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Research Article

Growth analysis of winter wheat cultivars as affected by nitrogen fertilization

Wachstumsanalyse von Winterweizensorten in Abhängigkeit von Stickstoffdüngung

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Summary

Growth analysis helps explain the differences in yield and growth potential between cultivars in response to management practices and environmental conditions. The aim of the research was: (i) to investigate the effect of nitrogen fertilization on the growth and growth parameters of different wheat (*Triticum aestivum* L.) cultivars and (ii) to study the relationship between yield and growth parameters at the individual plant and plant stand level. In the two-factorial, split-plot experiment, the main plot was the nitrogen (N) treatment and the sub-plot was the cultivar. In response to N fertilization, the values of growth rate parameters increased up to the N_{160} treatment. The mean values of crop growth rate (g m^{-2} day^{-1}) in the treatments were as follows: N_0: 10.4, N_{80}: 15.4, N_{160}: 17.2 and N_{240}: 16.3. The leaf area index, leaf area duration and especially the duration of the flag-leaf gave a good reflection of the effect of N fertilization. Multiple regression analysis demonstrated the significant effect of growth rates, size and duration of leaf area, biomass distribution and yield components on the yield. The results showed that understanding the growth of plants is important for optimizing management decisions.

Keywords: yield response, classical growth analysis, Hunt-Parsons model, growth rates, regression analysis

Zusammenfassung

Wachstumsanalyse hilft, die Unterschiede im Ertrag und Wachstumspotential zwischen Sorten als Reaktion auf Managementsverfahren und Umweltverhältnisse zu erklären. Das Ziel der Untersuchung war es, (i) den Einfluss der Stickstoffdüngung auf das Wachstum und die Wachstumsparameter von verschiedenen Weizensorten (*Triticum aestivum* L.) und (ii) den Zusammenhang zwischen dem Ertrag und den Wachstumsparametern auf Einzelpflanzen- und Bestandesebene zu untersuchen. In einer zweifaktoriellen Spaltanlage war die Großparzelle die Stickstoff (N)-Düngung und die Kleinparzelle die Sorte. Die Wachsumsraten stiegen mit zunehmender N-Düngung bis zur Behandlung N_{160}. Die mittleren Werte der absoluten Wachstumsraten (g m^{-2} Tag^{-1}) waren in den Behandlungen wie folgt: N_0: 10,4, N_{80}: 15,4, N_{160}: 17,2 and N_{240}: 16,3. Der Blattflächenindex, die Blattflächendauer und besonders die Fahnenblatt-Blattflächendauer gaben einen guten Hinweis auf den Effekt der N-Mineraldüngung. Eine Mehrfach-Regressionsanalyse hat den signifikanten Einfluss von Wachstumsraten, der Größe und der Dauer von Blattflächen, der Verteilung der Biomasse und der Ertragskomponenten auf den Ertrag gezeigt. Die Ergebnisse haben gezeigt, dass das Verstehen des Pflanzenwachstums für die Optimierung der Managementsentscheidungen wichtig ist.

Schlagworte: Ertragsreaktion, classical Wachstumsanalyse, Hunt-Parsons model, Wachstumsparameter, Regressionanalyse

1. Introduction

Identifying the physiological, biochemical or morphological characteristics responsible for inherent or environmentally induced variation in plant growth or yield requires careful growth analysis. Plant growth analysis is an explanatory, holistic and integrative approach for interpreting plant form and function. It uses simple primary data in the form of weights, areas, volumes and contents of plant components to investigate the processes within and involving the whole plant (Causton and Venus, 1981; Hunt, 1982).
Two distinct approaches to the growth analysis of plants have evolved. In the classical approach, parameters are calculated using various formulae. The functional approach involves fitting curves to experimental data, and the instantaneous values of growth parameters are calculated from the first derivative of the function fitted. Growth analysis helps to explain differences in growth potential between species and cultivars in response to environmental conditions and management practices (Lambers et al., 1998). Understanding the growth of plants is important for optimizing management decisions. Plant growth analysis can provide data to calibrate crop models and to test the effects of climatic factors on photosynthesis and partitioning (Boote et al., 2016). Combined with reduced rates of yield improvement, the increasing global population has led to reduced productivity per capita, hence the need to increase the grain yield by at least 50% over the next few decades (Reynolds et al., 2009; Slafer et al., 2014). A better understanding of crop yield physiology would help to achieve the rates of yield improvement required in the near future.
Various authors have published the results of growth analysis on various crops in terms of different management practices and cultivar comparisons, including maize (e.g., Bullock et al., 1993), wheat (Davidson and Campbell, 1984; Barneix, 1990; Karimi and Siddique, 1991; Ozturk et al., 2006; Neugschwandtner et al., 2015), triticale (Royo and Blanco, 1999), Bermuda grass (Silva et al., 2016), soybean (Clawson et al., 1986; Yusuf et al., 1999; Hu and Wiatrak, 2012), potato (Oliveira et al., 2016), sugar beet (Hoffman and Kluge-Severin, 2011) and peas (Silim et al., 1985; Munier-Jolain et al., 2010; Neugschwandtner et al., 2013). However, few studies appear to have been made on the effect of agronomic treatments on the growth and productivity of wheat at both the individual plant and plant stand levels.
The aim of the research was: (i) to investigate the effect of nitrogen fertilization on the growth and growth parameters of different wheat cultivars and (ii) to study the relationship between yield and growth parameters at both the individual plant and plant stand level in several years.

2. Materials and methods

2.1. Field experiments and growing conditions

The effect of nitrogen fertilization on the yield and yield components of various wheat cultivars was studied in a small-plot long-term experiment, with two factors arranged in a split-plot design in four replications. The experiment was carried out in the years 2006/2007, 2007/2008 and 2008/2009 at the Agricultural Institute of the Centre for Agricultural Research in Martonvásár. In the long-term crop rotation experiment, the crop sequence was pea, winter wheat, maize and spring barley. The dose of N fertilizer formed the main plot and wheat cultivar the subplots. The doses of N fertilizer (calcium ammonium nitrate) were 0, 80, 160 and 240 kg ha^{-1} (designated as N_0, N_{80}, N_{160} and N_{240}, respectively) and were applied in two splits: one-third before sowing and the other two-thirds in early spring at tillering. All the plots were given the same dosage of phosphorus and potassium (120 kg ha^{-1} of each). The three Martonvásár wheat genotypes sown in the subplots were Mv Toborzó (extra early), Mv Palotás (early) and Mv Verbunkos (mid-early). The ploughed layer of the chernozem soil, a humus-containing loam, was slightly acidic with moderate supplies of phosphorus and good supplies of potassium.
In the dry year of 2007, the total rainfall during the growing season was only one-third (200 mm) of that in 2008 and 2009 (638 and 617 mm, respectively). The rainfall distribution was also unfavorable in 2007, while in 2008 and 2009 both the quantity and distribution of rainfall were satisfactory (with the exception of lack of rain in April 2009). The mean temperature during the growing season was higher in 2007 (12°C) than in the other two years (10°C), which could be attributed partly to the very mild winter.

2.2. Sampling procedures

The sampling area for each treatment was 13.5 m^2 (9 m × 1.5 m). At each sampling date, destructive samples consisting of 5 plants were taken randomly from a 0.5 m^2 area once a week on a total of 25 occasions in 2007, 21 in 2008 and 17 in 2009, covering the whole growing season. Sampling was begun when the wheat reached the two-leaf stage. Leaf area was estimated by measuring the green leaf area of all the leaves with a leaf area meter (Model AM 300, BioScientific Ltd, UK). The dry mass of leaves, stems and spikes was determined after drying in a drying cabinet at 60°C for 48 h. The harvest index was derived from a 0.18 m² subplot. The plants were cut at the soil surface, bundles were weighed and threshed, and grain weights were recorded.

2.3. Growth analysis

The Hunt-Parsons program (HP curves) (Hunt and Parsons, 1974), which fits first-, second- or third-order polynomial exponential curves to the trends in lnY (dry weight) versus t (time) and lnZ (leaf area) versus t, was used for functional growth analysis. A polynomial exponential function is a polynomial function of the natural logarithm of a growth attribute in relation to time (Causton and Venus, 1981). The output consisted of observed and fitted values of lnY and lnZ and the values of dY/dt, dZ/dt, (1/Y)(dY/dt), (1/Z)(dZ/dt), Z/Y and (1/Z)(dY/dt), together with their standard errors and 95% confidence intervals.
The absolute growth rate (AGR), absolute growth rate of leaf area (ALGR), relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR), crop growth rate (CGR) and leaf area index (LAI) were calculated using the Hunt-Parsons program, while the method of classical growth analysis (Evans, 1972; Hunt, 1982) was used to calculate the harvest index (HI), leaf area duration (LAD), leaf area duration of the flag-leaf ($LAD_{flag-leaf}$) and biomass duration (BMD). The growth analysis indices (parameters) were characterized in terms of dynamics over time and average (mean) and maximum (max) values (Causton and Venus, 1981; Hunt, 1982).

2.4. Statistical analysis

The split-plot design from the General Analysis of Variance menu of the GenStat 18 program was applied to analyze the growth parameter data sets, while the relationships between growth parameters were studied by linear regression analysis. Multiple linear regression analysis was used to determine relationships between the yield per plant (g plant^{-1}) and yield per unit area (t ha^{-1}) (as dependent variables), and the yield components and growth indices (as independent variables) for all the data (n = 36). The individual and joint effects of independent variables on the yield were determined using the All Subsets Regression menu of multiple regression. Relationships were analyzed between the yield per plant and the following eight independent variables: grain number (GN) per spike, thousand kernel weight (TKW), RGR_{mean}, AGR_{mean}, $ALGR_{mean}$, NAR_{mean}, LAR_{mean} and LAD_{flag_leaf}. The relationships between yield per unit area (t ha^{-1}) and the following seven variables were analyzed: GN per m², TKW, CGR_{mean}, LAI_{max}, LAD_{LAI}, HI and BMD. The following indices: $\bar{R}^2$ (adjusted multiple correlation coefficient), R² (multiple correlation coefficient), Mallows C_p and AIC (Akaike's information criterion) were used as criteria in selecting the variables (Afifi et al., 2004).

3. Results

3.1. Above-ground dry matter and leaf area

The dynamics of dry matter accumulation per plant over time was expressed by a third-degree exponential function (Figure 1), the only exceptions being the dry matter accumulation of Mv Toborzó and Mv Verbunkos in the N_0 treatment in 2007, to which a quadratic exponential function was fitted. In all cases, the functions gave a good fit to the measurement data (R² = 94.7–99.3%). The dynamics of dry matter accumulation gave a good reflection of the effect of nitrogen treatments. In response to N fertilizer, the dry matter production increased up to the N_{240} treatment in 2007 and 2008, and up to N_{160} in 2009, the greatest differences generally being observed between the N_0 and N_{80} treatments. Averaged over the cultivars and years, the maximum values were as follows: N_0: 3.03, N_{80}: 4.01, N_{160}: 4.38, N_{240}: 4.37 g plant^{-1}.
In all cases, the dynamics of leaf area growth was depicted with a third-degree exponential function (Figure 2) (R² = 83.6–97.0%). The dynamics in the N_0 and N_{80} treatments was quite distinct from that in the N_{160} and N_{240} treatments. The maximum value of leaf area per plant was smallest in the N_0 treatment and significantly greater in the N_{80} treatment, while the highest values were obtained in the N_{160} and N_{240} treatments. Averaged over years and cultivars, the maximum leaf area in the N treatments was as follows (cm² plant^{-1}): N_0: 84.8, N_{80}: 134.9, N_{160}: 160.7, N_{240}: 169.5. The maximum leaf area was achieved by the plants immediately before heading. The dynamics of leaf area gave a clear indication of the different maturity dates of the cultivars. As a function of year and N treatment, the maximum leaf area was recorded 173–187 days after sowing (DAS) for Mv Toborzó, 180–194 DAS for Mv Palotás and 187–194 DAS for Mv Verbunkos. Averaged over years

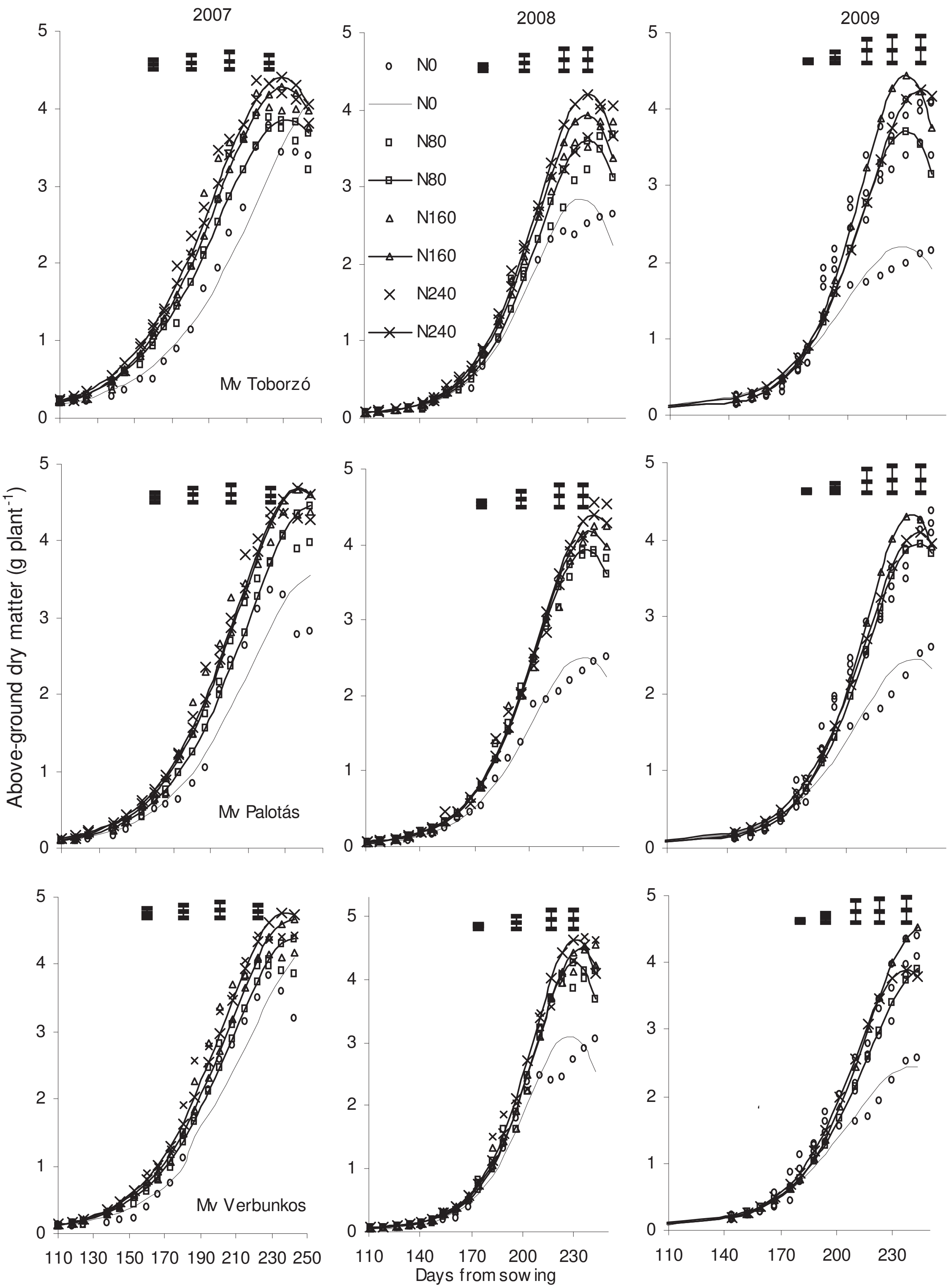

Figure 1. Effect of N treatment on the above-ground dry matter (g plant^{-1}) of wheat cultivars (mean values for the years 2007-2009)
Error bars are LSD (p<0.05) separating means of different fertilization treatments.
Abbildung 1. Einfluss der N-Düngung auf die oberirdische Trockenmasse (g Pflanze^{-1}) der Weizensorten (Mittelwerte für die Jahre 2007-2009)
Die Fehlerbalken zeigen Grenzdifferenzen (p<0,05), welche die Mittelwerte der Düngebehandlungen abgrenzen.

and N treatments, the leaf area of Mv Verbunkos was the greatest (144 cm²), followed by Mv Toborzó (135 cm²) and Mv Palotás (134 cm²). The maximum leaf area per plant (averaged over cultivars and N treatments) was considerably lower in 2009 (115 cm²) than in the other two years (2007: 135 cm², 2008: 155 cm²).

3.2. Growth parameters of individual plants

Absolute growth rate (AGR), the rate of change in size per unit time, is the simplest index of growth. Figure 3 shows the dynamics of AGR of Mv Palotás in 2008. The dynamics of growth parameters were similar in each year. Tables 1-3 give the detail data of the parameters. The dynamics of AGR could be characterized by a bell-shaped curve. The maximum values were obtained in the period around flowering (ca. 203 days after sowing). In the treatment where no N fertilizer was given, the dynamics of AGR was clearly distinct from that of the fertilized treatments. The value of AGR_{mean} (g day^{-1} 10^{-2}) rose to the N_{160} treatment (Table 1), with the following values in the individual treatments: N_0: 2.26, N_{80}: 3.17, N_{160}: 3.54, N_{240}: 3.51. There was little difference in the AGR_{mean} values of the different wheat cultivars: Mv Verbunkos and Mv Palotás: 3.13, Mv Toborzó: 3.09. The mean value of AGR was higher in 2008 and 2009 (3.16 and 3.55, respectively) than in 2007 (2.64).

Relative growth rate (RGR) expresses growth in terms of the rate of increase in size per unit of size. After the plants reached the 4-leaf stage (ca. 110 days after sowing), the dynamics of RGR exhibited an initial, relatively rapid increase. The maximum value was reached between mid-March and mid-April (around 154 days), at the beginning of shooting, after which it gradually declined, dropping to 0 when the foliage withered completely in mid-June (236 days) (Figure 3). The value of RGR_{mean} (g g^{-1} day^{-1} 10^{-2}) was the greatest in the N_{160} treatment (Table 1), with the following values per N treatment: N_0: 2.78, N_{80}: 3.07, N_{160}: 3.25, N_{240}: 3.12. There was no significant difference between the RGR values of the cultivars: Mv Toborzó: 2.97, Mv Palotás: 3.08, Mv Verbunkos: 3.01. In the wetter years of 2008 and 2009, the RGR_{mean} value (g g^{-1} day^{-1} 10^{-2}) was considerably higher (3.31 and 3.18, respectively) than in 2007 (2.67), when the rainfall supplies were less favorable.

The **absolute growth rate of the leaf area (ALGR)** was characterized by two successive bell-shaped curves (Figure 3), the first describing the growth of leaf area and the second describing the dynamics of leaf withering. The maximum value of ALGR was achieved at the end of tillering (174 days after sowing), immediately prior to shooting, with a difference of around a week between the cultivars due to differences in their maturity dates. The mean values of ALGR (cm² day^{-1} 10^{-2}) in each N treatment were as follows: N_0: 0.95, N_{80}: 1.67, N_{160}: 2.01, N_{240}: 2.15 (Table 1). Among the cultivars Mv Verbunkos exhibited a higher value of $ALGR_{mean}$ (1.79) than Mv Toborzó (1.60) or Mv Palotás (1.69). The mean value of ALGR (cm² day^{-1} 10^{-2}) was lowest in 2007 (1.34) and substantially higher in 2008 (1.94) and 2009 (1.81).

Net assimilation rate (NAR) is an index of the productive efficiency of plants, calculated in relation to total leaf area. Starting from the early growth stage (111 days after sowing), NAR increased rapidly for a few weeks, until the side-tillers had developed (Figure 3), after which the rate slowed and remained more or less constant until the foliage was fully developed. Then, as the leaf area decreased (about 174 days), NAR accelerated up to the end of the vegetation period. The mean value of NAR (Table 1) was smallest in the N_0 treatment (2.79), rising with the application of N fertilizer and reaching the highest value in the N_{80} (2.82) or N_{160} treatment (2.84), depending on the cultivar and year. The NAR values of Mv Palotás (3.05) and Mv Toborzó (2.71) exceeded that of Mv Verbunkos (2.58). The mean value of NAR was highest in 2009 (3.63), while there was little difference between the values recorded in 2007 (2.27) and 2008 (2.45).

Leaf area ratio (LAR) is a morphological index expressing the leafiness of the plant as the ratio between total leaf area per plant and total dry weight per plant. The LAR values reached a maximum at the end of tillering (160-168 days after sowing), after which they declined steeply until flowering, followed by a further, slower decrease (Figure 3). The mean values of LAR provided a good illustration of the effects of N treatments (Table 1), and exhibited the following values in the individual N treatments: N_0: 82.8, N_{80}: 91.4, N_{160}: 95.8, N_{240}: 94.3 cm² g^{-1}. Among the wheat cultivars, the LAR_{mean} values of Mv Toborzó (93.5) and Mv Verbunkos (94.3) were higher than that of Mv Palotás (85.4). The highest value of LAR_{mean} was recorded in 2008 (101.4), while the values in 2007 and 2009 were similar (89.2 and 82.6, respectively).

3.3. Growth parameters of the crop stand

Crop growth rate (CGR) is an index of agricultural productivity of land in terms of the plant biomass produced per unit area. The dynamics of CGR was similar to that of AGR, being characterized by a bell-shaped curve with maximum values during the flowering period. The mean value of CGR (CGR_{mean}: g m^{-2} day^{-1}) was lowest in the N_0 treatment, increasing significantly in the N_{80} treatment (15.4) and achieving the highest value in the N_{160} treatment (17.2), after which it dropped slightly (N_{240}: 16.3) (Table 1). Among the wheat cultivars, Mv Toborzó had the highest CGR_{mean} value (15.3), followed by Mv Verbunkos (14.9) and Mv Palotás (14.4). CGR_{mean} exhibited the lowest value in 2007 (13.9), with higher values in 2008 (15.6) and 2009 (15.1).

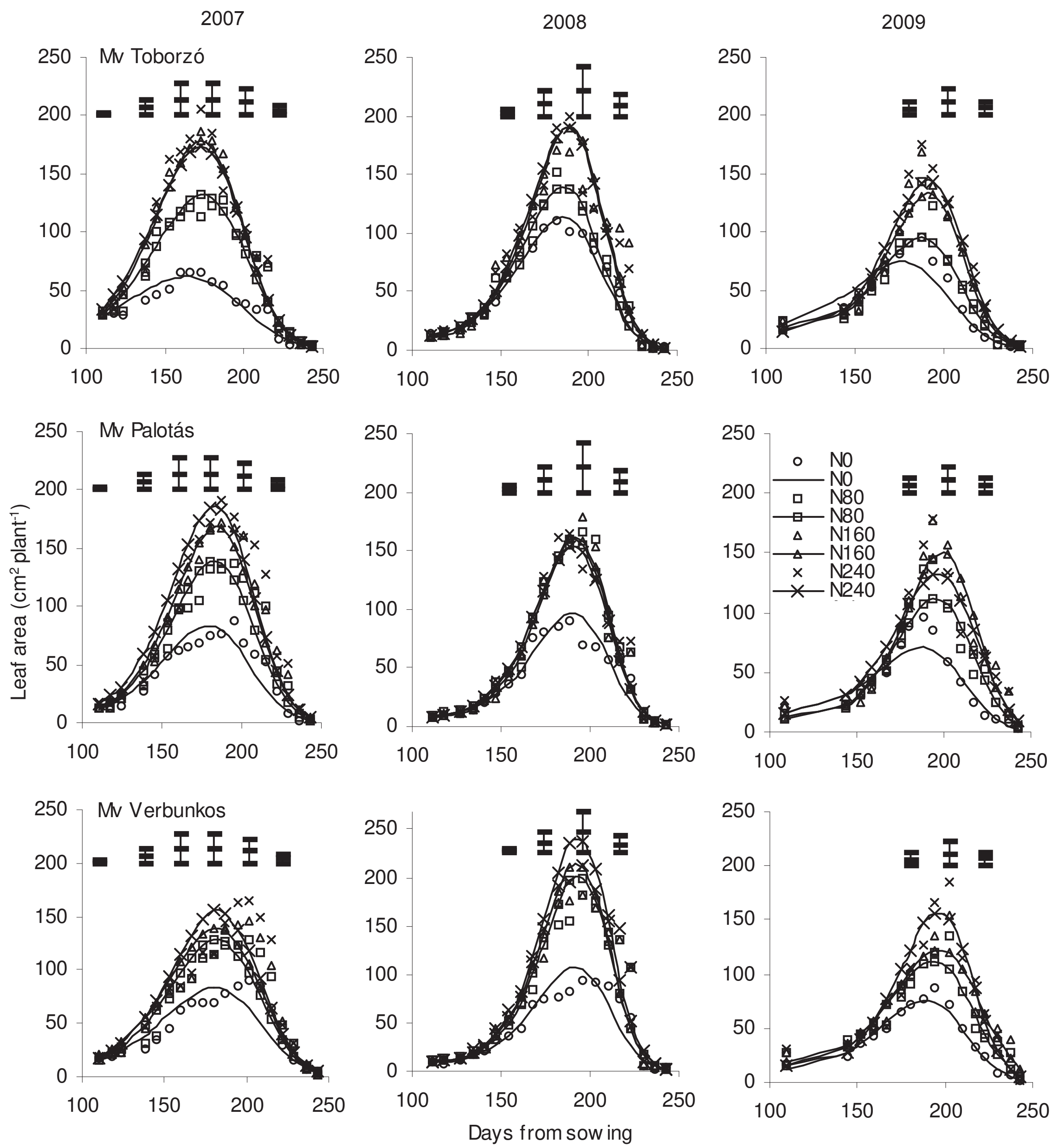

Figure 2. Effect of N treatment on the leaf area (cm^2 $plant^{-1}$) of wheat cultivars (mean values for the years 2007-2009)
Error bars are LSD ($p<0.05$) separating means of different fertilization treatments.
Abbildung 2. Einfluss der N-Düngung auf die Blattfläche (cm^2 $Pflanze^{-1}$) der Weizensorten (Mittelwerte für die Jahre 2007-2009)
Die Fehlerbalken zeigen Grenzdifferenzen ($p<0,05$), welche die Mittelwerte der Düngebehandlungen abgrenzen.

Table 1. Effect of N fertilization on the mean values of the growth parameters and the maximum leaf area index (LAI) of wheat cultivars, using the functional method of growth analysis (2007-2009)
Tabelle 1. Einfluss der N-Düngung auf die Mittelwerte der Wachstumsparameter und den maximalen Blattflächenindex (LAI) der Weizensorten nach der funktionellen Methode der Wachstumsanalyse (2007-2009)

		2007			2008			2009	
N rate	Toborzó	Palotás	Verbunkos	Toborzó	Palotás	Verbunkos	Toborzó	Palotás	Verbunkos
					AGR_{mean} [g day^{-1}10^{-2}]				
N_0	2.17	2.04	2.28	2.33	2.07	2.61	2.14	2.40	2.26
N_{80}	2.50	2.63	2.64	2.98	3.25	3.52	3.82	3.87	3.29
N_{160}	2.79	2.95	2.84	3.28	3.40	3.63	4.60	4.42	3.92
N_{240}	2.88	2.98	3.01	3.49	3.52	3.83	4.09	3.99	3.76
					LSD values				
N rate (N)		0.21^{***}			0.15^{***}			0.26^{***}	
Cultivar (C)		0.14^{NS}			0.14^{***}			0.17^{***}	
N × C		0.30^{*}			0.26^{***}			0.36^{*}	
					$ALGR_{mean}$ [cm^2 day^{-1}]†				
N_0	0.35	0.83	0.82	1.35	1.13	1.25	0.67	0.99	1.17
N_{80}	1.15	1.51	1.35	1.69	1.91	2.28	1.50	1.86	1.76
N_{160}	1.57	1.85	1.44	2.34	1.90	2.48	2.32	2.36	1.84
N_{240}	1.49	2.02	1.65	2.32	1.86	2.78	2.50	2.08	2.61
					LSD values				
N rate (N)		0.10^{***}			0.09^{***}			0.13^{***}	
Cultivar (C)		0.10^{***}			0.08^{***}			0.08^{***}	
N × C		0.18^{***}			0.15^{**}			0.17^{***}	
					RGR_{mean} [g g^{-1} day^{-1}10^{-2}]				
N_0	2.34	2.73	2.72	2.94	3.15	3.24	2.45	2.87	2.54
N_{80}	2.45	2.82	2.72	3.20	3.36	3.19	3.40	3.54	2.97
N_{160}	2.59	2.82	2.75	3.44	3.53	3.45	3.63	3.79	3.29
N_{240}	2.54	2.73	2.84	3.39	3.53	3.34	3.27	3.33	3.07
					LSD values				
N rate (N)		0.13^{**}			0.11^{***}			0.34^{***}	
Cultivar (C)		0.18^{***}			0.13^{NS}			0.30^{NS}	
N × C		0.31^{*}			0.22^{***}			0.58^{**}	
					NAR_{mean} [g m^{-2} day^{-1}]				
N_0	2.17	2.31	2.13	1.92	2.81	2.64	3.84	3.83	3.50
N_{80}	2.22	2.39	2.35	1.93	2.98	1.98	4.56	3.91	3.03
N_{160}	2.06	2.43	2.29	2.24	3.30	2.20	4.06	3.81	3.14
N_{240}	2.16	2.18	2.57	2.17	3.13	2.11	3.23	3.53	3.06
					LSD values				
N rate (N)		0.18^{***}			0.15^{***}			0.23^{***}	
Cultivar (C)		0.11^{***}			0.16^{**}			0.23^{**}	
N × C		0.24^{***}			0.30^{***}			0.42^{NS}	
					LAR_{mean}[cm^2 g^{-1}]				
N_0	75.2	84.8	88.1	107.7	82.8	93.0	74.4	75.2	64.1
N_{80}	84.5	90.8	88.6	113.2	85.0	113.2	81.6	79.6	85.8
N_{160}	95.2	91.6	92.9	112.8	80.6	115.3	88.0	88.9	97.1
N_{240}	90.5	98.7	89.1	113.4	82.7	117.1	85.8	83.8	87.3
					LSD values				
N rate (N)		2.4^{***}			3.0^{**}			6.0^{***}	
Cultivar (C)		2.6^{NS}			1.5^{***}			5.5^{*}	
N × C		4.7^{***}			3.7^{***}			10.4^{NS}	
					CGR_{mean} [g m^{-2} day^{-1}]				
N_0	10.3	9.3	10.9	12.5	10.1	13.0	9.8	8.4	9.6
N_{80}	14.8	12.6	14.4	15.3	16.1	16.8	17.3	16.1	15.2
N_{160}	17.2	15.4	15.3	17.2	16.3	18.3	20.1	18.1	16.9
N_{240}	16.6	14.7	14.9	16.3	17.0	18.2	15.8	17.9	15.6
					LSD values				
N rate (N)		1.2^{***}			0.9^{***}			0.9^{***}	
Cultivar (C)		1.0^{***}			0.6^{***}			0.8^{***}	
N × C		1.9^{**}			1.3^{***}			1.5^{*}	
					LAI_{max} [m^2 m^{-2}]				
N_0	2.95	3.85	4.43	5.77	4.53	5.13	3.71	2.63	3.43
N_{80}	7.49	6.79	7.06	6.88	7.64	9.39	4.76	4.95	5.59
N_{160}	10.49	8.67	7.50	9.70	7.51	10.56	6.59	6.38	5.74
N_{240}	9.58	9.23	7.64	8.51	7.38	10.93	7.13	5.26	6.88
					LSD values				
N rate (N)		0.37^{***}			0.34^{***}			0.25^{***}	
Cultivar (C)		0.60^{**}			0.23^{***}			0.30^{*}	
N × C		1.03^{***}			0.48^{***}			0.53^{**}	

Significance levels: *p<0.05, ** p<0.01, ***p<0.001, NS=non-significant; † ALGR values are for the leaf area increasing period

Table 2. Effect of N fertilizer treatments on the biomass duration (BMD) and the leaf area duration (LAD_{LAI}, $LAD_{flag-leaf}$) of wheat cultivars, using the classical method of growth analysis (2007-2009)
Tabelle 2. Einfluss der N-Düngung auf die Biomassedauer (BMD) und die Blattflächendauer (LAD_{LAI}, $LAD_{flag-leaf}$) der Weizensorten nach der klassischen Methode der Wachstumsanalyse (2007-2009)

	2007			2008			2009		
N rate	Toborzó	Palotás	Verbunkos	Toborzó	Palotás	Verbunkos	Toborzó	Palotás	Verbunkos
					BMD (g day)				
N_0	200	178	194	149	132	156	133	131	129
N_{80}	249	221	229	181	199	200	186	182	171
N_{160}	273	250	249	201	205	208	213	197	187
N_{240}	288	256	264	217	213	219	209	195	187
					LSD values				
N rate (N)		6***			4***			4***	
Cultivar (C)		3***			2***			3***	
N × C		8**			5***			6***	
					LAD_{LAI} (day)				
N_0	193	243	287	325	235	265	265	191	229
N_{80}	472	408	436	376	386	450	310	288	365
N_{160}	639	520	475	488	383	502	366	349	378
N_{240}	606	554	465	437	389	511	352	328	388
					LSD values				
N rate (N)		18***			8***			11***	
Cultivar (C)		12***			7***			6***	
N × C		25***			13***			14***	
					LAD_{flag_leaf} (cm^2 day)				
N_0	533	487	488	499	437	559	368	349	412
N_{80}	574	568	549	627	685	678	477	568	553
N_{160}	667	572	623	907	825	858	483	654	675
N_{240}	650	624	637	806	826	925	602	611	777
					LSD values				
N rate (N)		18***			30***			27***	
Cultivar (C)		19***			21***			38***	
N × C		35NS			43***			66**	

Significance levels: *p<0.05, **p<0.01, ***p<0.001, NS=non-significant

Leaf area index (LAI) is the ratio between the total leaf area of the crop and the total ground area on which it stands. The dynamics of LAI in response to N fertilization was similar to that of the leaf area (Figure 3). The maximum LAI values (Table 1) clearly reflected the effect of N fertilization (m^2 m^{-2}): N_0: 4.05, N_{80}: 6.73, N_{160}: 8.13, N_{240}: 8.06. Averaged over N treatments and years, the LAI_{max} values were lower for Mv Palotás (6.24) than for Mv Toborzó (6.96) and Mv Verbunkos (7.02). LAI_{max} was highest in 2008 (7.83), somewhat lower in 2007 (7.14) and much lower in 2009 (5.25).

Leaf area duration (LAD) is a quantitative expression of the length of time over which the plant stand maintains an active photosynthesizing leaf area. Both N fertilization and cultivar had a highly significant effect on the value of LAD_{LAI} in all three years, and there was also a significant N fertilizer × cultivar interaction (Table 2). The value of LAD_{LAI} (days) was lowest in the N_0 treatment (248), significantly higher in N_{80} (388) and N_{160} (448), and the highest in N_{240} (455). Averaged over the years and N treatments, the greatest value of LAD_{LAI} was obtained for Mv Toborzó (402), followed by Mv Verbunkos (296) and Mv Palotás (356); though in the favorable years of 2008 and 2009, Mv Verbunkos had the highest values. In the individual years, the LAD_{LAI} value was significantly higher in 2007 (442) than in 2008 (396) or 2009 (317).

The leaf area duration of the flag-leaf (LAD_{flag_leaf}) differed in terms of both N treatments and cultivars (Table 2). The lowest values were recorded in the N_0 treatment, rising with increases in N rate. The highest LAD_{flag_leaf} values were found in the N_{160} treatment in 2007 and 2008 (423 and 864 cm² day, respectively) and in the N_{240} treatment in 2009 (664 cm² day). In 2008 and 2009, the LAD_{flag_leaf} values of Mv Verbunkos exceeded those of the other two cultivars. In terms of the years, the highest LAD_{flag_leaf} value (cm^2 day) was recorded in 2008 (719), with a significantly lower value in 2007 (581) and the lowest in 2009 (544).

The biomass duration (BMD) takes into account not only how much dry weight develops, but also how long it lasts. The effects of both N fertilizer and cultivar on BMD were significant in all the years, and there was also a significant N fertilizer × cultivar interaction (Table 2). The value of BMD (g day) was lowest in the N_0 treatment (156), rising significantly with increasing N rates to 201.9 in N_{80}, 220 in N_{160} and 227 in N_{240} (Table 2). Averaged over the N treatments, Mv Toborzó had the highest BMD in 2007 and 2009 (252 and 185 g day, respectively), while in the favorable year of 2008, the highest value was recorded for Mv Verbunkos (196 g day). The value of BMD (g day) was the highest in the dry year of 2007 (248), with significantly lower values in 2008 (191) and 2009 (177).

3.4. Regression between growth parameters and yield

Significant linear regression was found between leaf area duration (LAD) and biomass duration (BMD) based on the data of three years (Y = 75.9 + 0.324BMD). The R^2 value showed that LAD explained 75.9% of the variance in BMD. On the basis of the 3-year data, linear regression was significant at P < 0.1% level between the absolute leaf area growth rate ($ALGR_{max}$) and the maximum value of the leaf area index (LAI_{max}) ($Y = 1.97 + 1.56ALGR_{max}$, R^2 = 79.6%). In each year, significant linear regression was detected between the mean absolute growth rate of dry matter (AGR_{mean}) and the biomass duration (BMD). Based on R^2, AGR_{mean} accounted for 75% of the variance in BMD in 2007, for 95.7% in 2008 and for 95.3% in 2009. Based on the three-year data (n = 36), there was a significant relationship between RGR_{mean} and its two components, NAR_{mean} and LAR_{mean}. The two components explained 62.7% of the variance in RGR_{mean} at P < 0.1% level. The two parameters had similar effects on the RGR_{mean}. In all three years and averaged over three years, significant linear regression (P < 0.1%) was found between CGR_{max} and its components, NAR_{mean} and LAI_{max}, which together determined 71.2% of the variance in CGR_{max}. In all three years, the effect of LAI_{max} was decisive, being more than three times as great as that of NAR_{mean}.

Relationships were investigated between the yield per plant (g $plant^{-1}$), as a dependent variable, and eight independent variables (Table 3). In decreasing order of $\bar{R}^2$, the individual variables having the greatest significant effect on the yield per plant were GN per spike, RGR_{mean}, AGR_{mean}, $ALGR_{mean}$ and LAD_{flag_leaf}. The two independent variables that had the greatest joint influence on the yield were GN $spike^{-1}$ and TKW, with the regression equation: Y = –1.133 + 0.04386GN + 0.02486TKW. This was followed (in decreasing order of $\bar{R}^2$) by the GN $spike^{-1}$ and RGR_{mean} and the GN per spike and AGR_{mean}. The three independent variables with the greatest joint effect on the yield per plant were the GN $spike^{-1}$, the TKW and RGR_{mean}, with the regression equation: $Y = –1.494 + 0.03971GN + 0.02381TKW + 0.1709RGR_{mean}$. The four independent variables with the greatest combined effect on yield per plant were GN $spike^{-1}$, TKW, RGR_{mean} and LAD_{flag_leaf}. In this case, the regression equation was: $Y = –1.029 + 0.04299GN + 0.02438TKW + 0.0896ALGR_{mean} + 0.000341LAD_{flag\_leaf}$.

The influence of seven independent variables was examined on the crop yield (t ha^{-1}) (Table 4). The independent variables that individually had a separate significant influence on the crop yield (in decreasing order of $\bar{R}^2$) were GN m^{-2}, CGR_{mean}, LAI_{max}, HI, TKW and LAD_{LAI}. The two independent variables having the greatest effect on the yield in combination were GN m^{-2} and LAD_{LAI}. The regression equation was: Y = 4.072 + 0.00009843 GN m^{-2} + 0.002947 LAD_{LAI}. This was followed (in decreasing order of $\bar{R}^2$) by GN m^{-2} and LAI_{max}, GN m^{-2} and CGR, GN m^{-2} and BMD and GN m^{-2} and HI. The three independent variables having the greatest combined influence on the yield (t ha^{-1}) were the GN m^{-2}, LAI_{max} and HI, with the regression equation: Y = 1.08 + 0.0000802 GN m^{-2} + $0.1398LAI_{max}$ + 0.0825HI.

4. Discussion

Growth analysis demonstrated significant relationships between growth rates and yield at both individual plant and plant stand level. This is in agreement with the results showing a significant relationship between growth rate and yield in maize (Tollenaar et al., 1992) and wheat (Serrago et al., 2013). The effect of N fertilization and cultivar on the yield was significant in all the years (Sugár et al., 2016). The grain yield was lowest in treatment N_0 (averaging 5.45 t ha^{-1}), with a significant increase from the N_{80} treat-

Table 3. Variables significantly influencing yield per plant (g $plant^{-1}$) alone or in combination, based on the stepwise method of multiple regression analysis (n = 36)
Tabelle 3. Variablen, die den Ertrag der Einzelpflanzen (g $Pflanze^{-1}$) signifikant beeinflussen, allein oder in Kombinationen, nach der schrittweisen Methode der Mehrfach-Regressionsanalyse (n = 36)

No. of variables	Variable	R^2	$\bar{R}^2$	C_p	AIC
1	GN† $spike^{-1}$	93.6	93.4	161	197
1	RGR_{mean}	70.8	70.0	848	884
1	AGR_{mean}	63.4	62.3	1072	1108
1	$ALGR_{mean}$	58.5	57.3	1219	1255
1	LAD_{flag_leaf}	30.9	28.8	2054	2090
2	GN $spike^{-1}$ TKW‡	98.2	98.1	24.5	60.5
2	GN $spike^{-1}$ RGR_{mean}	94.6	94.2	134	170
2	GN $spike^{-1}$ AGR_{mean}	94.3	93.9	143	179
3	GN $spike^{-1}$ TKW RGR_{mean}	98.7	98.6	11.0	47.0
3	GN $spike^{-1}$ LAR_{mean} NAR_{mean}	95.5	95.1	107	143
4	GN $spike^{-1}$ TKW RGR_{mean} LAD_{flag_leaf}	98.9	98.7	8.4	44.4
4	GN $spike^{-1}$ TKW $ALGR_{mean}$ LAD_{flag_leaf}	98.7	98.5	14.7	50.7
4	GN $spike^{-1}$ TKW LAR_{mean} NAR_{mean}	98.5	98.4	18.1	54.1

R2: multiple correlation coefficient, $\bar{R}^2$: adjusted R^2, Cp: Cp criterion, AIC: Akaike's information criterion
† GN, grain number
‡ TKW, thousand kernel weight

Table 4. Variables significantly influencing crop yield (t ha^{-1}) alone or in combination, based on the stepwise method of multiple regression analysis (n = 36)
Tabelle 4. Variablen, die den Ertrag des Pflanzenstandes (t ha^{-1}) signifikant beeinflussen, allein oder in Kombinationen, nach der schrittweisen Methode der Mehrfach-Regressionsanalyse (n = 36)

No. of variables	Variable	R^2	$\bar{R}^2$	C_p	AIC
1	GN† m^{-2}	71.4	70.5	16.5	52.5
1	CGR_{mean}	54.3	53.0	45.3	81
1	LAI_{max}	32.4	30.4	82	118
1	HI	25.3	23.1	94	130
1	TKW‡	19.4	17	104	140
1	LAD_{LAI}	17.8	15.4	107	143
2	GN m^{-2} LAD_{LAI}	80.6	79.4	2.9	38.9
2	GN m^{-2} LAI_{max}	78.3	77.0	6.8	42.8
2	GN m^{-2} CGR_{mean}	76.9	75.5	9.1	45.1
2	GN m^{-2} BMD	76.3	74.8	10.2	46.2
2	GN m^{-2} HI	74.6	73.1	12.9	48.9
3	GN m^{-2} LAI_{max} HI	81.7	80.0	2.9	38.9

R2: multiple correlation coefficient, $\bar{R}^2$: adjusted R^2, Cp: Cp criterion, AIC: Akaike's information criterion
† GN, grain number
‡ TKW, thousand kernel weight

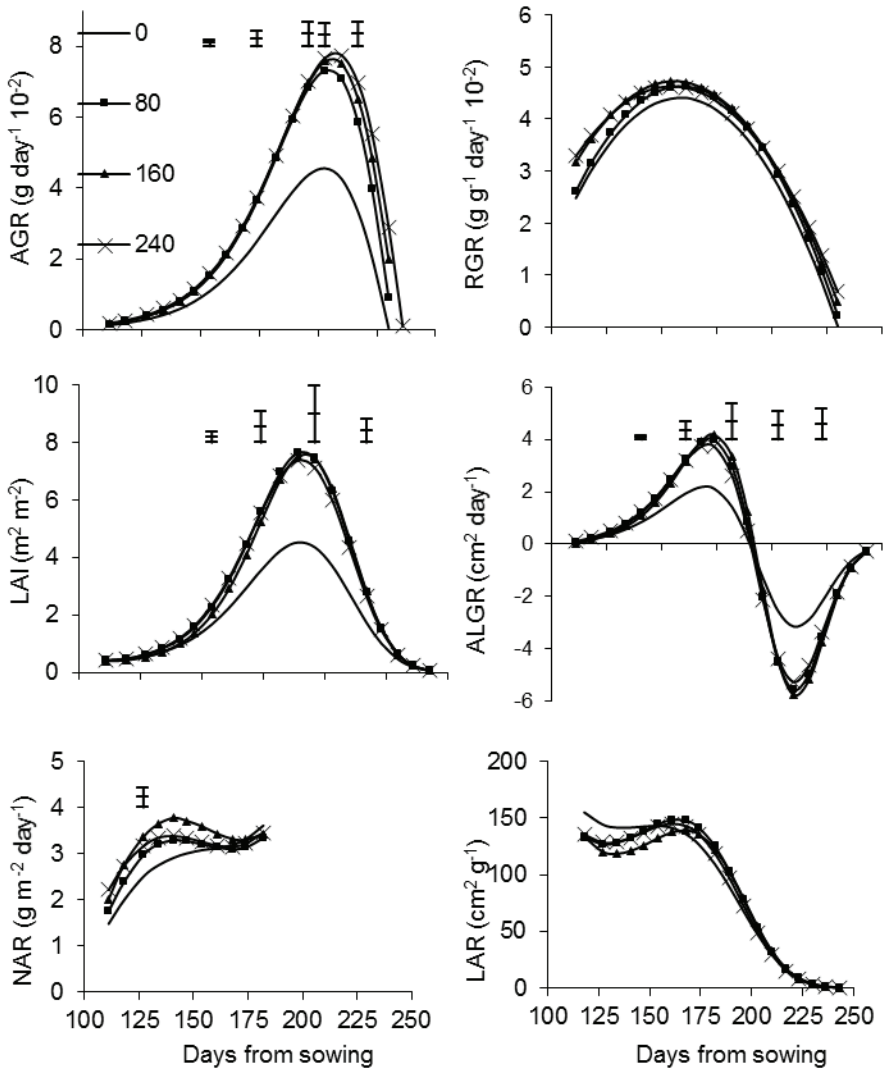

Figure 3. Effect of N treatment on the dynamics of the AGR, RGR, LAI, ALGR, NAR and LAR of Mv Palotás in 2008
Error bars are LSD (p<0.05) separating means of different fertilization treatments.
Abbildung 3. Einfluss der N-Düngung auf die Dynamik von AGR, RGR, LAI, ALGR, NAR und LAR der Sorte Mv Palotás in 2008
Die Fehlerbalken zeigen Grenzdifferenzen (p<0,05), welche die Mittelwerte der Düngebehandlungen abgrenzen.

ment in 2007 and 2008 (6.45 and 7.99 t ha^{-1}, respectively) and the N_{160} treatment in 2009 (7.44 t ha^{-1}). Higher N doses had no further significant yield-increasing effect. Averaged over the treatments, the grain yield was significantly higher in 2008 and 2009 (7.28 and 7.11 t ha^{-1}, respectively) than in 2007 (6.11 t ha^{-1}).
Nitrogen fertilization had a significant effect on the GN per spike (except in 2007) and the TKW. The GN per spike was highest in treatments N_{160} and N_{240}, while TKW dropped significantly in the N_{160} and N_{240} treatments (Sugár et al., 2016).
In response to N fertilization, the growth rates (AGR, RGR, CGR) rose up to the N_{160} level, in harmony with the increase in dry matter and yield. NAR and LAR made different contributions to RGR depending on the genotype and the environmental conditions. Breaking down the growth rates into their components demonstrated that at the individual plant level, NAR and LAR had similar effects; whereas at plant stand level, the effect of LAI was decisive and that of NAR only secondary. In studies on the interspecific variation in relative growth rate, Poorter (1990) concluded that in general, 80–90% of an inher-

ently higher RGR was explained by higher LAR and only 10–20% by higher NAR.

Higher values of dry matter productivity due to better N supplies have been associated with higher values of LAI and LAD. Better nitrogen supplies generally result in greater leaf area growth which, in turn, leads to better light absorption and further carbon fixation. Thorne (1973) mentioned the great dependence of grain yield on leaf area index. Positive associations between green leaf area duration and grain yield have been observed in a range of cereals, including wheat (Evans et al., 1975), maize (Tollenaar and Daynard, 1978; Wolfe et al., 1988), oats (Helsel and Frey, 1978) and sorghum (Borrell et al., 2000).

Flag-leaf photosynthesis in wheat contributes about 30–50% of the assimilates for grain filling (Shearman et al., 2005), and the onset and rate of senescence are clearly important factors for determining resistance to abiotic stress. Hansen et al. (2005) studied 20 spring wheat cultivars and found that modern cultivars tended to have higher yields and later senescing flag leaves. Blake et al. (2007) also reported that prolonged photosynthesis in the flag-leaf increased yield in a population of recombinant inbred lines. In the present experiments, the value of LAD_{flag_leaf}, like that of the growth rates, gave a good reflection of the effects of N fertilization, cultivar and year. LAD_{LAI} and the cumulative value of BMD, like the other parameters, clearly demonstrated the influence of mineral fertilization. The linear relationship between LAD and BMD pointed to the importance of size and duration of the leaf area (the major photosynthesizing organ of the plant) in biomass formation. The linear relationships between leaf area growth rate and LAI_{max}, and between AGR and BMD indicated the importance of growth rates in the formation of leaf area and biomass.

The positive effect of N fertilization up to N_{160} was demonstrated most consistently by the dynamics and mean (maximum and cumulative) values of growth parameters, in agreement with the yield response data (Sugár et al., 2016). Similarly, in spring wheat experiments performed by Farmaha et al. (2015), increasing N fertilization from low to medium generally increased the grain yield and above-ground dry matter, but no significant increases were observed when N fertilization increased from medium to high. In the present work, the growth parameters of wheat cultivars exhibited little difference, though in most cases, those of Mv Palotás and Mv Verbunkos had more similar values and were usually somewhat higher than those of Mv Toborzó. As regards the year effect, the growth rates and growth parameters were generally lowest in 2007, the year with unfavorable rainfall supplies, and higher in the favorable years of 2008 and 2009.

Multiple regression analysis demonstrated the significant effects of growth rates (AGR, RGR, ALGR, CGR), size and duration of leaf area (LAI_{max}, LAD_{flag_leaf}, LAD_{LAI}), the size and distribution of biomass (BMD, LAR, HI) and the yield components on the size of the yield (per plant and per hectare). In agreement with the present results, Heggenstaller et al. (2009) showed that across systems (sole-crop and double-crop corn), variation in yield was positively related to maximum crop growth rate, maximum leaf area index and leaf area duration, but was not associated with maximum or seasonal net assimilation rate. It can be concluded from the present experiments that if higher temperature during the vegetative growth stage is accompanied by rainfall deficit, substantial yield losses can be expected despite the increase in vegetative growth. This is particularly important in the light of climate change (Hatfield et al., 2011; Kimball et al., 2016). The results showed that the value of many agricultural experiments could be greatly enhanced if data were available on plant growth and the partitioning of this growth.

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