

PERFORMANCE OF MULTI-COMPONENT MIXTURES OF SPRING CEREALS. PART 2. COMPETITIVE HIERARCHY AND YIELD ADVANTAGE OF MIXTURES

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Abstract. In a field experiment conducted in 2009-2011 on light soil barley, oat, wheat and triticale were grown in 3- and 4-species mixtures and in pure stands. The aim of the study was to assess competition between species in mixtures and to determine yield advantage of mixtures over their components grown in pure stands. Competitive hierarchy observed at full maturity of cereals in 4-species mixture clearly reflected hierarchies seen in 3-species mixtures, with triticale showing the highest competitive ability followed by wheat then oat and finally barley. Five weeks after plant emergence all mixtures were more productive than pure stands ($LER > 1$) while no biomass or grain yield advantage of mixtures over pure stands was found at full maturity of cereals.

Key words: competitive dominance, competitive response, LER, overyielding

INTRODUCTION

In plant ecology relationship between biodiversity and ecosystem functioning have been extensively researched during recent years. Many studies were conducted with plants from natural ecosystems to ask whether increasing species richness increases community productivity. In those experiments some mixtures comprised several or even more than ten species in order to more closely resemble plant assemblages typical for natural ecosystem [Jumpponen *et al.* 2005, Roscher *et al.* 2008, Bonin and Tracy 2012]. The research showed that the more species constitute plant community the higher is the biomass yield.

The diversity-productivity relationship has also been investigated in crop science, however most experiments used only simplest form of biodiversity, the mixture of two species. This approach is natural because in those experiments and also in agricultural practice different role is often assigned to each component. Compensation for low yield

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of worse adapted component by higher yield of the second component may be the first example. Support providing by cereal component to prone to lodging legume species is the next one.

Increasing number of components in crop mixture reduces predictability of outcome of interspecific interactions. This is because in multicomponent plant assemblage there are direct and indirect interactions between species [Vandermeer 1989, Brooker *et al.* 2008]. For example, in 3-component mixture, the interaction between components A and B is affected by the presence of the component C which also interacts with component A and B. Based on theoretical considerations Huisman and Weissing [2001] argue that the outcome of multispecies competition cannot be predicted. Some other studies contradict that view. Sobkowicz [2003] observed that in two-species mixtures, barley was better competitor than triticale and oat, while triticale better competed for resources than oat. The same hierarchy of competitive abilities was reflected in 3-component mixture of the cereals. Also Weigelt *et al.* [2007] in experiment with herbage plants demonstrated that competitive effects in multi-species assemblages may be predicted from pair-wise interactions, however in their studies, there were also some plant combinations differing from that result.

Plant species use available resources needed for growth in different way or use different forms of the same resource (e.g. atmospheric N fixed by legumes). Thus the main idea in biodiversity studies implies that the more species constitutes plant community the more completely they use resources in space and time. This resource complementarity is perceived as the one cause of the increase of productivity of a community. The second cause is facilitation – the positive influence of one species on another, for example through secretions of root system or through N transfer from roots of legume species to the roots of non-legume [Hauggaard-Nielsen and Jensen 2005].

The first aim of the study was to assess competition between species in multi-component cereal mixtures and to determine competitive hierarchy of the cereals. It was assumed that due to direct and indirect interactions between three or four cereals in mixture, the response of a species to neighboring cereals would be different in different mixtures. It was also hypothesized that three or four species grown in mixture would be able to use available resources more completely for their growth than pure stands. Thus the second aim of the research was to detect resource complementarity or positive interactions between cereals in mixtures increasing their biomass and grain production.

MATERIAL AND METHODS

The experimental site and design, field management, plant sampling and weather conditions were described in the first part of the article [Sobkowicz *et al.* 2016].

To determine the response of a species to competition from another species in mixture in relative terms, the relative yield (RY) was calculated for each cereal. In original version, RY is the ratio of yield (biomass, grain etc.) of a species in mixture to yield of the species in pure stand [Weigelt and Jolliffe 2003]. Using relative yield it is possible to compare the response of a species to competition from another species only among mixtures having the same number of components. For the purpose of this study, modified equation was used in order to enable this comparison between 3- and 4-component mixtures, as follows:

$$RY_a = (Y_{ma} / Y_{sa}) \times n$$

where RY_a is the relative yield of species a in mixture, Y_{ma} is the yield of species a in mixture, Y_{sa} is the yield of species a in pure stand, and n is the number of species in mixture. Similar modification of RY in order to compare competitive interactions in multiple plant assemblages was done by Fowler [1982] and Dukes [2001]. The modification – multiplying original equation by number of species in mixture – scales up RY to unity in situation when for species a interspecific competition (competition of plants of species a with plants of other species in multi-species mixture) equals intraspecific competition (competition between plants of species a in pure stand). Thus $RY_a < 1$ means that species a is suppressed in mixture by the collective pressure of other species in multi-species mixture. If $RY_a > 1$, the competition from plants of neighboring species in multi-species mixture is weaker for species a than between plants of species a in pure stand.

To assess yield advantage of a mixture over its corresponding components grown in pure stands the land equivalent ratio (LER) [Mead and Willey 1980] was calculated. In original version LER is the sum of relative yields. For the purpose of this research the sum was divided by the number of species in mixture:

$$LER = (RY_a + RY_b + \dots + RY_x) / n$$

where RY_a , RY_b , and RY_x are relative yields of all components of the mixture. LER shows total area of land needed in pure stands to produce the same amount of each of them as unit of land of the mixture. $LER > 1$ means gain from mixed cropping (overyielding). The same method was used by Dukes [2001] to calculate similar index to LER – the relative yield total (RYT) in multi-species plant assemblage.

Competitive abilities of mixture components were compared using the competitive balance index (C_b) [Wilson 1988]. C_b is the natural logarithm of competitive ratio (CR) [Willey and Rao 1980]. In the present study C_b was calculated based on CR modified by Juskiw *et al.* [2001] for assessing competitive abilities of components in multispecies mixtures, as follows:

$$C_{ba} = \ln\{[RY_a/(RY_b + \dots + RY_x)] \times [(p_b + \dots + p_x)/p_a]\},$$

where C_{ba} is the competitive balance index of species a , while p_a , p_b and p_x are initial proportions of all component crops in a mixture (in the present study 0.33 or 0.25 for 3- and 4-component mixtures respectively). The index was calculated for all mixture components. $C_{ba} > 0$, means that species a is more competitive than other components in mixture considered as a whole, while $C_{ba} < 0$, means that the reverse is true. In other words, C_{ba} compares competitive ability of species a with the collective competitive ability of other mixture components. Value of C_b decided also on a place of a species in competitive hierarchy.

Separately for each mixture student's t-test was used to determine whether RY and LER means, differed from 1 and C_b means differed from 0 ($n = 12$). Simple linear correlation coefficient was calculated between some features of cereals grown in pure stand and competition indices calculated for the cereals in 4-species mixture (RY, C_b). The coefficient was also calculated in order to find relationship between competitive hierarchy of cereals in 4-species mixture and hierarchies found in 3-species mixtures. For this purpose values of C_b from 4-species mixture were correlated with values of C_b calculated for each cereal as a mean C_b of all 3-species mixtures.

RESULTS

Five weeks after plant emergence values of $RY_{\text{triticale}}$ calculated based on dry matter yield of plants were significantly greater than unity in all mixtures indicating positive response of triticale to mixed cropping (Table 1). Wheat responded in similar way when grown in mixtures with barley and triticale, oat and triticale and in 4-species mixture. For barley, interspecific competition was significantly lower than intraspecific competition only when the species was grown in barley-oat-wheat mixture and the same was true for oat in barley-oat-triticale mixture. At this stage of growth all mixtures were more productive than pure stands ($LER > 1$).

Table 1. Relative yields (RY) and the land equivalent ratios (LER) calculated on the basis of dry matter yields of plants during vegetation period and grain yields (mean for 2009-2011)
Tabela 1. Plony względne (RY) oraz współczynniki ekwiwalentu terenowego (LER) obliczone na podstawie plonów suchej masy roślin w okresie wegetacji i plonów ziarna (średnia z lat 2009-2011)

Mixture Mieszanka	RY_{barley} $RY_{\text{jęczmień}}$	RY_{oat} RY_{owies}	RY_{wheat} RY_{pszenica}	$RY_{\text{triticale}}$ $RY_{\text{pszenżyto}}$	LER
5 weeks after plant emergence – 5 tygodni po wschodach roślin (BBCH 31-32)					
BOW	1.15*	1.14	1.15	–	1.15*
BOT	1.12	1.11*	–	1.39*	1.21*
BWT	1.05	–	1.24*	1.22*	1.17*
OWT	–	1.12	1.23*	1.17*	1.17*
BOWT	1.19	1.04	1.20*	1.22*	1.16*
Full maturity – Dojrzałość pełna (BBCH 87-89)					
BOW	0.82*	0.94	1.09	–	0.95
BOT	0.74*	0.90	–	1.35*	1.00
BWT	0.78*	–	1.05	1.25*	1.03
OWT	–	0.80*	1.06	1.11	0.99
BOWT	0.79*	0.91	1.12	1.22*	1.01
Grain yield – Plon ziarna					
BOW	0.93	0.88	1.15*	–	0.99
BOT	0.78*	0.85	–	1.34*	0.99
BWT	0.81*	–	1.02	1.22*	1.02
OWT	–	0.78*	1.10	1.18*	1.02
BOWT	0.87*	0.85*	1.14	1.26*	1.03

B – barley – jęczmień, O – oat – owies, W – wheat – pszenica, T – triticale – pszenżyto

* significantly different from 1 at $P = 0.05$ – istotnie różne od 1 dla $P = 0,05$

At full maturity $RY_{\text{triticale}}$ calculated based on dry matter yield of plants significantly exceeded unity in barley-oat-triticale, barley-wheat-triticale and in 4-species mixture. No significant response to different neighboring species was noted for wheat. Barley was the only cereal that was negatively affected by competition from other cereals in all mixtures while significantly negative response of oat to mixed cropping was observed when the species was sown together with wheat and triticale. LER calculated for plant dry matter yield at full maturity of cereals did not differ significantly from unity indicating no gain from mixed cropping.

Relative yields calculated on the basis of grain yield confirm that barley was suppressed by other species in mixtures with the exception of barley growing with oat

and wheat for which RY_{barley} did not differ significantly from unity. Data also shows that triticale yielded relatively more grain in mixtures than in pure stand. Negative response of oat to neighboring species reflected in grain yield was noted when the cereal was grown in mixture with wheat and triticale and in 4-species mixture. Wheat yielded relatively more grain in mixture with barley and oat than in pure stand. Grain LER did not differ significantly from unity showing no advantage from mixed cropping.

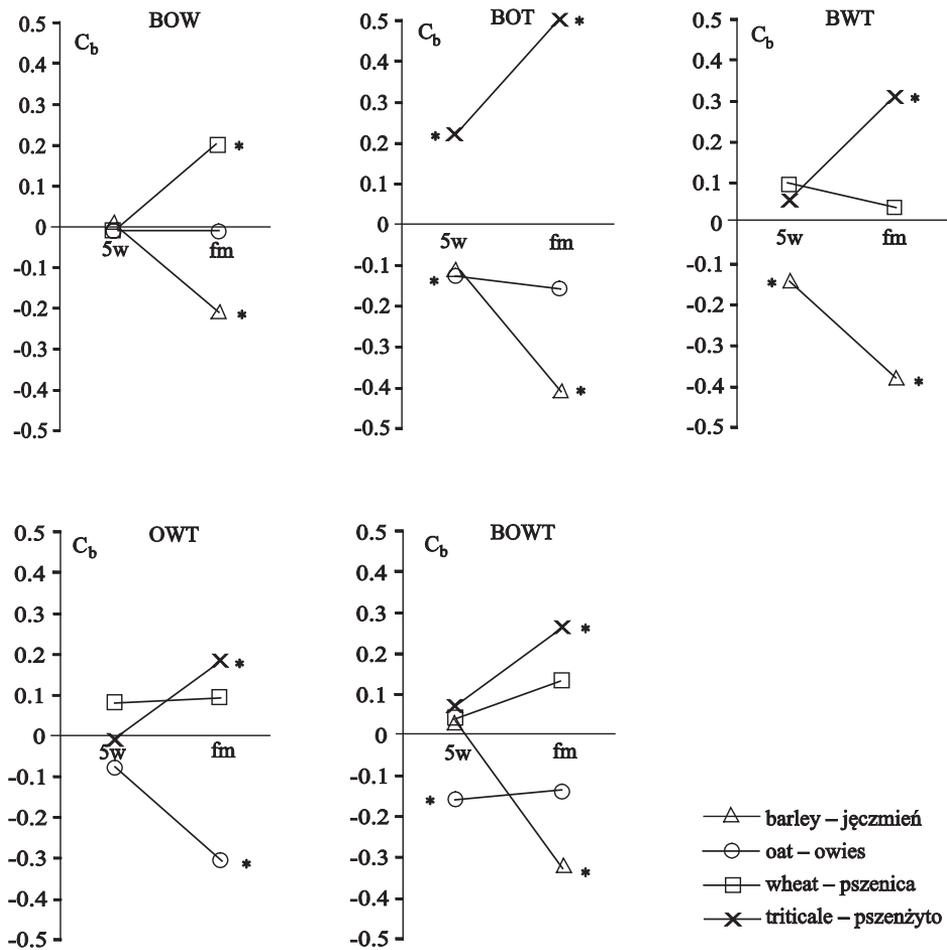
Figure 1 shows that competitive abilities of cereals calculated on the basis of dry matter yields of plants differed less during early growth of mixtures than later, during reproductive stages of growth. Five weeks after plant emergence no competitive dominance of any species was observed in mixtures with the exception of barley-oat-triticale mixture that was dominated by the last component. Oat was less competitive than other components in the same mixture and in 4-species mixture at this stage of growth. Competitive ability of barley was lower than other components in mixture with wheat and triticale.

Later during growing season competitive ability of triticale greatly increased while the reverse was true for barley. At full maturity competitive dominance of triticale was seen in mixtures, while barley was subordinate component. Competitiveness of oat and wheat was more stable than barley and triticale during plant growth, however wheat was never significantly less competitive than other mixture components, while oat was outcompeted by other components in oat-wheat-triticale mixture. Competitive hierarchy observed at full maturity in mixture comprising four cereals clearly reflected hierarchies seen in most 3-species mixtures, with triticale showing the highest competitive ability followed by wheat then oat and finally barley.

Dominance of triticale in mixtures is also seen when the competitive balance index was calculated on the basis of grain yield (Table 2). Triticale C_b ranged from 0.22 to 0.50 being significantly different from zero in all mixtures. Also the ranking order of the four cereals created on the basis of C_b was generally similar to that observed for plant dry matter yields. The only difference was in barley-oat-wheat mixture and in mixture comprising four cereals. In the first mixture oat was less competitive than other components ($C_b = -0.18$), while in 4-species mixture barley ($C_b = -0.23$) and oat ($C_b = -0.26$) were worse competitors than wheat and triticale.

In 4-species mixture, which demonstrates well the competitive hierarchy of cereals observed in the study, a significant linear relationship was found between some features of the cereals determined in pure stand and competition indices (RY , C_b) determined at full maturity (Table 3). Grain weight per inflorescence was positively correlated with plant dry matter relative yield, grain relative yield and C_b calculated on the basis of grain yield. Negative correlation was found between number of inflorescences per plant and C_b calculated on the basis of plant dry matter yield. Also there was negative linear relationship between number of inflorescences per unit area and both indices calculated on the basis of grain yield. No significant correlations were found between other yield components of cereals in pure stands and competition indices and also between plant dry matter yield, grain yield and crop growth rate in pure stands and the indices.

Five weeks after plant emergence no significant correlation was found between competitive balance indices (C_b) calculated for each cereal in 4-species mixture and values of the index calculated for the cereals as a mean C_b of 3-species mixtures ($r = 0.632$, $n = 4$). At full maturity the relationships were significant for plant dry matter yield ($r = 0.992^*$) and grain yield ($r = 0.997^{**}$) confirming the same competitive hierarchy of species in mixtures.



5w – five weeks after plant emergence (BBCH 31-32) – pięć tygodni po wschodach roślin

fm – full maturity (BBCH 87-89) – dojrzałość pełna

B – barley – jęczmień, O – oat – owies, W – wheat – pszenica, T – triticale – pszenżyto

* significantly different from 0 at $P = 0.05$ – istotnie różne od 0 dla $P = 0,05$

Fig. 1. Competitive balance indices (C_b) calculated for each mixture component on the basis of dry matter yields of plants during vegetation period (mean for 2009-2011)

Rys. 1. Współczynniki równowagi konkurencyjnej (C_b) obliczone dla każdego komponenta mieszanki na podstawie plonów suchej masy roślin w okresie wegetacji (średnia z lat 2009-2011)

Table 2. Competitive balance indices (C_b) calculated for each mixture component on the basis of grain yields (mean for 2009-2011)Tabela 2. Współczynniki równowagi konkurencyjnej (C_b) obliczone dla każdego komponenta mieszanki na podstawie plonów ziarna (średnia z lat 2009-2011)

Species Gatunek	Mixture – Mieszanka				
	BOW	BOT	BWT	OWT	BOWT
Barley – Jęczmień	-0.09	-0.34*	-0.33*	–	-0.23*
Oat – Owies	-0.18*	-0.25	–	-0.39*	-0.26*
Wheat – Pszenica	0.23*	–	0.00	0.11	0.12
Triticale – Pszenżyto	–	0.50*	0.29*	0.22*	0.28*

B – barley – jęczmień, O – oat – owies, W – wheat – pszenica, T – triticale – pszenżyto

* significantly different from 0 at $P = 0.05$ – istotnie różne od 0 dla $P = 0,05$ Table 3. Simple linear correlation coefficients between features of four cereals ($n = 4$) grown in pure stands and competition indices (RY, C_b) calculated for the cereals in 4-species mixture on the basis of plant dry matter yield determined at full maturity and grain yield (mean for 2009-2011)Tabela 3. Współczynniki korelacji liniowej pomiędzy cechami czterech zbóż ($n = 4$) uprawianych w siewie czystym a wskaźnikami konkurencji (RY, C_b) obliczonymi dla tych zbóż w mieszance 4-gatunkowej na podstawie plonów suchej masy roślin w fazie dojrzałości pełnej i plonu ziarna (średnia z lat 2009-2011)

Cereal traits in pure stands Cechy zbóż w zasiewach czystych	Dry matter yield of plants Plon suchej masy roślin		Grain yield Plon ziarna	
	RY	C_b	RY	C_b
No. of inflorescences per plant Liczba kwiatostanów z rośliny	-0.944	-0.955*	-0.810	-0.810
1000-grain weight Masa 1000 ziarn	-0.173	-0.191	0.106	0.114
Grain weight per inflorescence Masa ziarna z kwiatostanu	0.955*	0.945	0.962*	0.958*
Grain no. per inflorescence Liczba ziarn z kwiatostanu	0.311	0.326	0.047	0.039
No. of inflorescences per unit area Liczba kwiatostanów na jednostce powierzchni	-0.947	-0.943	-0.973*	-0.976*
Plant dry matter yield Plon suchej masy roślin	0.450	0.460	0.216	0.206
Crop growth rate: 5w – fm Szybkość wzrostu łanu 5w – fm	0.468	0.477	0.242	0.232
Grain yield Plon ziarna	-0.319	-0.345	-0.192	-0.203

5w – five weeks after plant emergence (BBCH 31-32) – pięć tygodni po wschodach roślin

fm – full maturity (BBCH 87-89) – dojrzałość pełna

* significant correlation at $P = 0.05$ – korelacja istotna dla $P = 0,05$

DISCUSSION

The experiment showed that barley was the weakest competitor among spring cereals which contradicts results of previous studies indicating high competitive abilities of the species in cereal mixtures [Michalski i Waligóra 1993, Rudnicki 1994,

Noworolnik i Leszczyńska 1999, Juskiw *et al.* 2000, Sobkowicz 2003, Wanic *et al.* 2007, Treder and Wanic 2011]. In our study barley having similar to other cereals growth dynamics in pure stand [Sobkowicz *et al.* 2016], was unable to gain advantage over them in mixtures during early growth. Studies demonstrate that high competitiveness of barley at first stages of plant growth usually leads to further success in interspecific competition [Sobkowicz 2003, Andersen *et al.* 2007, Wanic *et al.* 2007, Treder and Wanic 2011]. The reason for competitive failure of barley in the present study is not clear. Its competitive ability in relation to other cereals was probably affected by factors like cultivars chosen, soil conditions and weather. Michalski and Szolkowska [2007] found that competition between barley and oat in mixture depended on cultivars of both cereals. They also pointed out to barley dominance in grain yield of mixture in dry year. Zając *et al.* [2011] indicated greater competitive ability of oat than barley at site with worse environmental conditions while the reverse was true for site with more favorable conditions. In research of Klima and Pieczko [2002] triticale was better competitor than barley in mixture grown on different parts of the mountain slope, but in particular on the upper zone where soil conditions were more severe.

Competitive hierarchy of cereals in mixtures was established later during growing season when species reached maximum height of plants. It suggests that competition for light was an important factor for establishing the hierarchy, with barley having the smallest plants being the weakest competitor. Oat, wheat and triticale as later-maturing crops than barley continued growth longer and to some extent escaped from competitive pressure of barley. The results agree with those of Cousens *et al.* [2003] who observed that the competitive hierarchy in mixture may be established later during growing season when there are environmental conditions favoring initially weaker competitor. In the study presented here in June and July 2009 and 2011 there was more rainfall than in long-term average [Sobkowicz *et al.* 2016], and this conditions probably benefited plant growth and grain filling of later maturing cereals than barley. The importance of the second part of the growth period of plants in mixtures in establishing the competitive hierarchy is confirmed by relationships found between some yield components noted in pure stand and competitive indices. The correlations showed that triticale and wheat forming one heavy spike per plant outcompeted barley and oat. Thus, producing more tillers with inflorescences per plant like the latter two cereals was not profitable strategy to gain competitive advantage over neighboring species in mixtures. High competitiveness of triticale observed in our study was also found by Starczewski *et al.* [2010] when compared with competitiveness of wheat. Baron *et al.* [1996] underlined good performance of triticale in cereal mixtures due to its high tolerance to shade. Other results were noted by Tobiasz-Salach *et al.* [2011] in two-species mixtures who noted higher competitive advantage of barley over oat and triticale, and wheat over barley and triticale.

Taking into consideration the whole growth period, it seems that the main phenomenon present in multi-species mixtures was competition for resources. This was demonstrated by the same competitive hierarchy of species in mixtures and by significant positive correlation between competition indices calculated for 4-species mixture and the mean values of the indices calculated for 3-species mixtures. The hierarchy was thus transitive [Freckleton and Watkinson 2001, Brooker *et al.* 2008] which means that the hierarchy observed in 4-species mixture may be easily predicted from competitive hierarchies in 3-species mixtures and vice versa.

In the present study cereals in pure stand yielded each other similar biomass and grain during experimental years and only 3-year average shows that wheat yielded less grain than barley and triticale [Sobkowicz *et al.* 2016]. Wheat however was the second species in the competitive hierarchy in mixtures, after triticale but before oat and barley. Thus competitive hierarchy at maturity did not reflect the hierarchy formed based on pure stand grain yields of the cereals. The higher productive species in pure stand like barley or oat were outcompeted in mixtures by least productive wheat. This so called "Montgomery effect" [Blijenburg and Sneepe 1975] was probably the obstacle to better performance of mixtures with wheat. According to Dukes [2001] this situation may obscure existing positive interactions between remaining species in the mixtures or resource complementarity between them. Worse performance in mixtures of the highest yielding component in pure stand was also noted by Andersen *et al.* [2007]. Rudnicki and Wasilewski [1993] observed different than in our research, hierarchy of cereals built on their response to competition in equal proportion 3-species mixture of barley, oat and wheat. In that research only oat showed positive response, while it was negative for barley and severe for wheat.

Although cereals employed in the present experiment are adapted to different soil conditions, similar level of grain yield of pure stand cereals indicates that they used the same available resources in similar way. It may explain the lack of resource complementarity in mixtures, which was expressed by LER not different from unity. Only during stem elongation $LER > 1$ was noted for plant dry matter yields of mixtures, but it did not differ among mixtures. Wanic *et al.* [2007] also found greater resource complementarity in mixture of barley and wheat during stem elongation than at full maturity.

In our research other types of interactions including direct and indirect facilitation among components were absent in mixtures or if they were present, their influence was too small to increase biomass or grain production of mixtures. In previous study, oat and triticale performed supporting function for barley in mixtures preventing it from early lodging and grain yield decrease [Sobkowicz 2003]. That facilitative mechanism increased RYT calculated for grain yield, the index of similar meaning to LER used in this study. In the present study pure stands and mixtures did not lodge. Lack of resource complementarity or facilitation in two-species mixtures of spring cereals was also observed by Tobiasz-Salach *et al.* [2011], who noted $LER < 1$ for four out of six mixtures comprising wheat, triticale and hulled cultivars of barley and oat.

The study showed no positive diversity – productivity relationship even when the diversity was represented by 4-species mixture, being very high in terms of agricultural practice. Thus the cereals were almost perfectly substitutable in the sense that regardless of mixture composition, each mixture produced similar plant dry matter and grain yield.

CONCLUSIONS

1. Competitive hierarchy of spring cereals grown in 3 and 4 species mixtures determined on the basis of competitive balance index (C_b) indicated triticale with the highest competitive ability followed by wheat, oats and finally barley.

2. Correlations between yield components of pure stand cereals and competition indices (RY and C_b) shows that creating one heavy inflorescence per plant like triticale and wheat was better competitive strategy than producing more fertile tillers like barley and oat.

3. Land equivalent ratio (LER) calculated on the basis of dry matter yields of plants showed higher productivity of mixtures than pure stands five weeks after plant emergence, however at full maturity of cereals the values of LER indicated no gain from mixed cropping.

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WYDAJNOŚĆ WIELOSŁADNIKOWYCH MIESZANEK ZBÓŻ JARYCH. CZĘŚĆ 2. HIERARCHIA KONKURENCYJNA I NADPRODUKTYWNOŚĆ MIESZANEK

Streszczenie. W doświadczeniu polowym przeprowadzonym w latach 2009-2011 na glebie lekkiej uprawiano 3- i 4-gatunkowe mieszanki zbożowe z udziałem jęczmienia, owsa, pszenicy i pszenżyta oraz zasiewy czyste tych zbóż. Celem badań była ocena konkurencji między gatunkami w mieszankach i określenie nadprodukcyjności mieszanek. Hierarchia konkurencyjna stwierdzona w okresie dojrzałości pełnej zbóż w mieszance 4-składnikowej odzwierciedlała hierarchie obserwowane w mieszankach 3-składnikowych, w których najbardziej konkurencyjne było pszenżyto, a mniej kolejno: pszenica, owies i jęczmień. Pięć tygodni po wschodach roślin wszystkie mieszanki były bardziej produktywne niż zasiewy czyste ($LER > 1$), podczas gdy w okresie dojrzałości pełnej nie stwierdzono nadprodukcyjności mieszanek w odniesieniu do plonu biomasy i ziarna.

Słowa kluczowe: dominacja konkurencyjna, LER, nadprodukcyjność, reakcja na konkurencję

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