Agronomy Research **14**(4), 1467–1485, 2016

Canopy traits in rye, triticale and wheat under varying N supply

K. Sieling*, U. Böttcher and H. Kage

Christian-Albrechts-University Kiel, Institute of Crop Science and Plant Breeding, Hermann-Rodewald-Strasse 9, DE-24118 Kiel, Germany
*Correspondence: sieling@pflanzenbau.uni-kiel.de

Abstract. Information on growth of rye (*Secale cereale* L.) and triticale (*X Triticosecale* Wittmark) are scarce. In 2007/08 and 2008/09, winter rye, winter triticale and winter wheat (*Triticum aestivum* L.) were simultaneously grown in combination with 4 nitrogen (N) treatments (0/0, 40/40, 80/80 and 120/120 kg N ha^{-1}) at the Hohenschulen Experimental Farm in northern Germany allowing for a comparison of the resource capture and biomass accumulation during spring growth. Several canopy traits (e.g. green area index (GAI), specific leaf area (SLA), light use efficiency (LUE)) as well as N dilution curves of the whole shoots, leaves and stems were determined.

Triticale achieved highest GAI in throughout both growth periods. An extended growth period of wheat partly compensated for a lower GAI, thus the differences in the amount of intercepted photosynthetically active radiation (Q) between the crops remained small. In general, rye leaves were thinner (higher SLA) compared to wheat and triticale showing similar SLA, except at ear emergence in both years. Total above-ground dry matter accumulation at dough ripening was lowest in wheat mainly due to a lower LUE which in turn may be the result of a lower specific leaf area. The N dilution curves revealed a clear reduction of stem N concentration with increasing dry matter accumulation, whereas leaf N concentration only slightly decreased presumably in order to maintain optimal photosynthesis. The presented results enhance the understanding of the growth of rye and triticale and allow improving crop growth modeling of both crops.

Key words: Specific leaf area; light use efficiency; green area index; N dilution curve.

INTRODUCTION

In the European Union, wheat (*Triticum aestivum* L.) was grown on 26.1 Mio. ha compared to rye (*Secale cereale* L.) with 2.4 Mio. ha and triticale (*X Triticosecale* Wittmark) with 2.7 Mio. ha on average of 2012–2014. With 5.3 t ha^{-1} wheat clearly outyielded rye (3.67 t ha^{-1}) and triticale (4.21 t ha^{-1}) (FAO 2016). However, under less favorable growing conditions e.g. limited water availability in a Mediterranean environment, triticale may achieve higher grain yields than wheat, due to a longer spike formation phase or a greater early vigor leading to more grains per unit area (López-Castañeda & Richards 1994a; 1994b). In the last decade, the use of whole plant silage of winter rye and winter triticale as energy crops for biogas production increased (Amon et al., 2007; Gissén et al., 2014; Mayer et al., 2014).

In general, the key factor for plant growth is the absorption of the incoming radiation being a function of the total leaf area resp. the total green area. The ratio of leaf area to leaf mass i.e. the specific leaf area (SLA) – or its inverse, leaf mass per unit area

(LMA) (g m^{-2}) – thereby is often used in growth analysis because it is positively related to potential relative growth rate across species (Gunn et al., 1999; Poorter et al., 2009; Pérez-Harguindeguy et al., 2013). SLA tends to scale negatively with area-based light-saturated photosynthetic rate, but positively and linearly with mass-based light-saturated photosynthetic rate as well as with leaf nitrogen (N) concentration (Wright et al., 2005; Shipley, 2006; Lemaire et al. 2008; Poorter et al., 2009; Pérez-Harguindeguy et al., 2013).

Shortly after emergence, canopy SLA of winter wheat showed an initial increase, thus young plants producing large, but thin leaves to intercept as much irradiation as possible, followed by a levelling off (Hotsonyame & Hundt, 1998; van Delden et al., 2000). A meta-analysis on the causes and consequences of variation in leaf mass per area (=1/SLA) is presented by Poorter et al. (2009). According to Ratjen & Kage (2013) both drought and N shortage lead to a reduced SLA in wheat mainly due to reduced mutual shading under stress situation.

While for wheat a lot of information on canopy traits is available (e.g. Rawson et al., 1987; Hotsonyame & Hundt, 1998; Poorter et al., 2009; Qin et al, 2013), respective data for rye and triticale are scarce. Comparing spring rye, spring triticale and spring wheat, Sheng & Hunt (1991) found significant differences in total plant dry weight with rye showing consistently the highest total plant dry weight at several sampling dates during the growth period. Giunta et al. (2009) attributed the higher biomass accumulation of spring triticale to the higher amount of intercepted photosynthetically active radiation (PAR) compared to durum wheat under the Mediterranean conditions of Sardinia (Italy), mainly due to earlier build-up of the leaf area (López-Castañeda & Richards, 1994b). However, Estrada-Campuzano et al. (2012) and Motzo et al. (2013) observed a higher radiation use efficiency of triticale. Based on pot experiments Amanullah (2015) and Amanullah & Stewart (2015) reported that rye developed a higher leaf area per plant and a higher SLA than wheat at 30, 60 and 90 days after emergence.

Beside the radiation interception, N content of the plant plays an important role for the carbon assimilation. Justes et al. (1994) published a critical N dilution curve for winter wheat crops relating shoot N concentration to the corresponding above-ground dry matter based on a power function. However, some authors argued that leaf N concentration and also its vertical gradient within the plant have to be taken into account (e.g. Grindley, 1997; Moreau et al., 2012). Unfortunately, to our knowledge, N dilution curves do exist neither for rye nor for triticale.

Limited experimental data compare rye, triticale and wheat simultaneously in the same (field) experiment allowing to investigate their growth under similar conditions. Therefore, based on a 2 year field trial with different N treatments (0–240 kg N ha^{-1}), the objectives of this study were (i) to identify canopy traits (e.g. green area index (GAI), SLA) affecting dry matter (DM) accumulation of rye, triticale and wheat and (ii) to analyze differences in the crop behavior. It is hypothesized that the importance of the canopy traits differs with the crops.

MATERIALS AND METHODS

Site and soils

The field trial was carried out at the Hohenschulen Experimental Farm (northern Germany, 10.0° E, 54.3° N, 30 m a.s.l.) on a pseudogleyic sandy loam (Luvisol: 170 g kg^{-1} clay, pH 6.7, 13 g kg^{-1} Corg, 1.1 g kg^{-1} Norg in 0–30 cm). The climate of northern Germany can be described as humid temperate with a long-term mean annual temperature of about 8.4 °C. Total rainfall averages 800 mm annually, of this ca. 400 mm occur during the main growing season (April–September) (Table 1).

Table 1. Monthly rainfall (mm), mean air temperature (°C), and mean global radiation at Hohenschulen, Germany

	Total rainfall (mm)			Mean air temperature (°C)			Mean global radiation (MJ m^{-2} d^{-1})		
	2007/ 2008	2008/ 2009	long-term average	2007/ 2008	2008/ 2009	long-term average	2007/ 2008	2008/ 2009	long-term average
September	71	64	61	13.1	13.2	14.2	9.79	9.45	10.38
October	25	124	75	8.9	9.5	9.8	5.76	5.17	5.76
November	38	45	58	5.0	6.4	4.9	2.85	1.88	2.34
December	77	20	62	3.3	2.8	1.6	1.00	1.19	1.38
January	64	16	48	4.4	-0.1	1.2	1.37	1.97	1.82
February	40	25	50	4.7	0.5	2.0	3.90	3.52	3.81
March	62	45	44	4.3	4.1	3.4	8.06	6.66	8.54
April	41	7	44	7.6	10.4	8.0	14.11	17.65	14.79
May	19	52	62	13.7	11.7	11.9	23.18	20.36	17.96
June	42	104	69	15.7	13.2	14.8	21.58	19.89	19.72
July	69	101	100	17.6	17.3	16.9	18.70	18.16	18.77
August	131	69	59	16.7	17.8	17.9	12.15	16.04	14.41

Field trials

In 2007/08 and 2008/09, winter rye (cvs. Amato; Balistic in 2007/08 and Palazzo in 2008/09, all hybrids), winter triticale (cvs. Inpetto; Korpus) and winter wheat (cvs. Mulan; Winnetou) were grown in a field trial. Preceding crops were field beans in 2007 and oilseed rape in 2007/08. Each variety was combined with 4 N treatments: N1 – 0/0, N2 – 40/40, N3 – 80/80, N4 – 120/120 kg N ha^{-1}). The experimental design was a completely randomized block design with four replicates. The whole plot size was 12 m x 3 m, using a row width of 0.12 m. Sowing density was 240 and 200 kernels m^{-2} for rye, 270 and 230 kernels m^{-2} for triticale and 300 and 250 kernels m^{-2} for wheat in 2007/08 and 2008/009, respectively. Nitrogen (calcium ammonium nitrate, 27% N) was applied in split-dressings at the beginning of spring growth (growth stage 25 (GS according to Zadoks et al., 1974) and at stem elongation (GS 30/31) (details see Table 2). During the second N application in 2009, the attribution of the N treatments to the respective plots was not correct, resulting in N levels differing from the aimed ones.

The straw of all crops remained on the plots. In general, the trials were ploughed within one day before sowing. Crop management not involving the treatments (e. g. P and K supply, soil tillage, sowing dates, pesticide application) were applied according to local recommendations to achieve optimal yield.

Table 2. Dates of crop management and plant sampling

	2007/08			2008/09		
	Rye	Triticale	Wheat	Rye	Triticale	Wheat
Crop management						
Sowing	08 Oct	08 Oct	08 Oct	18 Sep	18 Sep	18 Sep
1st N application	20 Feb	20 Feb	20 Feb	18 Mar	18 Mar	18 Mar
2nd N application	08 Apr	08 Apr	08 Apr	16 Apr	16 Apr	16 Apr
Harvest	01 Aug	01 Aug	01 Aug	14 Aug	14 Aug	14 Aug
Plant sampling						
End of autumn growth	13 Nov	13 Nov	13 Nov	01 Dec	01 Dec	01 Dec
Start of spring growth	20 Feb	20 Feb	20 Feb	12 Mar	12 Mar	12 Mar
GS 30/31#	14 Apr	14 Apr	14 Apr	14 Apr	16 Apr	16 Apr
GS 55	20 May	28 May	02 Jun	04 May	18 May	25 May
GS 75	23 Jun	23 Jun	30 Jun	22 Jun	24 Jun	30 Jun

GS 30/31 – stem elongation; GS 55 ear emergence; GS 75 milk ripe.

Measurements, calculations, and statistical analysis

Starting in Mid-April, green area index (GAI) and the mean leaf angle (MTA) of all plots was determined non-destructively each week using a LAI 2000 (LiCor Inc., NE, USA). In addition, the extinction coefficient k was derived from the LAI2000 readings GAI and DIFN (diffuse non-interceptance):

$$k = -\ln(DIFN)/GAI \tag{1}$$

At the end of autumn growth, beginning of spring growth, stem elongation (GS 30/31), ear emergence (GS 55) and milk ripe (GS 75), plants from 2 x 50 cm drilling row (at GS 75: 5 x 50 cm) per plot were harvested (sampling dates see Table 2). In the N1, N2 and N4 treatment, above-ground dry matter (DM) was determined. Plants of the N3 treatment (80/80) were subdivided into a leaf fraction (leaf blades = leaf DM), a stem fraction (leaf sheaths and stem = stem DM), and an ear fraction (= ear DM; GS 55 and GS 75 only). From a sub-sample of the leaf fraction, leaf area (LAI) was determined using a LiCor 3100 leaf area meter (LiCor Inc., NE, USA). After drying and weighing, the fractions were ground and analyzed separately for the N concentration by using near infrared spectroscopy (NIRS). Total above-ground DM and total nitrogen content were calculated by adding the fractions, and, if appropriate, standardized to m^2. At maturity, to minimize border effects, a core of 6 m x 1.75 m of each plot was combine harvested and seed yield was corrected to t ha^{-1} at 86% DM based on the moisture content of a grain subsample.

The amount of photosynthetically active radiation intercepted by the crops (Q) was calculated on a daily basis from GAI and k which have been linearly interpolated between the dates of GAI measurements:

$$Q = PAR\ (1-e^{(-kGAI)}) \tag{2}$$

where PAR denotes the amount of incoming photosynthetically active radiation (measured by a weather station nearby), GAI the green area index and k the extinction coefficient derived from Eq. 1.

The light use efficiency (LUE) was estimated for each plot separately by relating the DM accumulation between the GS 30/31 and GS 75 to the corresponding cumulated radiation intercepted by the canopy (Q).

The fractionation of the plants from the N3 treatment allowed for deriving additional parameters. However, the last sampling date (GS 75) was excluded due to progressive leaf senescence. Separately for each plot, specific leaf area (SLA), leaf area ratio (LAR) and leaf mass ratio (LMR) were calculated as following

$$SLA = LAI/DM_{leaf} \quad (3)$$

$$LAR = LAI/DM_{shoot} \quad (4)$$

$$LMR = DM_{leaf}/DM_{shoot} \quad (5)$$

Please note that the destructively measured leaf area (LAI) was used.

This paper mainly focusses on the crop effects; therefore, the effects of the varieties are not presented and were considered as replications. All statistics were done for each year separately using the SAS procedures PROC MIXED with the block effect as random factor. Due to the inaccurate N fertilization in 2009, N fertilization has to be characterized as quantitative factor (as total fertilizer N amount) requiring a covariance analysis (parameters see Table 3). N dilution curves were fitted by PROC NLIN separately for each crop. Function parameters were compared by a modified *t*-test based on Zar (2009) (parameters see Table 5).

RESULTS

Dry matter at GS 75 and grain yield at maturity

In both years (2008, 2009 and all crops, N supply significantly ($P < 0.001$) increased above-ground dry matter (DM) at the milk ripe stage (growth stage (GS) 75) (Fig. 1); however, no effects occurred if N fertilization equaled or exceeded 160 kg N ha^{-1}. In 2008, winter rye outyielded winter triticale and winter wheat, but the differences were not significant ($P > 0.20$), whereas in 2009, rye and triticale DM were significantly higher than that of wheat, especially at lower N supply, but similar for all crops in the 240 kg N ha^{-1} treatment.

Grain yield at maturity ranged in the order rye > triticale > wheat at low N fertilization, while at N amounts higher than 200 kg N ha^{-1} triticale outyielded rye and wheat (Fig. 2). Wheat achieved in both years the lowest grain yields.

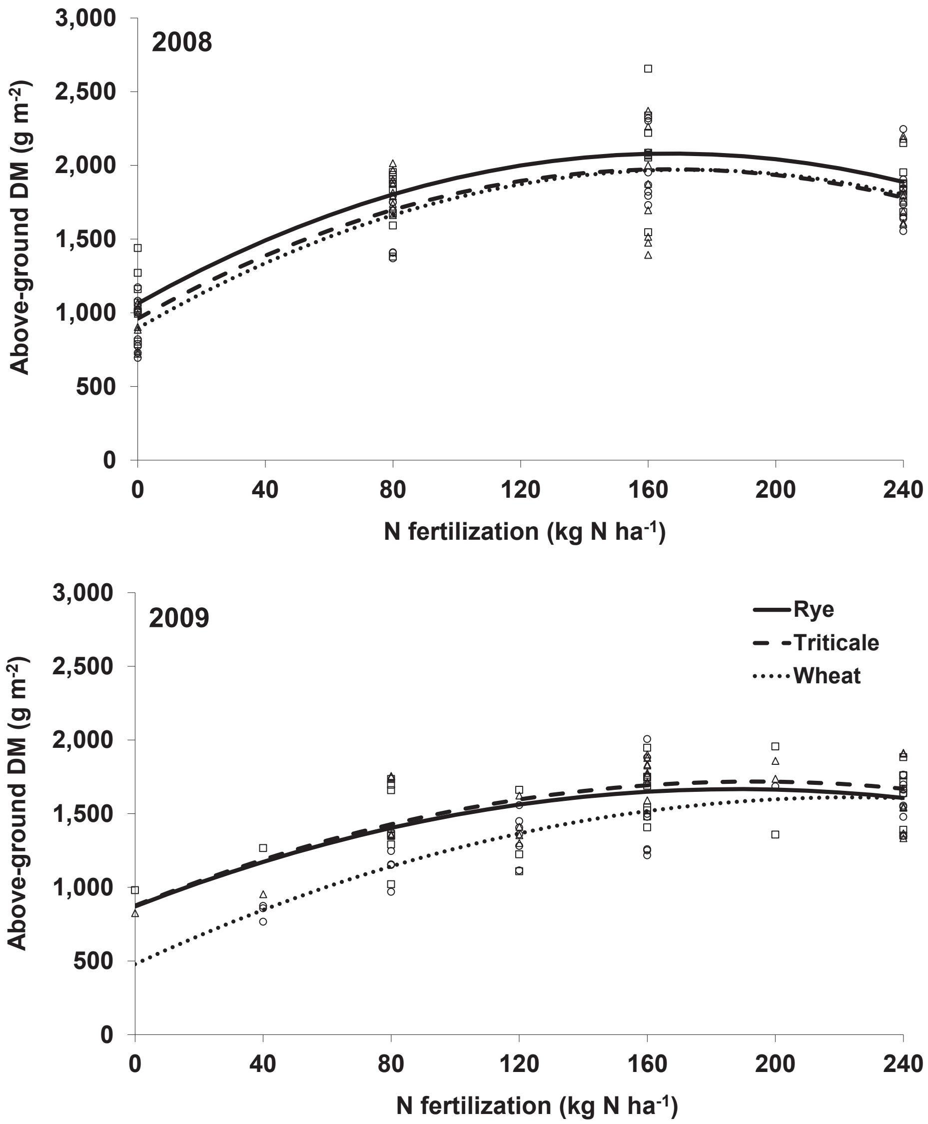

Figure 1. Effect of N fertilization on above-ground dry matter (DM; g m^{-2}) at GS 75 of rye (□), triticale (Δ) and wheat (○) in 2008 and 2009 (function parameters see Table 3).

Table 3. Parameters of the N response curves of rye, triticale and wheat in 2008 and 2009 ($Y = a + b*N + c*N^2$)

Crop	2008 n	a	b	c	R^2	2009 n	a	b	c	R^2
Above-ground dry matter at GS 75# (g m^{-2}) (Fig. 1)										
Rye		1,062.8	12.16				869.9	8.47		
Triticale	96	960.2	12.15	-0.03634	0.76***	87	875.8	8.70	-0.02249	0.54***
Wheat		895.2	12.50				478.9	10.09		
Grain yield (t ha^{-1}) (Fig. 2)										
Rye		7.32	0.0519				6.45	0.0455		
Triticale	91	6.48	0.0585	-0.00014	0.89***	87	5.12	0.0526	-0.00011	0.82***
Wheat		5.85	0.0553				4.10	0.0536		
Amount of intercepted photosynthetically active radiation between GS 30/31 and GS 75 (MJ m^{-2}) (Fig. 5)										
Rye		505.2	2.274				494.0	0.817		
Triticale	96	531.7	2.159	-0.00588	0.88***	96	519.7	0.742	-0.00082	0.57***
Wheat		505.9	2.441				466.4	1.043		
Light use efficiency between GS 30/31 and GS 75 (g MJ^{-1}) (Fig. 6)										
Rye		1.840					1.515			
Triticale	96	1.692	0.00998	-0.00003	0.43***	86	1.523	0.01102	-0.00003	0.34***
Wheat		1.676					1.248			

GS 30/31 – stem elongation; GS 55 ear emergence; GS 75 milk ripe.

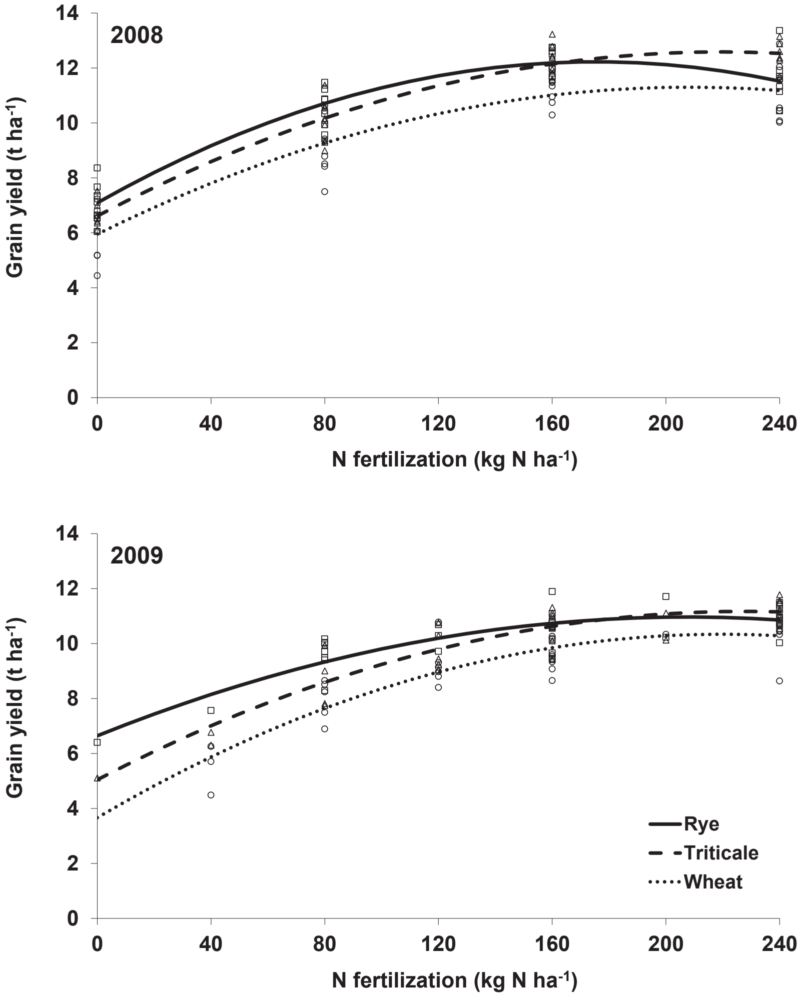

Figure 2. Effect of N fertilization on grain yield (t ha^{-1}) at maturity of rye (□), triticale (Δ) and wheat (○) in 2008 and 2009 (function parameters see Table 3).

Green area index, extinction coefficient, and mean leaf angle

In general, all crops achieved a lower green area index (GAI) in 2009 than in 2008 (Figs 3a, 4a). The course of GAI of the three crops during both growth periods revealed highest GAI in rye in April and May, but from Mid-May onwards triticale clearly outyielded rye and wheat, especially in 2008. Wheat GAI was lower or similar (end of May until Mid-July 2008) to that of rye. Even maximum GAI did not reach the level of rye or triticale. In general, N fertilization increased GAI. In 2008, the difference between the crops became larger with increasing N supply, while in 2009 GAI increase was similarly in all crops (not shown).

The extinction coefficient k varied within the growth period (Figs. 3b, 4b). While no consistent differences between rye and triticale occurred, k of wheat was lowest at most of the sampling dates. In contrast, leaves of the wheat plants showed the highest leaf angle (Figs 3c, 4c).

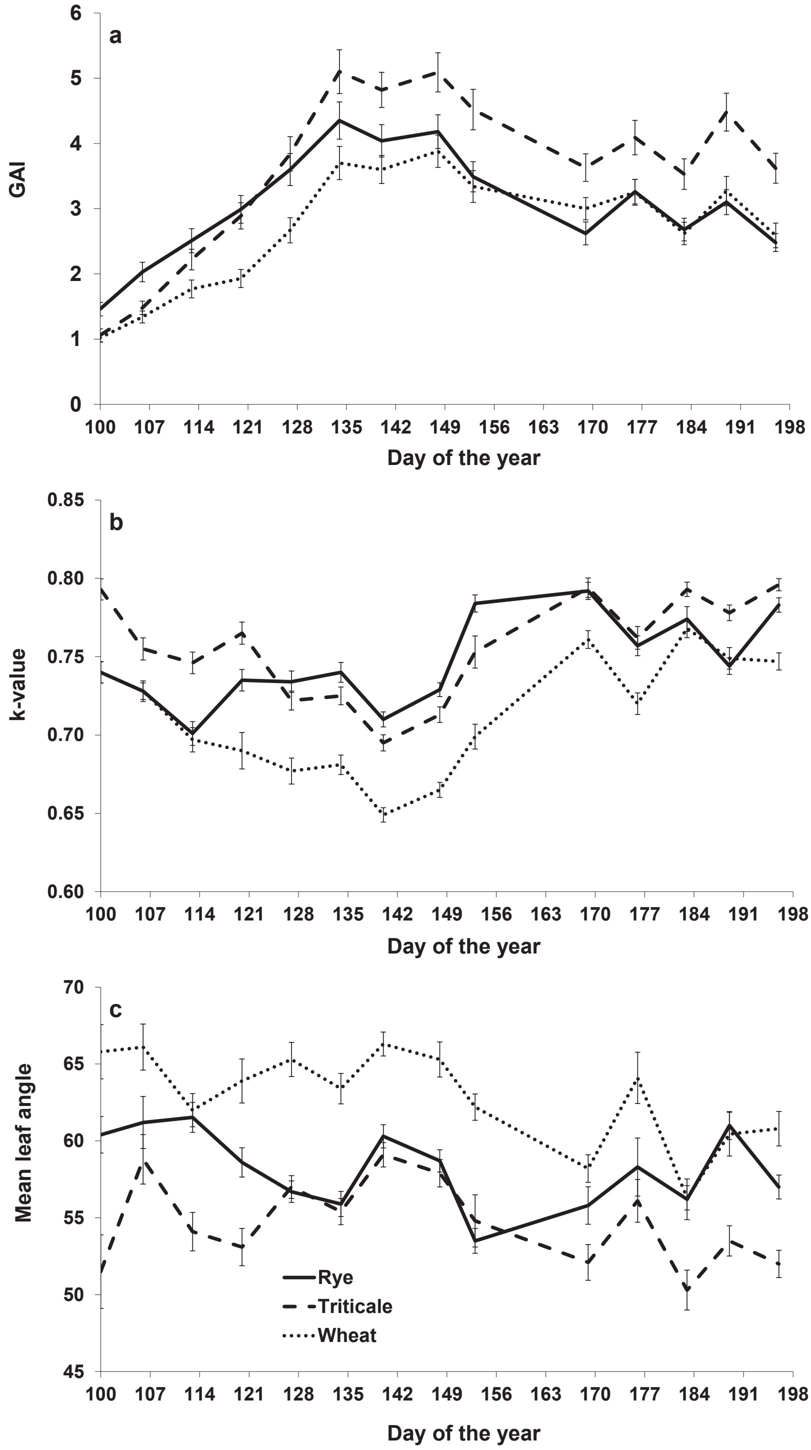

Figure 3. Course of green area index (GAI) (a), extinction coefficient k (b) and mean leaf angle (c) of rye, triticale and wheat in 2008 (N3 treatment).

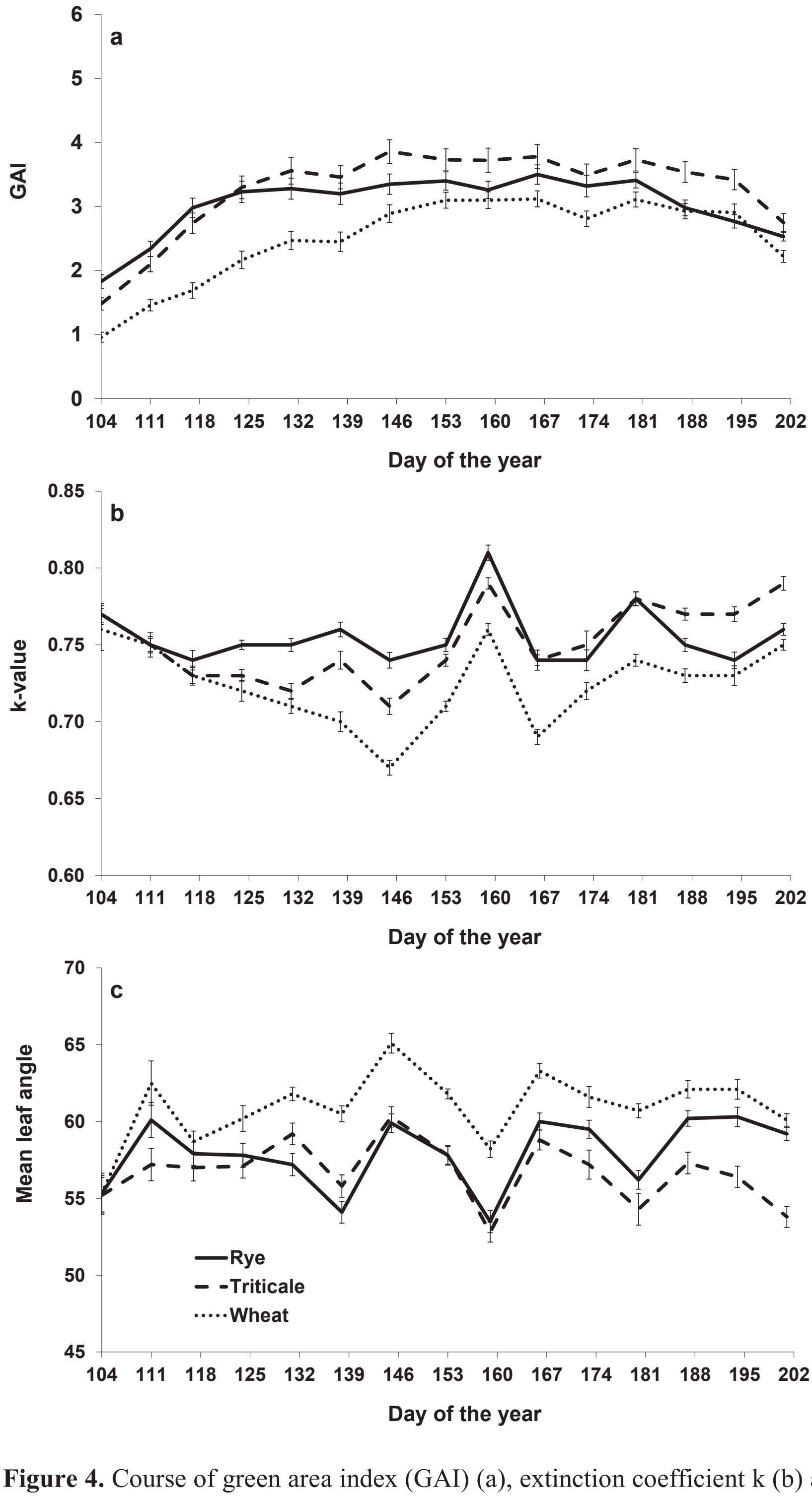

Figure 4. Course of green area index (GAI) (a), extinction coefficient k (b) and mean leaf angle (c) of rye, triticale and wheat in 2009 (N3 treatment).

Photosynthetically active radiation interception and light use efficiency

In 2008, the amount of photosynthetically active radiation (PAR) intercepted by the crops (Q) was higher than 2009 and its increase due to the N fertilization became smaller in all crops, whereas it was linear in 2009 (Fig. 5). In both years, triticale intercepted more PAR at low N levels than rye and wheat. In the 240 kg N ha^{-1} treatment, wheat outyielded rye and triticale which intercepted similar Q amounts during this period. The larger variation in 2009 was mainly due to canopy heterogeneities.

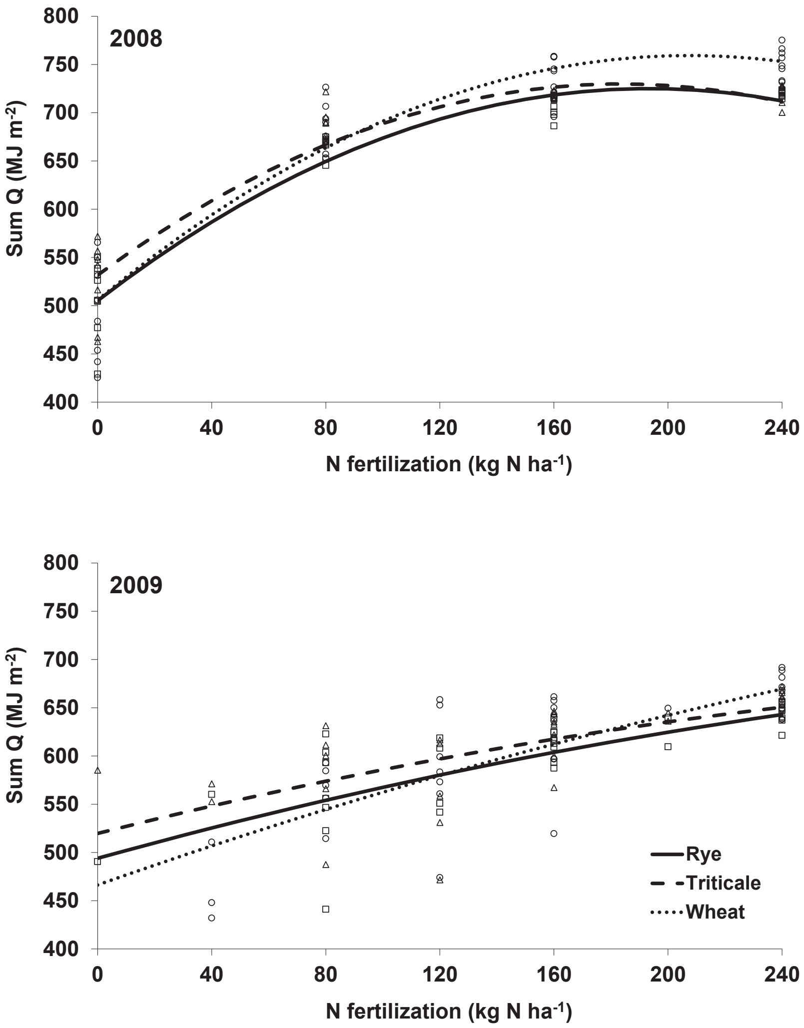

Figure 5. Effect of N fertilization on the amount of photosynthetically active radiation intercepted by the crops (Sum Q; MJ m^{-2}) between GS 30/31 and GS 75 of rye (□), triticale (Δ) and wheat (○) in 2008 and 2009 (function parameters see Table 3).

In order to estimate the light use efficiency (LUE), Q was estimated for the period between GS 30/31 and GS 75 and related to the corresponding DM increase. It should be noted that the duration of this period varied with the year and the crop. In both years, LUE increased with increasing N supply; however, only the plots receiving 0 or 40 kg N ha^{-1} significantly differed from the other N treatments (Fig. 6). While in 2008 no differences between the crops were observed, LUE of wheat was significantly lower compared to rye and triticale in 2009. In both years, N fertilization similarly affected LUE of all crops indicating no N x crop interaction.

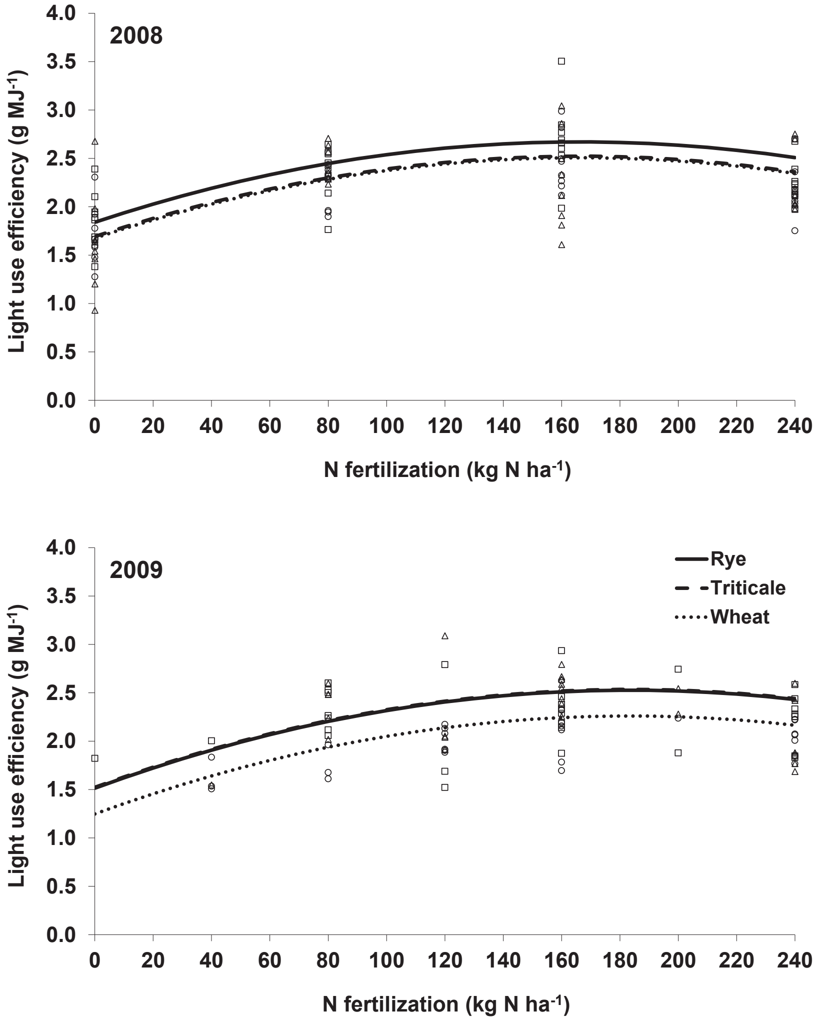

Figure 6. Effect of N fertilization on light use efficiency (g MJ^{-1}) of rye (□), triticale (Δ) and wheat (○) in 2008 and 2009 (function parameters see Table 3).

Leaf area ratio, specific leaf area and leaf mass ratio

The following presented parameters were derived from the plants being fractionated from the N3 treatment only. Therefore, no N effects can be analyzed.

At most of the sampling dates, rye achieved highest leaf area in relation to the total above-ground DM (leaf area ratio, LAR) except at ear emergence (Table 4). In contrast, wheat showed lowest LAR; however, without being significant from triticale.

Table 4. Selected canopy traits (specific leaf area, leaf area ratio, leaf mass ratio) of rye, triticale and wheat at different growth stages in 2008 and 2009

	2008			2009		
	Rye	Triticale	Wheat	Rye	Triticale	Wheat
Specific leaf area (SLA) (cm^2 g^{-1})						
End of autumn growth	156.7[a]	133.2[b]	142.9[ab]	168.9[a]	137.2[b]	149.0[ab]
Beginning of spring growth	222.9[a]	194.6[b]	192.3[b]	184.2[ns]	169.9[ns]	170.1[ns]
GS 30/31[#]	205.3[a]	146.0[b]	140.8[b]	220.0[a]	153.5[b]	153.2[b]
GS 55	227.5[a]	219.5[a]	171.6[b]	235.3[a]	199.6[b]	171.0[c]
Leaf area ratio (LAR) (m^2 kg^{-1})						
End of autumn growth	11.71[a]	10.15[b]	10.07[b]	10.26[ns]	8.58[ns]	8.43[ns]
Beginning of spring growth	14.71[a]	13.43[ab]	12.86[b]	10.53[ns]	10.81[ns]	10.16[ns]
GS 30/31	10.00[a]	8.99[b]	8.26[b]	10.87[a]	8.68[b]	7.92[b]
GS 55	3.33[b]	4.55[a]	2.68[c]	4.66[a]	4.87[a]	3.67[b]
Leaf mass ratio (LMR) (g g^{-1})						
End of autumn growth	0.728[ab]	0.743[a]	0.680[b]	0.608[ab]	0.625[a]	0.563[b]
Beginning of spring growth	0.659[ns]	0.688[ns]	0.665[ns]	0.572[b]	0.636[a]	0.596[b]
GS 30/31	0.482[c]	0.616[a]	0.582[b]	0.492[b]	0.567[a]	0.516[b]
GS 55	0.153[b]	0.217[a]	0.170[b]	0.199[b]	0.245[a]	0.216[b]

‡Different letters indicate significant differences at $P = 0.05$ between the crops within a year and a row;
GS 30/31 – stem elongation; GS 55 ear emergence; GS 75 milk ripe.

In 2008 and 2009, rye achieved the highest specific leaf area (SLA = leaf area per unit leaf DM) indicating thinner leaves compared to the other crops (Table 4). Triticale and wheat had similar SLA except at ear emergence (GS 55) when SLA of triticale markedly increased especially in 2008. Relating SLA to the destructively determined leaf area revealed a positive correlation of both parameters (Fig. 7). SLA increase was similar for all crops ($P > 0.10$), but at different levels.

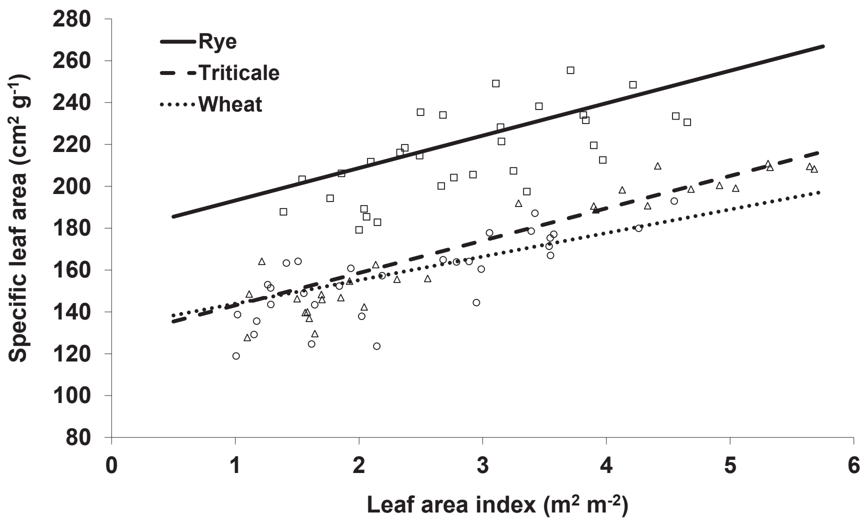

Figure 7. Relation between leaf area index (LAI) and specific leaf area (SLA = leaf area/leaf DM) of rye (□; SLA = 177.8 + 15.49*LAI), triticale (Δ; SLA = 127.7 + 15.45*LAI) and wheat (○; SLA = 132.66 + 11.25*LAI) (2008 and 2009).

Leaf mass ratio (LMR) increased during winter, especially in 2008, and then decreased (Table 4). Compared to rye and wheat, triticale produced more leaf DM in relation to the total shoot DM at all sampling dates in in both years, whereas the ratio of the LMR values for rye and wheat changed during the vegetation period with higher LMR values for wheat compared to rye during the later growth stages (Table 4).

N dilution curves

The N dilution curves of the shoot and the different parts stem, leaves and ear of all crops reveal a negative correlation between the N concentration and the corresponding DM from the N3 treatment (Fig. 8, curve parameters see Table 5); however, the decrease was more pronounced in the stem fraction and the total shoot DM, since shoot DM mainly consisted of stem DM, especially at later growth stages. Leaf N concentration only varied between 4 and 6%, whereas ear N concentration only slightly decreased. Due to advancing senescence, data from GS 75 was excluded from the estimation of the leaf curves, whereas the ear curves only based on data from GS 55 and GS 75. Rye had higher N concentrations in all plant parts, but the difference in shoot and stem N concentrations between the crops decreased during the growth period. The scattered data around 2 t ha^{-1} shoot DM resp. 1 t ha^{-1} stem DM mainly correspond to plants sampled at GS 30/31 in 2008.

Table 5. Parameters of the N dilution curves for the shoot (%N = 1/(a+b*DM), stem (%N = 1/(a+b*DM), leaf (%N = 1/(a+b*DM) and ear (%N = a+b*DM) fraction of rye, triticale and wheat (Figure 8; 2008 and 2009)

Crop	n	a	b	R^2
Shoot (End of autumn growth–GS 75[#])				
Rye	240	0.1705[c]	0.0320[ns]	0.95***
Triticale	240	0.1894[a]	0.0330[ns]	0.96***
Wheat	240	0.1826[b]	0.0366[ns]	0.94***
Stem (End of autumn growth–GS 75)				
Rye	80	0.1849[c]	0.0812[ns]	0.95***
Triticale	80	0.2141[a]	0.0812[ns]	0.95***
Wheat	80	0.2042[b]	0.0995[ns]	0.93***
Leaf (End of autumn growth–GS 55)				
Rye	64	0.1668[c]	0.0396[ns]	0.67***
Triticale	64	0.1831[a]	0.0398[ns]	0.81***
Wheat	64	0.1740[b]	0.0478[ns]	0.70***
Ear (GS 55–GS 75)				
Rye		2.26[a]		
Triticale	72	2.05[b]	-0.067	0.50***
Wheat		2.10[b]		

‡Different letters indicate significant differences at $P = 0.05$ between the N treatments according to Zar (2009); ns – not significant;
GS 30/31 – stem elongation; GS 55 ear emergence; GS 75 milk ripe.

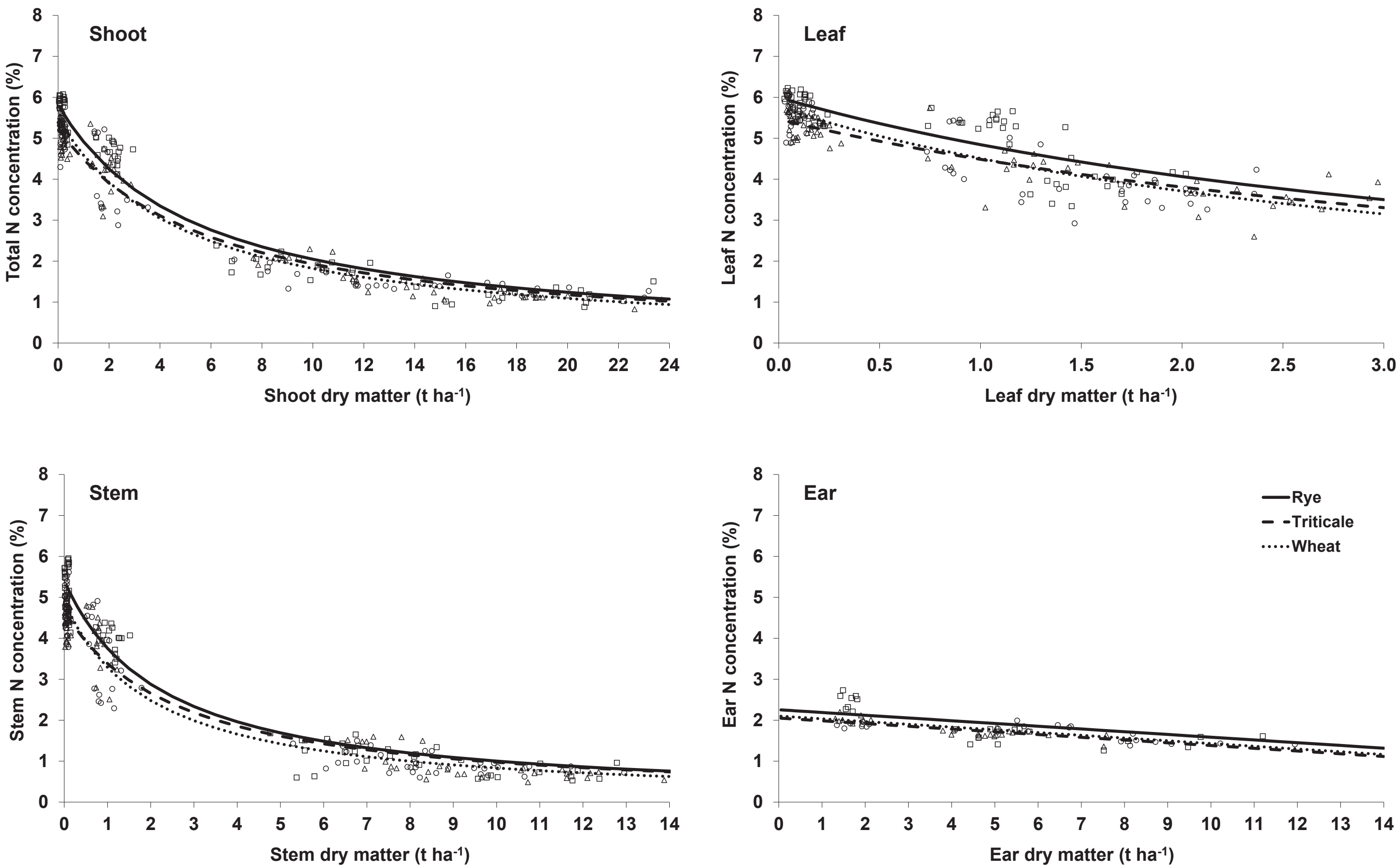

Figure 8. N dilution curves for shoot (end of autumn growth–GS 75), stem (end of autumn growth–GS 75), leaves (end of autumn growth–GS 55) and ear (GS55–GS 75) of rye (□), triticale (Δ) and wheat (○) (only N3 treatment; 2008 and 2009; function parameters see Table 5).

DISCUSSION

Several papers compared the yield formation of rye, triticale and (durum) wheat (e.g. López-Castañeda & Richards, 1994a; Motzo et al., 2015); however, no concurrent growth analysis of the three cereals exists. The presented field trial was designed to compare rye, triticale and wheat for their suitability feeding biogas plants to produce biomethane. For this purpose, a harvest as whole-plant silage during milk and dough ripening was aimed for. Since grain N concentration was of no importance, total N supply was split into 2 applications at the beginning of spring growth and at stem elongation, thus skipping the 3rd N application normally given at ear emergence. Therefore, the crop and N effect on final grain yield should not be overestimated. Nevertheless, the simultaneous cropping of rye, triticale and wheat allows for a comparison of the resource capture and biomass accumulation during spring growth of all three crops. The preceding crops differed in both years (faba beans vs. oilseed rape) probably affecting soil N dynamic; however, several other trials at the experimental site suggested similar preceding crop effects of legumes and oilseed rape on a subsequent winter wheat crop (e.g. Sieling & Christen, 2015).

It was somewhat surprising that DM yield at GS 75 and grain yield at maturity (Fig. 2) of wheat was lower than those of rye and triticale. The course of GAI revealed that wheat developed less green area for PAR interception and showed a lower extinction coefficient at most of the sampling dates throughout the growth period compared rye and triticale (Figs 3a, 3b, 4a, 4b). This can partly explained by the more erectophile leaf angle of wheat (Fig. 3c & 4c). In addition, even the maximum GAI of wheat remained below that of the other tested cereals. On the other hand, triticale produced highest GAI as revealed by Giunta et al. (2009). Although N supply clearly affects leaf formation (Sieling et al. 2016), GAI course is presented on average of the N treatments, since the paper mainly focusses on crop effects and no significant crop by N interactions were observed.

The lower extinction coefficient of wheat compared to triticale is in contrast to findings of Estrada-Campuzano et al. (2012) who observed wheat exhibiting a higher extinction coefficient than triticale. Since k varied throughout the growth period, a stage-specific k was estimated by linear interpolation between the respective sampling dates when calculating the amount of intercepted PAR. Therefore, using a constant k seems to be debatable. A more detailed analysis revealed only small N effects on the extinction coefficient which was in agreement with Estrada-Campuzano et al. (2012). Therefore, a similar k for all N treatments was used. Variation between measurement dates may be due to canopy heterogeneity as well as different weather conditions (cloudy vs. sunny).

N fertilization increased the amount of intercepted PAR (Q) mainly due to an increased GAI (data not shown). In addition, differences between the crops occurred with rye showing almost lowest amounts of Q, while triticale and wheat intercepted most PAR with low and high N supply, respectively. Giunta et al. (2009) reported of higher Q amounts for triticale compared to durum wheat at, however, one N level. Combining Q with the corresponding DM increase allows for the estimation the effective light use efficiency (LUE) (Fig. 6), thus possibly including biotic or abiotic stress (e.g. drought stress). LUE was reduced in the unfertilized plots in all crops being in agreement with Muurinen & Peltonen-Sainio (2006) and Sieling et al. (2016). Rye used Q more efficiently for above-ground DM accumulation than wheat in both years, while triticale behavior was similar to that of wheat in 2008. Sanchez et al. (2015) also reported of higher LUE for rye than for wheat. Compared triticale with (durum) wheat, Motzo et al. (2013) observed higher LUE for triticale due to a higher stomatal conductance during vegetative growth, whereas Winzeler et al. (1989) attributed the lower growth rate to a substantially lower leaf respiration for triticale and rye than for wheat, the difference being more pronounced at the cooler temperatures.

Specific leaf area (SLA) often is a key factor in growth analysis because SLA positively correlates with relative growth rate at early growth stages. In general, rye leaves were thinner (higher SLA) compared to wheat and triticale showing similar SLA, except at ear emergence in both years (Table 4). Winzeler et al. (1989) determined the specific leaf weight (= 1/SLA) being similar for rye and triticale, but higher for wheat. These thicker leaves went along with an increased leaf respiration (see above). In pot experiments, Amanullah (2015) and Amanullah & Stewart (2015) also observed that rye SLA outyielded wheat SLA at 30, 60 and 90 days after emergence. It should be noted that each pot contained 15 plants of which 5 plants were harvested at each sampling date; therefore, the situation will be different from a canopy in the field. In the presented data herein, triticale SLA clearly increased at ear emergence indicating that the leaves became thinner, probably indicating an intensified translocation of assimilates into the growing ear. In addition, as already observed in wheat and barley, SLA positively correlated with GAI (Fig. 7) presumably due to mutual shading (Rawson et al., 1987; Ratjen & Kage, 2013; Sieling et al., 2016).

The N dilution curve relates the N concentration of the shoot or of parts of it to the corresponding DM during vegetative growth. Justes et al. (1994) for wheat and Colnenne et al. (1998) for oilseed rape used a power equation (%N = a*W-b; W is total shoot biomass) to describe the relationship. Comparing additional approaches revealed lowest residual error if a rational equation (%N = 1/(a + b*W)) was used instead of a power function or a ln-function (%N = a + b*ln(W)) (not shown). The fractionation of the total shoot into stem, leaves and ear (if appropriate) allowed for estimating separate N dilution curves (Fig. 8). While leaf N only slightly decreased during spring growth, stem N was dramatically reduced. This can at least partly be explained by the fact that the plant tries to maintain a high leaf N concentration to ensure maximum photosynthesis whereas stem N mainly achieves structural functions. The larger variation around 2 t ha^{-1} shoot DM resp. 1 t ha^{-1} stem DM (Fig. 8) mainly corresponding sampling at GS 30/31 in 2008 may be explained by the fact that the 2nd N application occurred in that year 1 week before sampling. The plants took up fertilizer N which, however, was not yet converted into leaves. If the N1, N2 and N4 treatments were additionally taken into account, the variation of the data at that sampling date markedly increased (data not shown). In 2009, plant sampling was just before N application.

CONCLUSIONS

The simultaneous growth analysis of rye, triticale and wheat reveals that the lower DM yield of wheat at GS 75 mainly resulted from a lower light use efficiency, which in turn may be due to a lower specific leaf area. An extended growth period of wheat partly compensated for a lower GAI, thus the differences in the amount of intercepted PAR between the crops remained small. The higher leaf DM related to the total shoot DM (leaf mass ratio) did not outweigh the lower SLA. On the other hand, rye produced the thinnest leaves with the highest leaf N concentrations resulting in the highest light use efficiency.

The results presented here revealed small, but remarkable differences in the resource capture and above-ground biomass accumulation between the crops. They may allow improving crop growth models for rye and triticale, since respective data are scarce compared to wheat.

ACKNOWLEDGEMENTS. The authors thank Gunda Schnack for the plant sampling and Achim Seidel for collecting and handling the data.

REFERENCES

Amanullah. 2015. Specific leaf area and specific leaf weight in small grain crops wheat, rye, barley, and oats differ at various growth stages and NPK source. *J. Plant Nutr.* **38**, 1694–1708.

Amanullah & Stewart, B.A. 2015. Analysis of growth response of cool season cereals 'wheat vs. rye' grown in organic and inorganic soils. *Emir. J. Food Agric*. **27**, 430–440.

Amon, T., Amon, B., Kryvoruchko, V., Machmüller, A., Hopfner-Sixt, K., Bodiroza, V. Hrbek, R., Friedel, J., Pötsch, E., Wagentristl, H., Schreiner, M. & Zollitsch, W. 2007. Methane production through anaerobic digestion of various energy crops grown in sustainable crop rotations. *Biores. Techn.* **98**, 3204–3212.

Colnenne, C., Meynard, J.-M., Roche, R. & Reau, R. 2002. Effects of nitrogen deficiencies on autumnal growth of oilseed rape. *Eur. J. Agron.* **17**, 11–28.

Estrada-Campuzano, G., Slafer, G.A. & Miralles, D.J. 2012. Differences in yield, biomass and their components between triticale and wheat grown under contrasting water and nitrogen environments. *Field Crops Res.* **128**, 167–179.

FAO 2016. Statistics of harvested area and yield. http://faostat3.fao.org/home/E (07.03.2016).

Gissén, C., Prade, T., Kreuger, E., Achu Nges, I., Rosenqvist, H., Svensson, S.-E., Lantz, M., Mattsson, J.E., Börjesson, P. & Björnsson, L. 2014. Comparing energy crops for biogas production – Yields, energy input and costs in cultivation using digestate and mineral fertilisation. *Biomass Bioenergy* **64**, 199–210.

Giunta, F., Pruneddu, G. & Motzo, R. 2009. Radiation interception and biomass and nitrogen accumulation in different cereal and grain legume species. *Field Crops Res*. **110**, 76–84.

Grindlay, D.J.C. 1997. Towards an explanation of crop nitrogen demand based on the optimization of leaf nitrogen per unit leaf area. *J. Agric. Sci.* **128**, 377–396.

Gunn, S., Farrar, J.F., Collis, B.E. & Nason, M. 1999. Specific leaf area in barley: individual leaves versus whole plants. *New Phytol.* **143**, 45–51.

Hotsonyame, G.K. & Hundt, L.A. 1998. Seeding date, photoperiod and nitrogen effects on specific leaf area of field-grown wheat. *Can. J. Plant Sci.* **77**, 51–61.

Justes, E., Mary, B., Meynard, J.-M., Machet, J.-M. & Thelier-Huche, L. 1994. Determination of a critical nitrogen dilution curve for winter wheat crops. *Ann. Bot.* **74**, 397–407.

Lemaire, G., Jeuffroy, M.-H. & Gastal, F. 2008. Diagnosis tool for plant and crop N status in vegetative stage: Theory and practices for crop N management. *Eur. J. Agron.* **28**, 614–624.

López-Castañeda, C. & Richards, R.A. 1994a. Variation in temperate cereals in rainfed environments I. Grain yield, biomass and agronomic characteristics. *Field Crops Res.* **37**, 51–62.

López-Castañeda, C. & Richards, R.A. 1994b. Variation in temperate cereals in rainfed environments II. Phasic development and growth. *Field Crops Res.* **37**, 63–75.

Mayer, F., Gerin, P.A., Noo, A., Lemaigre, S., Stilmant, D., Schmit, T., Leclech, N., Ruelle, L., Gennen, J., von Francken-Welz, H., Foucart, G., Flammang, J., Weyland, M. &

Delfaosse, P. 2014. Assessment of energy crops alternative to maize for biogas production in the Greater Region. *Biores. Techn*. **166**, 358–367.
Moreau, D., Allrad, V., Gaju, O., Le Gouis, J., Foulkes, M.J. & Matre, P. 2012. Acclimation of leaf nitrogen to vertical light gradient at anthesis in wheat is a whole-plant process that scales with the size of the canopy. *Plant Physiol.* **160**, 1479–1490.
Motzo, R., Pruneddu, G. & Giunta, F. 2013. The role of stomatal conductance for water and radiation use efficiency of durum wheat and triticale in a Mediterranean environment. *Eur. J. Agron.* **44**, 87–97.
Muurinen, S. & Peltonen-Sainio, P. 2006. Radiation-use efficiency of modern and old spring cereal cultivars and its response to nitrogen in northern growing conditions. *Field Crops Res.* **96**, 363–373.
Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D,E., Urcelay, C., Veneklaas, E.J., ReichI, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter Steege, H., van der Heijden, M.G.A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S. & Cornelissen, J.H.C. 2013. New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.* **61**, 167–234.
Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J. & Villar, R. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytol.* **182**, 565–588.
Qin, X., Weiner, J., Qi, L., Xiong, Y. & Li, F. 2013. Allometric analysis of the effects of density on reproductive allocation and Harvest Index in 6 varieties of wheat (*Triticum*). *Field Crops Res*. **144**, 162–166.
Ratjen, A.M. & Kage, H. 2013. Is mutual shading a decisive factor for differences in overall canopy specific leaf area of winter wheat crops? *Field Crops Res*. **149**, 338–346.
Rawson, H.M., Gardner, P. A. & Long, M.J. 1987. Sources of variation in specific leaf area in wheat grown at high temperature. *Aust. J. Plant Physiol.* **14**, 287–289.
Sánchez, M.L., Pardo, N., Pérez, I.A. & García, M.A. 2015. GPP and maximum light use efficiency estimates using different approaches over a rotating biodiesel crop. *Agric. Forest Meteo*. **214–215**, 444–455.
Sheng, Q. & Hunt, L.A. 1991. Shoot and root dry weight and soilwater in wheat, triticale and rye. *Can. J. Plant Sci.* **71**, 41–49.
Shipley, B. 2006. Net assimilation rate, specific leaf area and leaf mass ratio: which is most closely correlated with relative growth rate? A meta-analysis. *Funct. Ecol.* **20**, 565–574.
Sieling, K. & Christen O. 2015. Crop rotation effects on yield of oilseed rape, wheat and barley and residual effects on the subsequent wheat. *Arch. Agron. Soil Sci.* **61**, 1531–1549.
Sieling, K., Böttcher, U. & Kage, H. 2016. Dry matter partitioning and canopy traits in wheat and barley under varying N supply. *Eur. J. Agron.* **74**, 1–8.
van Delden, A., Pecios, A. & Haverkort, A.J. 2000. Temperature response of early foliar expansion of potato and wheat. *Ann. Bot.* **86**, 355–369.
Winzeler, M., McCullough, D.E. & Hunt, L.A. 1989. Leaf gas exchange and plant growth of winter rye, triticale, and wheat under contrasting temperature regimes. *Crop Sci.* **29**, 1256–1260.
Wright, I.J., Peter, B., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Eric Garnier, E., Hikosaka, K., Lamont, B.B., Lee, W., Oleksyn, J., Osada, N., Poorter, H., Villar, R., Warton, D.I. & Westoby, M. 2005. Assessing the generality of global leaf trait relationships. *New Phytol.* **166**, 485–496.
Zadoks, J.C., Chang, T.T. & Konzak, C.F. 1974. A decimal code for growth stages of cereals. *Weed Res.* **14**, 415–421.
Zar, J.H. 2009. *Biostatistical Analysis*. 5th Edition, Prentice Hall, 960 pp.