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## CROPPING SYSTEMS

### Yield and Growth Components of Potato and Wheat under Organic Nitrogen Management

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#### ABSTRACT

In order to optimize N management in organic farming systems, knowledge of crop growth processes in relation to N limitation is necessary. The present paper examines the response of potato (*Solanum tuberosum* L.) and wheat (*Triticum aestivum* L.) to N with respect to intercepted photosynthetically active radiation (PAR), light use efficiency (LUE), and leaf N concentration ([N]). Potato and wheat cultivars were grown in field experiments (1997 and 1998) at three N levels: no N (N1), cattle (*Bos taurus*) slurry (N2), and cattle slurry supplemented by mineral N fertilizers (N3). Estimated available N from the soil (0–0.9 m) plus added fertilizer was 80 (N1), 150 (N2), and 320 (N3) kg ha<sup>-1</sup> for potato and 115 (N1), 160 (N2), and 230 (N3) kg ha<sup>-1</sup> for wheat. Nitrogen deficiency was quantified by an N nutrition index (NNI; 1 = hardly limited, 0 = severely limited). Nitrogen deficiency increased in the N1 and N2 treatments up to 20 (potato) and 50 (wheat) d after emergence, with small changes thereafter. An increasing N limitation in potato (NNI = 1–0.55) resulted in a linear decrease in crop dry weight and cumulative intercepted PAR and in a linear increase of the harvest index, whereas the LUE decreased only at NNI values below 0.65. Crop dry weight and cumulative intercepted PAR for wheat decreased linearly with N limitation (NNI = 0.9–0.6), but the harvest index and LUE were unaffected. For both crops, N limitation to 0.55 caused a linear decrease in maximum leaf area index, the rate of foliar expansion, leaf area duration, and to a lesser extent, leaf [N]. In conclusion, both crops respond to N limitation by reducing light interception while maximizing the LUE and leaf [N].

NITROGEN MANAGEMENT in organic farming systems is complex. The supply of N from organic sources is difficult to synchronize with crop demand (Pang and Letey, 2000). Nitrogen deficiencies limit crop growth, whereas N excesses are often lost to the environment. Smaller arable crop yields in organic farming systems compared with those from conventional practices have been attributed to a mismatch between N supply and demand (Korva and Varis, 1990; Haraldsen et al., 2000). Thus, in organic farming, the limited amounts of avail-

able N require more effective distribution among the various crops to optimize farm results.

Optimization of organic N management requires knowledge of the response of crop growth processes to N. Variation in dry matter yield in response to N may arise from differences in the amount of intercepted photosynthetically active radiation (PAR) by the canopy, the light use efficiency (LUE), and harvest index (Charles-Edwards, 1982). Depletion and/or shortage of N indicates that either the crop cannot maintain its leaf area expansion rate or cannot maintain its leaf and plant N concentration ([N]). Theoretical studies (Sinclair and Horie, 1989) and experiments (Muchow and Sinclair, 1994) showed a curvilinear increase in LUE with an increase in areal leaf N content (N<sub>LA</sub>; g m<sup>-2</sup>).

Plant species differ in their degree of response. Two extreme types of responses are (i) maintenance of the N<sub>LA</sub> necessary for unrestricted productivity per unit of leaf area (i.e., maintain LUE at the cost of a reduced rate of leaf area expansion) and (ii) maximization of the leaf area expansion and intercepted PAR at the cost of a reduced N<sub>LA</sub> and a reduced LUE. In the second response, leaf area expansion is also somewhat reduced because of a smaller LUE.

According to simulation studies, maximum daily gross (Goudriaan, 1995) and net crop photosynthesis (Dewar, 1996) per unit of ground area are achieved when a crop maintains an optimal N<sub>LA</sub> necessary for unrestricted productivity per unit of leaf area, which corresponds to the first type of response. Goudriaan (1995) also showed that maintaining a smaller N<sub>LA</sub> increased the light interception but decreased the daily gross photosynthesis. The second strategy, i.e., maximization of leaf area expansion with smaller values of N<sub>LA</sub>, may be useful for maximizing N use efficiency, which in turn may be useful under natural ecosystems where N is limited. A large leaf area may also be useful in a mixed stand to achieve a competitive advantage in large canopy (Grindlay, 1997).

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**Abbreviations:** DAE, days after emergence; LAI, leaf area index; LUE, light use efficiency; [N], N concentration; N1, unfertilized; N2, fertilizations with cattle slurry; N3, fertilizations with cattle slurry supplemented by mineral N; N<sub>LA</sub>, areal leaf N content; NNI, nitrogen nutrition index; N<sub>min</sub>, soil mineral N content; PAR, photosynthetically active radiation; REML, residual maximum likelihood.

The N deficiency responses of potato and wheat crops were compared for two reasons. First, both species are important in an organic farming rotation system: Potato is an economically high-value crop, and wheat improves the soil structure. Second, both crops may exhibit different types of responses. According to Vos and Van der Putten (1998), the leaf area expansion in potato is responsive to N deficiency, whereas its LUE shows little response (Millard and Marshall, 1986; Duchenne et al., 1997), a response also found in other dicotyledonous C<sub>3</sub> crops (Booij et al., 1996). For wheat, a C<sub>3</sub> monocot, some studies showed a clear response of LUE to N (e.g., Green, 1987), whereas others did not (e.g., Meinke et al., 1997). Radin (1983) found the leaf area expansion of four cereal species, including C<sub>3</sub> and C<sub>4</sub> species, to be less responsive to N than that of dicotyledons. The LUE of the C<sub>4</sub> cereals maize (*Zea mays* L.) and sorghum (*Sorghum bicolor* L.) responded to the N supply (Muechow and Sinclair, 1994).

Comparison of crop responses to N deficiency requires quantification. To that end, Lemaire et al. (1989) proposed a N nutrition index (NNI), defined as:

$$\text{NNI} = \text{actual crop [N]}/\text{critical crop [N]} \quad [1]$$

where the critical crop [N] barely limits the growth rate of the crop. To calculate mean NNI values over time, a maximum value of 1 is used because crop growth rates are at their maximum for  $\text{NNI} \geq 1$  and  $\text{NNI} > 1$  indicates luxury N consumption (Lemaire et al., 1989). The NNI has been used in various studies to quantify N deficiency (e.g., Belanger et al., 1992). The critical crop [N] can be derived from the relationship between crop N uptake

and dry matter production (Greenwood et al., 1990; Booij et al., 1996). A widely used relationship between critical crop [N] and crop dry weight for potato has been derived by Greenwood et al. (1990) and for the vegetative stage of winter wheat by Justes et al. (1994). Such a relationship has not yet been established for spring wheat until crop maturity.

The objectives of the present work are to (i) establish relationships between N uptake and dry matter production for potato and spring wheat cultivars, (ii) use these relationships to quantify crop N demand and deficiency, (iii) establish relationships between N deficiency and growth characteristics, and (iv) use the findings to compare the responses of a potato and wheat crop to N supply under organic N management. To that end, sampled potato and wheat crops were grown at different rates of organic and mineral N supplies in the field.

## MATERIALS AND METHODS

### Experimental Site

In 1997 and 1998, potato and wheat were grown in the field at the experimental farm Lovinkhoeve at Marknesse (52°42' N, 5°53' E), the Netherlands. The soil was a silt loam, with 12% sand (>50 µm), 68% silt (2–50 µm), 20% clay (<2 µm), 2.3% (kg kg<sup>-1</sup>) organic matter (Lebbink et al., 1994), and pH (KCl) of 7.4 (sampling in December 1998). Soil P and K contents (Table 1) were sufficiently high to enable unrestricted growth of potato and wheat according to Van Dijk (1999). Water was not considered limiting because the pF (log<sub>10</sub> of water pressure in centimeters) value in the rhizosphere was below 2.85 for potato and below 3.0 for wheat at all sample times.

**Table 1.** Description of the experimental site Lovinkhoeve and experimental methods for potato and wheat.

	Potato	Spring wheat
Year	1997	1997
Planting/sowing date	18 Apr. 1997	14 Apr. 1997
Previous crop	Winter wheat	Fodder beet
Green manure crop	Mustard	–
Sampling date P (water) and K (HCl)	30 Mar. 1998	24 Sept. 1998
P (water), mg I <sup>-1</sup> P <sub>2</sub> O <sub>5</sub> †	44	30
K (HCl), mg K <sub>2</sub> O (100 g dm <sup>-1</sup> )‡	27	21
Plant density, pl m <sup>-2</sup>	4.44	260
Row spacing, m	0.75	0.3
Gross plot size, m <sup>2</sup>	19.8	6
Net plot size, m <sup>2</sup>	9.45	1.05
Cultivars	Junior	Baldus and Axona
Emergence date	1 June	27 Apr.
Sampling, DAE§	3, 8, 15, 36, 50, 58 (N1), 65 (N2), N3), and 99	4, 9, 16, 23, 39, 53, 59 (N1), 75 (N2), 79 (N3), and 100
		9, 23, 30, 45, 67, 81, 102, and 114
Year	1998	1998
Planting/sowing date	13 May 1998	9 May 1998
Previous crop	Spring wheat	Fodder beet
Green manure crop	Mustard	–
Sampling date P (water) and K (HCl)	24 Sept. 1998	14 Sept. 1998
P (water), I <sup>-1</sup> P <sub>2</sub> O <sub>5</sub> †	44	30
K (HCl), mg K <sub>2</sub> O (100 g dm <sup>-1</sup> )‡	27	21
Plant density, pl m <sup>-2</sup>	4.44	230
Row spacing, m	0.75	0.3
Gross plot size, m <sup>2</sup>	23.4	10
Net plot size, m <sup>2</sup>	9.45	1.2
Cultivars	Junior	Baldus and Axona
Emergence date	28 May	17 May
Sampling, DAE§	7, 18, 27, 46, 63, and 94	5, 15, 32, 53, 85, and 117

† Soil P content  $\geq 21$  is sufficient for good crop growth of potato and wheat.

‡ Soil K content  $\geq 21$  is sufficient for good crop growth of potato and wheat.

§ DAE, days after emergence.

### Treatments

For each year and crop, N was supplied at three rates (Table 2A and 2B): (i) unfertilized or only garden compost (N1); (ii) fertilizations with cattle slurry at a level corresponding to current organic farming systems in the Netherlands (N2); and (iii) twice the N2 treatment, supplemented with mineral N according to recommended rates (Van Dijk, 1999) for potato and wheat based on soil analysis (N3). Supplementary N fertilizer was applied as calcium ammonium nitrate (Table 2B) and corrected for expected net N mineralization from organic sources (Table 2A) during the growing season, as explained in Appendix 1.

For each crop, two cultivars differing in leaf area dynamics were used: potato cultivars Junior (early) and Agria (mid to late) and wheat cultivars Axona [relatively small maximum leaf area index (LAI)] and Baldus (larger maximum LAI).

### Design and Plot Size

For each crop, a separate experiment was laid out as a randomized complete block design in a split-plot arrangement with three replicates of each individual treatment. Fertilization rates were whole plots, cultivars were subplots, and sampling dates were randomized within each individual treatment. To avoid carry-over effects, low, intermediate, and high relative fertilization rates of the main plots within experimental fields were maintained since summer 1995.

### Crop Husbandry

Potato tubers were presprouted and planted by machine. Pests and diseases [notably late blight (*Phytophthora infestans*)] of potato and wheat were controlled using standard farming practices for the area to avoid interaction of N with

**Table 2A. Dates and levels of N application, actual total N content in organic N sources, and expected net N mineralization during the growing season for potato and spring wheat at three N treatments (N1, N2, and N3)† in 1997 and 1998.**

Crop and year	Date and manure treatment	Application rate		Total N content		Expected net N mineralization‡			Sum
		Compost	Cattle slurry	Compost	Cattle slurry	Compost	Cattle slurry	Previous crop	
		Mg ha <sup>-1</sup> fm§		kg N ha <sup>-1</sup>					
Potato 1997	2 Sept. 1996								
	N1	10	0	116	0	12	0	0	12
	N2	0	40	0	188	0	28	0	28
	N3	0	80	0	376	0	55	0	55
1998	30 Sept. 1997								
	N1	5	0	57	0	6	0	0	6
	N2	5	45	57	270	6	43	0	49
	N3	5	80	57	480	6	77	0	83
Wheat 1997	10 Apr. 1997								
	N1	0	0	0	0	0	0	30	30
	N2	0	15	0	33	0	5	30	35
	N3	0	30	0	66	0	11	30	41
1998	8 May 1998								
	N1	0	0	0	0	0	0	30	30
	N2	0	20	0	78	0	13	30	43
	N3	0	40	0	156	0	25	30	55

† N1, no N; N2, cattle slurry corresponding to current organic N management; and N3, cattle slurry supplemented by mineral N fertilizers according to recommended levels used in conventional farming.

‡ Calculation of expected net N mineralization is explained in Appendix 1, and presented values of Table 2A are based on measured total and organic N contents of slurry and garden compost. Calculated amount of supplied mineral fertilizer N was based on standard values for organic N contents, as manure samplings were not available at the time.

§ fm, fresh matter.

**Table 2B. Sampling date and soil mineral N content just after planting and sowing, and expected net N mineralization [expected net N mineralization (ENM), from Table 2A] from organic sources. Dates and levels of mineral N application are just after planting and sowing (first) and at stem extension of wheat (second). Total N is available N for the crops, estimated as the sum of soil mineral N (0–0.9 m), ENM, and mineral fertilizer N. Crops and treatments are as in Table 2A.**

Crop and year	N treatment†	Soil mineral N		Total ENM	Mineral fertilizer N		Total N
		0–0.6 m	0–0.9 m		First	Second	
		kg N ha <sup>-1</sup>					
Potato 1997		21 Apr. 1997			26 May 1997		
	N1	50	61	12	0	0	72
	N2	80	101	28	0	0	129
	N3	112	148	55	110	0	313
1998		18 May 1998			20 May 1998		
	N1	65	89	6	0	0	94
	N2	84	121	49	0	0	169
	N3	94	127	83	120	0	330
Wheat 1997		21 Apr. 1997			5 June 1997		
	N1	67	79	30	0	0	109
	N2	90	101	35	0	0	136
	N3	84	94	41	0	75	210
1998		19 May 1998			20 May 1998		26 June 1998
	N1	66	88	30	0	0	118
	N2	107	139	43	0	0	182
	N3	82	108	55	15	75	253

† N1, no N; N2, cattle slurry corresponding to current organic N management; and N3, cattle slurry supplemented by mineral N fertilizers according to recommended levels used in conventional farming.

biotic factors. In 1998, tubers were disinfected with validamycin (Solacol, Hoechst Schering AgrEvo, Berlin) against *Rhizoctonia solani*. By omission, tubers were not disinfected in 1997, and about 5% of the tubers of cultivar Junior were infected by *R. solani*, but hardly any tubers of cultivar Agria were infected. Weeds were mechanically controlled by harrowing and hoeing.

### Measurements

At regular intervals, growth was analyzed by assessing crop biomass of all organs except fibrous roots. Leaf area was measured with a Li-COR 3100 area meter (Li-COR, Lincoln, NE). Sampling areas, dates, plant densities, and row distances are given in Table 1. Wheat was sampled up to maturity. Potato was harvested on 8 Sept. 1997 when soil cover of Junior was nearly zero while the soil cover of Agria was still about 75% (N3) or below 50% (N1 and N2). In 1998, final potato harvest was conducted when soil cover was nearly zero.

The various plant parts were dried (105°C for 24 h) and weighed. Total N was determined using the Dumas method (Macro N; Foss Heraeus Analysensysteme, Hanau, Germany). Nitrate in green leaves and stems was extracted with water and determined using a continuous-flow analyzer (TRAACS 800, Bran and Luebbe, De Meern, the Netherlands). Previous studies showed that NO<sub>3</sub> contents in tubers and stolons are a negligible proportion of total N content (Biemond and Vos, 1992). Nitrate was determined in wheat up to anthesis. After anthesis, the NO<sub>3</sub> concentration was determined in one replicate and was found to be very small. The NO<sub>3</sub> content of potato was determined until it dropped below 5% of total N content, which occurred at about maximum LAI. Nitrogen uptakes were determined in three replicates in 1997 but usually in two replicates in 1998. Nitrogen uptake by each organ was calculated as the product of dry matter yield and [N]. Throughout the paper, [N] refers to organic N only, calculated as total N minus NO<sub>3</sub>-N. Ammonium concentrations in the plants were assumed to be small because soil-derived NH<sub>4</sub> is quickly assimilated in the root tissue itself and is not considered to be transported in the xylem to other plant organs (Pearson and Stewart, 1993). Moreover, foliar NH<sub>4</sub> taken from atmospheric deposition results in low leaf NH<sub>4</sub> concentrations. Yin et al. (1996) found NH<sub>4</sub> concentrations in leaves of zonal geranium (*Pelargonium zonale* L.) to be about 0.3 μg NH<sub>4</sub>-N g<sup>-1</sup> leaf fresh weight, with hardly any increase by NH<sub>3</sub> fumigation.

Soil inorganic N was analyzed (NH<sub>4</sub>-N and NO<sub>3</sub>-N) after combining four cores from all plots per treatment using a 30-mm-diam. probe. Exchangeable NH<sub>4</sub>-N and NO<sub>3</sub>-N were determined in 1 M KCl with a continuous-flow analyser (TRAACS 800, Bran and Luebbe, De Meern, the Netherlands).

### Interception of Photosynthetically Active Radiation and Light Use Efficiency

Intercepted PAR was measured once or twice a week for wheat, 10 times per recording, with a portable line sensor (TFDL, Wageningen, the Netherlands). Recordings were taken within 1 h of solar noon for either a clear or an overcast sky. Previous studies showed that recordings of interception at solar noon were within 2% of the average interception as weighted over 1 d (Kiniry et al., 1999). Global radiation data were obtained from a weather station located at the farm, and PAR was taken as 50% of global radiation. The proportion of soil cover by green potato leaves was observed once or twice a week using a frame divided into 100 rectangles and with dimensions that were a multiple of the planting pattern.

Daily values of intercepted PAR (wheat) and soil cover (potato) were obtained by fitting a nonlinear relationship with thermal time [modified from Spitters (1990), see Appendix 2]. Less frequently, intercepted PAR was also measured for potato, and both methods correlated well. Daily soil cover values were transformed into the fraction intercepted of PAR, according to a relationship similar to that published by Van der Zaag (1984).

The average LUE was calculated by linear regression of cumulative intercepted PAR and crop biomass production, using weighted residuals to obtain homogeneity of variances. Crop biomass production was set equal to the actual crop dry weight, except during the period of foliar decrease when the maximum leaf dry weight recorded was taken as total production of leaf dry weight for subsequent periodic harvests. Crop biomass production and growth components were compared well before the final harvest (see Results section) because PAR at later dates was mainly intercepted by yellow stems and leaves.

### Thermal Time

Thermal time was calculated as cumulative daily effective temperature (daily mean air temperature minus a base temperature of 2°C for potato and 0°C for wheat). Average daily air temperature was calculated as the mean of the daily minimum and maximum temperatures.

### Relationship between Crop Dry Weight and Nitrogen Uptake

For both crops, crop dry weight ( $W$ ; Mg ha<sup>-1</sup>) was related to the corresponding N uptake ( $N_U$ ; kg ha<sup>-1</sup>) at each sampling date and N application rate. An exponential function given by Booij et al. (1996) was used to describe the relationship at each sampling date:

$$W = W_m(1 - e^{-K_{NU}N_U}) \quad [2]$$

where  $W_m$  = maximum crop dry weight, and  $K_{NU}$  is a constant (ha kg<sup>-1</sup> N). The relationship was fitted to each replicate, and the parameters ( $K$  and  $W_m$ ) were subjected to analysis of variance using residual maximum likelihood (REML; see Statistical Analysis section) after a log<sub>10</sub> transformation.

At each fertilizer level, crop dry weight was related to N uptake, according to a relationship found to be appropriate for both C<sub>3</sub> and C<sub>4</sub> crops (Lemaire and Gastal, 1997):

$$W = \left(\frac{N_U}{A}\right)^B \text{ for } W \geq 1 \text{ and} \\ W = \left(\frac{N_U}{A}\right) \text{ for } W < 1 \quad [3]$$

where  $A$  = crop [N] (kg N Mg<sup>-1</sup>) of a young crop with  $W < 1$  (Mg ha<sup>-1</sup>) and  $B$  is a constant. The relationship was fitted to each replicate, and residuals were weighted because the variance was a function of the mean. Each year, the parameters ( $A$  and  $B$ ) were subjected to analysis of variance (see Statistical Analysis section) after a log<sub>10</sub> transformation.

### Calculation of Nitrogen Nutrition Index and Leaf Area Duration

Nitrogen nutrition index was calculated according to Eq. [1]. To calculate mean NNI values over time, a maximum value of 1 was used. Critical crop [N] was calculated as the [N] at near-maximum dry matter production at each harvest date. The near-maximum dry matter production was defined

as 95% of the asymptotic value ( $W_m$ ) in Eq. [2], as was done previously by Booij et al. (1996). Values for critical [N] were compared with reference lines for potato (Greenwood et al., 1990) and for the vegetative stage of winter wheat (Justes et al., 1994). Leaf area duration was calculated as the area under the LAI curve vs. days after emergence (DAE) where LAI was linearly interpolated between successive sampling times. Throughout the paper, weighted averages for growth components are calculated as the average weighted for DAE.

### Statistical Analysis

All data and parameters were subjected to analysis of variance using Genstat (Genstat 5 Committee, 1993). Analysis of data with only factors was based on the classical ANOVA procedure, and data with both factors (year and cultivar) and variates (e.g., NNI and DAE) were analyzed with a linear mixed model, using the REML procedure. Both procedures take treatment structure into account, and the results are identical when data with factors only are used. The variation with year was also tested by analysis of variance, using the pooled residual variance as the estimate of within-treatment variance. Differences between individual treatments were tested by least significant difference. All effects mentioned in the Results and Discussion section refer to significant effects at a  $P \leq 0.05$  significance level unless otherwise stated.

## RESULTS AND DISCUSSION

### Final Crop Yields, Harvest Index, and Nitrogen Uptake

For potato at final harvest, higher N rates increased tuber dry weight and tuber N uptake, independent of year and cultivar (Table 3). Averaged over years and cultivars, tuber dry weight increased by 15 and 60% and tuber N uptake by 24 and 128% in N2 and N3, respectively. The early cultivar Junior had both a

smaller tuber weight and a smaller N uptake than the later cultivar Agria.

For wheat at crop maturity, crop dry weight varied with year and increased with N (Table 3). The increase of dry weight with N was larger for Axona than for Baldus. Total N uptake increased with N supply from 124 to 180 kg N ha<sup>-1</sup> in N1 and N3, respectively, for both years and cultivars. Higher rates of N increased grain yield in 1997 but not in 1998. Averaged over years and N treatments, grain yield was slightly larger (7.6%) for Baldus than for Axona, which was associated with the higher (9.5%) harvest index of Baldus (Table 3).

### Relationship between Dry Matter Production and Nitrogen Uptake

Dry matter production and N uptake were affected by N application and growth stage of the crop (Fig. 1). At each harvest date, dry matter production increased asymptotically with N uptake, eventually approaching a maximum. The parameters in Eq. [2] ( $K_{NU}$  and  $W_m$ ) varied with sampling date in both years for potato but did not vary with cultivar. For wheat,  $W_m$  varied with sampling date in both years and  $K_{NU}$  varied with sampling date only in 1997. The parameters did not vary with wheat cultivar, except at 23 DAE in 1997. Generally, the relationship between N uptake and dry matter production at a given date did not vary between the cultivars of potato and wheat during the growth period tested.

At a set fertilizer level, dry matter production increased with N uptake until it approached a maximum. For both crops, the parameters in Eq. [3] ( $A$  and  $B$ ) were affected by N ( $B$  in 1997 and  $A$  in 1998) but did not vary with cultivar. Thus, for a given N treatment and year, the increase in crop dry matter with N uptake

**Table 3. Values and effects of analysis of variance of year (Y), nitrogen (N), and cultivar (C) on tuber dry weight and N uptake of potato and total crop biomass, grains, harvest index (HI) and total N uptake of wheat at maturity in 1997 and 1998.**

Year	N treatment†	Potato			Spring wheat				
		Cultivar	Tuber weight Mg ha <sup>-1</sup>	Tuber N uptake kg N ha <sup>-1</sup>	Cultivar	Total biomass Mg ha <sup>-1</sup>	Grain weight Mg ha <sup>-1</sup>	Harvest index kg kg <sup>-1</sup>	Total N uptake kg N ha <sup>-1</sup>
1997	N1	Junior	4.03	44.4	Axona	10.8	4.59	0.426	111
	N2		4.67	58.2		11.5	4.88	0.424	123
	N3		8.14	145.2		14.5	6.01	0.416	190
1997	N1	Agria	6.44	60.8	Baldus	11.8	5.45	0.463	142
	N2		8.35	89.3		10.2	4.79	0.468	109
	N3		9.90	142.8		13.6	6.39	0.470	184
1998	N1	Junior	5.38	50.3	Axona	9.37	3.95	0.422	122
	N2		5.83	57.2		11.7	4.95	0.423	139
	N3		7.61	92.5		11.6	4.77	0.413	174
1998	N1	Agria	7.92	73.6	Baldus	9.92	4.71	0.474	123
	N2		8.54	78.9		10.8	5.06	0.469	134
	N3		12.38	141.8		10.6	4.99	0.470	172
Sig. Y			ns‡	ns	*	**	ns	ns	
Sig. N			**	***	*	*	ns	*	
Sig. C			***	***	ns	**	***	ns	
Sig. interactions			Y × N × C:§	Y × N × C:§	Y × N:§	Y × N:*	ns	ns	
					N × C:*	N × C:§			
LSD ( $P = 0.05$ ) N			1.67	18.6	1.46	0.54	0.012	28.8	
LSD ( $P = 0.05$ ) N within Y.C			2.54	29.9	2.17	0.84	0.023	42.1	

\* Significant at the 0.05 level.

\*\* Significant at the 0.01 level.

\*\*\* Significant at the 0.001 level.

† N1, no N; N2, cattle slurry corresponding to current organic N management; and N3, cattle slurry supplemented by mineral N fertilizers according to recommended levels used in conventional farming.

‡ ns, nonsignificant at  $P \geq 0.1$ .

§ Significant at the 0.1 level.

did not vary between the cultivars of potato and wheat. Therefore, data of cultivars were pooled to calculate critical [N].

### Critical Crop Nitrogen Concentration

The critical crop [N] decreased with crop dry weight in both species (Fig. 2). The calculated critical [N] <1 Mg ha<sup>-1</sup> in potato and wheat were not included because the initial effects of N were small, which resulted in strong overestimations of the critical [N] ([N] ≥ 7%).

Calculated critical [N] for potato (Fig. 2A) was clearly larger than that found by Greenwood et al. (1990), whereas calculated critical [N] values for spring wheat (Fig. 2B), also after anthesis, were consistent with data from Justes et al. (1994). Our relationship for potato probably overestimated critical [N] because crop dry matter production at a given date as a function of N supplies (Fig. 1A and 1B) did not yet reach its maximum. Further calculations were based on the reference lines

by Greenwood et al. (1990) and Justes et al. (1994), as they were appropriate (explained below). The ratio of actual/near-maximum crop dry weight was found to be 1 at a NNI = 1, as expected from the definition of NNI (Eq. [1]; Lemaire et al., 1989), whereas an overestimation of crop N content at the near-maximum crop dry weight would have resulted in underestimations of NNI.

### Nitrogen Nutrition Index

In both years, the NNI (see Eq. [1]) for potato cultivars decreased in the N1 and N2 treatments from 0.8 to 0.9 at emergence to 0.6 to 0.7 at about 15 DAE in 1997 and to 0.4 to 0.5 at about 25 DAE (1998). From then on, changes in NNI were much smaller (Fig. 3A and 3B). The NNI for potato cultivars at high N (N3) in 1997 also decreased, but after 20 DAE, it remained above 1. In 1998, the changes were small throughout the growth period. Averaged over years and cultivars, higher levels of N increased the average NNI (emer-

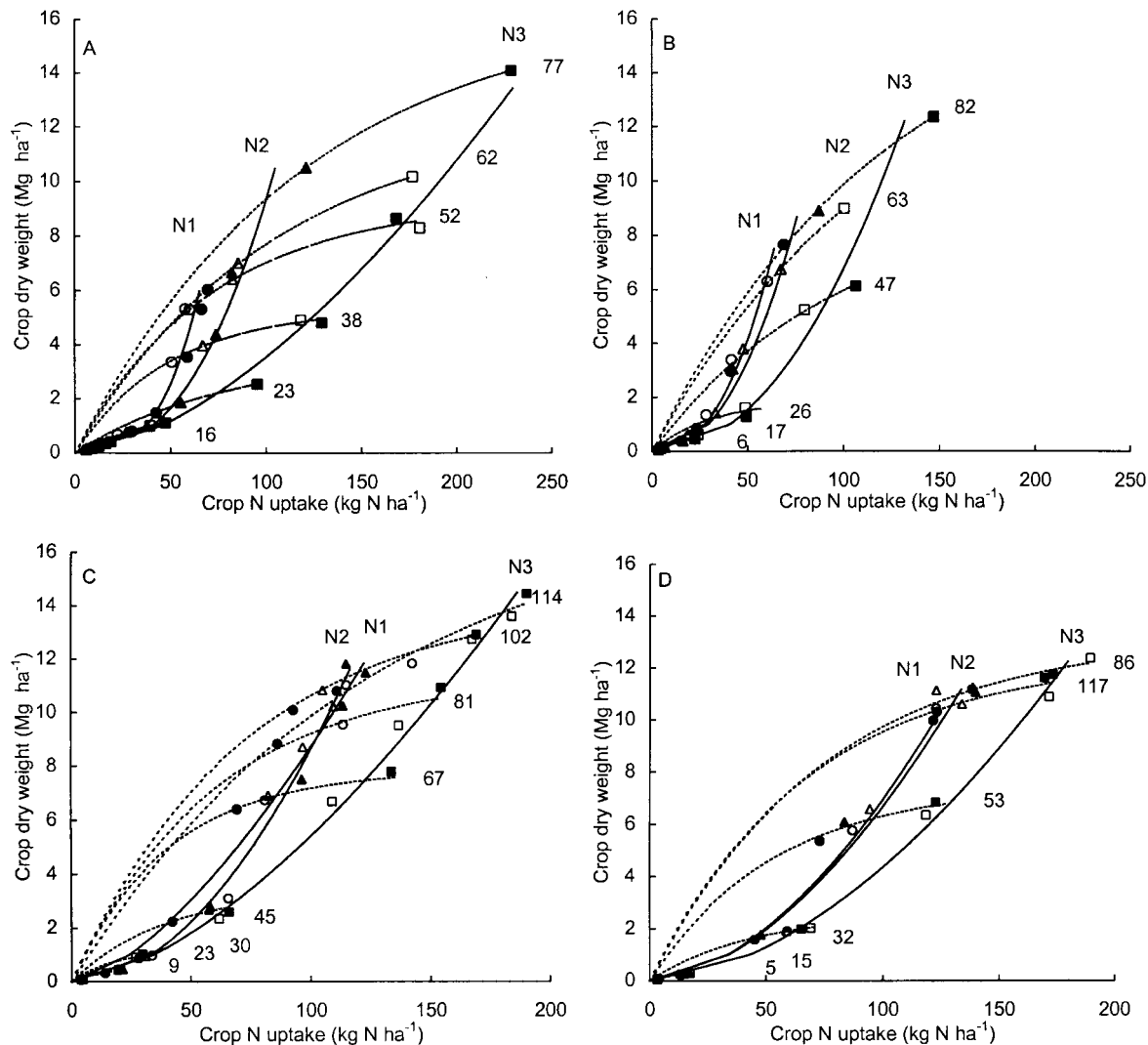


Fig. 1. Relationship between N uptake and total dry matter production of (A and B) potato and (C and D) wheat in (A and C) 1997 and (B and D) 1998. For each day after emergence (DAE), the line was fitted according to Eq. [2] (broken lines) and at each N level according to Eq. [3] (solid lines). Data values are DAE of periodic samplings. Open symbols represent potato cultivar Junior and wheat cultivar Axona, and closed symbols represent potato cultivar Agria and wheat cultivar Baldus for N1 (circles), N2 (triangles), and N3 (squares).

gence to 60 DAE) for potato by 10% in N2 and by 48% in N3 (Fig. 3B). The average NNI was larger for Agria (0.712) than for Junior (0.657) in both years.

The NNI for wheat cultivars followed the same pattern (Fig. 3C and 3D) in both years. The NNI for all N treatments for wheat was well above 1 from emergence until about 20 to 30 DAE. Thereafter, the NNI remained about 0.8 in N3 but decreased in N1 and N2 until about 0.6 at 50 DAE, hardly changing thereafter. Averaged over years and cultivars, higher N levels increased the average NNI (emergence to maturity) for wheat by 2% (N2) and 20% (N3) (Fig. 3C and 3D). The average NNI for wheat varied slightly with year but was not affected by cultivar.

### Relationship between Dry Matter Production, Growth Components, and Nitrogen Nutrition Index

Throughout the current section, crop biomass production (actual weight corrected for leaf shedding) and its components (Table 4 and 5) were compared well before final harvest (to avoid interception by yellow leaves). For the comparison, the latest possible harvest was used at which both cultivars of a crop were harvested at about the same harvest date (potato, 52 DAE in 1997 and 47 DAE in 1998; wheat, the next-to-last harvest).

Biomass production, tuber dry matter, cumulative intercepted PAR, and harvest index (excluding outliers) for potato were larger in 1997 than in 1998 (Table 4). These results were associated with a later harvest in 1997 (52 DAE) than in 1998 (47 DAE) and with a higher average daily air temperature and daily PAR from emergence until harvest in 1997 (14.2°C; 9.4 MJ m<sup>-2</sup> d<sup>-1</sup>) than in 1998 (13.4°C; 7.2 MJ m<sup>-2</sup> d<sup>-1</sup>). A small but significant year × cultivar interaction was found for the cumulative intercepted PAR and LUE. Averaged over cultivars and years, N supply increased biomass production by 18% in N2 and 60% for N3, the cumulative intercepted PAR by 8% in N2 and 27% for N3, and the LUE by 9.1% for N2 and 25% for N3. Biomass production for potato did not differ between cultivars, but the early cultivar Junior had a larger tuber dry weight (3.89 Mg ha<sup>-1</sup>) than Agria (3.62 Mg ha<sup>-1</sup>) due to a larger harvest index.

The wheat biomass production, cumulative intercepted PAR, harvest index, and grain yield were larger in 1997 than in 1998 because crops were harvested later in 1997 (102 vs. 86 DAE) (Table 5) and average temperature and daily PAR during growth were higher (see above). The LUE for wheat was smaller in 1997 than in 1998, which was associated with a larger average daily PAR from emergence until harvest in 1997 (8.9 vs. 7.9 MJ m<sup>-2</sup> d<sup>-1</sup>). Averaged over cultivars and years, the N supply tended to increase ( $P = 0.06$ ) the biomass production by 10 (N2) and 19% (N3) and increased cumulative intercepted PAR by 5 (N2) and 14% (N3), but it did not affect the LUE. Averaged over years and N treatments, the harvest index was larger for cultivar Baldus (0.386) than for Axona (0.328), and the difference was slightly larger in 1998 than in 1997.

The response of crop dry weight and growth components to the average NNI, across years and cultivars, is shown in Fig. 4 and 5. The response is expressed relative to the maximum or critical value for each year and cultivar. Crop dry weight for potato and cumulative intercepted PAR decreased strongly with decreasing NNI (Fig. 4A and 4B). Analysis of REML showed that the relationship between relative cumulative intercepted PAR and the NNI varied with year. For a given NNI, the relative cumulative intercepted PAR was smaller in 1998 than in 1997. The LUE for potato barely decreased with NNI, from 1 to 0.65, but decreased strongly thereafter (Fig. 4C). The relative harvest index for potato increased slightly with decreasing NNI (Fig. 4D), but it was no longer affected by average NNI

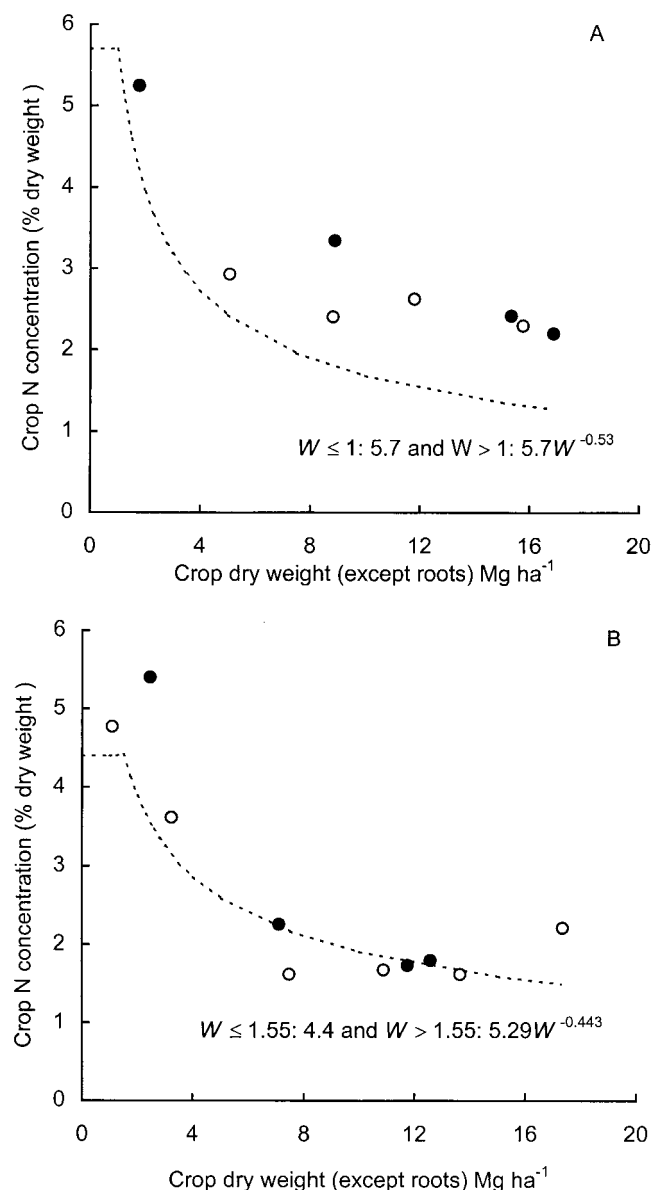


Fig. 2. Relationship between crop dry matter production ( $W$ ; Mg ha<sup>-1</sup>) and critical N concentration ( $[N]$ ) in (A) potato (Greenwood et al., 1990) and (B) wheat (Justus et al., 1994). Symbols are 95% of the calculated maximum  $W$  (Eq. [2] in text), as derived from Fig. 1. Open symbols are for 1997 and closed symbols are for 1998.

at the next-to-last harvest (not shown). As with potato, the crop dry weight and cumulative intercepted PAR for wheat cultivars decreased strongly with decreasing NNI (Fig. 5A and 5B). Neither the relative LUE nor the relative harvest index for wheat was affected by the average NNI, with NNI ranging from 0.61 to 0.92 (Fig. 5C and 5D).

Other studies also found potato and wheat harvest index near crop maturity to be unaffected by N depletion (Millard and Marshall, 1986; Duchenne et al., 1997; Green, 1987). During early tuber growth, however, potato harvest index may decrease with increased N supply, as high N supply is known to decrease the dry matter partitioning to tubers during early tuber growth (e.g., Millard and Marshall, 1986).

Results in Fig. 4 corroborate the hypothesis by Vos and van der Putten (1998) that, in response to N limitation, potato maximizes LUE but reduces light interception, as explained below. For NNI of 1 to 0.65, the

cumulative intercepted PAR for potato decreased strongly with increasing N deficiency, whereas the LUE hardly changed. At a NNI below 0.65, the LUE was also reduced with NNI. Duchenne et al. (1997) also found no effect of N supply on the LUE for potato and usually observed NNI values above 0.7. Millard and Marshall (1986) found only the LUE for potato in their unfertilized treatment to be reduced compared with their other N rates of 50 to 250 kg N ha<sup>-1</sup>.

Results in Fig. 5 showed that wheat reduces its intercepted PAR with decreasing NNI, whereas its LUE was not reduced at NNI of 1 to 0.7. The results of the present study agreed with those of Meinke et al. (1997) but contrasted with other studies. Green (1987) reported a quasi-linear increase of LUE with N supply in spring and winter wheat crops even though only the zero N treatment differed significantly from the other N supply levels of ≥40 kg N ha<sup>-1</sup>.

The contrasting results in previous wheat studies

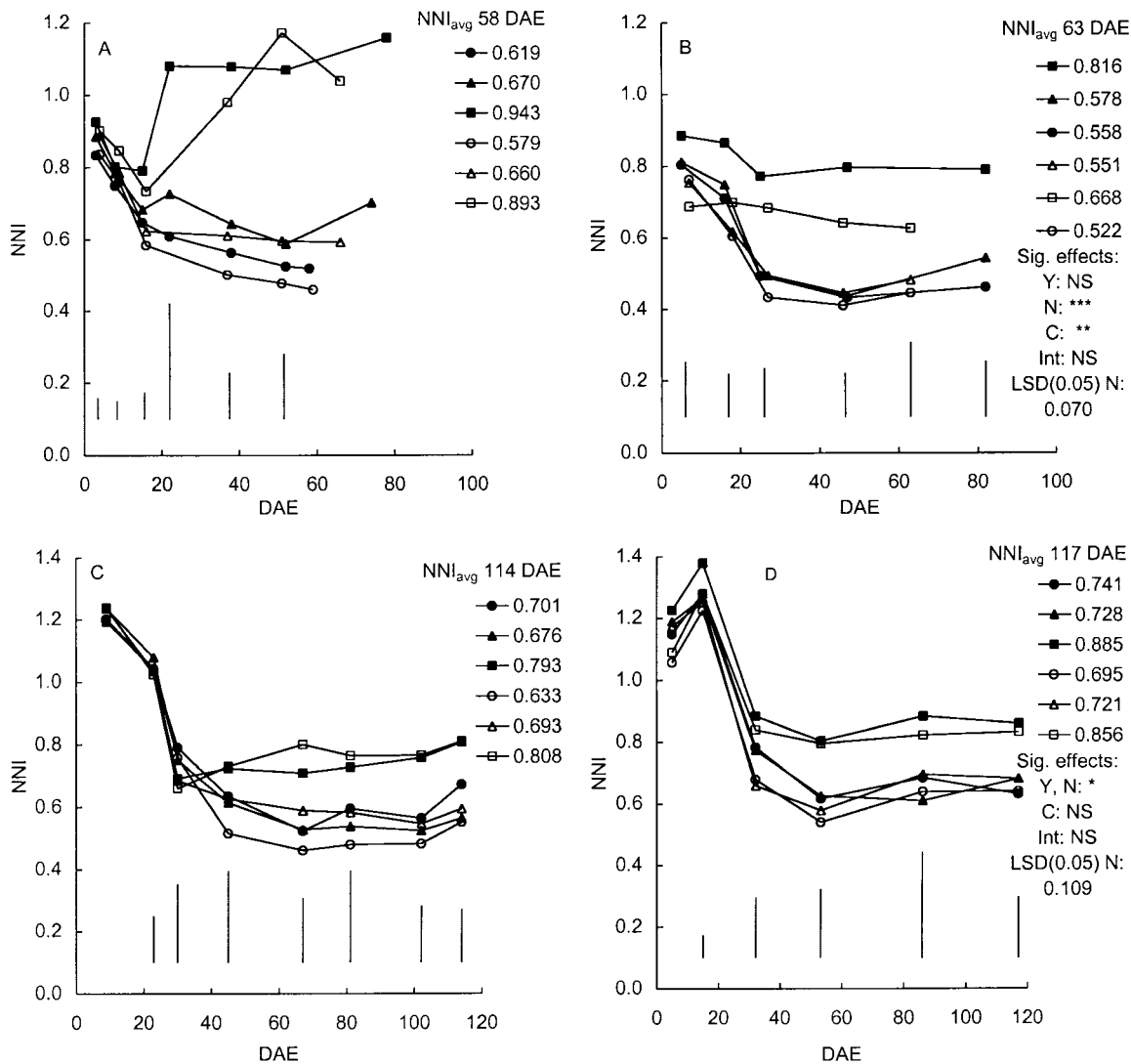


Fig. 3. Course of the N nutrition index (NNI) (see Eq. [1]) with days after emergence (DAE) of (A and B) potato and (C and D) wheat in (A and C) 1997 and (B and D) 1998. Bars represent the LSD ( $P = 0.05$ ) at each sampling date. Data values are average NNI values at the largest possible DAE that cultivars could be compared. Open symbols represent potato cultivar Axona, and closed symbols represent potato cultivar Agria and wheat cultivar Baldus for N1 (circles), N2 (triangles), and N3 (squares). Y, year; N, nitrogen; C, cultivar; \*, \*\*, and \*\*\*, significant at the 0.05, 0.01, and 0.001 levels, respectively; NS, nonsignificant at the 0.1 level.



**Table 4.** Means and effects of year (Y), nitrogen (N), and cultivar (C) on average N nutrition index (NNI), crop biomass, tuber dry weight, harvest index, light use efficiency (LUE), and cumulative intercepted photosynthetically active radiation (PAR) of potato at about 52 d after emergence (DAE) in 1997 and 47 DAE in 1998. Actual = measured biomass, Critical = 95% of maximum biomass (just barely N limited), and Total = total biomass production, including shed leaves.

Y	C	N	NNI	Crop dry weight			Tubers†	Harvest index†		LUE	Cum. interc. PAR‡	
				Actual	Critical	Total		Total	LUE		Actual	Critical
				Mg ha <sup>-1</sup>			g g <sup>-1</sup>		g MJ <sup>-1</sup>		MJ m <sup>-2</sup>	
1997	Junior	N1	0.594	5.31	8.23	5.71	4.95	0.770	2.07	259	345	
		N2	0.669	6.43	8.23	6.82	5.01	0.734	2.38	276	345	
		N3	0.881	8.31	8.23	8.35	5.28	0.631	2.40	327	345	
	Agria	N1	0.630	5.33	8.23	5.66	4.99	0.711	1.98	271	357	
		N2	0.702	6.68	8.23	6.93	4.52	0.652	2.19	306	357	
		N3	0.936	8.67	8.23	8.83	5.15	0.582	2.35	350	357	
1998	Junior	N2	0.557	3.15	7.16	3.17	2.27	0.715	1.93	163	297	
		N2	0.583	3.78	7.16	3.78	2.68	0.708	2.04	175	297	
		N3	0.680	5.19	7.16	5.19	3.13	0.603	2.42	197	297	
	Agria	N1	0.596	3.01	7.16	3.01	1.86	0.619	2.03	139	257	
		N2	0.607	3.23	7.16	3.23	1.92	0.594	2.13	140	257	
		N3	0.824	5.85	7.16	5.85	3.28	0.559	2.79	187	257	
Sig. Y§		ns	**	**	**	***	*	ns	***			
Sig. N		***	**	**	**	§	**	*	***			
Sig. C		***	ns	ns	ns	*	***	ns	ns			
Sig. interactions		N × C§	ns	ns	ns	N × C§	*	Y × C*	Y × N§	Y × C***		
LSD <i>P</i> = 0.05 N			0.065	1.23		1.15	0.62	0.044	0.34	14.7		
LSD <i>P</i> = 0.05 N, within Y × C			0.086 (1997) 0.106 (1998)	1.81		1.69	0.92	0.063	0.51	24.2		

\* Significant at the 0.05 level.

\*\* Significant at the 0.01 level.

\*\*\* Significant at the 0.001 level.

‡ Critical value for cumulative intercepted PAR was calculated according to (critical W/actual W) × total W divided by the maximum LUE per N treatment for each year and cultivar.

§ Significant at the 0.1 level.

¶ Nonsignificant at the 0.1 level.

**Table 5.** Means and effects of year (Y), nitrogen (N), and cultivar (C) on average N nutrition index (NNI), crop biomass, grain dry weight, harvest index, light use efficiency (LUE), and cumulative intercepted photosynthetically active radiation (PAR) of wheat at 102 d after emergence (DAE) in 1997 and 86 DAE in 1998. Actual = measured biomass, Critical = 95% of maximum biomass (just barely N limited), and Total = total biomass production, including shed leaves.

Y	C	N	NNI	Crop dry weight			Grains Actual	Harvest index		LUE	Cum. interc. PAR†	
				Actual	Critical	Total		Total	LUE		Actual	Critical
				Mg ha <sup>-1</sup>			g g <sup>-1</sup>		g MJ <sup>-1</sup>		MJ m <sup>-2</sup>	
1997	Axona	N1	0.647	10.1	13.7	10.6	4.01	0.378	2.25	510	649	
		N2	0.708	11.8	13.7	12.3	4.58	0.371	2.25	575	649	
		N3	0.811	12.9	13.7	13.5	4.94	0.366	2.20	624	649	
	Baldus	N1	0.711	11.0	13.7	11.6	4.89	0.424	2.17	580	636	
		N2	0.692	10.8	13.7	11.3	4.74	0.420	2.17	540	636	
		N3	0.794	12.8	13.7	13.1	5.58	0.425	2.11	602	636	
1998	Axona	N1	0.715	10.0	12.5	10.1	2.90	0.286	2.61	399	481	
		N2	0.733	11.5	12.5	11.8	3.37	0.287	2.77	444	481	
		N3	0.866	11.8	12.5	12.2	3.33	0.273	2.67	487	481	
	Baldus	N1	0.771	10.4	12.5	10.6	3.80	0.357	2.46	448	465	
		N2	0.757	11.3	12.5	11.7	4.06	0.345	2.64	471	465	
		N3	0.890	11.9	12.5	12.2	4.18	0.344	2.53	492	465	
Sig. Year (Y)†		*	‡	*	***	***	***	***	***			
Sig. Nitrogen (N)		*	‡	‡	ns§	‡	ns	ns	**			
Sig. Cultivar (C)		ns	ns	ns	ns	***	***	ns	ns			
Sig. interactions		ns	ns	ns	ns	Y × C‡	ns	ns	ns			
LSD ( <i>P</i> = 0.05) N			0.098	1.6		1.6	0.27	0.008	0.23	32.2		
LSD ( <i>P</i> = 0.05) N, within Y × C			0.062	2.4		1.2	0.98	0.017	0.18	30.2		

\* Significant at the 0.05 level.

\*\* Significant at the 0.01 level.

\*\*\* Significant at the 0.001 level.

† Critical cumulative intercepted PAR calculated as explained in Table 4.

‡ Significant at the 0.1 level.

§ ns, nonsignificant at the 0.1 level.

might have resulted from differences in crop N deficiency, cultivars, and timing of N deficiency. Sivasankar et al. (1998) recently reported a differential response in leaf area expansion of two wheat genotypes to N supply. One genotype reduced leaf area expansion and maintained leaf [N] per unit of dry weight with reduced N

supply, but leaf area expansion for the other genotype was hardly reduced. According to Grindlay (1997), all cultivated C<sub>3</sub> species adjust their leaf area expansion rate and maintain their N<sub>LA</sub> with decreasing N. Grindlay (1997) suggested that the variation of cultivated species in response of LUE and photosynthesis to N<sub>LA</sub> has been

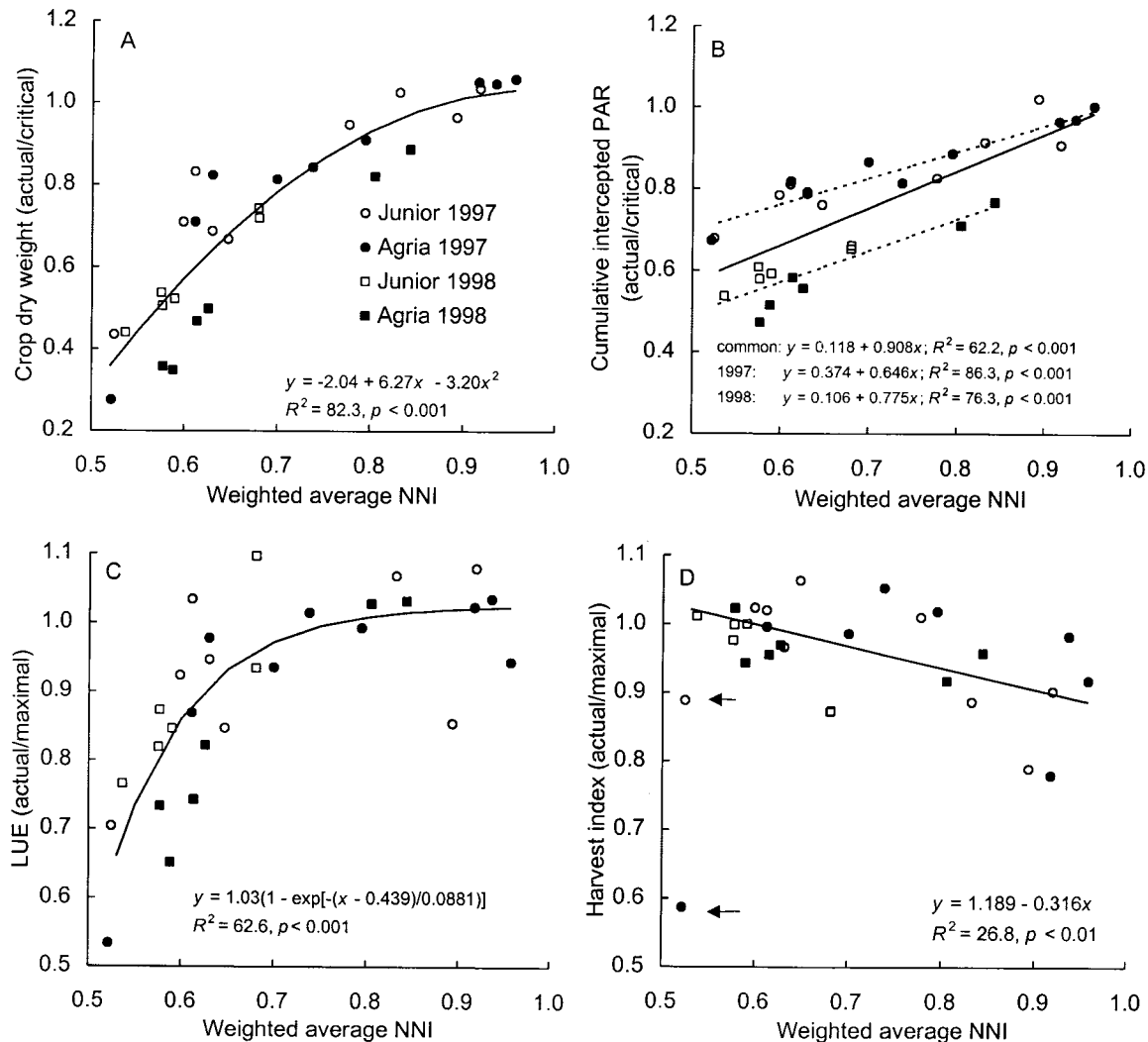


Fig. 4. Influence of average N nutrition index (NNI) on the relative values of (A) crop dry weight, (B) cumulative intercepted photosynthetically active radiation (PAR), (C) light use efficiency (LUE), and (D) harvest index of potato at about 52 d after emergence (DAE) in 1997 and 47 DAE in 1998. The values are relative to maximum or critical values given in Table 4. Points represent individual replicates. Solid regression lines include all points, except those indicated by arrows. Dotted lines represent separate years.

decreased as a result of selection. Photosynthesis decreases much faster with decreasing N per unit of leaf area for  $C_4$  crops than for  $C_3$  crops (Grindlay, 1997), which may explain the higher sensitivity of LUE to N shortage in maize and sorghum (compare Muchow and Sinclair, 1994 with Booij et al., 1996).

Although N limitations starting during early growth stages of wheat generally do not reduce the LUE under field conditions (e.g., Meinke et al., 1997), N limitations during the postanthesis period may cause N loss from leaves and a reduction in photosynthesis of flag leaves (Gregory et al., 1981). Under such conditions, the LUE of wheat may be reduced. In contrast to wheat, a potato crop sheds its leaves upon a late N limitation while maintaining its leaf [N] of the remaining leaves.

#### Relationship between Leaf Parameters and Nitrogen Nutrition Index

A smaller N deficiency (larger NNI) increased the average leaf [N] in potato based on dry weight (Fig. 6B)

but had no effect on the mean  $N_{LA}$  (Fig. 6A) (Table 6). The slope of these relationships did not vary with year or cultivar, but the intercept did (Table 6). A smaller N deficiency increased the total leaf area duration for potato (Fig. 6C), decreased the thermal duration from emergence to 50% intercepted PAR (Fig. 6D), and increased the maximum LAI (Fig. 6E). Within each year, the early cultivar Junior had a smaller leaf area duration at any given NNI compared with the later cultivar Agria (Table 6).

For wheat, a smaller N deficiency increased the leaf [N] based on both dry weight (Fig. 7B) and leaf area (Fig. 7A). The slopes did not vary with year or cultivar (Table 7). The response of wheat to a smaller N deficiency was comparable to that of potato with respect to total leaf area duration (Fig. 7C), early foliar expansion (Fig. 7D), and maximum LAI (Fig. 7E). At a given average NNI, the leaf area duration was larger for cultivar Baldus than for cultivar Axona (Fig. 7C and Table 7).

For potato and wheat, the present study (Fig. 6 and 7) showed that the response of  $N_{LA}$  to average NNI

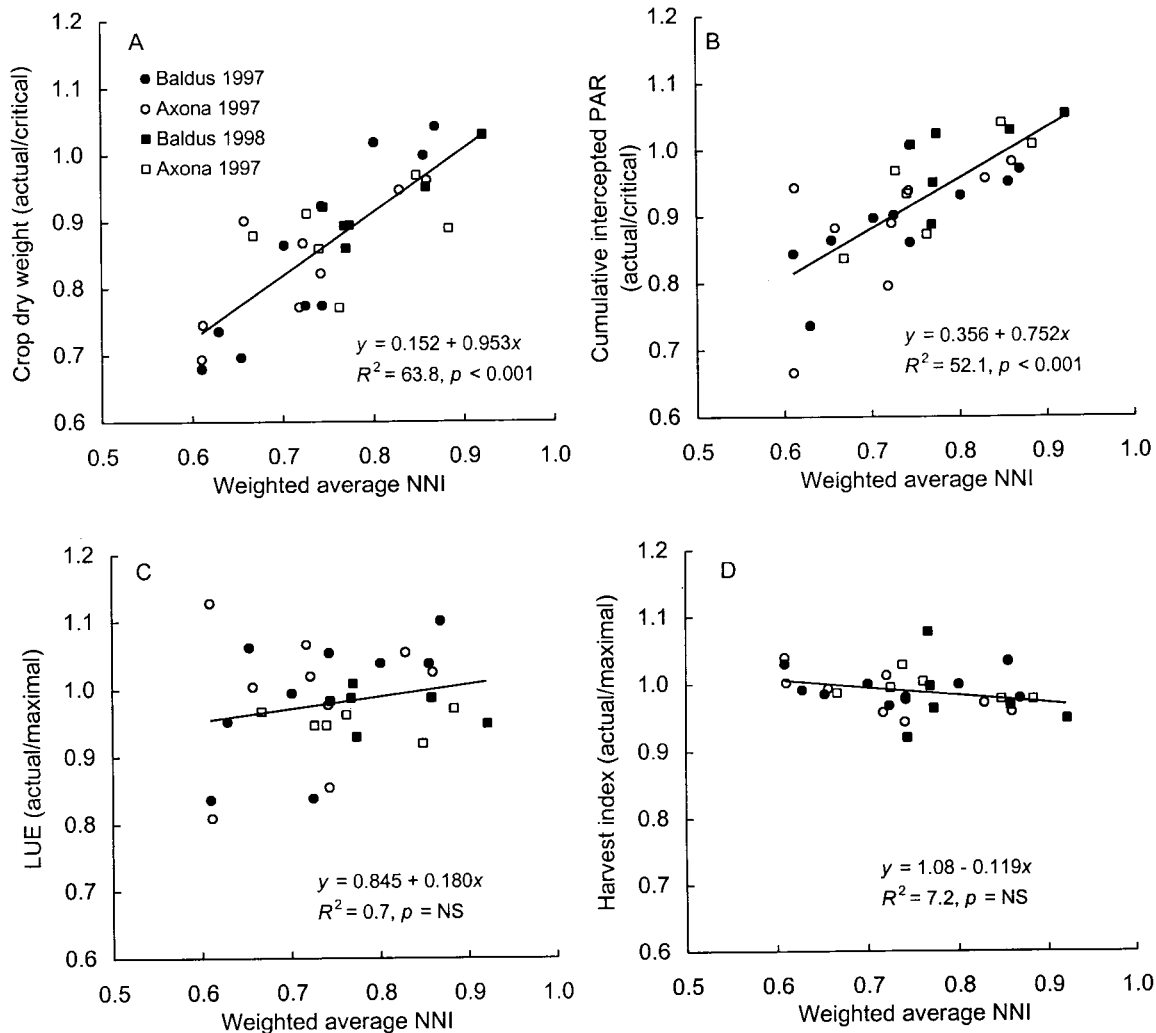


Fig. 5. Influence of average N nutrition index (NNI) on relative values of (A) crop dry weight, (B) cumulative intercepted photosynthetically active radiation (PAR), (C) light use efficiency (LUE), and (D) harvest index for wheat at 102 d after emergence (DAE) in 1997 and 86 DAE in 1998. The values are relative to maximum or critical values given in Table 5. Points are for individual replicates. Solid regression lines include all points. NS, nonsignificant at the 0.1 level.

was smaller than the LAI response, supporting earlier observations for potato (Vos and van der Putten, 1998), wheat (Evans, 1983), and other  $C_3$  species (see Grindlay, 1997). Those results also support the conclusion that both crops adjusted leaf area expansion to the limiting N supply while maximizing  $N_{LA}$  and LUE. Potato leaf [N] ( $\text{kg kg}^{-1}$ ) increased more with increased N supply than did  $N_{LA}$  ( $\text{g m}^{-2}$ ) because the specific leaf area increased with increasing N. When leaf expansion is N limited, the specific leaf area may decrease due to accumulation of starch and cell wall material (Grindlay, 1997). In a field study, Vos (1995) found no effect of N supply on specific leaf area of main-stem leaves for potato up to 43 DAE. No change was found in specific leaf area of wheat in the present study, which supports earlier results of Meinke et al. (1997).

Observed patterns of LUE with NNI (Fig. 4 and 5) could not be explained solely from average  $N_{LA}$ . To explain those patterns, measurements of leaf N distribution would be required, as explained below. A decrease

of NNI from 1 to 0.44 decreased the LUE in potato by 34% while average  $N_{LA}$  remained constant. In contrast, the LUE for wheat did not decrease with N deficiency, whereas the average  $N_{LA}$  for both cultivars decreased by about 20%. This difference between crops may have resulted from a decrease in leaf [N] with increased canopy depth, which has been found in wheat (Dreccer et al., 2000) and potato (Osaki, 1995). The photosynthesis and leaf [N] of top leaves in a canopy is of main importance for the LUE of a crop (Yin et al., 2000).

### Towards Optimization of Organic Nitrogen Management

The present study was conducted to improve our knowledge of the responses of light interception, LUE, and harvest index to N. Ultimately, these findings are to be used to improve organic N management. Longer leaf area duration, and thus an increased light interception, increased yields with increased N supply. Shortage

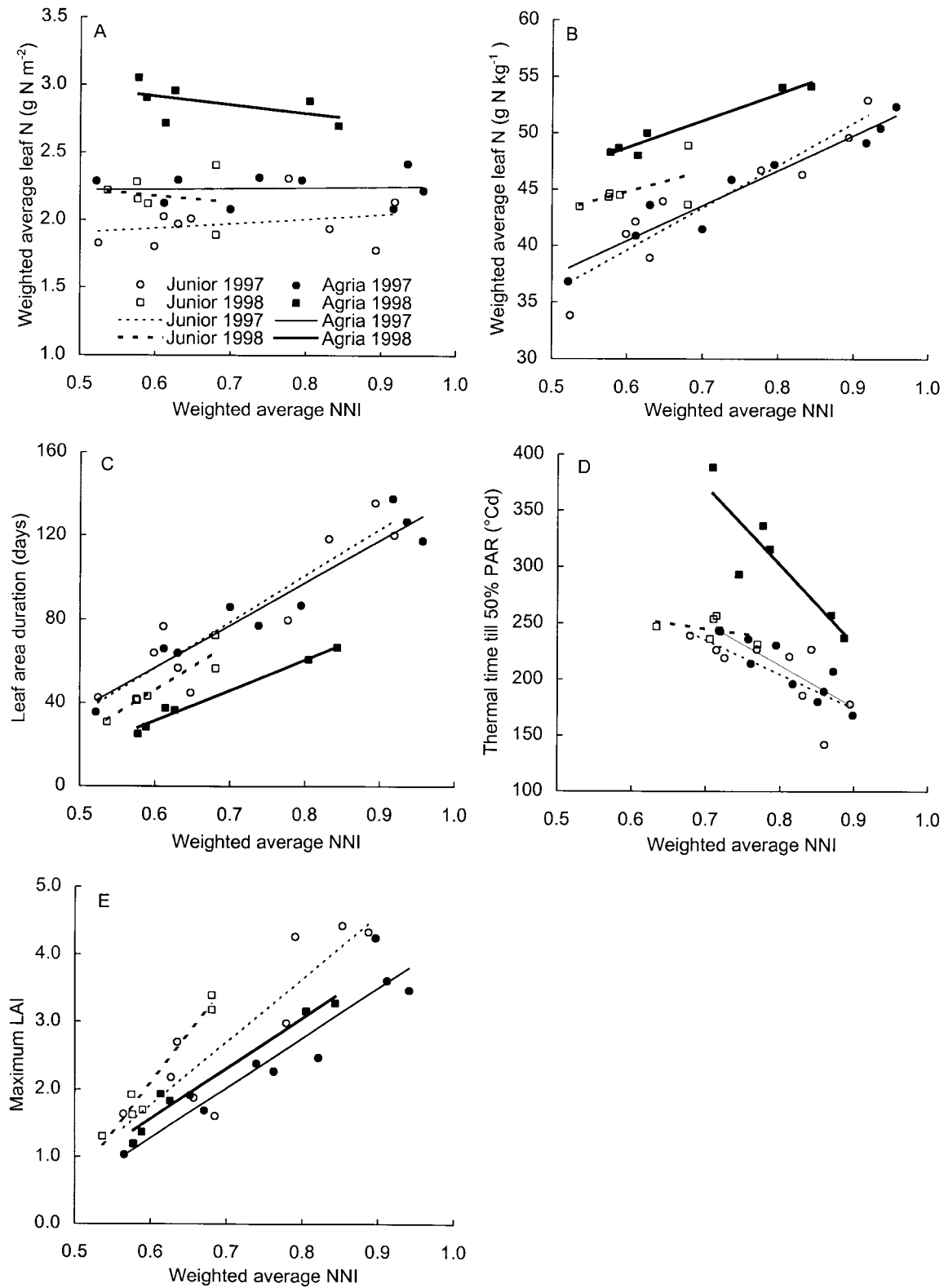


Fig. 6. Influence of average N nutrition index (NNI) on average (A) areal leaf N content ( $N_{LA}$ ;  $\text{g m}^{-2}$ ), (B) leaf N concentration ( $[N]$ ;  $\text{g kg}^{-1}$ ), and (C) leaf area duration of potato at about 52 d after emergence (DAE) in 1997 and 47 DAE in 1998. Influence of NNI on (D) thermal time till 50% intercepted photosynthetically active radiation (PAR) at start of the season and (E) maximum leaf area index (LAI) of potato. Points are for individual replicates. Lines are regression lines for each cultivar and year separately. Parameter estimates of lines are in Table 6.

**Table 6. Linear regressions between N nutrition index (NNI) (independent variable) and average areal leaf N content ( $N_{LA}$ ; g N m<sup>-2</sup>), leaf N concentration ( $[N_L]$ ; g N kg dm<sup>-1</sup>), and leaf area duration (LAD; days) of potato at about 52 d after emergence (DAE) in 1997 and 47 DAE in 1998. Regressions also are given for NNI and thermal time from emergence till 50% intercepted photosynthetically active radiation (PAR) ( $t_{50}$ ; °Cd) and maximum leaf area index ( $LAI_m$ ). Residual maximum likelihood (REML) analysis for effects of year (Y) and cultivar (C) on regression parameters.**

	Y	C	Intercept		Slope		Regression		Slope	Among slopes	Among lines	LSD ( $P = 0.05$ )
			Mean	SE	Mean	SE	$R^2$	$P$				
$N_{LA}$	1997	Junior	1.74	0.32	0.34	0.43	–	ns†	ns	ns	Y × C	a
	1997	Agria	2.19	0.22	0.06	0.28	–	ns			***	b
	1998	Junior	2.47	0.88	–0.48	1.44	–	ns				ab
	1998	Agria	3.30	0.34	–0.63	0.5	10.4	ns				c
$[N_L]$	1997	Junior	16.8	3.9	38.0	5.3	86.1	***	***	ns	Y × C	a
	1997	Agria	21.7	2.5	31.3	3.3	91.8	***			***	a
	1998	Junior	33.5	8.5	18.9	13.9	14.5	ns				b
	1998	Agria	34.4	1.8	23.9	2.7	94.1	***				c
LAD	1997	Junior	–77.1	26.5	223	37	82.0	***	***	Y	C	
	1997	Agria	–65.2	17.7	204	23	90.7	***		***	***	
	1998	Junior	–92.0	26.0	230	43	84.9	**				
	1998	Agria	–56.3	7.1	146	10	97.5	***				
$t_{50}$	1997	Junior	450	90	–307	114	44.0	*	***	ns	Y × C	a
	1997	Agria	511	65	–373	79	72.7	**			***	a
	1998	Junior	312	73	–95	103	–	ns				a
	1998	Agria	862	145	–701	181	73.6	*				b
$LAI_m$	1997	Junior	–3.91	1.34	9.45	1.84	76.0	**	***	C		
	1997	Agria	–3.17	0.82	7.42	1.05	86.0	***		*		
	1998	Junior	–6.54	0.91	14.39	1.49	94.8	***				
	1998	Agria	–2.93	0.49	7.48	0.72	95.5	***				

\* Significant at the 0.05 level.

\*\* Significant at the 0.01 level.

\*\*\* Significant at the 0.001 level.

† ns, nonsignificant.

of N in the N1 and N2 treatments developed early in the season and resulted in a reduced rate of early leaf-area expansion (Fig. 6D and 7D). Shortages were greater for potato than for wheat (Fig. 3) based on soil mineral N contents ( $N_{min}$ ) and expected net N mineralization from manure. The  $N_{min}$  of 82 kg N ha<sup>-1</sup> (0–0.6 m; Table 2B, N2) at planting of potato and subsequent

expected net mineralisation of 30 to 50 kg N ha<sup>-1</sup> (Table 2B) totaled about 120 kg N ha<sup>-1</sup>. Such N contents are well below the recommended values in regular farming of 265 – 1.1 ×  $N_{min}$  (Van Dijk, 1999). The  $N_{min}$  of 99 kg N ha<sup>-1</sup> at planting (Table 2B, N2) for wheat plus the expected net N mineralization during the first half of the season (20 kg N ha<sup>-1</sup>, half values of Table 2B)

**Table 7. Linear regressions between the average N nutrition index (NNI) (independent variable) and weighted average areal leaf N content ( $N_{LA}$ ; g N m<sup>-2</sup>), leaf N concentration ( $[N_L]$ ; g N kg dm<sup>-1</sup>), and leaf area duration (LAD; days) of wheat at 102 d after emergence (DAE) in 1997 and 86 DAE in 1998. Linear regressions also are given for NNI and thermal time until 50% intercepted photosynthetically active radiation (PAR) ( $t_{50}$ ; °Cd) and maximum leaf area index ( $LAI_m$ ). Residual maximum likelihood (REML) analysis for effects of year (Y) and cultivar (C) on regression parameters is given.**

	Y	C	Intercept		Slope		Regression		Slope	Among slopes	Among lines
			Mean	SE	Mean	SE	$R^2$	$P$			
$N_{LA}$	1997	Axona	0.73	0.16	1.29	0.22	80.1	***	***	ns†	C
	1997	Baldus	0.78	0.20	0.96	0.28	58.2	*			***
	1998	Axona	0.89	0.22	1.04	0.28	71.2	*			
	1998	Baldus	0.44	0.32	1.38	0.40	69.1	*			
$[N_L]$	1997	Axona	11.7	1.8	29.6	2.5	94.6	***	***	ns	Y
	1997	Baldus	13.7	3.2	27.1	4.3	82.8	***			***
	1998	Axona	18.4	2.9	24.8	3.8	89.4	**			
	1998	Baldus	11.0	6.8	34.7	8.4	76.1	*			
LAD	1997	Axona	–76.5	46.1	305	63.4	73.4	**	***	ns	C
	1997	Baldus	–80.4	57.2	340	78.1	69.1	**			***
	1998	Axona	–85.5	68.6	317	88.5	70.4	*			
	1998	Baldus	55.0	109.0	169	134.0	10.3	ns			
$t_{50}$	1997	Axona	1553	367	–1225	390	52.5	*	***	ns	Y
	1997	Baldus	962	156	–600	165	60.4	**			***
	1998	Axona	2487	555	–2219	565	74.3	*			
	1998	Baldus	2974	726	–2700	735	71.4	*			
$LAI_m$	1997	Axona	3.62	3.29	7.65	3.96	25.5	‡	***	Y × C	
	1997	Baldus	–10.47	2.18	16.04	2.52	83.1	***		*	
	1998	Axona	–6.49	3.12	12.27	3.75	66.0	*			
	1998	Baldus	–2.89	6.90	8.20	7.92	1.4	ns			

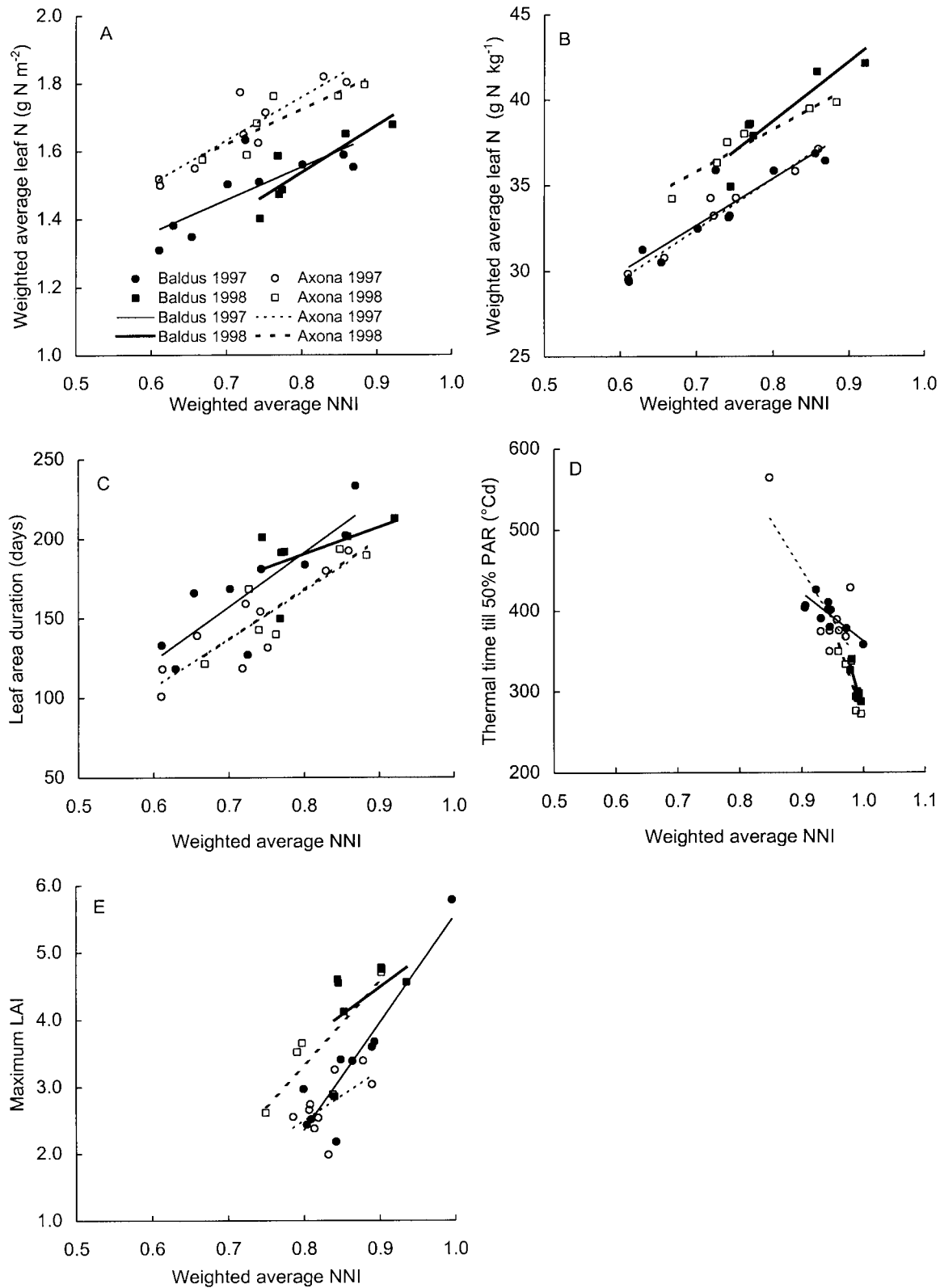
\* Significant at the 0.05 level.

\*\* Significant at the 0.01 level.

\*\*\* Significant at the 0.001 level.

† ns, nonsignificant at the 0.1 level.

‡ Significant at the 0.1 level.



**Fig. 7.** Influence of average N nutrition index (NNI) on average (A) areal leaf N content ( $N_{LA}$ ; g m<sup>-2</sup>), (B) leaf N concentration ([N]; g kg<sup>-1</sup>), and (C) leaf area duration of wheat at 102 d after emergence (DAE) in 1997 and 86 DAE in 1998. Influence of NNI on (D) thermal time till 50% intercepted photosynthetically active radiation (PAR) at start of the season and (E) maximum leaf area index (LAI) of wheat. Points are for individual replicates. Lines are regression lines for each cultivar and year separately. Parameter estimates of lines are in Table 7.

totalled about 120 kg N ha<sup>-1</sup>. Such values were close to recommended rates in regular farming until stem extension, being 120 – N<sub>min</sub> (Van Dijk, 1999). In the present study, and in others (Korva and Varis, 1990), crops supplied with organic N sources were N limited early in the season because initial N<sub>min</sub> plus released N was too small to meet crop demands. Early N limitation by crops may depend on weather conditions determining N leaching during winter, rates of N mineralization, and the kind of organic N sources. Early N limitations are expected to be smaller, with an organic N source that decomposes rapidly (e.g., green manure) and contains a large proportion of mineral N (e.g., a slurry compared with farmyard manure). Further research is required on (i) matching crop N supply with demand while subjecting the crop to a range of organic N sources and (ii) comparing the LUE and leaf area dynamics among C<sub>3</sub> and C<sub>4</sub> crops under a range of mineral N fertilizer levels. Once established, this should be followed by a comparison of their yield response under organic N management.

### Appendix 1: Calculation of Expected Nitrogen Mineralization from Organic Sources

#### Cattle Slurry

Expected N mineralisation (ENM) from cattle slurry was calculated according to Lammers (1983):

$$\begin{aligned} ENM &= S \times N_{\text{tot}} \times \left( \frac{N_{\text{org}}}{N_{\text{tot}}} \right) \times \left( \frac{N_e}{N_{\text{org}}} \right) \times \left( \frac{N_{\text{season}}}{N_e} \right) \\ &= S \times 4.9\% \times 0.5 \times 0.5 \\ &\quad \times \{0.60 \text{ potato}, 0.66 \text{ wheat}\} \end{aligned}$$

where  $S$  is the amount of applied cattle slurry (Mg ha<sup>-1</sup>),  $N_{\text{tot}}$  is the N content of the slurry (kg N Mg<sup>-1</sup>),  $N_{\text{org}}$  is the organic N content,  $N_e$  is the organic N content released within the first year after application, and  $N_{\text{season}}$  is the amount of mineralized N that becomes available during the months of the growing season.  $N_{\text{tot}}$  of cattle slurry is, on average, 4.9 kg N Mg<sup>-1</sup> fresh matter (Van Dijk, 1999). The different N fractions are from Lammers (1983).  $N_{\text{season}}/N_e$  is smaller for potato than for wheat because cattle slurry for potato was applied in the autumn, whereas that for wheat was applied in spring and more N is lost with the autumn application than with the spring application.

#### Garden Compost

Expected N mineralization from garden compost was estimated to be 10% from total N content (Van Dijk, 1999), with a N content of 10.7 kg N Mg<sup>-1</sup> fresh matter (Schröder, unpublished, 1996).

#### Leaves of Sugarbeet

Nitrogen mineralization from leaves of sugarbeet (*Beta vulgaris* L.) was estimated to be 30 kg N ha<sup>-1</sup> (Van Dijk, 1999)

### Appendix 2: Calculation of Daily Intercepted Photosynthetically Active Radiation

Spitters (1990) described the course of light interception during the growing season with a logistic function:

$$F_t = \frac{F_0 M}{F_0 + (M - F_0)e^{-R_0 t}} \quad [A1]$$

where  $F_t$  is the fraction of intercepted light,  $F_0$  is the initial fraction of intercepted light at crop emergence,  $M$  is the maximum fraction of intercepted light,  $R_0$  (°Cd)<sup>-1</sup> is the relative increase rate for light interception, and  $t$  (°Cd) is the thermal time with a base temperature of 2°C (potato) and 0°C (wheat). The decline in light interception was assumed to be linear, which was a simple but adequate description for this study:

$$F_t = M - at \quad [A2]$$

where  $a$  (°Cd)<sup>-1</sup> is the slope of the linear decline of the fraction of intercepted light with thermal time. Because it was not clear which points to include up to the maximum and which thereafter, equations A1 and A2 were combined:

$$F_t = \frac{F_0 (M - at)}{F_0 + (M - F_0)e^{-R_0 t}}$$

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