

Dry matter and nitrogen accumulation and use in spring barley

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ABSTRACT

During growth, kernel of cereals can be provided with carbohydrate and nitrogen (N) from the translocation of pre-anthesis accumulated reserves stored either in the vegetative plant parts or from current assimilation during kernel development. This study was conducted to assess the effects of nitrogen level and cultivars on dry matter and N accumulation and mobilization during pre-anthesis and post-anthesis. Twenty two-rowed spring barley (*Hordeum vulgare* L.) cultivars were grown on a non-calcareous chernozem soil in four growing seasons (1995–1998) at Novi Sad (45°20'N, 15°51'E, 86 m a.s.l.) at two nitrogen levels. Dry matter accumulation before anthesis ranged from less than 50% in unfavorable to 90% in favorable growing conditions. Dry matter translocation occurred in favorable growing conditions only. Pre-anthesis accumulated N represented 57–92% and 54–129% of total N at maturity at the low and high N levels, respectively. Translocated N represented 41–85% and 37–153% of grain N at the low and high N level, respectively. N losses occurred in favorable growing conditions when anthesis N exceeded 150 kg/ha. N accumulation during grain filling was in negative correlation with dry matter and N accumulation before anthesis. The N harvest index was 0.57–0.63 and 0.71–0.74 in unfavorable and favorable growing conditions, respectively. Selection of genotypes with a higher ability of pre-anthesis reserve utilization or genotypes with longer leaf area duration after anthesis may be two possible solutions in spring barley breeding for Mediterranean growing conditions.

Keywords: spring barley (*Hordeum vulgare* ssp. *distichum* L.); dry matter; nitrogen; accumulation; translocation; nitrogen concentration; nitrogen harvest index; correlation

The supply of assimilate to growing kernels of barley (*Hordeum vulgare* L.) can come from current assimilation and matter assimilated before anthesis and stored temporarily in the vegetative parts of the plant (Austin et al. 1980, Sanford and MacKown 1987). The contribution of pre-anthesis assimilates to kernel weight depends on the amount of matter that is mobilized between anthesis and maturity and the efficiency of conversion of the mobilized matter into kernel (Gebbing et al. 1999). It was estimated that pre-anthesis reserves contributed up to 74% to the grain yield of barley (Gallagher et al. 1975) and 57% to the grain yield of wheat (Gallagher et al. 1976) when crops suffered from severe postanthesis drought.

In cereals, research on N accumulation and utilization has been carried out mainly on wheat. Studies have shown that grain N in wheat mainly represents N accumulated in the vegetative parts until anthesis and translocated to kernel during the reproductive phase. N in the form of protein and amino acids is a component of the pre-anthesis portion that is potentially available for grain filling (Schnyder 1993). In barley, 10–100% of grain N is taken up during vegetative growth and translocated during the grain filling period (Carreck and Christian 1991, Bulman and Smith 1994). The importance of both N sources has been emphasized by Sanford and MacKown (1987), who have found that variation in final spike N can be associated with variation in total N uptake. Bulman and Smith (1994) established that post-heading N uptake in barley was generally not related to N concentration and N per plant at heading, instead, it was highly correlated with total dry matter accumulation after anthesis and to-

tal plant N and grain at harvest. Environmental conditions during the pre- and post-anthesis periods are likely to have different effects on N accumulation. N uptake is influenced by available water (Clarke et al. 1990), degree of association between the roots and the soil, the supply of nitrate (Cox et al. 1985, Papakosta and Gagianas 1991), genotype requirements and efficiency of N use, and other properties of the genotype and conditions of growing. In wheat, a surplus of soil N at grain filling favors post-anthesis N uptake and reduces the mobilization of pre-anthesis N (Papakosta and Gagianas 1991).

This study's objectives were to examine the accumulation of dry matter and nitrogen during pre-anthesis and grain filling periods, the contribution of pre-anthesis dry matter and nitrogen to grain development, and the relationships among the investigated characters.

MATERIAL AND METHODS

Field trials. Detailed procedures for the field experiments and laboratory analysis have been described elsewhere (Przulj and Momčilović 2001a, b). Briefly, the trials were conducted in a four-year period (1995–1998) on non-calcareous chernozem at Novi Sad, Yugoslavia (45°20'N, 15°51'E, 86 m a.s.l.). In all four years, preceding crop was soybean and 45 kg/ha of each N, P and K in winter before plowing were applied. In springs two N levels were applied, a low N level with no additional N and a high N level with 50 kg/ha N as ammonium nitrate at mid-tillering (Zadoks GS 23). The crop was grown under the

usual agronomic practises for spring barley in Panonian plane conditions. Around mid-anthesis, five plants from the second row in each replication, 30 cm from end of the row, were cut at ground level and they represented one sample/replication in the analysis. These samples were separated in two components at anthesis (leaf + culm and chaff-flowered spikes) and in three components at maturity [leaf + culm, chaff (rachis, glumes, awns), and grain] and dry matter (DM) and N have determined.

Measurements. The following parameters related to dry matter and N accumulation and movement within the barley plant are discussed in this paper:

1. Pre-anthesis and post-anthesis dry matter accumulation (kg/ha)
2. Dry matter translocation (kg/ha) = dry matter at anthesis – dry matter (leaf + culm + chaff) at maturity
3. Dry matter translocation efficiency (%) = dry matter translocation/dry matter at anthesis × 100
4. Contribution of pre-anthesis assimilates to grain (%) = dry matter translocation/grain yield × 100 (Papakosta and Gagianas 1991)
5. Pre-anthesis and post-anthesis nitrogen accumulation (kg/ha)
6. N translocation from vegetative tissues at anthesis to the kernel (kg/ha) = N content at anthesis – N content at maturity (leaf + culm + chaff) (Cox et al. 1986)
7. Proportion of vegetative N in the plant at anthesis that was translocated to kernel: nitrogen translocation efficiency = N translocation/N content at anthesis
8. Proportion of the N in grain in relation to total above-ground N at maturity: nitrogen harvest index = grain N/total N content in aboveground parts at maturity

Statistical analysis. Three-way analysis of variance and estimates of the components of variance due to nitrogen, cultivar, year, and all interactions were made as well. A mixed model was used, with N level and cultivar considered as fixed and years as random effects (Zar 1996). The analysis of variance and estimates of the components of variance due to cultivar (σ^2_G), cultivar by nitrogen level interaction (σ^2_{NG}), and error (σ^2_E) were

calculated for each year according to Comstock and Moll (1963). The significance of mean squares for nitrogen levels and cultivars was tested using mean squares of $G \times Y$ interaction and significance of cultivar × year interaction ($G \times Y$) by pooled error. The percentage contribution of each variance component was estimated by summing the appropriate terms to give an estimate of total variance and then dividing the specific variance component by the total variance (Brandle and McVetty 1988). The Pearson coefficient of correlation was used to calculate the simple correlation between the characters based on their yearly mean performance. Accumulated growing degree-days (GDD) from emergence to heading were calculated by summing daily degree-days. Daily degree-days were calculated as $T_n = (T_7 + T_{14} + 2T_{21})/4$, where T_7 , T_{14} , and T_{21} are temperatures at 7 a.m., 14 p.m. and 21 p.m.

Weather. Barley growing season in 1995 characterized by moderate temperatures with no high extremes and sufficient precipitations. In 1996, temperatures were low during emergence, tillering, and high during stem elongation and anthesis. At grain filling, a drought was recorded. In 1997 temperatures were low during tillering and high during stem elongation while amount of precipitation was lower than the long-term average and unevenly distributed across the vegetative cycle. Favorable temperatures for germination and higher temperatures at grain filling characterized the temperature conditions in 1998. Water deficit occurred at tillering and middle of grain filling.

RESULTS

Dry matter accumulation and mobilization

ANOVA (Table 1) shows that main differences in dry matter accumulated until anthesis were due to year and its interactions with N level and genotype. In 1996, 1997, and 1998 accumulated dry matter at anthesis was positively correlated ($P < 0.05$) with the sum of GDD, while there was no significant relation in 1995, when the high-

Table 1. ANOVA for two N levels, four years, and 20 barley cultivars

Source	Df	Anthesis		PANU	Maturity				DMTE	NTE	NHI
		DM	BAN		VDM	GY	VN	GN			
Nitrogen (N)	1	ns	ns	ns	ns	ns	ns	ns	*	ns	*
Cultivars (G)	19	*	**	ns	**	ns	**	ns	ns	ns	**
N × G	19	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Year (Y)	3	**	**	**	**	**	**	**	**	**	**
N × Y	3	**	**	**	**	**	**	**	**	**	ns
G × Y	57	**	**	**	**	**	**	**	**	**	*
N × G × Y	57	**	**	**	**	**	**	**	**	**	*

DM – dry matter, BAN – amount of N accumulated till anthesis, PANU – amount of N taken up during grain filling, VDM – vegetative dry matter at maturity, GY – grain yield, VN – amount of vegetative N at maturity, GN – amount of grain N, DMTE – dry matter translocation efficiency, NTE – N translocation efficiency, NHI – N harvest index

*, ** significant at the 0.05 and 0.01 probability levels, respectively

est amount of dry matter accumulated (data not shown). Cultivar differences in aboveground dry matter per hectare at anthesis were observed in 1998 only, although variation due to cultivar was high (39.3%) in 1996 also (Table 2). Aboveground dry matter at anthesis was higher in favorable years, when temperature and precipitation were not limiting factors for plant development. Without exception, all cultivars had the lowest dry matter in the least favorable year (1996). Dry matter at anthesis was not influenced by N level, although in 1995 dry matter was 20% higher with the high N. N level \times cultivar interaction occurred for dry matter at anthesis in all four years, with the contribution of this component of variance ranging from 30.9 to 84.6%.

There were no differences among the cultivars in any year in vegetative dry matter at maturity and grain yield, despite the numerically high values for the cultivar component of variance (Table 3). The observed differences for both traits were due to N level in 1995 and 1998 and N level \times cultivar interactions in all years. The main part of the total aboveground dry matter found at maturity at the high N level had been accumulated by anthesis, 98% in 1995 and 69% in 1998. At the low N level, in the same years, 58 and 53% of total aboveground dry matter at maturity had been accumulated by anthesis. However, in unfavorable years the N level influenced the amount of dry matter neither at anthesis and maturity nor grain yield (Tables 2 and 3). Across N levels, 48 and 46% of total dry

Table 2. Main effects of cultivar and N level on dry matter and N content at anthesis in vegetative parts in 20 spring barley cultivars in four years (1995–1998)

Cultivar	Dry matter				N content			
	leaf + culm + chaff (kg/ha)				1996	1997	1998	
	1995	1996	1997	1998	1995	1996	1997	1998
NS.294	11 331	3 994	4 405	5 444	248	93	65	124
NS.301	6 109	2 816	5 459	4 218	154	48	73	90
Vihor	8 013	2 804	5 369	3 787	197	51	83	83
Pek	7 473	2 913	5 383	3 242	161	58	83	72
Jelen	8 195	2 323	5 279	4 172	193	52	80	99
Lazar	8 499	2 264	6 229	5 959	221	51	82	127
Arapiles	8 970	3 087	3 825	3 805	199	67	58	83
Shcooner	9 979	2 500	3 353	4 425	222	50	44	92
Cantala	8 181	2 600	4 320	4 648	204	56	61	96
K.M.184	10 932	3 720	6 584	10 211	297	78	97	231
Orbit	8 423	4 848	7 640	10 847	199	100	108	188
Triumph	9 203	3 975	8 269	8 629	227	98	123	199
Gimpel	6 330	5 551	5 813	8 362	145	113	110	160
Amsel	6 132	3 646	5 293	6 510	129	71	80	126
Aramir	8 245	5 347	7 885	5 993	184	103	116	113
Kaskade	7 216	3 361	6 097	4 123	155	74	99	86
Berolina	6 765	3 349	7 771	6 528	151	75	127	129
Menuet	8 120	3 067	7 014	7 923	196	56	103	173
Berencie	7 907	3 657	7 477	9 853	189	60	132	194
Hiproly	9 929	2 388	5 853	12 708	239	46	109	277
<i>LSD</i> _{0.05}			409		5		9	
Nitrogen level								
Low N	7 564	3 464	5 504	6 539	175	69	77	130
High N	9 031	3 357	6 428	6 600	216	71	106	143
Significance								
N level (N)	ns	ns	ns	ns	*	ns	**	ns
Cultivar (G)	ns	ns	ns	**	ns	*	ns	**
N \times G	**	**	**	**	**	**	**	**
Components of variance (%)								
N level (N)	11.9	0.0	8.4	0.0	17.9	0.0	28.3	0.0
Cultivar (G)	0.0	39.3	20.5	64.6	2.8	44.8	20.3	60.1
N \times G	84.6	57.5	64.7	30.9	75.8	51.6	46.4	38.2
Error	3.5	3.2	6.4	4.5	3.5	3.6	5.0	1.7

*, ** significant at the 0.05 and 0.01 probability levels, respectively *LSD*_{0.05}, least significant difference at the 0.05 level of significance

matter found at maturity in 1996 and 1997 respectively had been accumulated by anthesis.

In favorable seasons during the vegetative period, plants accumulated sufficient amounts of dry matter for various biological functions, and the surplus was translocated to the growing kernels. Changes in vegetative dry matter between anthesis and maturity, i.e. dry matter translocation, were influenced by the N level ($P < 0.05$), year, and interactions of year with N level and cultivars ($P < 0.01$) (Table 1). At the high N level, dry matter translocation was 3032 kg/ha in 1995 and 1100 kg/ha in 1998, i.e. the dry matter translocation efficiency was 34 and 17% in the studied years (Tables 2 and 3). Generally, greater dry matter at anthesis resulted in greater dry mat-

ter translocation efficiency. Across the N levels, the highest dry matter translocation efficiency in 1995 was found in the cultivar Schooner 58%, followed by Orbit 45%, Arapiles 36%, KM184 34%, Berenice 32%, and Menuet 28%. Grain yields in 1995 and 1998 were lower by 32 and 30% at the high N level compared with the low one. This could be explained by the loss of a significant amount of dry matter for maintaining a large quantity of vegetative mass. In growing seasons with unfavorable conditions during the vegetative period, plants must accumulate dry matter during the grain filling period for growth of their vegetative parts as well as for kernel development. Therefore, across the N levels in 1996 and 1997, 52 and 54% of total dry matter at maturity accumulated during

Table 3. Main effects of cultivar and N level on vegetative dry matter and grain yield at maturity in 20 spring barley cultivars in four years (1995–1998)

Cultivar	Maturity							
	leaf + culm + chaff (kg/ha)				grain (kg/ha)			
	1995	1996	1997	1998	1995	1996	1997	1998
NS.294	7 607	3 500	7 447	10 005	5 633	5 866	3 451	5 565
NS.301	8 009	3 580	6 177	6 328	5 370	6 252	3 222	6 291
Vihor	8 023	3 692	6 191	4 775	4 351	6 190	2 677	4 625
Pek	7 581	3 059	6 743	5 479	4 784	6 305	2 326	5 703
Jelen	7 167	3 829	4 907	6 316	4 819	5 759	3 718	4 715
Lazar	4 785	4 299	6 200	7 863	4 704	3 885	4 119	4 017
Arapiles	5 141	3 165	5 577	5 761	4 475	3 441	3 303	5 750
Shcooner	4 251	3 476	5 098	4 098	4 206	3 721	3 799	5 049
Cantala	5 310	2 845	5 675	5 422	4 349	4 071	2 421	6 015
K.M.184	7 157	4 473	4 696	7 657	3 921	2 802	3 212	4 800
Orbit	6 482	5 063	9 506	6 050	5 330	5 094	3 179	8 428
Triumph	6 965	6 178	9 123	6 296	4 792	4 560	3 689	6 661
Gimpel	8 785	4 300	9 506	6 571	5 186	6 315	2 918	6 937
Amsel	5 443	4 439	9 337	4 828	3 972	2 997	2 766	7 015
Aramir	9 051	3 709	8 997	6 644	5 215	6 619	2 883	6 829
Kaskade	6 011	3 871	6 173	4 484	4 445	4 477	3 315	6 690
Berolina	5 425	2 977	6 382	5 883	4 336	4 159	2 288	6 037
Menuet	5 267	2 950	5 492	6 098	4 044	3 999	2 426	5 144
Berenice	4 861	5 158	9 841	6 421	4 641	3 002	3 373	8 085
Hipoly	12 283	4 486	9 218	8 806	3 129	5 282	2 767	2 386
Nitrogen level								
Low N	7 562	3 967	6 890	7 079	5 392	3 152	5 225	5 280
High N	5 999	3 938	7 239	5 500	4 088	3 033	6 449	4 061
Significance								
N level (N)	*	ns	ns	*	*	ns	ns	*
Cultivar (G)	ns	ns	ns	ns	ns	ns	ns	ns
N × G	**	**	**	**	**	**	**	**
Components of variance (%)								
N level (N)	14.9	0.0	0.0	13.2	19.7	0.0	0.1	19.8
Cultivar (G)	24.2	31.7	31.4	42.6	9.7	10.0	12.1	13.9
N × G	56.9	61.8	60.6	41.3	65.2	81.4	83.2	59.7
Error	4.0	6.4	8.0	2.9	5.4	8.6	4.6	6.6

*, ** significant at the 0.05 and 0.01 probability levels, respectively

grain filling, which represents the total grain yield and part of vegetative dry matter. In the two unfavorable years, only the cultivar Menuet had a positive value of dry matter translocation. The possible contribution of dry matter accumulated pre-anthesis to the growing kernel is in proportion with dry matter translocation efficiency. Cultivars did not differ in the contribution in any year, while the N level resulted in marked differences in the contribution in 1995 with higher contribution at the high N level (data not shown).

The harvest index had close values in the two favorable years, 0.42 and 0.43 for low and 0.41 and 0.42 for high N level in 1995 and 1998, respectively. The harvest index in 1996 was 0.44 for both N levels and in 1997 0.43 for high and 0.47 for low N level.

Nitrogen accumulation and translocation

ANOVA (Table 1) showed non-significant effects of applied N but significant effects of cultivar and year ($P < 0.01$) on N accumulation until anthesis. Effect of N was more prominent through its interactions with cultivar and year. N accumulated during the pre-anthesis period represented 92, 69, 57 and 76% of the total N at maturity under low N level and 129, 68, 54 and 104% of the total N at maturity under high N level in 1995, 1996, 1997 and 1998, respectively. The N amount at anthesis was strongly correlated with accumulated dry matter, the highest N content was in 1995 and the lowest in 1996. Cultivars differed in total N at anthesis in vegetative parts in 1996 and 1998, with high values of the cultivar components of variance. In 1995 and 1997, N accumulation at anthesis was 23 and 38% higher with high than with low N level (Table 2).

With the low N level, plant N concentration at anthesis was lower in relation to high N level in all years (Table 4). The effect of N level on the concentration of N at anthesis was significant in unfavorable 1996 and 1997, with 7% ($P < 0.05$) and 20% ($P < 0.01$) higher N concentration at high than at low N level. Cultivar differences ($P < 0.05$) in N concentration at anthesis were also observed in these two years. Thus, cultivar differences were more prominent in unfavorable than in favorable growing conditions. Components of variance due to N \times G interaction in 1995 and 1998, cultivar and N \times G in 1996, and N level in 1997 had the highest proportion of the total variation. Chaff N concentration at anthesis was 16.4, 17.0, 14.3 and 17.8 g/kg for the low N level and 18.3, 17.8, 15.5 and 18.8 g/kg for the high N level in 1995, 1996, 1997 and 1998, respectively (data not shown). No one cultivar across the years and no year across the cultivars had higher chaff than leaf + culm N concentration at anthesis. Grain N concentration depended on N levels in the three growing seasons, with higher concentration at the high N level. The highest N concentration across the cultivars was found in the unfavorable year 1996. Values of variance components for grain N concentration depended on the year (Table 4).

The ratio of N content at anthesis to grain N at maturity was 1.61, 0.97, 0.77 and 1.20 for the low N level and 2.27, 0.96, 0.75 and 1.68 for the high N level in 1995, 1996, 1997 and 1998, respectively (Tables 2 and 5). The ratio was larger at high than at low N level in favorable years, while in unfavorable years it was not dependent on the N level. The higher ratio observed at the high N level was due to increased N content at this level at anthesis and similar grain yields at both N levels (Table 3).

N content at anthesis and GDD had a similar relationship to dry matter and GDD, non-significant in 1995 and significant in the other three years. In all four years, cultivar differences in N accumulation at anthesis were related to dry matter accumulation rather than to plant N concentration (data not shown). Coefficients of correlation between N and dry matter at anthesis were over 0.87 ($P < 0.01$) for the high N level and over 0.94 for the low one (data not shown). Correlation between N content at anthesis and plant N concentration were inconsistent, in 1995 at the low N level they were non-significant and in 1998 at the low N level significant and negative, while in the other years they were positive and significant ($P < 0.05$). Coefficients of determination (R^2) between N and dry matter at anthesis were over 0.76, while those between N accumulation and plant N concentration were lower than 0.34.

By maturity, the N amount in leaf + culm + chaff declined considerably more than dry matter. At the low N level 33, 42, 52 and 36% and at the high N level 49, 42, 45 and 49% of anthesis N were found in vegetative plant parts at maturity in 1995, 1996, 1997 and 1998, respectively. Differences in vegetative N per plant at maturity were recorded among cultivars in three years 1995, 1996 and 1997 (Table 5). In the favorable years, more N was retained in the vegetative plant parts at maturity at the low N level, although the differences were not significant. In the years which were adverse for barley growing the amount of retained N was not consistent with respect to N level, in 1996 the same proportion of N was retained at both N levels, while in 1997 more N was retained at the high N level. N level \times cultivar interactions occurred in all four growing seasons. The highest variation was due to the N level \times cultivar interaction in 1995 and 1998 and to the interaction and cultivars in the other two years. In addition to cultivar significance, ANOVA showed a significant influence of year and its interaction with N level and year on vegetative N at maturity (Table 1).

Although the differences for grain N content among the cultivars were large, they were not significant in any of the growing seasons (Table 5). Differences due to N level were recorded in 1997 and 1998, when grain N was 41% higher at the high N level in 1997 and 27% higher at the low N level in 1998. At the low N level in unfavorable years the cultivars accumulated more N than at the high N level, although the differences were not significant. This situation was probably due to insufficient differences in available soil N under these growing conditions. Significant N level \times cultivar interactions and the highest values of this variance component were observed in all growing seasons. ANOVA showed that only year and its

Table 4. Main effects of cultivar and N level on N concentration at anthesis and maturity in vegetative parts and grain in 20 spring barley cultivars in four years (1995–1998)

Cultivar	Anthesis				Maturity							
	leaf + culm (g/kg)				leaf + culm (g/kg)				grain (g/kg)			
	1995	1996	1997	1998	1995	1996	1997	1998	1995	1996	1997	1998
NS.294	22.5	24.9	14.9	23.7	9.9	8.5	6.9	9.7	21.1	22.4	19.7	20.6
NS.301	26.3	17.3	12.9	21.9	11.8	6.1	5.3	9.1	20.6	23.1	20.4	20.5
Vihor	25.9	17.7	15.4	22.7	12.4	8.5	5.3	10.4	19.2	25.3	21.3	21.8
Pek	22.1	20.8	15.3	23.4	10.0	7.3	7.0	8.8	21.7	24.9	20.0	20.5
Jelen	24.0	23.4	15.5	24.9	10.5	9.0	6.5	9.7	20.2	20.8	18.9	20.4
Lazar	26.7	23.6	12.6	21.8	12.5	6.5	6.9	8.9	23.1	23.2	20.8	19.8
Arapiles	23.5	22.9	15.4	23.1	9.4	7.0	5.3	9.6	22.6	21.3	18.5	18.0
Shcooner	23.2	20.9	13.0	21.6	13.2	6.3	6.2	8.2	26.1	22.1	19.5	18.4
Cantala	25.8	22.2	14.4	21.0	12.8	5.5	5.8	8.8	21.4	23.2	20.0	20.2
KM.184	27.7	21.5	14.7	23.2	14.7	8.9	6.1	8.4	22.6	25.4	19.1	20.2
Orbit	24.8	21.2	13.7	17.3	11.2	8.1	5.4	8.9	22.2	24.6	21.4	21.5
Triumph	25.8	25.8	14.3	23.2	12.4	8.5	7.3	8.4	22.0	24.0	21.2	21.7
Gimpel	24.3	20.7	18.5	19.8	11.1	8.1	6.8	9.9	22.6	24.2	20.5	20.4
Amsel	23.0	19.9	14.7	19.6	12.2	8.9	7.8	9.3	23.8	24.0	20.3	22.6
Aramir	23.7	19.6	14.6	18.7	10.5	8.4	5.2	9.5	21.6	25.8	22.5	22.6
Kaskade	22.6	22.9	16.2	21.7	9.2	6.7	5.4	8.1	21.5	22.0	20.2	19.3
Berolina	23.3	23.3	16.9	19.6	11.1	7.4	6.1	8.5	22.0	24.5	20.3	18.0
Menuet	25.8	19.5	14.7	21.5	11.7	7.4	6.0	8.8	25.1	24.3	19.7	22.8
Berence	24.6	16.6	18.0	19.7	11.9	7.1	6.7	10.4	22.2	26.4	21.6	22.0
Hiproly	25.0	19.4	18.5	22.5	12.5	6.9	9.4	12.6	22.1	21.2	29.5	26.6
<i>LSD</i> _{0.05}		0.97	0.56			0.54	0.60				0.75	0.41
Nitrogen level												
Low N	24.5	20.5	13.8	22.0	10.9	7.3	5.1	9.0	20.4	22.6	19.3	20.7
High N	24.6	21.9	16.6	22.1	12.1	7.8	7.6	9.6	23.9	24.7	22.2	21.1
Significance												
N level (N)	ns	*	**	ns	*	ns	**	ns	**	**	**	ns
Cultivar (G)	ns	*	*	ns	ns	*	*	ns	ns	ns	**	**
N × G	**	**	**	**	**	**	**	**	**	**	**	**
Components of variance (%)												
N level (N)	0.0	9.3	46.8	7.1	14.0	6.0	65.8	7.9	55.4	28.7	40.9	0.2
Cultivar (G)	5.3	41.2	23.4	20.8	8.3	42.1	13.4	28.7	3.7	9.2	45.7	63.6
N × G	88.1	42.1	26.8	70.0	74.2	38.7	15.4	60.7	38.3	56.0	9.2	33.6
Error	6.6	7.4	3.0	2.1	3.5	13.2	5.4	2.7	2.6	6.1	4.2	2.6

*, ** significant at the 0.05 and 0.01 probability levels, respectively *LSD*_{0.05}, least significant difference at the 0.05 level of significance

interaction with N level and cultivars had a significant effect on grain N yield (Table 1).

In favorable years, post-anthesis N uptake (PANU) depended on the N level, while in unfavorable years no difference was found. Across the cultivars, the amount of N accumulated after anthesis contributed from 8 to 43% and 32 to 46% to total N at maturity at the low and high N level, respectively. In favorable years, at the low N level, PANU represented 8 and 27% of total N at maturity, while at the high N level the total N amount was accumulated during the pre-anthesis period. At the high N level, 23 and 5% of pre-anthesis accumulated N was lost during grain filling. In unfavorable years for barley development, there was no

difference between post-anthesis N uptake at the low and high N level. PANU contributed 31 and 43% at the low and 32 and 46% at the high N level at maturity in 1996 and 1997, respectively. Cultivar differences in PANU were found only in 1998, although a large range for this was observed among the cultivars in the other years. In 1998, the cultivar NS.294 accumulated 131 kg/ha during grain filling, while the cultivar Hiproly lost 111 kg/ha at the same stage. N level × cultivar interactions for PANU were significant in all the years, and the corresponding component of variation was the highest.

The ratio of N accumulated pre-anthesis to grain N depended on N level and cultivars only in 1998, while N lev-

Table 5. Main effects of cultivar and N level on N content at maturity in vegetative parts and grain in 20 spring barley cultivars in four years (1995–1998)

Cultivar	Leaf + culm + chaff (kg/ha)				Grain (kg/ha)			
	1995	1996	1997	1998	1995	1996	1997	1998
NS.294	78	29	49	93	124	79	111	162
NS.301	93	21	34	56	129	74	132	119
Vihor	100	31	32	50	118	68	98	84
Pek	76	22	45	46	137	57	114	98
Jelen	76	32	33	58	116	77	89	104
Lazar	60	28	41	67	87	96	84	133
Arapiles	46	21	30	52	77	71	108	97
Shcooner	54	21	29	32	92	84	99	78
Cantala	64	16	33	46	85	56	124	98
KM.184	102	39	26	63	57	82	92	98
Orbit	72	41	51	52	107	76	182	100
Triumph	85	52	64	57	98	87	135	91
Gimpel	98	33	67	63	138	70	144	94
Amsel	58	38	63	45	70	67	142	70
Aramir	93	29	45	63	145	74	148	102
Kaskade	55	25	33	37	94	73	136	63
Berolina	58	23	38	53	91	56	123	87
Menuet	61	23	33	58	99	58	102	105
Berenice	53	37	71	66	65	87	179	90
Hipoly	150	30	81	110	114	58	71	56
<i>LSD</i> _{0.05}	8	4	6					
Nitrogen level								
Low N	82	29	35	64	109	71	100	108
High N	72	30	55	52	95	74	141	85
Significance								
N level (N)	ns	ns	**	ns	ns	ns	**	*
Cultivar (G)	*	*	*	ns	ns	ns	ns	ns
N × G	**	**	**	**	**	**	**	**
Components of variance (%)								
N level (N)	3.1	0.0	32.0	10.8	3.5	0.0	30.6	16.5
Cultivar (G)	39.2	43.0	28.4	21.6	11.9	4.3	3.1	4.4
N × G	52.3	46.8	34.9	63.5	77.0	85.6	62.5	71.5
Error	5.0	10.2	4.7	4.1	7.6	10.1	3.8	7.6

*, ** significant at the 0.05 and 0.01 probability levels, respectively *LSD*_{0.05}, least significant difference at the 0.05 level of significance

el × cultivar interactions occurred in all years. In unfavorable years, the ratio was similar at both N levels. In general, in 1996 all grain N had been accumulated by anthesis. That year, those cultivars that we considered better adapted continued N accumulation after anthesis, while the cultivars that were supposed to have poorer adaptation to these growing conditions accumulated gross N during the vegetative phase. The Australian cultivars were also able to continue N accumulation during grain filling. In favorable 1995, N level did not influence the ratio of pre-anthesis and grain N, although at the high N level this ratio was much higher than at the low N level. That year, the cultivar KM.184 accumulated 10 times more N at pre-anthesis than was found in the grain at harvesting. In 1995, the Yugoslav cultivars accu-

mulated between 1 and 2 and the other cultivars between 2 and 3 times the amount of N found in the grain.

N accumulation during grain filling responded negatively to dry matter and N accumulation before anthesis, while the relation with N concentration in leaf + culm and flowed spike was not significant. dry matter accumulated during grain filling is a fairly accurate indicator of PANU, the coefficient of determination was higher than 0.80. In general, the amount of N accumulated after anthesis was in positive correlation with all the characters that represent dry matter and N accumulation during grain filling, i.e. vegetative dry matter and grain yield at maturity, total N at maturity and grain protein yield and kernel number per plant. PANU was negatively correlated with N and dry matter translocation characters.

Table 6. Main effects of cultivar and N level on N translocation (NT), N translocation efficiency (NTE), and N harvest index (NHI) in 20 spring barley cultivars in four years (1995–1998)

Cultivar	NT (kg/ha)				NTE (kg/ha)				NHI (kg/ha)			
	1995	1996	1997	1998	1995	1996	1997	1998	1995	1996	1997	1998
NS.294	171	64	16	31	0.67	0.68	0.24	0.25	0.62	0.74	0.67	0.62
NS.301	61	26	39	34	0.28	0.54	0.55	0.38	0.59	0.78	0.79	0.68
Vihor	97	20	51	33	0.47	0.36	0.62	0.39	0.55	0.69	0.76	0.64
Pek	85	36	38	27	0.45	0.61	0.43	0.35	0.64	0.72	0.72	0.69
Jelen	117	19	47	41	0.54	0.33	0.59	0.39	0.60	0.70	0.72	0.64
Lazar	161	23	41	60	0.73	0.46	0.49	0.46	0.60	0.78	0.67	0.67
Arapiles	152	46	27	31	0.74	0.67	0.50	0.35	0.62	0.77	0.79	0.64
Shcooner	168	28	15	60	0.75	0.48	0.32	0.63	0.63	0.80	0.77	0.71
Cantala	140	40	28	50	0.64	0.72	0.43	0.47	0.57	0.78	0.78	0.68
KM.184	195	38	70	167	0.66	0.50	0.72	0.70	0.33	0.68	0.78	0.61
Orbit	128	60	57	136	0.64	0.59	0.48	0.72	0.60	0.65	0.78	0.66
Triumph	142	47	59	142	0.62	0.44	0.46	0.72	0.53	0.63	0.65	0.62
Gimpel	46	79	43	97	0.30	0.67	0.39	0.59	0.59	0.68	0.69	0.59
Amsel	71	33	18	81	0.55	0.46	0.08	0.64	0.53	0.63	0.70	0.61
Aramir	91	74	71	50	0.50	0.72	0.61	0.42	0.61	0.72	0.76	0.62
Kaskade	100	50	66	49	0.60	0.67	0.66	0.57	0.62	0.75	0.81	0.63
Berolina	93	53	89	76	0.61	0.70	0.70	0.59	0.61	0.71	0.76	0.63
Menuet	134	34	71	115	0.66	0.59	0.68	0.62	0.62	0.72	0.75	0.64
Berénice	136	23	61	129	0.69	0.39	0.39	0.66	0.55	0.71	0.74	0.58
Hiproly	89	16	29	167	0.36	0.31	0.23	0.60	0.43	0.66	0.47	0.34
<i>LSD</i> _{0.05}				11						0.03	0.04	0.04
Nitrogen level												
Low N	93	40	42	66	0.50	0.52	0.49	0.47	0.57	0.72	0.74	0.63
High N	145	41	52	92	0.65	0.57	0.47	0.58	0.57	0.71	0.72	0.62
Significance												
N level (N)	**	ns	ns	*	*	ns	ns	ns	ns	ns	ns	ns
Cultivar (G)	ns	ns	ns	*	ns	ns	ns	ns	ns	**	**	**
N × G	**	**	**	**	**	**	**	**	**	**	**	*
Components of variance (%)												
N level (N)	25.9	0.0	0.0	7.6	20.9	0.0	0.0	10.9	0.0	0.0	0.0	0.0
Cultivar (G)	0.0	25.8	0.0	45.1	4.5	17.6	9.3	8.6	31.8	33.3	63.3	75.0
N × G	70.8	68.5	92.1	44.4	70.4	70.6	81.9	73.6	56.8	65.0	22.9	10.0
Error	3.3	5.7	7.9	2.9	4.2	11.8	8.8	6.9	11.4	1.7	13.8	15.0

*, ** significant at the 0.05 and 0.01 probability levels, respectively *LSD*_{0.05}, least significant difference at the 0.05 level of significance

Higher amounts of plant N were recorded at the high N level at anthesis (Table 2). This means that at the high N level the cultivars had a greater potential for nitrogen translocation (NT) to the kernel. Compared with the low N level, NT at the high N level was higher by 56% in 1995 and 39% in 1998. Cultivar differences in NT were significant only in 1998 (Table 6). If it is assumed that all translocated N was used for kernel development, then the translocated N represented 85, 56, 41 and 61% of grain N at the low N level and 153, 55, 37 and 108% of grain N at the high N level in 1995, 1996, 1997 and 1998, respectively. In favorable years at high N level, the amount of translocated N was 53 and 8% higher than the amount of N found in the grain at harvesting (Tables 5 and 6), which indicates N losses during the grain filling stage.

Nitrogen translocation efficiency (NTE) represents the proportion of N at anthesis that was lost from the vegetative plant parts during grain filling. ANOVA revealed a significant effect of year and its interactions with nitrogen levels and cultivars on NTE (Table 1). The high N level increased NTE in 1995 and 1998, although the differences between N levels in 1998 were not statistically significant (Table 6). Cultivar differences in NTE were not recorded in any of the growing seasons, while significant N level × cultivar interactions were observed in all the years. The highest NTE was recorded for the Australian cultivars and the lowest for the Yugoslav ones as well as Gimpel and Hiproly. Variation in NT and NTE was mainly caused by N level × cultivar interactions, with the partition of this variance component of over 70%.

Translocated N from the vegetative plant parts to the kernel was in positive correlation with dry matter and N at anthesis (data not shown). Relation to plant N concentration was not consistent, it was positive and significant in unfavorable and nonexistent in favorable years. Logically, the amount of translocated N from the vegetative plant parts was related to dry matter translocation efficiency and contribution of pre-anthesis dry matter to kernel weight. Post-anthesis dry matter and N accumulation decreased translocation of N accumulated by anthesis. NT is a good indicator of NTE, the coefficients of determination were over 0.50. There was no relation between NT and NHI. In general, higher dry matter at maturity, grain yield, total amount of N at maturity, grain protein yield and kernel number per plant decreased NT. Vegetative and grain N concentration did not influence NT to the kernel.

The cultivars differed significantly in nitrogen harvest index (NHI) in three years, while N level \times cultivar interactions occurred in all four years (Table 6). Despite the increased N content at anthesis resulting from the application of N fertilizer (Table 2), NHI was not significantly affected by N level. The most important component of variance was the cultivar in 1997 and 1998 and N level \times cultivar interaction in 1995 and 1996. The highest proportion of aboveground N was retained in straw in favorable 1995, when only 57% of N was translocated into kernel. In unfavorable growing seasons close to three quarters of aboveground N were translocated into kernel, and NHI was 0.72 and 0.74 for the low and 0.71 and 0.72 for the high N level, respectively. Across the years, the lowest NHI (0.47) was found in the cultivar Hiproly and the highest (over 0.70) in the Yugoslav cultivar NS.301, all the Australian cultivars (Arapiles, Schooner and Cantala), and the German cultivar Kaskade. In principle, higher amounts of dry matter and N at anthesis resulted in lower NHI. At maturity, none of the listed traits except N concentration in the vegetative plant parts was in consistent relationship with NHI. Lower N concentration in leaf, culm and chaff at maturity was in a positive ($P < 0.01$) correlation with higher partition of aboveground N in the grain at maturity (data not shown).

DISCUSSION

Dry matter accumulation until anthesis in conditions with available water and moderate temperature represented 90% at high and 58% at low N level of total dry matter at maturity, respectively. It is obvious that N level in conditions with available water is the important factor influencing dry matter accumulation. However, the grain yield was 32% higher at the low than at the high N level. This situation can be explained by a state of disharmony between plant growth in the vegetative phase and plant growth and kernel development during grain filling. When environmental factors (available water, abundant N, less sunshine, etc.) favor the growth of culm and leaves, huge vegetative mass will develop. If during fertiliza-

tion and grain filling environmental conditions become unfavorable, much of photoassimilate may be used for the maintenance of green parts instead of being translocated into the kernel. In adverse growing circumstances during vegetative phase, regardless of the N level, less than 50% of total dry matter at maturity had been accumulated by anthesis.

If it is assumed that all losses from anthesis to maturity were used for kernel development, then the contribution of pre-anthesis dry matter to kernel weight was 74 and 27% at the high N level in two favorable years, respectively. Some cultivars in favorable conditions lost much more dry matter from anthesis to maturity than was their grain yield, i. e. a major quantity of pre-anthesis dry matter was used for sinks other than kernel. Austin et al. (1977) found that only 73% of the losses of vegetative weight were used for kernel growth. Respiratory losses (Rawson and Evans 1971) and the losses of dead leaves (Bidingger et al. 1977) can account for the rest of the losses. The mobilization of dry matter stored pre-anthesis in the vegetative parts starts during the period of the maximum rate of grain filling (Küchbauch and Thome 1989, Bell and Incoll 1990). However, earlier dry matter mobilization, i.e. that taking place at anthesis, can occur as a result of decreased photosynthesis (Küchbauch and Thome 1989) or in response to water stress. Cultivars with larger contribution of pre-anthesis dry matter to grain yield tended to have lower yields although the coefficient of correlation between translocated pre-anthesis dry matter and grain yield was significant ($P < 0.01$). However, the coefficient of determination (R^2) was only 0.21, which means that the measurement of dry matter translocation was not useful for grain yield prediction.

Contribution of stem reserves may be greater under conditions of severe stress during grain development and in cultivars adapted to short growing seasons if plant had developed large vegetative mass during the pre-anthesis period. However, if growing conditions are adverse during the pre-anthesis stage and plants are not able to accumulate enough dry matter, as was the case in 1996 and 1997, dry matter accumulation during grain filling becomes more important. The pre-anthesis reserves can be used for grain filling without the alteration of weight of vegetative plant parts. Thus, in cultivars that have an increase of weight of vegetative plant parts from anthesis to maturity there is also a possibility of pre-anthesis dry matter contribution to grain yield. In a study where pulse-labelling and growth analysis were combined, Bidingger et al. (1977) found contributions of pre-anthesis photosynthate that ranged between 12 and 27% of grain yield, although there was no decrease in the weight of the vegetative parts after anthesis. In most barley-growing regions, grain filling occurs under biotic and abiotic stresses, increased temperature, water deficit, and severe foliar diseases. All these factors, together with natural senescence, cause a decrease of assimilation, although growing kernels as well as plant respiration and maintenance demands are increased. Genotypes that are developed and adapted for particular growing

conditions satisfy these demands by current photosynthesis efficiently, while those that are less adapted make larger use of their vegetative reserves. Wardlaw and Porter (1967) and Schnyder (1993) found that in the absence of stress effects on crop photosynthesis, most of the WSC reserves accumulate during the first part of the grain filling period.

Since there is a positive relationship between dry matter and N accumulation until anthesis, the highest N accumulation was found in the seasons favorable for high vegetative mass formation. Although some quantity of N could be accumulated after anthesis, it is assumed that all N had been accumulated by anthesis at the high N level and 92 and 73% at the low N level in 1995 and 1998, respectively. In adverse seasons, N level did not influence N accumulation until anthesis and 54 to 69% of total N had been accumulated by anthesis. Halloran (1981) and Heitholt et al. (1990) found higher vegetative N exploration for grain filling in poor N supply. Contrary to the state, in our study the lowest NT and the lowest grain and biological yields were recorded in 1996, which was the most unfavorable year for spring barley production. In extremely poor growing conditions with low N accumulation until anthesis, NT is lower than in better conditions because of the necessity of retaining some N quantity in the vegetative plant parts after anthesis. Poor N nutrition does not always result in a low level of N in the soil. Unfavorable weather conditions, e.g. low temperature and water deficit, lead to the inhibition of N absorption even if N is present in the soil.

The amount of pre-anthesis N utilized in the kernel is considerably higher when nutrition is rich, because of the higher N content and larger mass of vegetative organs. The amount of translocated N was the highest in 1995 and 1998, i.e. in years with the highest grain and biological yields. High amount of the utilization usually results in low protein concentration in the grain, where the higher efficiency of N utilization is used for the increase in the grain yield. Regardless of the growing conditions, significant positive correlation was established between NT and NTE. Cox et al. (1986) obtained different results, the participation of translocated vegetative N in total amount of grain N was high, but there was no significant correlation between grain protein, the amount of translocated N and NTE.

The ratio of translocated N to grain N was 0.85, 0.56, 0.42 and 0.61 at the low and 1.53, 0.55, 0.37 and 1.08 at the high N level in 1995, 1996, 1997 and 1998, respectively. Thus, in favorable growing conditions the highest grain N amount came from pre-anthesis, while in the less favorable ones half or more of the grain N was accumulated during grain filling. These data were not unexpected, since the climatic conditions in 1996 and 1997 were unfavorable at pre-anthesis and dry matter and N accumulation was extremely low. Because the soil was provided with N reserves, a significant portion of grain N in 1996 and 1997 was taken up during grain filling.

Wetselaar and Farquhar (1980) and Papakosta and Gagianas (1991) reported N losses from anthesis to maturity

under field conditions. In our study, most of the cultivars had a negative N balance at the high N level in 1995 and 1998, across cultivars 53 and 8% NT was higher in relation to kernel sink capacity. Papakosta and Gagianas (1991) stated that N losses depend primarily on N content at anthesis, i.e. when N content in wheat at anthesis exceeds 200 kg/ha, N losses are inevitable regardless of yield. In barley, similar to wheat, it can be assumed that N content at anthesis of over 150kg/ha causes N losses (Przulj and Momčilović 2001b). Volatilization of N and leaching of mobile N compounds from the surface of plants (Haper et al. 1987), environmental factors (high temperature and low air humidity during grain filling) (Denmead et al. 1976, Spiertz 1977), and inadequate usage of nitrogen fertilizer (Papakosta and Gagianas 1991) are the main causes of N losses. N losses from anthesis to maturity in the above-ground plant parts could also be due to loss of some plant parts during the post-anthesis period, e.g., old leaves, or due to translocation of a part of N to other sinks. Some results are erroneous due to analytical errors, non-representative sample size of very variable plant replicates, etc.

CONCLUSION

Cultivar, year, and their interaction influenced pre-anthesis dry matter and nitrogen accumulation and translocation. In the years with favorable growing conditions during vegetative growth the main portion of dry matter was stored before anthesis, while in the years with unfavorable conditions during that period significant amounts of dry matter were accumulated during grain filling as well. The more adapted cultivars continued the accumulation of dry matter and nitrogen during the grain filling period, while in the less adapted ones the main portion accumulated before anthesis. Poor growing conditions during pre-anthesis inhibited N accumulation, decreased the amount of translocated N, and increased post-anthesis N uptake. Plant N content over 150 kg/ha at anthesis caused N losses. The cultivars with a high capacity for N accumulation at pre-anthesis, high translocation efficiency and high NHI could be used in the development of cultivars with the desired N balance. Straw N concentration could be a useful and cheaper indicator in the selection of genotypes with efficient N utilization.

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ABSTRAKT

Akumulace a využití sušiny a dusíku u jarního ječmene

Obilky obilnin mohou během růstu získávat sacharidy a dusík (N) buď z translokace zásob akumulovaných před obdobím kvetení ve vegetativních částech rostlin, nebo z běžné asimilace během vývoje obilky. Tuto studii jsme zaměřili na vyhodnocení vlivů úrovně dusíku a odrůd na akumulaci a mobilizaci sušiny a N před obdobím kvetení a po něm. Dvacet odrůd dvouřadého jarního ječmene (*Hordeum vulgare* L.) jsme pěstovali na nevápnité černozemní půdě při dvou dávkách dusíku ve čtyřech vegetačních obdobích (1995–1998) v lokalitě Novi Sad (45° 20' severní zeměpisné šířky, 15° 51' východní zeměpisné délky, 86 m nad mořem). Akumulace sušiny před obdobím kvetení se pohybovala od méně než 50 % v nepříznivých pěstebních podmínkách do 90 % v příznivých podmínkách. K translokaci sušiny docházelo pouze v příznivých pěstebních podmínkách. Dusík akumulovaný před obdobím kvetení dosahoval ve zralosti 57–92 % z celkového N při nízké a 54–129 % při vysoké hladině N. Hodnoty translokovaného dusíku činily 41–85 % N v obilkách při nízké a 37–153 % N při vysoké hladině N. Ke ztrátám dusíku docházelo za příznivých pěstebních podmínek tehdy, když dusík v období kvetení

přesáhl 150 kg/ha. Akumulace dusíku během nalévání zrna vykazovala zápornou korelaci s akumulací sušiny a N před obdobím kvetení. Sklizňový index N činil 0,57–0,63 v příznivých a 0,71–0,74 v nepříznivých pěstebních podmínkách. Dvě možná řešení ve šlechtění jarního ječmene pro středomořské pěstební podmínky může představovat selekce genotypů s vyšší schopností využívat zásoby vytvořené před obdobím kvetení nebo genotypů s delší listovou pokryvností po skončení období kvetení.

Klíčová slova: jarní ječmen (*Hordeum vulgare* ssp. *distichum* L.); sušina; dusík; akumulace; translokace; koncentrace dusíku; sklizňový index dusíku; korelace

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