RADIATION USE EFFICIENCY IN SPRING BARLEY UNDER DROUGHT: A CROSSTALK BETWEEN SURVIVAL STRATEGY AND CANOPY STRUCTURE

ZMENA EFEKTÍVNOSTI VYUŽITIA ŽIARENIA U JARNÉHO JAČMEŇA POČAS SUCHA: INTERAKCIA STRATÉGIE PREŽITIA A ŠTRUKTÚRY PORASTU

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Manuscript received: February 16, 2009; Reviewed: August 6, 2009; Accepted for publication: August 18, 2009

ABSTRACT

In order to evaluate effects of different survival strategy and canopy structure on cereal radiation use efficiency (RUE) under drought during grain filling, a pot experiment in spring barley (Hordeum vulgare L.) of cultivar Dobla (able for escape, no productive tiller) and Kompakt (one productive tiller) was conducted. There was no difference in current RUE for leaf dry mass (RUE$_{L}$) between main stems of tested cultivars, observed. However, in productive tillers of cultivar Kompakt it was approximately double. Taking together, RUE$_{L}$ for whole plants was significantly higher in cultivar Kompakt than in cultivar Dobla. Current RUE for spike dry mass (RUE$_{S}$) in hydrated plants was markedly higher than RUE$_{L}$, in main stems of cultivar Kompakt with round double values of cultivar Dobla. Productive tillers of cultivar Kompakt were the most efficient PAR (photosynthetic active radiation) utilizator for spike growth. Drought decreased RUE$_{S}$ in cultivar Kompakt (in main stems as well as productive tillers) to a half but in cultivar Dobla 20 %, only. Evaluating final RUE for spikes, almost fivefold higher values in hydrated plants of cultivar Kompakt fell to double ones under drought. In this context, important role played the productive tiller. Thus, model of more intensively tillering cereal crop seems to be more efficient in radiation use.

Key words: radiation use efficiency, drought, survival strategy, canopy structure, spring barley

ABSTRAKT

Za účelom zhodnotenia účinku odlišnej stratégie prežitia a štruktúry porastu na efektívnosť využitia žiarenia (RUE) obilnín v podmienkach sucha počas nalievania zŕn, bol realizovaný nádobový vegetačný pokus s jarným jačmeňom (Hordeum vulgare L.), kultivaru Dobla (schopnosť úniku, bez produktívnych odnoží) a Kompakt (1 produktívna odnož). Medzi aktuálnou RUE pre tvorbu sušiny listov (RUE$_{L}$) na hlavných steblách nebol u rastlín jednotlivých kultivarov pozorovaný žiadny rozdiel. Na druhej strane, produktívne odnože u kultivaru Kompakt dosiahli približne dvojnásobnú hodnotu. Zohľadňujúc obe časti rastliny, tento genotyp výrazne prevýšil kultivar Dobla. Aktuálna RUE pre tvorbu sušiny klasov (RUE$_{S}$) bola všeobecne vyššia ako RUE$_{L}$, pričom u hlavných stebiel kultivaru Kompakt sme zistili oproti kultivaru Dobla asi dvojnásobnú hodnotu. Najefektívnejšie využívali PAR (fotosynteticky aktívne žiarenie) pre tvorbu sušiny klasov produktívne odnože. Sucho znížilo RUE$_{S}$ u kultivaru Kompakt o polovicu, no u kultivaru Dobla len o 20%. Pozberová analýza RUE ukázala suchom indukovaný pokles u kultivaru Kompakt z asi päťnásobne vyššej hodnoty na približne dvojnásobnú, čo do značnej miery súvisí s prítomnosťou produktívnej odnože. Model obilniny s väščou odnožovacou schopnosťou sa teda javí ako efektívnejší.

Kľúčové slová: efektívnosť využitia žiarenia, sucho, stratégia prežitia, štruktúra porastu, jarný jačmeň

DETAILNÝ ABSTRAKT

Sucho môže výrazne redukovať úrodu zrna cereálií. Toto zníženie je spôsobené poklesom efektívnosti, ktorou je využívané slnečné žiarenie (efektívnosť využitia žiarenia, RUE). V tomto kontexte sú najcitlivejšími miestami fotosyntéza (zdroj asimilátov) a procesy spojené s nalievaním zrna (akceptor asimilátov). Za účelom zmiernenia strát na úrode ako aj zlepšenia efektívnosti využitia žiarenia a vody vzniklo množstvo šľachtiteľských programov zameraných na osmotické prispôsobenie, prieduchovú vodivosť, aktívny povrch koreňa, translokáciu uhlíkových rezerv, fenologický posun a štruktúru porastu. V tejto štúdii sme hodnotili efektívnosť využitia žiarenia u genotypov jačmeňa jarného líšiacich sa štruktúrou porastu (odnožovacia schopnosť) a stratégiou prežitia (únik/tolerancia) počas sucha.

Mikroporasty jačmeňa jarného (Hordeum vulgare L.) – kultivarov Kompakt (SVK, 1 produktívna odnož) a Dobla (ESP, schopnosť úniku, bez odnoží) boli založené do nádob s pôdnym substrátom v hustote 392 rastlín na meter štvorcový (optimum pre južné Slovensko). Na začiatku kvitnutia skoršieho kultivaru Dobla (DC 61) sa časť nádob prestala zalievať. Listová plocha, hmotnosť sušiny listov a po prechode do generatívnej fázy aj sušiny klasov boli zisťované jedenkrát týždenne. Z údajov o dennom príkone fotosynteticky aktívneho žiarenia (PAR), získané na báze merania absolútneho slnečného svitu, sme počítali aktuálnu RUE pre tvorbu sušiny listov (RUE_L) resp. klasov (RUE_S) na hlavnom steble a produktívnej odnoži. Po zbere sa tiež zistila finálna RUE pre tvorbu sušiny klasov.

V porovnaní s kultivarom Dobla s dynamikou rastu listovej plochy v tvare písmena „S“, vykazoval kultivar Kompakt homogénnejší rast s maximálnym indexom listovej pokryvnosti (LAI) väčším asi o 1 $m^2.m^{-2}$ (Obr. 1). Listová plocha na produktívnej odnoži tohto genotypu sa začala vyvíjať približne o 10 dní neskôr, oproti hlavnému steblu expandovala s polovičnou intenzitou a dosiahla len 60 % jeho maximálneho LAI. Vzhľadom k podobnej špecifickej listovej ploche (SLA) na hlavných steblách oboch kultivarov (Tab. 1), hmotnosť sušiny listov sledovala dynamiku LAI. Avšak výrazne vyššia SLA u produktívnych odnoží rastlín Kompaktu poukazuje na relatívne nižšiu produkciu sušiny. Medzi hlavnými steblami rastlín jednotlivých kultivarov sme nepozorovali markantný rozdiel v RUE_L, no produktívne odnože kultivaru Kompakt dosahovali dvojnásobok (Obr. 2). Berúc do úvahy obe časti rastliny, v RUE_L dominoval kultivar Kompakt.

Klasové primordiá boli najskôr detekované v hlavných steblách genotypu Dobla, čo potvrdzuje jeho skorosť (Obr. 3; Tab. 2). Na druhej strane, kultivar Kompakt priniesol na hlavných steblách o 100 $g.m^{-2}$ väčšiu úrodu klasov. O niekoľko dní neskôr objavujúce sa klasy produktívnych odnoží vykazovali polovičnú finálnu hmotnosť. RUE_S dosahovala výrazne vyššie hodnoty ako RUE_L, pričom na hlavných steblách u kultivaru Kompakt to bol takmer dvojnásobok pozorovaný u kultivaru Dobla (Obr. 4, 5). Podobne ako v prípade tvorby sušiny listov, aj pri tvorbe sušiny klasov boli najefektívnejšie utilizátory PAR produktívne odnože kultivaru Kompakt. Analyzujúc finálnu RUE, takmer päťnásobne vyššie hodnoty u rastlín kultivaru Kompakt (Obr. 6) boli zabezpečené dlhšie prebiehajúcou akumuláciou sušiny v klasoch ako aj prítomnosťou produktívnej odnože.

Sucho znížilo RUE_S u oboch kultivarov ako aj častí rastlín (Obr. 4). U kultivaru Kompakt (na hlavných steblách aj produktívnych odnožiach) klesla približne o polovicu, u kultivaru Dobla asi o 20 %. Preukazné zníženie finálnej hmotnosti klasov bolo však pozorované len u kultivaru Kompakt (Obr. 3), a tomu zodpovedá aj zmena finálnej RUE (Obr. 6). Zohľadňujúc formovanie klasov na odnožiach, kultivar Kompakt využíval PAR efektívnejšie ako kultivar Dobla aj v podmienkach progresívneho sucha. Predpokladáme však, že pozitívny efekt rýchleho prechodu do generatívnej fázy (úniku) v reakcii na sucho by sa u kultivaru Dobla prejavil zvýšením hustoty porastu.

INTRODUCTION

Grain (the harvestable part) yield (GY) of cereals is a function of radiation input throughtout the growing period (RAD), fraction of RAD intercepted (%RI), radiation use efficiency (RUE) and harvest index (HI) [1]:

$$GY = RAD * \%RI * RUE * HI \qquad (1)$$

Crop management practices, such as changing planting date, or crop breeding strategies modifying plant duration will affect RAD. %RI by the canopy may be increased by a faster approach to full cover and a higher leaf expansion. RUE may be increased by improving the distribution of PAR among the various leaves as well as enhancing the photosynthetic performance under stress conditions [1].

According to Nam et al. [18] cummulative intercepted radiation and RUE accounted for 99 per cent of the genotypic variation in pigeonpea crop growth rate (CGR). RUE per se contributed by nearly 90 per cent, documenting its important position in yield formation.

In the study of RUE, both photosynthesizing source as

Table 1: Specific leaf area (SLA) in main stems and productive tillers of cultivar Kompakt as well as main stems of cultivar Dobla. Letters indicate statistically significant difference at P=0,01.
Tabuľka 1: Špecifická listová plocha na hlavnom steble a produktívnej odnoži rastlín kultivaru Kompakt ako aj na hlavnom steble rastlín kultivaru Dobla. Analýza rozptylu zodpovedá hladine významnosti 99%.

Genotype	***Plant part***	***SLA ($m^2.g^{-1}$)***
Kompakt	main stems	0,0330 ± 0,0021 a
	productive tillers	0,0448 ± 0,0055 b
Dobla	main stems	0,0352 ± 0,0020 a

Table 2: Course of phenological changes (according to Zadoks scale) in spring barley genotypes Kompakt and Dobla under sufficient and insufficient water supply.
Tabuľka 2: Priebeh fenologických zmien (podľa Zadoksovej stupnice) u genotypov jačmeňa jarného s odlišnou stratégiou prežitia a štruktúrou porastu (Kompakt a Dobla) v podmienkach dostatočnej a nedostatočnej zásoby vody v pôde.

DAS*	***Genotype***			
	Kompakt		***Dobla***	
8	DC 12		DC 12	
14	DC 25		DC 25	
21	DC 31		DC 32	
28	DC 36		DC 49	
35	DC 45		DC 55	
40	DC 49		DC 61	
	hydrated	***dehydrated***	***hydrated***	***dehydrated***
47		DC 71		DC 75
48	DC 71		DC 75	
56	DC 75		DC 85	
57		DC 75		DC 85
62	DC 77		DC 87	
64		DC 85		DC 87
71	DC 87		DC 92	

*days after sowing

well as accumulating sink must be targeted. Key research areas includes: i) photosynthetic metabolism, ii) canopy photosynthesis, iii) determination of grain number and size (sink strength), iv) vascular transport of water, nutrients and assimilates, v) respiratory costs, and vi) buffering of these processes to environmental fluxes [19].

Although high effort has been given to improvement RUE, only some per cent of photosynthetically active radiation is fixed in plant biomass under favourable conditions. Environmental constraints further reduce RUE [23].

In semiarid conditions, source is mainly limited by water deficit and sink by elevated temperature [9]. Photosynthesis down-regulation follows decrease in stomatal conductivity, ribulose bisphosphate carboxylase/oxygenase (Rubisco) activity and ribulose bisphosphate (RuBP) regeneration probably caused by inhibition of ATP synthesis [15]. Thylakoid electron transport is stable till 30 per cent of water deficit [8]. Limitation on the sink side is represented by lower division of endosperm cells in early periods of grain filling, and by impairment of starch synthesis in later ones [2].

To alleviate yield losses and improve radiation and water utilization, wide breeding programs focused on osmotic adjustment, stomatal conductivity, root active surface, carbon reserves translocation, phenological shift and canopy structure have been established [20].

In this study, we evaluated radiation use efficiency of two spring barley genotypes differing in canopy structure (tillering ability) and survival strategy (escape/tolerance) under drought. Simultaneously, we analyzed RUE in respective plant/canopy components (main stems and productive tillers).

MATERIAL AND METHODS

Plant material and cultivation

Microcanopies of two spring barley (Hordeum vulgare L.) cultivars – Kompakt (Slovak provenience, one productive tiller) and Dobla (Spanish provenience, escape ability, no productive tiller) were established in twenty 10-litres plastic pots with loamy-clayey soil substrate supplemented by mineral fertilization. Density of the microcanopies was arranged to 392 plants per square meter, meeting optimal range for Southern Slovakia. Plants were cultivated in external conditions with regular water supply and protection against pests and diseases. At the beginning of flowering stage of the more precocious cultivar Dobla (DC 61) a part of both microcanopies was subjected to progressing drought by water witholding.

Measurements and calculations

During canopy development leaf area (leaf area meter CI-203, CID Inc., USA) and leaf dry mass per square meter (A and W_L, respectively) were determined weekly. From these parameters specific leaf area (SLA) was calculated:

$$SLA = A/W_L \qquad (m^2.g^{-1}) \qquad (2)$$

Swiching to generative phase of the plant ontogeny, spike dry weight (W_S) was ascertained, as well.

Incident photosynthetically active radiation (PAR) over microcanopies (direct and diffuse component), was calculated using global radiation (GR), obtained from measurement of absolute sunshine duration:

$$GR = GR_o*(1-K*(1-s/s_o)) \ (kWh.m^{-2}), \qquad (3)$$

where GR is real global radiation, GR_o is global radiation at clear sky, K is coefficient of GR reflection and diffusion, s – absolute sunshine (h), s_o – astronomic sunshine (h). Thereafter:

$$PAR = GR* H_{PAR}/H_{GR} \ (kWh.m^{-2}), \qquad (4)$$

where H_{PAR}/H_{GR} is average monthly ratio of PAR to GR. For every month of vegetation period a distinct H_{PAR}/H_{GR} ratio was utilized, as indicated in [11]. PAR values were then expressed in $MJ.m^{-2}$.

Dynamics of photosynthetically active radiation efficiency (RUE) in main stems and productive tillers was determined indirectly as a slope of linear regresion of cummulative incident PAR corrected by relative participation of plant parts (main stems and productive tillers) on total leaf area to total leaf dry mass (current RUE_L) or spike dry mass (current RUE_S) in these plant parts. At the harvest it was determined as a ratio of final spike dry mass (W_S) and cummulative incident PAR per plant part related to spike formation (ΣPAR):

$$RUE = W_S/\Sigma PAR \ \ (g.MJ^{-1}) \qquad (5)$$

Statistical analysis

Data were submitted to statistical analysis of variance (ANOVA) using application Statgraphics Plus v. 4.0. LSD tests on confidence level of 95 and 99 per cent were performed for leaf area, specific leaf area, spike dry weight and radiation use efficiency.

RESULTS

Leaf formation

Leaf area expansion in main stems of more precocious cultivar Dobla at first showed slow dynamics, followed by intense one, and slowed down again at the end of leaf formation period (Figure 1). On the other hand, cultivar Kompakt exhibited more homogenous dynamics with final leaf area index (LAI) almost 1 $m^2.m^{-2}$ larger. Leaf area in productive tillers of this cultivar started to develop approximately 10 days later, with a half intensity and only 60 per cent of final LAI, as compared to main stems.

Because of similar specific leaf area (SLA) of main stem leaves in both cultivars (Table 1) accumulation of leaf dry weight corresponded with LAI formation. But significantly higher SLA in productive tillers of cultivar Kompakt pointed to lower leaf dry weight production.

The slope of linear regression between cummulative incident PAR corrected to actual participarion of main stems/productive tillers on total LAI, and average growth of leaf dry weight in main stems and productive tillers, respectively, denoting current PAR use efficiency (RUE_L), was very similar in main stems of tested cultivars (Figure 2). However, in productive tillers of cultivar Kompakt it was approximately double. Taking together, RUE_L for whole plants was significantly higher in cultivar Kompakt than in cultivar Dobla.

Spike formation

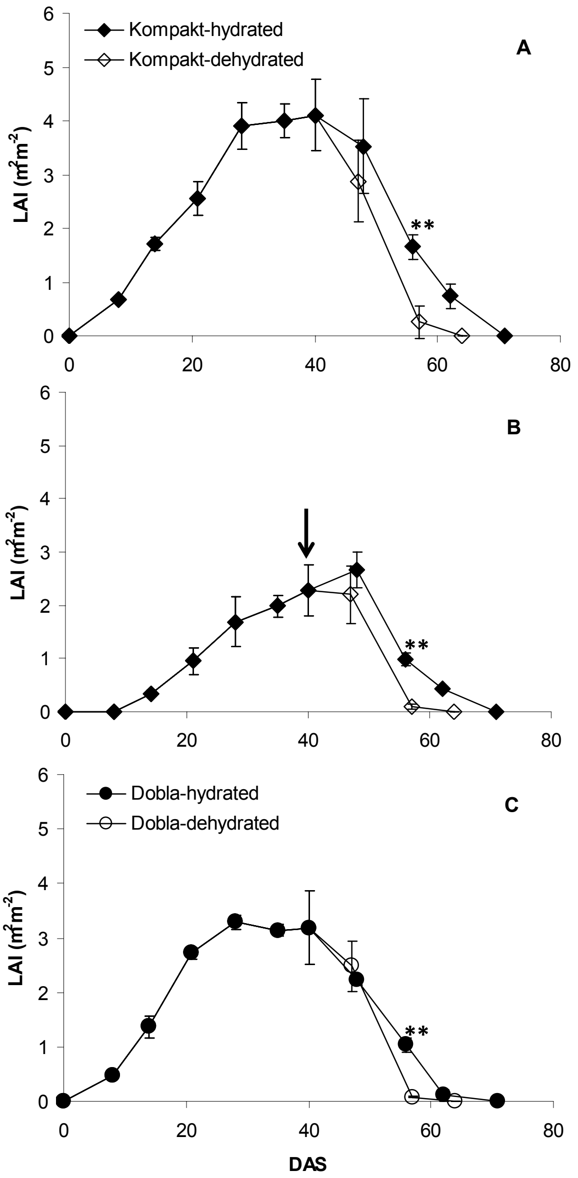

Figure 1: Dynamics of leaf area index (LAI) in main stems (A, C) and productive tillers (B) of spring barley genotypes Kompakt and Dobla as affected by developing drought. Legend: DAS – days after sowing, arrow - start of dehydration, and double asterisk statistical difference at P=0,01.

Obrázok 1: Dynamika indexu listovej pokryvnosti (LAI) na hlavných steblách (A, C) a produktívnych odnožiach (B) rastlín jačmeňa jarného genotypov Kompakt a Dobla zasiahnutá prehlbujúcim sa suchom. Legenda: DAS – dni po výseve; šípka – začiatok dehydratácie; tmavé symboly – hydratované rastliny, svetlé symboly – dehydratované rastliny; ** - štatisticky významný rozdiel pri P=0,01.

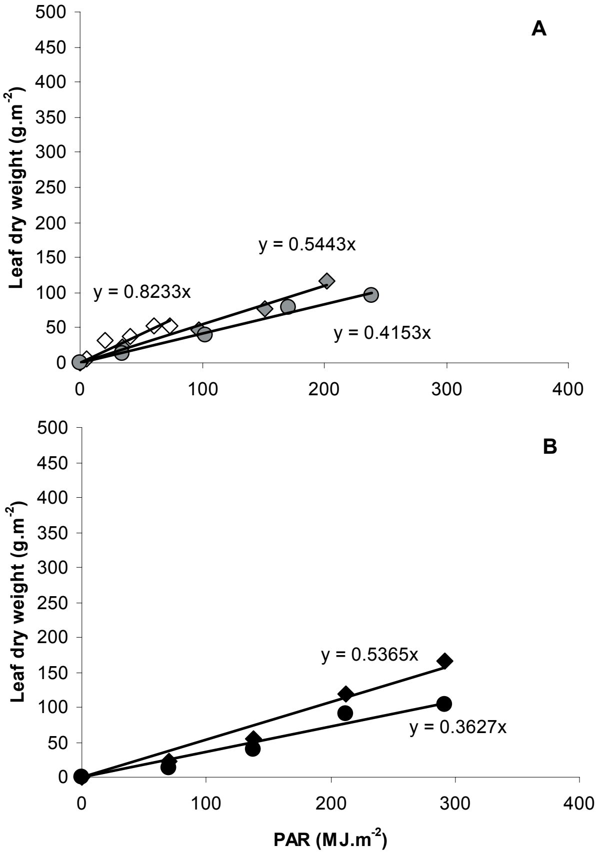

Figure 2: Linear regresion of cummulative incident PAR and growing leaf dry mass (current radiation use efficiency for leaf dry mass, RUE$_L$) in distinct parts of spring barley plants (A) as well as whole individuals (B). Legend: diamonds – cultivar Kompakt, circles – cultivar Dobla, light symbols – productive tillers, grey symbols – main stems, and dark symbols – whole plants.

Obrázok 2: Lineárna regresia príkonu fotosynteticky aktívneho žiarenia (PAR) nad porastom a rastúcej hmotnosti sušiny listov (aktuálna efektívnosť využitia žiarenia pre tvorbu sušiny listov, RUE$_L$) v jednotlivých častiach rastlín jačmeňa (A) a na úrovni celých rastlín (B). Legenda: kosoštvorce – kultivar Kompakt, kruhy – kultivar Dobla; prázdne symboly – produktívne odnože, sivé symboly – hlavné steblo, čierne symboly – celé rastliny.

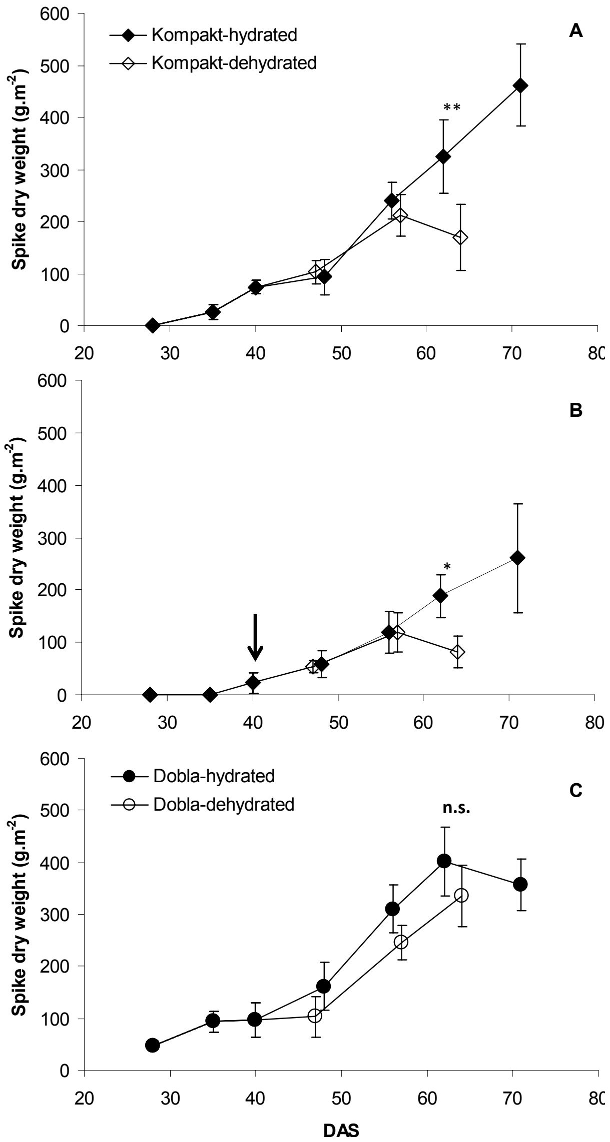

Figure 3: Dynamics of spike dry weight growth in main stems (A, C) and productive tillers (B) of spring barley cultivars Kompakt and Dobla as influenced by rising water deficit. Legenda: DAS – days after sowing, arrow - start of dehydration, n.s. - non-significant statistical difference at P=0,05, * - significant statistical difference at P=0,05, and ** - significcant statistical difference at P=0,01.

Obrázok 3: Dynamika rastu hmotnosti sušiny klasov na hlavnom steble (A, C) a produktívnej odnoži (B) rastlín jačmeňa kultivaru Kompakt a Dobla ovplyvnená nrastajúcim vodným deficitom. Legenda: DAS – dni po výseve; šípka – začiatok dehydratácie; tmavé symboly – hydratované rastliny, svetlé symboly – dehydratované rastliny; n.s. – bez štatisticky významného rozdielu pri P=0,05, * - štatisticky významný rozdiel pri P=0,05, ** - štatisticky významný rozdiel at P=0,01.

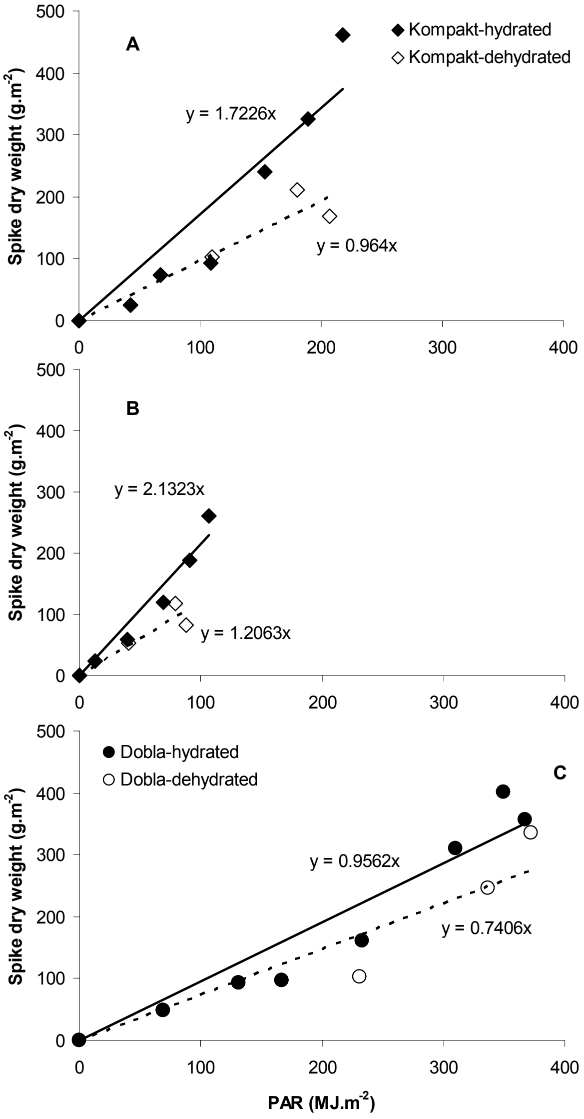

Figure 4: Spike dry weight in main stems (A) and productive tillers (B) of cultivar Kompakt, and in main stems of cultivar Dobla (C) as correlated to cummulative incident PAR (current radiation use efficiency for spike dry mass, RUE$_S$) in conditions of continuing and interrupted water supply.

Obrázok 4: Hmotnosť sušiny klasov na hlavnom steble (A) a produktívnej odnoži (B) kultivaru Kompakt, a hlavnom steble kultivaru Dobla (C) korelovaná s kumulatívnou hodnotou fotosynteticky aktívneho žiarenia (PAR) dopadajúceho na porast (aktuálna efektívnosť využitia žiarenia pre tvorbu sušiny klasu, RUE$_S$) v podmienkach s nepretržitým a zastaveným prísunom vody (tmavé symboly – hydratované rastliny, svetlé symboly – dehydratované rastliny).

Spike primordia were first detected in main stems of cultivar Dobla, at 28th day after sowing (DAS) (Figure 3), confirming its enhanced precocity (Table 2). Slow growth was followed by an intense phase after 48th DAS. Similar tendency we observed in main stems of cultivar Kompakt but final dry weight of their spikes was round 100 g.m^{-2} larger than in cultivar Dobla. Tiller spikes in this cultivar appeared some days later and grew more homogenously. However their final dry mass reached only half values of main stems.

Water witholding caused a temporar decrease of spike growth in main stems of cultivar Dobla, which was conserved till harvesting. On the other hand, in cultivar Kompakt (main stems as well as productive tillers) longer lasting no change in spike growth intensity followed by sudden cessation after 57th DAS was observed. Drought caused 15 and 55 per cent reduction of spike dry weight in cultivar Dobla and Kompakt, respectively. There was no difference between main stems and productive tillers in cultivar Kompakt.

Intense spike growth was associated with a sequential decrease of photosynthetically active leaf area (Figure 1), having a significant effect on current radiation use efficiency (RUE_S). In comparison to main stems of cultivar Kompakt with values round 1,72 MJ.g^{-1}, in cultivar Dobla we obtained only 0,96 MJ.g^{-1} (Figure 4). Productive tillers of cultivar Kompakt were much more efficient (RUE_S = 2,13 MJ.g^{-1}). Drought markedly affected radiation use efficiency. Particularly, almost a half RUE_S decrease was observed in both parts of cultivar Kompakt plants. However, it was very mild in main stems of cultivar Dobla. Expression on whole plant (Figure 5) showed a general decrease of RUE_S.

Evaluating final RUE at the harvest (Figure 6), in main stems as well as productive tillers of hydrated plants of cultivar Kompakt we observed more than double values of those in main stems of cultivar Dobla; and when plant parts were added together cultivar Kompakt showed almost fivefold higher RUE. Nevertheless, under drought conditions RUE in cultivar Kompakt (main stems as well as productive tillers) fell to the level of main stems of cultivar Dobla. Despite of this, thanks to presence of productive tillers, it was always double in comparison to cultivar Dobla.

DISCUSSION

In order to better utilization of solar radiation for biomass production, breeders are asked for rapid emerging crop genotypes with fast forming and long lasting optimal total leaf area of suitable architecture and high photosynthetic rates [21].

Following own internal programme [6], leaf formation in studied cultivars has specific patterns. In main stems of cultivar Kompakt more homogenous leaf growth dynamics was accompanied by larger final leaf biomass (Figure 1) – mainly because of higher leaf number (8 instead of 7 in cultivar Dobla). However, important contribution to total leaf dry mass in this cultivar was productive tiller, though its leaf growth intensity and final dry weight were only half of the main stem´s ones. Resulting higher canopy density, probably raising PAR interception, could then enhance current RUE_L (Figure 2B).

This is in contrast with observation of Kemanian et al. [13] in two barley cultivars, stating that plant density do not affect RUE. The same was valid for 2 winter wheat and 5 spring wheat cultivars in the study of Choudhuri [10]. However, in our case different canopy densities were associated with distinct genotypes.

What is interesting, partial RUE_L analysis generally showed higher values, with more efficient productive tillers (Figure 2A). Reason for this could be temporal secondary tillering.

In the work of Miralles and Slafer [16], among near isogenic lines of wheat, differing in dwarfing allele dosage, significant loss of pre-anthesis RUE was associated with both Rht1 and Rht2 alleles, only. Taking account more intense stem elongation in cultivar Dobla associated with escape ability, canopy density seems to be more important for RUE_L than plant height. However, for final RUE grain yield is important.

Once met external conditions for inflorescence initiation, plants can swich from vegetative to generative phase of their ontogenesis. First, assimilates produced in photosynthetic apparatus start to be utilized in formation both organ types (spike and leaves/stem), as mirrored in slow phase of spike dry weight accumulation (Figure 3). After fertilization, forming grains are the only sink for assimilates, therefore they grew more intensively. At the same time, photosynthetically active leaf area diminished gradually pointing to loss of its role in this process. Much more important seems to be spike and stem photosynthesis as well as sustained assimilate transport provided by intense grain filling [25]. As comprehenced by Roitch [22], sugars play the key role in this feedforward and feedback regulation of source-sink relationship.

Larger spike dry weight in cultivar Kompakt was achieved by higher RUE_S, prolonged assimilate accumulation, and the presence of productive tillers. They showed larger radiation use efficiency but shorter spike growth (Figure 3, 4). Getting together, spring barley plants of this cultivar, composed from two autonomous parts, represent a more productive model suitable for more precipitated areas. This is in agreement with [4] that later flowering genotypes have a greater production potential.

According to Calderini et al. [7], recently bred wheat cultivars show almost the same RUE in pre-anthesis as well as post-anthesis period. In older ones pre-anthesis RUE prevails. This was not our case because in both cultivars post-anthesis RUE showed higher values.

To reduce transpirating area and preserve water for grain filling [17], plants significantly accelerated leaf senescence under rising water deficit (Figure 1). Nevertheless, there are some studies concerning higher drought tolerance associated with larger leaf area at maturity [5].

Spike dry weight accumulation was affected by drought, as well (Figure 3). In main stems of cultivar Dobla there was one week breakdown followed by normal growth, in cultivar Kompakt we found out no change in spike growth for 17 days but cessation thereafter (this is valid for main stems as well as productive tillers). However, in no cultivar drought fastened the grain filling process [2]. Possibly, water deficit raised stem and spike tissue temperature imposing a stress for grain filling in cultivar Kompakt because, as indicated by Voltas et al. [24], grain filling rate seems to be more genotype-dependent and grain filling duration is influenced mainly by post-anthesis temperature. On the other hand, reason for spike growth failure in main stems of cultivar Dobla is questioned when mostly a mild drought stress is suggested. What is important, in this cultivar spike growth continued in intensity similar to that in hydrated plants. Therefore the radiation use efficiency as well as final spike dry mass reduction were lower.

When photosynthesis is affected, grain filling depends largely or even exclusively on remobilization of stem reserves under developing drought [9, 4]. And this is what we take for crucial cause for lower grain yield and RUE in spring barley [3], not the rapid leaf loss typical for drought stress imposed far before anthesis [12]. Very efficient way how to improve assimilate translocation of a cereal crop is to anchor ability for escape (faster switch

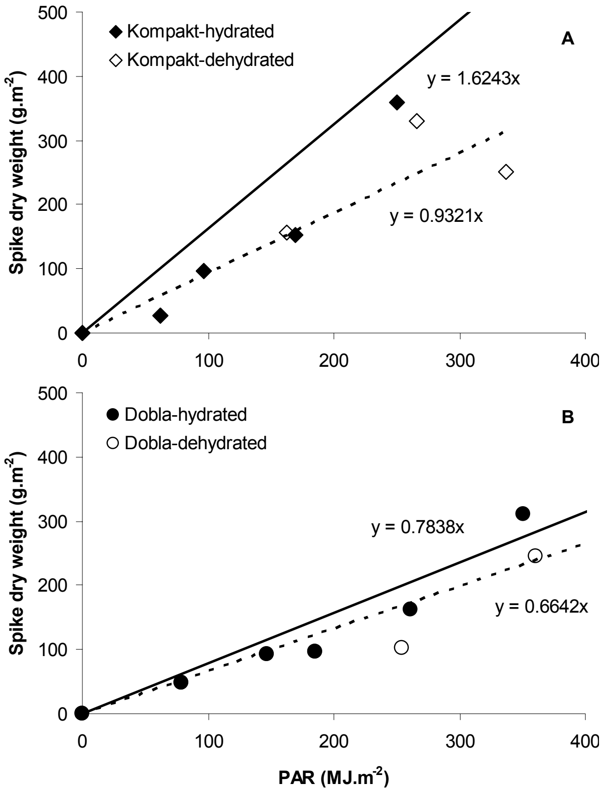

Figure 5: Current radiation use efficiency (RUE_S) in whole spring barley plants of cultivars Kompakt (A) and Dobla (B) under two water regimes, as a relationship of cummulative incident PAR and spike dry mass.

Obrázok 5: Aktuálna efektívnosť využitia žiarenia (RUE_S) na úrovni celých rastlín jačmeňa kultivaru Kompakt (A) a Dobla (B) v odlišných vlahových podmienkach (tmavé symboly – hydratované rastliny, svetlé symboly – dehydratované rastliny), vyjadrená ako lineárny vzťah kumulatívnej hodnoty fotosynteticky aktívneho žiarenia (PAR) dopadajúceho na porast a hmotnosti sušiny klasov.

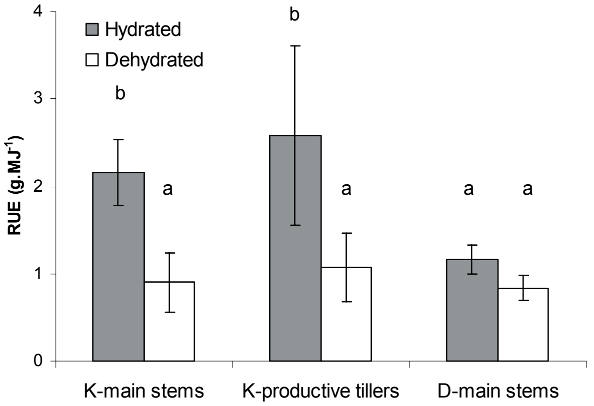

Figure 6: Drought effect on final radiation use efficiency (RUE) in respective plant parts of spring barley cultivars Kompakt (K) and Dobla (D). Letters indicate statistical difference at P=0,05.

Obrázok 6: Efekt sucha na finálnu efektívnosť využitia žiarenia (RUE) v jednotlivých častiach rastlín dvoch genotypov jačmeňa jarného (K - Kompakt, D – Dobla; main stem - hlavné steblo, productive tiller - produktívna odnož; tmavé stĺpce – hydratované rastliny, svetlé stĺpce – dehydratované rastliny). Analýza rozptylu zodpovedá hladine významnosti 95%.

into generative phase) in its genetic equipment. In cultivar Dobla this trait is combined with higher capacity for osmotic adjustment enabling better coping with drought affecting its life cycle [14]. But from the viewpoint of radiation use efficiency this was not sufficient (Figure 5, 6) because an important portion of PAR was not intercepted by photosynthetic apparatus and impinged to the ground. This could be overcome by higher canopy density determined by sowing.

We can conclude that thanks to higher tillering ability, cultivar Kompakt more efficiently utilized incident photosynthetically active radiation for biomass production and yield under sufficient as well as insufficient water supply. However, drought escaping cultivar Dobla more reduced loss of spike dry weight per stem. Therefore it is strongly suggested that modification of canopy density in this cultivar can markedly enhance its radiation use efficiency.

ACKNOWLEDGEMENT

This study was supported by the research project of the Grant Agency for Applied Research of the Slovak Ministry of Education (AV/1109/2004).

REFERENCES

[1] Araus J.L., Slafer G.A., Reynolds M.P., Royo C., Plant breeding and drought in C3 cereals: what should we breed for? Annals Bot. (2002) 89: 925–940.

[2] Barnabás B., Jäger K., Fehér A., The effect of drought and heat on stress reproductive processes in cereals, Plant Cell Env. (2008) 31: 11-38.

[3] Bingham I.J., Blake J., Foulkes M.J., Spink J., Is barley yield in UK sink limited? I. Post-anthesis radiation interception, radiation-use efficiency and souce-sink balance, Field Crop Res. (2007) 101: 198-211.

[4] Blum A., Crop responses to drought and the interpretation of adaption, Plant Growth Reg. (1996) 20:135-148.

[5] Borell A.K., Hammer G.L., Douglas A.C.L., Does maintaining green leaf area in Sorghum improve yield under drought? II. Dry matter production and yield, Crop Sci. (2000) 40: 1037–1048.

[6] Bos H.J., Neuteboom J.H., Growth of individual leaves of spring wheat (Triticum aestivum L.) as influenced by temperature and light intensity, Annals Bot. (1998) 81: 141-149.

[7] Calderini D.F., Dreccer M.F., Slafer G.A., Consequences of breeding on biomass, radiation interception and radiation-use efficiency in wheat, Field Crop Res. (1997) 52: 271–281.

[8] Cornic G., Massacci, A., Leaf photosynthesis under drought stress, in: Baker, N. R.(Eds.) Photosynthesis and the environment. Kluwer Academic Publishers, (1996) pp. 347–366.

[9] Evans L.T., Crop evolution, adaptation and yield. Cambridge University Press, 1993.

[10] Choudhuri B.J., A sensitive analysis of the radiation use efficincy for gross photosynthesis and net carbon accumulation by wheat, Agr. For. Met. (2000) 101: 217-234.

[11] Jacovides C.P., Tymvios F.S., Asimakopoulos D.N., Theofilou K.M., Pashiardes S., Global photosynthetically active radiation and its relationship with global solar radiation in the Eastern Mediterranean basin, Theor. Appl. Climatol. (2003) 74: 227–233.

[12] Jamieson P.D., Martin R.J., Francis G.S., Wilson D.R., Drought effect on biomass production and radiation-use efficiency in barley, Field Crop Res. (1995) 43: 77-86.

[13] Kemanian A.R., Stoeckle C.O., Huggins D.R., Variability of barley radiation-use efficiency, Crop Sci. (2004) 44:1662-1672.

[14] Kovár M., Brestič M., Olšovská K., Drought tolerance mechanisms of spring barley. I. Osmotic adjustment and methods of its determination, Acta fytotechnica et zootechnica (2003) 3: 76-81.

[15] Lawlor D., Limitation to photosynthesis in water-stressed leaves: Stomata vs. metabolism and the role of ATP, Annals Bot. (2002) 89: 871-885.

[16] Miralles D.J., Slafer G., Radiation interception and radiation use efficiency of near-isogenic lines with different height, Euphytica (1997) 97: 201-208.

[17] Munné-Bosch S., Alegre E., Die and let live: Leaf senescence contributes to plant survival under drought, Func. Plant Biol. (2004) 31: 203-216.

[18] Nam N.H., Subbarao G.V., Chauhan Y.S., Johansen C., Importance of canopy attributes in determining dry matter accumulation of pigeonpea under contrasting moisture regimes, Crop Sci. (1998) 38: 955 – 961.

[19] Reynolds M.P., van Ginkel M., Ribaut J.-M., Avenues for genetic modification of radiation use efficiency in wheat, J. Exp. Bot. (2000) 51: 459-473.

[20] Richards R.A., Condon A.G., Rebetzke G.J., Trait to improve yield in dry environment. in: Reynolds M.P., Ortiz-Monasterio J.I., McNab A. (Eds.), Application of physiology in wheat breeding. Cimmyt, 2001, pp. 88-100.

[21] Richards R.A., Rebetzke G.J., Condon A.G., van Herwaarden A.F., Breeding opportunities for increasing the efficiency of water use and crop yield in temperate cereals. In: Crop Sci. (2002) 42: 111–121.

[22] Roitch T., Source-sink regulation by sugar and stress, Curr. Opin. Plant Biol. (1999) 2: 198-206.

[23] Sinclair T. R., Limits to crop yield? in: Physiology and determination of crop yield. Madison, American Society of Agronomy, 1994, pp. 509 – 532.

[24] Voltas J., Romagosa I., Araus J.L., Growth and final weight of central and lateral barley grains under Mediterranean conditions as influenced by sink strength, Crop Sci. (1998) 38: 84 – 89.

[25] Yang J.C., Zhang J.H., Grain filling of cereals under soil drying, New Phytol. (2006) 169: 223-236.