for height data only) and generalized linear mixed model results of sessile and Turkey oak saplings. Control black locust plots (CLP) were used as reference categories in the model. TLP: treated black locust plots, COP: control oak plots

4. táblázat. A kocsánytalan és csertölgycsemeték biometriai adataival végzett lineáris kevert modell (csak magassági adatokra) és általánosított lineáris kevert modell eredményei. A modellben a kontroll akácparcellákon (CLP) található tölgycsemeték adatait használtuk referenciakategóriaként. TLP: kezelt akácparcellák, COP: kontroll tölgyparcellák

	fixed effects			random effects	autocorrelation (AR1)		
	coefficient	SE	z		variance (SD)	variance (SD)	correlation
height	<i>intercept</i>	16.96***	2.14	7.91	<i>plot</i> 91.9 (9.59)	1.31 (1.15)	0.43
	<i>time</i>	1.08***	0.12	8.87			
	<i>plot (TLP)</i>	-0.993	3.07	-0.32			
	<i>plot (COP)</i>	-2.73	3.26	-0.84			
	<i>intercept</i>	0.71***	0.1	7.12	<i>plot</i> 0.2 (0.5)	-	-
shoot density	<i>time</i>	0.48***	0.01	11.5			
	<i>plot (TLP)</i>	0.13	0.15	0.38			
	<i>plot (COP)</i>	0.22	0.16	0.16			
leaf density	<i>intercept</i>	1.97***	0.15	13.5	<i>plot</i> 0.3 (0.54)	0.03 (0.2)	0.14
	<i>time</i>	0.05**	0.01	3.2			
	<i>plot (TLP)</i>	0.01	0.18	0.95			
	<i>plot (COP)</i>	0.18	0.19	0.34			

	<i>intercept</i>	15.54	53.9	0.29	<i>plot</i> 16.8 (4.1)	2914 (53.9)	0.9
height	<i>time</i>	0.63***	0.13	4.71			
	<i>plot</i> (TLP)	-1.69	1.27	-1.33			
	<i>plot</i> (COP)	-0.28	1.24	-0.22			
	<i>intercept</i>	0.83***	0.09	8.64	<i>plot</i> 0.23 (0.48)	-	-
shoot density	<i>time</i>	0.04***	0.01	7.46			
	<i>plot</i> (TLP)	-0.18	0.14	-1.23			
	<i>plot</i> (COP)	-0.29*	0.14	-2.16			
	<i>intercept</i>	1.83***	0.24	7.62	<i>plot</i> 0.3 (0.55)	0.04 (0.21)	0.48
leaf density	<i>time</i>	0.03	0.02	1.31			
	<i>plot</i> (TLP)	-0.14	0.15	-0.9			
	<i>plot</i> (COP)	-0.26	0.15	-1.73			

*** $p < 0.001$ ** $p < 0.01$ * $p < 0.05$

The very low pH and significant compaction (at 15–20 cm depth) represent disadvantageous soil conditions for black locust and oak saplings. The shallow humus-rich layer made seedling development more difficult in all vegetation plots regardless of the satisfactory levels of humus content (4.8 ± 1.5 %) which were equal among vegetation plots (KW = 1.02, $p = 0.6$). According to the KA plasticity index, the soil texture was identified as clay or clay loam (min = 43; max = 58), which was not seriously affected by the humus content, due to the shallow A horizon and relatively low humus concentration.

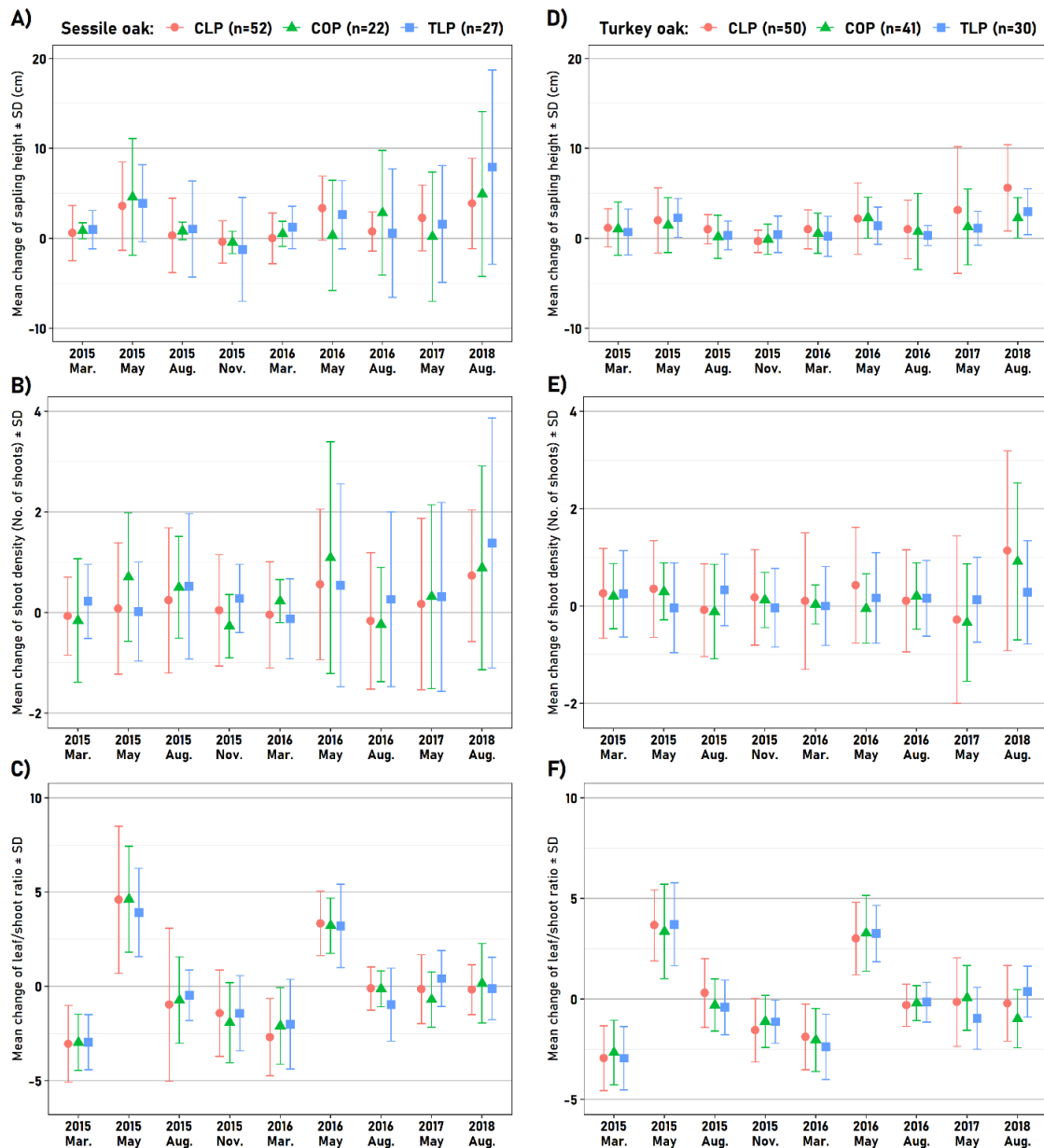


Figure 4. Average changes between consecutive time points in height (A, D), shoot density (B, E) and leaf density (C, F) of sessile oak and Turkey oak saplings, in different vegetation plots inside the enclosure. CLP: control black locust plots, COP: control oak plots, TLP: treated black locust plots

4. ábra. A tölgycsemék magasságának (A-D), hajtásszámának (B-E) és levélszámának (C-F) átlagos változása a vizsgálat alatt a vadkizáró kerítésen belüli területen kijelölt növényzeti foltokban. CLP: kontroll akácparcellák, COP: kontroll tölgyes parcellák, TLP: kezelt akácparcellák

No major differences were found in soil ammonium and nitrate N concentrations (KW = 3.13–6.82, $p = 0.2$ – 0.4) between vegetation patches with black locust ($\text{NH}_4^+\text{-N}$: 5.4 ± 2.3 mg/kg; $\text{NO}_3^-\text{-N}$: 16.6 ± 4.7 mg/kg) and without it ($\text{NH}_4^+\text{-N}$: 7.3 ± 2 mg/kg; $\text{NO}_3^-\text{-N}$: 13.7 ± 7.1 mg/kg). Potassium and phosphorus levels were similar in the presence (K_2O : 149 ± 75 mg/kg, P_2O_5 : 43 ± 11 mg/kg) and in the absence (K_2O : 192 ± 117 mg/kg, P_2O_5 : 35 ± 4 mg/kg) of black locust, as well (K_2O : KW = 3.13, $p = 0.2$; P_2O_5 : KW = 1.2, $p = 0.6$).

Discussion

The full-time response of black locust saplings to simulated browsing confirmed our first hypothesis that clipping treatments will significantly reduce the vitality of saplings for growth and further development. These effects were not evident in the short-term analyses (2 years, until August 2016), but turned out as significant in the background of the longer monitoring process. The first clipping only caused slight and temporary disturbances in the treated saplings and we observed compensation in height growth (Figure 2A) and shoot development (Figure 2B) after the first treatment. Compensatory growth is a common phenomenon after browsing, which was observed in many plant species (Hilton et al. 1987, Hester et al. 2004), but very few studies performed experiments on black locusts. Significant overcompensation did not occur in this study though it was observed earlier (Fehér and Katona 2013). The increasing mortality from November 2015 points out the importance of other (abiotic) contributing factors in the survival of black locusts. In July 2015 the experienced temperatures were significantly above the seasonal norm (above 34–35 °C) and the water balance was 100 mm below the long-term average in Hungary according to the ICPDR report (International Commission for the Protection of the Danube River 2017). We presume that the heavy drought period in the summer of 2015 significantly influenced sapling survival, even though black locusts can effectively adapt to prolonged drought conditions by reducing water loss through reduced transpiration and leaf size (Mantovani 2014). Stochastic weather phenomena and abiotic features of the habitat like soil moisture (Kullberg and Welander 2003) or shade patterns (Canham 1994) can also have a strong effect on plant development and survival in the long run. Therefore, these effects have to be considered as important determinants causing continuous mortality of black locust saplings observed in our study (Figure 3A), which might surpass the effects of the clipping treatments. Decreased spine production (Figure 2D and Table 2) could be also related to the actual abiotic stress since the development of structural plant defenses requires significant resource allocation and trade-off (Baraza et al. 2007).

The N fixation of black locust, rather than its allelopathy – which had only been confirmed under laboratory conditions (Vítková et al. 2015) – can lead to its dominance over native species and alter plant communities. However, we did not find higher nitrogen concentrations in TLP or CLP compared to COP, due to which we rejected our second hypothesis. This result corresponds with the findings of Wang et al. (2012), who examined black locust forests at different ages (up to 50 years) and found that N fixation is more evident in 25–30 years old mature black locust stands. The prevalent soil conditions as low pH, low nutrient content and high compaction with surface water erosion represent unsatisfactory conditions for oak and black locust saplings (Fehér et al. 2014, 2016). The extremely high soil resistance experienced during core sampling also implies significant compaction for all horizons. Resource acquisition was also limited: the pH below 4.5 represents extremely acidic soil, where nutrient uptake decreases significantly.

The typical “slow-growing” attribute of sessile oak and Turkey oak saplings was also confirmed in their shoot development (Figure 4B and 4E, Table 2). However, black locust did not have a significant negative effect on saplings of either oak species, which might be due to its high mortality that could largely reduce its competitive effect and thus hindered the detection of obvious clues. Thereby our results could not confirm our third hypothesis. Furthermore, in the case of Turkey oak, the overall shoot development was significantly the lowest in COP where no black locust saplings were around. The intensity of interference competition which is manifested in exploitation, overgrowing, or allelopathy can be the highest in high-productivity habitats at high soil resource supply rates (Reynolds and Rajaniemi 2007). In the case of our study site, the soil resources may be limiting for black locusts and occasional drought periods can reduce competition intensity between oak and black locust saplings. Black locust saplings take more risk than oaks because of their intensive height growth, shoot development and leaf production (Table 2), and higher investment can also mean higher potential losses in bad years. It is also worth noting that root architecture (depth and width) is different between oaks and black locusts. While oaks tend to develop a “heart-sinker root system” (Köstler et al. 1968) consisting of horizontal roots and a significant taproot reaching deep in the soil (Drexhage et al. 1999), black locust creates only vertical roots with 1.5–3 m depth on loose, sandy and moist soils. It has no taproot on shallow soils or eroded slopes but a fine flat, wide-spread horizontal root close to the surface (Nicolescu et al. 2020). The different responses of the two oak species in growth and shoot development in plots with black locusts indicate slightly diverging needs and use of resources, which also represents the priority of other contributing factors.

Fatalities of both oak species occurred in TLP at the latest, where neighboring black locust saplings were clipped, therefore, neither the mortality rates nor the changes in biometric data provided satisfactory proof to confirm our fourth hypothesis that oak sapling development will be the highest where black locust saplings were clipped.

Conclusions

Considering the potential effects of summer drought and actual soil attributes on black locust sapling development we can agree with Belsky et al. (1993), who also stated, that herbivory (i.e., ungulate browsing) itself is just one of the many biotic and abiotic disturbance factors which can influence sapling growth. In some cases, the effects of abiotic factors on sapling survival could be much higher than ungulate browsing, even if ungulates can play a significant role in forest regeneration. This statement is in accordance with our result, that mortality rates of black locust saplings were statistically similar between the treatment and the control group (Table 3). Furthermore, changes in environmental conditions can induce completely different plant responses to herbivory (Hjältén et al. 1993). The negative effects of browsing on sapling development are strongly dependent on the shade tolerance of the species and the current intensity of competition from neighbours (Vandenbergh 2008). On the other hand, it seems that black locust saplings were not able to express their competitive ability in this short period. Therefore, the negative effects of black locust presence on

oak sapling conditions could be assumed, but a significant difference was not confirmed at any time. Allelopathic effects and soil nitrogen enrichment by black locusts could not be significant at the sapling life stage, due to unsatisfactory leaf development, which plays an important role in the allelopathic potential of the species through releasing allelopathic compounds by fallen leaves (Nasir et al 2005). The primary competitive advantage of black locust saplings might arise from their fast growth instead of their allelopathy in the early life stages, which was at least 1.5 times higher in clipped and 2 times higher in control black locust saplings than in oaks (Table 2). This trait makes them able to overgrow other plants under favorable circumstances. The different response of sessile oak and Turkey oak in black locust plots indicates potential microclimatic differences (especially light and moisture levels) among the vegetation plots as well, because the two oak species have slightly different optimum conditions for these factors (Cutini and Mercurio 2007), which can modify their survival.

The invasion of black locusts is strongly dependent on the actual light conditions on the forest floor which can drastically hinder its competitive success in moderate shade and summer drought. Hence, it seems that ungulate browsing plays a secondary role in steering competition between native oak species and non-native locust, and only delays the spread of this invasive species in temperate forests. Still, this selective browsing can function as a valuable ecosystem service of ungulates by mitigating black locust invasion; even has the potential to hinder its spread into native forest communities when abiotic conditions are suboptimal to black locusts.

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Vadrágás hatása az akácok versenyképességére egy mérsékelt égövi tölgyesben

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Kulcsszavak: kerítés; növényi kompetíció, *Robinia pseudoacacia*; csertölgy; szimulált vadrágás; nitrogén a talajban

Összefoglalás: Az olyan inváziós fajok, mint a fehér akác (*Robinia pseudoacacia*), számos problémát okoznak az európai természetközeli erdők megőrzésében. A csülkös vadfajok szelektív rágása kiemelt szabályozó tényező lehet a fehér akác terjedésének megállításában is. Egy 4 éves kísérletet végeztünk egy magyarországi csertölgy (*Quercus cerris*) és kocsánytalan tölgy (*Quercus petraea*) elegyes erdő-részlet bekerített területén, hogy 1) értékeljük az akáccsometék rövidtávú reakcióit a szimulált vadrágásra; 2) meghatározzuk a vadrágás és a talajviszonyok hatását az akác- és a tölgycsometék közötti kompetícióra. Feltételeztük, hogy a szimulált vadrágás kezelések csökkentik a fehér akác növekedését és vitalitását, valamint közvetve fokozzák a tölgycsometék fejlődését. A kezelt és kontroll akáccsometék, illetve akáccsometék nélkül álló tölgy-csometék elkülönítésére parcellákat jelöltünk ki a vadkizárás területén. Az első, 2014 szeptemberben végzett kezelések után a kezelt akácok kompenzálták a magasság- és a hajtásvesztésüket. A 2015-ös nyári aszály csökkentette a fehér akácok túlélését, függetlenül a kezeléstől, és sok csemete elpusztult a korábban elfoglalt parcellákról. Emellett a 2015 szeptemberben végzett második kezelés jelentősen lelassította a növekedésüket, pár esetben megállította azt. A talaj nitrogéntartalma nem volt magasabb az akácos parcellákban, ugyanakkor az alacsony pH és a jelentős talajtömörődés korlátozó tényező lehetett valamennyi csemete számára. Eredményeink nem erősítették meg a fehér akácnak a tölgycsometék fejlődésére gyakorolt szignifikáns gátló hatását sem a kezelt-, sem a kontroll akác parcellákon, továbbá a kocsánytalan tölgy növekedési üteme magasabb volt az akácos parcellákon az ugyanott megtalálható csertölgyekéhez képest. Feltételezhető, hogy ez esetben a rágás csak egy másodlagos zavaró tényező, amely befolyásolja ugyan a fehér akácok növekedését és versenyképességét, de csak egy erős aszályos időszakot követő ismételt vadrágás képes megakadályozni, hogy a fehér akác csometék kompenzálják a veszteségeiket.

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