DOI: 10.5586/aa.1692

Publication history Received: 2016-04-06 Accepted: 2016-11-10 Published: 2016-12-06

Handling editor

Alina Syp, Institute of Soil Science and Plant Cultivation, State Research Institute, Poland

Authors' contributions

MW, MJ: idea; MJ, MKK, KT, PM: execution of studies; MJ, MKK: analysis of results; MJ, MKK: writing the paper

Funding

This work was supported by the Polish Ministry of Science and Higher Education as part of the statutory activities of the Department of Agroecosystems, University of Warmia and Mazury in Olsztyn.

Competing interests

No competing interests have been declared.

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Citation

Jastrzębska M, Kostrzewska MK, Wanic M, Treder K, Makowski P. The effect of interspecies interactions and water deficit on spring barley and red clover biomass accumulation at successive growth stages. Acta Agrobot. 2016;69(4):1692. http://dx.doi.org/10.5586/ aa.1692

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ORIGINAL RESEARCH PAPER

The effect of interspecies interactions and water deficit on spring barley and red clover biomass accumulation at successive growth stages

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Abstract

A pot experiment was conducted in a greenhouse in Olsztyn, Poland, in the period 2010-2012. The aim of the study was to examine whether soil water deficit would change biomass volume and distribution of pure sown spring barley and red clover as well as growth rate during their joint vegetation and mutual interactions. The interactions between spring barley and red clover were of a competitive character, and the cereal was the stronger crop. The strength of this competition increased in time with the growing season. Through most of the growing season, the competition was poorer in water deficit conditions.

The impact of clover on barley before the heading stage showed facilitation symptoms. Interspecific competition reduced the rate of barley biomass accumulation and decreased stem and leaf biomass towards the end of the growing season. Intensified translocation of assimilates from the vegetative parts to grain minimized the decrease in spike biomass.

Water deficit stress had a more inhibitory effect on the biomass and growth rate of barley than competition, and competition did not exacerbate the adverse influence of water deficit stress on barley. Competition from barley significantly reduced the biomass and biomass accumulation rate of clover. Water deficit stress did not exacerbate barley's competitive effect on clover, but it strongly inhibited the growth of aboveground biomass in pure-sown clover.

Keywords

intercropping; competition; growth stages; crop growth rate; dry matter translocation

Introduction

Intercropping is usually defined as a multiple cropping system in which two or more crop species are planted simultaneously in a field during a growing season [1]. In Northern Europe, it is a popular practice to use undersown crops. An undersown crop is a plant sown simultaneously with the main crop, or during its initial vegetation, which stays after the main crop harvest until fall of the same year [2]. An undersown crop may be used for fodder, green manure, or mulch. The main crop, which is supplemented by the undersown crop, is called the nurse crop [3]. It should be characterized by a short growing season, poor foliage, and minor water demand [4]. The most common undersown crops are legume plants and grasses. Red clover (Trifolium pratense L.) is one of the most popular undersown legume crops [5,6], whereas spring barley (Hordeum vulgare L.) is regarded as the most effective nurse crop in intercropped stands [7]. The benefits of using undersown crops have been evidenced in literature

for a long time now [5,6,8]. They have been shown to reduce soil erosion, increase organic matter content in soil and soil fertility, suppress weeds, improve soil structure and water holding capacity, provide suitable habitat for beneficial fauna (including insect pollinators), and act as non-host crops for pests in the rotation. Legume crops also participate in symbiotic nitrogen fixation and contribute to the nitrogen requirements of the subsequent crops. There are also less optimistic reports, e.g., concerning reduced cereal yield as a result of using these crops [9,10].

During joint vegetation, interspecies interactions take place between the undersown plant and its nurse crop. Their mechanism is not fully recognized [11,12]. Studies to date on interspecies interactions in mixed crops indicate that they may take the form of competition for environment resources, their complementary utilization or even facilitation – making it easier for the partner to exploit them [13].

Competition is generally understood to mean the negative effects caused by the presence of neighbors, usually by reducing the availability of resources [14]. Whilst definitions of competition abound, they can typically be divided into two categories: those that focus on mechanisms and resource acquisition [15,16] and those that focus on the reduction in fitness brought about by a shared requirement for a resource in limited supply [17].

Complementarity may be defined as a decrease in interspecific competition and competitive exclusion through resource partitioning between intercropped species. Species may use a given resource differently in time, in space, and in forms [18]. Facilitation occurs when one species enhances the growth, survival, or fitness of another [19]. This can occur through (i) direct positive mechanisms, such as favorable alteration of light, temperature, soil moisture, soil nutrients, soil oxygenation, or substrate, and (ii) indirect mechanisms, as protection from herbivores, attraction of shared pollinators, root grafts, and beneficial changes in soil mycorrhizal or microbial communities [19].

In the configuration main (nurse) crop – undersown crop, when environmental resources do not fully meet the requirements of the main (nurse) crop, the undersown crop, and weeds, the undersown species may compete with the main crop for the available resources [20,21]. Undersown crops are also significantly influenced by the nurse crop [12,22]. In recent years, the mechanisms of competition between the undersown plant and the nurse crop have been analyzed in numerous field [23–25] and greenhouse experiments [10,12].

In light of the studies carried out to date, the interactions between plants appear as an extremely complex phenomenon. The type and intensity of interactions may differ at individual plant growth stages, and their effects are often difficult to foresee [11,12]. Competitive ability is determined by individual and group traits of coexisting plant populations, as well as the influence of abiotic and biotic factors [11,26]. In the climate of Poland, the deficit of precipitation is the main reason for crop yield reduction [27]. Insufficient precipitation decreases red clover yield [28], whereas barley is the most drought sensitive cereal crop due to its poor root system and the shortest vegetation period [29]. Low soil moisture levels can alter the strength and direction of interactions between species growing in the same habitat.

The above condition constituted the basis for studies carried out to analyze the impact of interactions between spring barley and red clover on their biomass accumulation, its distribution and plant growth rate in the conditions of diverse water supply. An alternative hypothesis has been tested – that interspecies interactions and water deficit modify the plant characteristics specified above, in comparison to the zero hypothesis stating that these factors have no influence on them.

Material and methods

A pot experiment was performed in the greenhouse of the Faculty of Biology and Biotechnology of the University of Warmia and Mazury in Olsztyn, Poland, in the period 2010–2012. The successive growth periods (in the months between April and July) lasted 102, 97, and 98 days. The tested crops were spring barley 'Rastik' (hull-less) and red clover 'Bona'.

The experimental factors were:

- stand type: each species grown in a pure stand (pure-sown barley PB, pure-sown clover PC) and a mixed stand (barley mixed-sown with clover MB, clover mixed-sown with barley MC);
- water supply: optimal for the analyzed species (HW) and reduced by 50% (LW).

A higher dose of water ("optimal") was determined in a trial experiment in which plants' irrigation requirements were established on the basis of water loss estimated by daily measurements of pot weight. At the beginning of the trial experiment, the pots with plants were well irrigated and then every day the soil moisture content was maintained by re-watering with the water lost in the previous 24 h. Daily amounts of water supplied to the pots with barley, clover, and barley-clover mixture were recorded during the successive growth stages. Soil moisture was simultaneously measured by TDR method as well as evaporation, transpiration, and water content in plants were monitored. After finishing the trial experiment, on the basis of the recorded data of water amounts, the pattern of plant watering with the higher dose for the proper experiment was established. Higher daily dose of water, common for the three types of sowing, was calculated as an average of barley, clover, and barley-clover mixture requirements at a given stage of plant growth. This dose was dynamic according to the plant development (changeable during vegetation) as well as it was slightly verified during each growing season. The reduced dose was always equal to one-half of the higher one. At the beginning of each experimental series of the proper experiment (sowing), the soil moisture was about 20% (measured by TDR method). Eventually, in treatments with optimal water conditions, water was supplied in the amount of 13.4, 12.3, and 10.9 dm³ per pot as a total in each experimental series. Plants in reduced water treatments were supplied with half the above amounts, respectively. Soil moisture was monitored by TDR method. The results of those measurements will be presented in a separate article.

Plants were sown in Kick-Brauckmann pots (diameter – 22 cm, depth – 25 cm) with 18 barley plants and eight clover plants per pot in pure-sown treatments. Mixed stands had an additive design [30] where the number of plants representing each species in a mixed stand was identical to that of pure stands, and the total number of plants per pot was the sum of plants in pure stands (18 + 8). Kernels and seeds were planted in pots at a depth of 3 cm (barley) and 1.5 cm (clover) with the use of templates to ensure equal distance between seeds. Each year, experiments were set up according to completely randomized design in four replications.

The pots were filled with soil material in the form of Eutric Cambisol (Humic) soil [31] which included: 64% the fraction with a diameter below 0.02 mm, 12% the fraction with a diameter of 0.02–0.1 mm, and 24% the fraction with a diameter of 0.1–1.0 mm. The soil was characterized by an organic matter content of 1.84% to 2.52%, a slightly acidic pH (5.6 to 6.2 in 1 M KCl), a high content of phosphorus (9.24–11.61 mg × 100 g⁻¹ soil) and magnesium (8.80–9.11 mg), and average potassium concentrations (12.87–14.53 mg). The soil was mixed with mineral fertilizers: P – 0.2 g per pot (monopotassium phosphate), K – 0.45 (potassium sulfate) at identical rates for all pots, and N – 0.5 for barley, 0.3 for mixed-sown treatments and 0.125 for clover (urea). The greenhouse temperature was maintained at 20–22°C throughout the experiment (during the day and night). It was lowered to 6–8°C for 9 days at full leaf development to support barley vernalization. Air humidity in the greenhouse was maintained at a level of 45–50%.

Competition between the analyzed species was studied at five growth stages (BBCH [32]) of spring barley grown in a pure stand under optimal water supply conditions: leaf development (BBCH 10–13), tillering (BBCH 25–29), stem elongation (BBCH 35–37), heading (BBCH 57–59), and ripening (BBCH 87–91), for each growth stage separately. When the plants had reached each of the above growth stages, they were removed from the pots, rinsed in mesh sieves, and the aboveground parts (shoots) were separated from the roots. Plant samples were dried to constant weight in a separate dry room (drying room) and then weighed. Beginning from the stem elongation stage, barley shoots were separated into stems and leaves, and beginning from the heading stage – also into spikes.

The crop growth rate (CGR) was determined based on shoot biomass yield according to the formula proposed by Watson [33]: $CGR = dW dt^{-1} PA^{-1}$; g m⁻² day⁻¹, where: dW – increase in shoot biomass, dt – time interval, PA – pot area.

The following parameters were determined for barley based on the formula proposed by Dordas [34]:

- dry matter translocation (DMT): DMT = DMH (DMR G); g pot⁻¹, where: DMH
 shoot dry matter at the heading stage, DMR shoot dry matter at the ripening stage, G grain yield;
- dry matter translocation efficiency (DMTE): $DMTE = DMT \times 100 \times DMH^{-1}$; %;
- contribution of pre-heading assimilates to grain (CpHAG): $CpHAG = DMT \times 100 \times G^{-1}$; %.

The results were processed statistically using variance analysis for two-factor experiments in a fully randomized configuration. An individual variance analysis was carried out for each growth stage. Differences between treatments were evaluated by Duncan's test at p = 0.05.

The tables present average values from three experimental cycles, due to the fact that no significant differences have been observed among the individual cycles.

Results

Spring barley

Undersowing with clover increased the biomass of barley roots (MB > PB) at the stem elongation stage, but had no significant effect on the evaluated parameter in the remaining growth stages (Tab. 1). In comparison with HW treatments, water deficit (LW) reduced root biomass from the beginning of the growing season until the end of the stem elongation stage. The inhibitory effect of water deficit stress was reduced during heading, but it was accentuated towards the end of the vegetation stage. The combined effect of experimental factors was manifested at the stem elongation stage when the root biomass of MB-HW treatments was 61–137% greater than that of PB-HW, PB-LW, and MB-LW plants. In MB-HW plants, the root biomass began to decrease at the heading stage, while in the remaining treatments the above process began during ripening.

The effect of clover on the biomass of barley shoots (MB relative to PB) was observed only at the ripening stage, and it was manifested by lower stem and leaf biomass, whereas no significant differences were noted in spike biomass. Water deficit stress (LW) inhibited the accumulation of barley shoot biomass throughout the growing season, and it reduced the biomass of all plant parts. Stand type and water supply exerted a combined effect on barley shoot biomass during the ripening stage. In treatments with optimal water supply (HW), MB-HW plants produced lower stem, leaf and spike biomass in comparison with HW treatments, no significant differences in stem and spike biomass were observed between PB-LW and MB-LW plants, but the analyzed stressor exacerbated the decrease in leaf biomass in MB-LW plants.

Barley was characterized by the highest crop growth rate (CGR) between the stem elongation and heading stages (Tab. 2). The slowest rate of biomass accumulation was noted between sowing and leaf development, and the biomass of MB-HW plants was also reduced towards the end of the growing season. Stand type (PB or MB) did not affect CGR values from the beginning of the growing season until tillering and from stem elongation until heading. MB plants were characterized by lower CGR values than PB plants between tillering and stem elongation stages and between heading and ripening stages.

In barley, water deficit stress (LW) lowered the CGR values from the beginning of the growing season until heading. The combined effect of water supply and stand type was manifested between tillering and stem elongation when the CGR values of PB-LW, MB-HW, and MB-LW plants were lower in comparison with PB-HW plants. The combined effect of the experimental factors on the CGR of barley was also observed

			Source of variability (experimental factors)									
Barley				stand type		water supply		stand type × water supply				
stages	Plant parts		РВ	MB	HW	LW	PB-HW	PB-LW	MB-HW	MB-LW		
LD	Roots		0.32 ª	0.31 ª	0.36 ª	0.27 ^b	0.35 ª	0.29 ª	0.36 ª	0.26 ª		
	Shoots		0.66 ª	0.74 ª	0.78 ª	0.63 ^b	0.71 ^{ab}	0.62 ^b	0.85 ª	0.64 ^b		
Т	Roots		1.08 ª	1.28 ª	1.32 ª	1.03 ^b	1.23 ^{ab}	0.93 ^b	1.41 ª	1.14 ^{ab}		
	Shoots		3.83 ª	4.14 ª	5.44 ª	2.56 ^b	5.09 ^b	2.58 °	5.78 ª	2.55 °		
SE	Roots		1.32 ^b	1.84 ª	2.06 ª	1.10 ^b	1.58 ^b	1.07 ^b	2.54 ª	1.14 ^b		
	Shoots, including:		6.38 ª	6.25 ª	8.64 ª	3.99 ^b	8.88 ª	3.88 ^b	8.41 ª	4.09 ^b		
		stems	2.94 ª	2.82 ª	4.08 ª	1.68 ^b	4.31 ª	1.56 °	3.85 ^b	1.79 °		
		leaves	3.45 ª	3.46 ª	4.56 ª	2.31 ^b	4.57 ª	2.32 ^b	4.56 ª	2.30 ^b		
Н	Roots		1.61 ª	1.76 ª	1.80 ª	1.56 ª	1.74 ª	1.48 ª	1.87 ª	1.65 ª		
	Shoots, including:		18.20 ª	17.59 ª	22.42 ª	13.37 ^b	22.85 ª	13.55 ^b	22.00 ª	13.18 ^b		
		stems	9.03 ª	8.40 ª	10.85 ª	6.57 ^b	11.06 ª	6.99 ^b	10.65 ª	6.15 ^b		
		leaves	7.06 ª	6.57 ª	7.82 ª	5.81 ^b	8.34 ª	5.77 ^ь	7.30 ª	5.84 ^b		
		spikes	2.16 ª	2.62 ª	3.75 ª	0.99 ^b	3.45 ª	0.79 ^b	4.05 ª	1.19 ^b		
R	Roots		0.92 ª	0.87 ª	1.03 ª	0.76 ^b	1.08 ª	0.75 ^b	0.98 ab	0.77 ^b		
	Shoots, inc	Shoots, including:		17.96 ^b	23.98 ª	15.00 ^b	26.51 ª	15.53 °	21.45 ^b	14.48 °		
		stems	9.08 ª	8.08 ^b	9.99 ª	7.17 ^b	11.10 ª	7.06 ^c	8.87 ^b	7.29 °		
		leaves	6.70 ª	5.62 ^b	7.75 ª	4.57 ^b	8.28 ª	5.13 °	7.22 ^b	4.01 ^d		
		spikes	5.24 ª	4.27 ª	6.25 ª	3.26 ^b	7.13 ª	3.34 °	5.36 ^b	3.18 °		

Tab. 1Spring barley biomass (g pot⁻¹).

LD – leaf development; T – tillering; SE – stem elongation; H – heading; R – ripening; PB – pure-sown barley; MB – barley mixedsown with clover; HW – optimal water supply for the analyzed species (higher dose); LW – water supply reduced by 50% (lower dose); a, b, c, d – homogeneous groups: in each individual line of the table (separately for each stage and each plant organ) within each experimental factor and their interactions, values marked with the same letter do not differ significantly at p = 0.05.

Tab. 2 Spring barley crop growth rate (CGR) ($g m^{-2} da y^{-1}$).

	Source of va	Source of variability (experimental factors)										
Barley growth stages (No. of days)	stand type		water supply		stand type × water supply							
	РВ	MB	HW	LW	PB-HW	PB-LW	MB-HW	MB-LW				
S-LD (18-21)	0.79 ª	0.92 ª	0.95 ª	0.76 ^b	0.87 ^b	0.74 ^b	1.05 ª	0.79 ^b				
LD-T (18-20)	4.76 ª	5.16 ª	6.92 ª	2.97 ^b	6.52 ª	3.00 ^b	7.31 ª	2.97 ^b				
T–SE (20–23)	4.34 ª	2.87 ^b	4.95 ª	2.24 ^b	6.55 ª	2.13 ^b	3.34 ^b	2.37 ^b				
SE-H (17-20)	6.76 ª	6.13 ª	8.29 ª	4.60 ^b	8.55 ª	4.97 ^b	8.02 ª	4.24 ^b				
H–R (20–22)	3.39 ª	0.79 ^b	2.13 ª	2.08 ª	4.47 ª	2.34 ^{ab}	–0.18 ^c	1.79 ^{bc}				

S – sowing; LD – leaf development; T – tillering; SE – stem elongation; H – heading; R – ripening; PB – pure-sown barley; MB – barley mixed-sown with clover; HW – optimal water supply for the analyzed species (higher dose); LW – water supply reduced by 50% (lower dose); a, b, c – homogeneous groups: in each individual line of the table (separately for each period between stages) within each experimental factor and their interactions, values marked with the same letter do not differ significantly at p = 0.05.

Tab. 3	Dry matter translocation (DMT),	dry matter trans	location efficiency	(DMTE), and	l contribution of p	ore-heading a	assimi-
lates to g	grain (CpHAG) of spring barley.						

	Source of variability (experimental factors)									
	stand type		water supply		stand type × water supply					
Item	РВ	MB	HW	LW	PB-HW	PB-LW	MB-HW	MB-LW		
DMT, g pot ⁻¹	1.30 ^b	3.57 ª	3.31 ª	1.55 ^b	1.89 ^{bc}	0.70 ^c	4.73 ^a	2.41 ^b		
DMTE, %	5.28 ^b	15.83 ª	12.29 ª	8.83 ª	6.58 ^b	3.98 ^b	18.00 ª	13.67 ª		
CpHAG, %	32.9 ^b	82.4 ª	67.4 ª	48.4 ª	41.4 ^b	24.4 °	93.3 ª	72.3 ^{ab}		

PB – pure-sown barley; MB – barley mixed-sown with clover; HW – optimal water supply for the analyzed species (higher dose); LW – water supply reduced by 50% (lower dose); a, b, c – homogeneous groups: in each individual line of the table within each experimental factor and their interactions, values marked with the same letter do not differ significantly at p = 0.05.

between heading and ripening: in comparison with PB-HW plants, the growing season in MB-HW plants ended earlier and was followed by a decrease in plant biomass, whereas no significant differences were noted between PB-LW and MB-LW treatments.

In comparison with pure-sown treatments (PB), mixed-sown treatments with undersown red clover (MB) were characterized by significantly higher dry matter translocation (DMT) from vegetative parts to grain, higher translocation efficiency (DMTE), and higher contribution of pre-heading assimilates to grain yield (CpHAG) (Tab. 3). In comparison with optimally watered treatments (HW), water deficit stress (LW) significantly reduced DMT values and produced a minor decrease in DMTE and CpHAG values.

Red clover

Red clover was significantly more sensitive to competition and water deficit stress than barley. Competition had a significantly more inhibitory effect on plant growth than water deficit stress (Tab. 4). The reduction in shoot and root biomass induced by interspecific competition and water deficit during the initial growth stages of red clover (until the stem elongation stage of barley) was statistically significant, but low in terms of absolute numbers. During the rapid development of red clover (heading and ripening stages of barley), the root biomass of MC plants was 95% lower (heading stage) and 86% lower (ripening stage) in comparison with PC plants. During the heading stage, PC-LW plants were characterized by lower root biomass than PC-HW plants, whereas no significant differences were reported between MC-HW and MC-LW treatments. During the ripening stage of barley, water deficit stress did not differentiate clover root biomass.

Competition from barley also exerted a strong adverse influence on shoot biomass of clover during intensive growth. The shoot biomass of MC plants was 91% lower during the heading stage and 88% lower during the ripening stage in comparison with PC plants. Water deficit stress exerted a significant effect, but it was somewhat weaker and was observed only in PC plants: the shoot biomass of PC-LW plants was lower in comparison with PC-HW plants. In MC treatments, competition from barley was so strong that it marginalized the influence of water deficit stress.

The negative effect of interspecific competition on the CGR values of clover was first noted between the leaf development and tillering stages of barley, and it intensified until the end of the growing season (Tab. 5). The CGR values of MC plants between the stem elongation and heading stages and between the heading and ripening stages were 6-fold and 7-fold lower, respectively, in comparison with PC plants.

Water deficit stress lowered the CGR values of clover between the sowing and tillering stages of barley. Between the leaf development and tillering stages, the inhibitory effect of water deficit on the CGR values of pure-sown clover was equal to

	Plant parts	Source of variability (experimental factors)								
Barley growth stages		stand type		water supply		stand type × water supply				
		PC	МС	HW	LW	PC-HW	PC-LW	MC-HW	MC-LW	
LD	Roots	0.015 ª	0.013 ª	0.015 ª	0.013 ª	0.016 ª	0.014 ª	0.014 ª	0.012 ª	
	Shoots	0.042 ª	0.048 ª	0.053 ª	0.037 ^b	0.056 ª	0.039 ^b	0.050 ª	0.034 ^b	
Т	Roots	0.10 ª	0.05 ^b	0.12 ª	0.03 ^b	0.16 ª	0.05 °	0.08 ^b	0.02 °	
	Shoots	0.52 ª	0.20 ^b	0.54 ª	0.18 ^b	0.86 ª	0.17 ^b	0.22 ^b	0.19 ^b	
SE	Roots	0.47 ª	0.19 ^b	0.38 ª	0.28 ^b	0.56 ª	0.38 ^b	0.20 °	0.18 °	
	Shoots	1.36 ª	0.47 ^b	1.08 ª	0.75 ^b	1.65 ª	1.07 ^b	0.51 °	0.43 ^c	
Н	Roots	3.65 ª	0.19 ^b	2.18 ª	1.66 ª	4.08 ª	3.22 ^b	0.27 °	0.10 ^c	
	Shoots	8.33 ª	0.72 ^b	6.29 ª	2.76 ^b	11.70 ª	4.97 ^b	0.89 °	0.55 °	
R	Roots	6.52 ª	0.88 ^b	3.61 ª	3.79 ª	6.59 ª	6.45 ª	0.63 ^b	1.13 ^b	
	Shoots	16.92 ª	1.99 ^b	11.21 ª	7.71 ^b	20.54 ª	13.30 ^b	1.87 °	2.12 °	

Tab. 4Red clover biomass (g pot⁻¹).

LD – leaf development; T – tillering; SE – stem elongation; H – heading; R – ripening; PC – pure-sown clover; MC – clover mixedsown with barley; HW – optimal water supply for the analyzed species (higher dose); LW – water supply reduced by 50% (lower dose); a, b, c – homogeneous groups: in each individual line of the table (separately for each stage and each plant organ) within each experimental factor and their interactions, values marked with the same letter do not differ significantly at p = 0.05.

Tab. 5 Red clover crop growth rate (CGR) (g $m^{-2} day^{-1}$).										
	Source of variability (experimental factors)									
Barley growth stages (No. of days)	stand type		water supply		stand type × water supply					
	РС	МС	HW	LW	PC-HW	PC-LW	MC-HW	MC-LW		
S-LD (18-21)	0.06 ª	0.06 ª	0.07 ª	0.05 ^b	0.07 ª	0.05 ^b	0.07 ª	0.04 ^b		
LD-T (18-20)	0.66 ª	0.24 ^b	0.68 ª	0.21 ^b	1.12 ª	0.20 ^b	0.24 ^b	0.23 ^b		
T–SE (20–23)	1.04 ª	0.25 ^b	0.52 ^b	0.77 ª	0.64 ^b	1.44 ª	0.40 ^b	0.10 ^b		
SE-H (17–20)	5.53 ª	0.88 ^b	4.80 ª	1.62 ^b	9.00 ^a	2.07 ^b	0.60 ^c	1.16 ^{bc}		
H–R (20–22)	7.79 ^a	1.11 ^b	4.50 ª	4.40 ª	8.12 ª	7.46 ª	0.88 ^b	1.34 ^b		

S – sowing; LD – leaf development; T – tillering; SE – stem elongation; H – heading; R – ripening; PC – pure-sown clover; MC – clover mixed-sown with barley; HW – optimal water supply for the analyzed species (higher dose); LW – water supply reduced by 50% (lower dose); a, b, c – homogeneous groups: in each individual line of the table (separately for each period between stages) within each experimental factor and their interactions, values marked with the same letter do not differ significantly at p = 0.05.

the competitive influence of barley, whereas the combination of water deficit and interspecific competition produced a similar effect to that noted separately for each experimental factor (PC-HW > PC-LW \cong MC-HW \cong MC-LW). Between the tillering and stem elongation stages of barley, PC-LW plants increased their CGR and partially compensated for the loss of biomass relative to PC-HW plants. Between stem elongation and heading, water deficit stress significantly reduced the CGR values of PC plants (PC-HW > PC-LW), but it had no effect on the CGR values of MC plants (MC-HW \cong MC-LW). In the above period, PC-HW plants were characterized by the highest CGR values during the entire growing season. In PC-LW treatments, the highest CGR values were noted between the heading and ripening stages of barley, when the analyzed trait was not differentiated by water supply.

Discussion

Published sources contain contradictory information about the effect of undersown species on the main cereal crop. According to some authors, undersown crops lower the grain yield or the biomass of the main crop [9,10,12]. Other authors did not observe such effects [25,35], whereas different studies demonstrated a positive influence of undersown species on the yield of cereal plants [36,37]. These variations could result from different effects exerted by the undersown species that may compete for natural resources with the cereal plant (undersown crop takes the role of a weed – [22]), support the complementary use of resources by both intercropped species or facilitate the uptake of cereal plant resources (by reducing competition from weeds or by establishing mutualistic relationships with fungi or bacteria). A good example of facilitation is where the legume contributes N from symbiotic N₂ fixation for use by other crops [38]. The use of atmospheric N can also be considered as a form of niche differentiation (complementarity) [19].

The undersowing of legumes delivers positive effects by increasing N_2 fixation and making nitrogen available for cereals [37,39].

According to Giller [38], if the benefits of including the legume into the cropping system are attributable to sparing effects, then it is just a case of reduced competition. In a study by Njad et al. [25], the increase in N₂ fixation by undersown Trifolium alexanderium did not produce the expected increase in barley yield. The above authors attributed their results to insufficient N transfer between clover and barley in response to interspecific competition. In this study, barley responded to the presence of red clover in mixed stands by increasing its root biomass during the stem elongation stage (this may be qualified as facilitation) and decreasing its stem and leaf biomass (competition effect), without the accompanying loss in spike biomass, towards the end of the growing season, which could be explained by the translocation of assimilates from vegetative parts to spikes. Further evidence for the complexity of interspecific competition was provided by Mariotti et al. [40] who reported an increase in the aboveground biomass of barley undersown with white lupine (Lupinus albus L.) and a decrease in both underground and aboveground biomass of barley intercropped with common vetch (Vicia sativa L.). According to some authors, interspecific competition and facilitation are two aspects of the same interaction and can exist simultaneously [41,42].

Unlike grass intercrops, such as ryegrass, clover weakly competes with cereal nurse crops [21,22]. The results of this study corroborate the above observation. However, Askegaard and Eriksen [43] found that red clover and Persian clover competed more intensively with barley than seven other undersown plants that exerted a weaker effect on the grain yield of the main crop. In a study with white clover (*Trifolium repens*), Thorsted et al. [9] demonstrated that the strength of interspecific competition can be determined by varietal traits.

In the present study, water supply had a greater influence on the accumulation of spring barley biomass than competition. Biomass accumulation in all plant organs decreased in response to water deficit stress throughout the growing season. Puresown barley responded similarly to lower soil moisture content in a pot experiment conducted by Wanic et al. [12]. In a field experiment, the grain yield and dry matter accumulation of barley decreased in years with low precipitation, in particular during the grain filling stage [34]. In this study, the combined effect of water deficit and competition from clover did not exacerbate the negative influence of water deficit on barley biomass (excluding leaves). The combined effect of water deficit stress and competition from Italian ryegrass was observed by Wanic et al. [12] in a study of barley.

The results of this study and the findings of Michalska et al. [44], Treder et al. [45], and Wanic et al. [12] indicate that competition from different species lowers the rate of biomass accumulation in barley in comparison with pure-sown treatments at various growth stages, but the commencement and end of the above interactions, their duration, continuity, and strength differed in the above studies. In studies of barley undersown with peas [44] and Italian ryegrass [12], the competition from the undersown crop ceased to influence the CGR values of barley between the heading and ripening stages, whereas in this study, clover had the greatest effect on the CGR of

barley in the above period. These observations suggest that the strength of competitive interactions is determined by the specific traits of intercropped plants.

The results of this study and the findings of Mollah and Paul [46], Wanic et al. [12], and Hossain and Akhtar [47] indicate that optimal water supply increases plant growth rates throughout the growing season in comparison with treatments subjected to water deficit stress. In the current study and in the work of Mollah and Paul [46] and Hossain and Akhtar [47], water supply was a less influential experimental factor towards the end of the growing season. The decrease in the significance of water supply was observed previously between the stem elongation and heading stages by Wanic et al. [12]. The cited authors noted negative CGR values in barley treatments with optimal water supply between the heading and ripening stages, whereas plants subjected to water deficit stress continued to accumulate biomass during that period. In this study, negative CGR values were observed towards the end of the growing season only in barley undersown with clover in treatments with optimal water supply. Pure-sown barley with optimal water supply demonstrated relatively high CGR values.

In all cereals, grain is filled by the transfer of assimilates from photosynthesis or the remobilization of assimilates accumulated temporarily in vegetative parts [48]. The reserves accumulated before the flowering stage are utilized when environmental conditions during grain filling do not support photosynthesis or the uptake of mineral nutrients [49–51]. Pireivatlou and Aliyev [52] reported that water deficit stress significantly increased dry matter translocation to kernels, dry matter translocation efficiency, and the contribution of pre-flowering assimilates to wheat grain yield. In the present study, water deficit stress decreased dry matter translocation, but it had no effect on translocation efficiency or the contribution of pre-heading assimilates to grain yield. Competition from clover induced the remobilization of assimilates and their translocation to kernels. Arduini et al. [51] and Fang et al. [53] observed an increase in dry matter translocation to wheat spikes with an increase in seeding rate and, consequently, intraspecific competition, but the contribution of pre-flowering assimilates to wheat grain yield remained unchanged.

In barley and clover intercropping systems with optimal water and nutrient supply for both species, the growth rate of clover plants is reduced by more than 50% [22]. The results of our study are consistent with the above observation in treatments with optimal water supply. During intensive growth, clover root and shoot biomass was reduced by 90% or more in response to competition from barley. Due to its specific features, in particular slow growth in the first year [54], red clover is easily dominated by a stronger competitor, such as spring barley. Barley's high initial growth rate, welldeveloped roots, effective nutrient uptake from soil, and a relatively short growing season contribute to its status as the dominant species in intercropped stands [20,55–57]. In own research, both at the initial phase of the vegetation period and during further growth stages, barley formed greater aboveground mass and roots mass than clover. Moreover, before the heading stage, its roots in the mixture were developed better than in pure sowing, which increased their competitive abilities as regards the acquisition of water and nutrients. Therefore, barley could successfully compete with clover under the ground and absorb water and nutrients more efficiently. Moreover, its larger and more massive plants with more foliage allowed them to absorb more light. The negative allelopathic influence of barley on clover should not be excluded. This is indirectly confirmed by the research of Księżak [58], who observed the harmful effect of cereal root secretions on the growth of vetch roots and sprouts.

Main (nurse) crops are undersown with red clover despite the main crop's inhibitory influence on clover biomass. Intercropping contributes to weed control and minimizes the resulting loss of legume seedlings, which is frequently noted in pure-sown stands, but it does not reduce the density of legume plants and delivers positive effects in successive years of production [59].

In this study, spring barley continued to exert a negative influence on dry matter accumulation in clover roots and shoots until the end of the growing season. Lamb et al. [60] demonstrated that the negative effects of intercropping are most readily manifested in young plants. The mutual adverse effects of intercropped species were weakened towards the end of the growing season in experiments conducted by Bulson et al. [61], Sobkowicz [56], Michalska et al. [44], Treder et al. [45], and Wanic et al. [12]. The cited authors attributed their findings to differences in the growth rates of

the tested plant species. The life needs of the species are minimized towards the end of development, and the available resources are largely utilized by its competitor. The above observations were not confirmed by this study.

In the present experiment, water deficit stress had an adverse influence on the aboveground biomass of clover in a pure-sown stand. The above effect had been anticipated due to clover's high water demand and its particular sensitivity to drought, which was noted by Lang and Vejražka [62]. According to the cited authors, red clover rapidly decreases its biomass accumulation in response to water deficit stress, but under optimal water conditions its biomass accumulation rates are similar to those of alfalfa. In this study, red clover produced large amounts of biomass in treatments with optimal water supply. The positive correlation between clover biomass yield and soil moisture was validated in a mathematical model by Queen et al. [23].

In this study, low soil moisture levels did not exacerbate barley's strong negative effects on biomass development in clover. In an experiment investigating the effect of mutual competition and water deficit stress on biomass development in white clover (*T. repens*) and perennial ryegrass (*L. perenne*), mild water deficit in a competitive environment stimulated the growth of clover biomass, but severe water deficit significantly intensified the reduction in biomass (total biomass and above-ground biomass, without changes in root biomass) caused by competition [63].

Competition from barley slowed down the growth of red clover as early as in the leaf development stage. Barley had a similar effect on peas [44] and Italian ryegrass [12]. In this study and in the experiment by Michalska et al. [44], barley's inhibitory influence was intensified with time in stands undersown with legume crop, whereas in the work of Wanic et al. [12] barley's limiting effect on ryegrass was minimized towards the end of the growing season.

In this study, water deficit stress lowered the CGR values of red clover between the leaf development and heading stages in pure-sown treatments, but it did not exacerbate the effect of interspecific competition on the evaluated trait. Similar results were reported by Lucero et al. [64], in whose study the relative growth rate (RGR) of white clover decreased with the intensification of water deficit stress. In the cited study, aboveground competition from *L. perenne* under significant water deficit stress did not lower RGR values, whereas total competition (aboveground and underground) contributed to a further drop in RGR values. In selected growth stages, the CGR values of Italian ryegrass were also reduced by the combined effects of water deficit stress and competition from barley [12].

Zhang et al. [11] observed different patterns of interspecific competition in a study of interactions between *Festuca rubra* and *T. pratense* under varied conditions. According to the cited authors, competitive strength is determined by the partners' biological traits, which can be modified by environmental factors to stimulate or inhibit the plants' competitive effects. The above observations corroborate the results of this study. Our research showed that barley had a negative influence on clover. The barley effect increased in time with the growing season. The clover had a slight (mainly positive) influence on barley until the heading stage. Throughout most of the growing season, the competition of barley was stronger in the treatment with a larger water supply. Meanwhile, Cousens et al. [65] consider that better water conditions strengthen the competitive power of a legume over cereal.

Summary

The interactions between spring barley and red clover had a competitive character, and the cereal was the stronger crop. The strength of this competition increased in time with the growing season. Through most of the growing season, the competition was poorer in water deficit conditions. The impact of clover on barley before the heading stage showed facilitation symptoms.

In mixed stands, competition from red clover increased barley root biomass during the stem elongation stage, but it lowered the rate of biomass accumulation at the tillering stage and led to the loss of stem and leaf biomass in barley plants towards the end of the growing season. Intensified translocation of assimilates from vegetative parts to grain minimized the loss of spike biomass. Water deficit stress had a more inhibitory influence than competition on biomass accumulation in all parts of barley plants and the rate of biomass accumulation throughout the growing season. The strongest effect of clover competition on barley CGR was observed between heading and ripening. In treatments with reduced water supply, competition from barley did not exacerbate the negative effects of water deficit on barley.

Competition from spring barley significantly reduced biomass accumulation and the growth rate of red clover until the end of the growing season. Water deficit stress strongly inhibited the growth of aboveground biomass of pure-sown clover. Water deficit stress did not exacerbate the strong competitive influence of barley on biomass accumulation or the growth rate of red clover.

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Wpływ interakcji międzygatunkowych i deficytu wody na akumulację biomasy jęczmienia jarego i koniczyny czerwonej na kolejnych etapach wzrostu

Streszczenie

Oddziaływania między jęczmieniem jarym a koniczyną miały charakter konkurencji, w której silniejszą stroną było zboże. Siła tej konkurencji zwiększała się w miarę postępu wegetacji. Przez większą część wegetacji konkurencja była słabsza w warunkach deficytu wody. Wpływ koniczyny na jęczmień do fazy kłoszenia wykazywał symptomy ułatwiania.

Obecność koniczyny czerwonej we wspólnym środowisku skutkowała przyrostem biomasy korzeni jęczmienia w fazie strzelania w źdźbło, ale począwszy od fazy krzewienia przyczyniła się do ograniczenia tempa nagromadzania biomasy u zboża i strat w masie łodyg i liści pod koniec wegetacji. Zwiększenie translokacji asymilatów z części wegetatywnych do ziarna zapobiegło stratom w masie kłosów. Deficyt wody silniej niż konkurencja z koniczyną redukował nagromadzanie masy jęczmienia we wszystkich organach i tempo jej przyrostów niemal przez cały okres wegetacji. Najsilniejszy wpływ konkurencji ze strony koniczyny na CGR jęczmienia zaznaczył się okresie kłoszenie–dojrzałość. W warunkach deficytu wody konkurencja ze strony koniczyny nie pogłębiła już negatywnego wpływu samego stresu wodnego na jęczmień.

Konkurencja ze strony jęczmienia jarego skutkowała znaczącą redukcją biomasy koniczyny czerwonej i tempa jej wzrostu, nasilając te procesy do końca wegetacji. Deficyt wody silnie ograniczył rozwój biomasy nadziemnej koniczyny w siewie czystym. Niedostatek wody w podłożu w zasadzie nie pogłębił już silnego negatywnego wpływu konkurencji ze strony jęczmienia na nagromadzanie masy i tempo wzrostu koniczyny.