

**Yielding ability and weed suppression of  
potato and wheat under organic  
nitrogen management**

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# **Yielding ability and weed suppression of potato and wheat under organic nitrogen management**

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Proefschrift  
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## Stellingen

behorende bij het proefschrift van Arnout van Delden, Yielding ability and weed suppression of potato and wheat under organic nitrogen management. Wageningen University, 26 November 2001.

1. De bladoppervlaktetoename van aardappel en tarwe in het veld kan beter verklaard worden met een wisseling tussen temperatuur- en stralingsgestuurde expansie, dan door uitsluitend temperatuur of straling.  
(dit proefschrift)
2. In gewassystemen met weinig beschikbare stikstof in de bodem verhoogt een stikstofgift de reproductie van laatopkomende onkruiden, ondanks een verhoogde lichtonderschepping door het gewas.  
(dit proefschrift)
3. De lichtbenuttingsefficiënte van aardappel kan beter berekend worden op basis van de lichtonderschepping door groene gewasdelen, dan op basis van de bodembedekking door groen blad.  
(dit proefschrift)
4. Opbrengsten van akkerbouwgewassen in de biologische landbouw kunnen worden verhoogd door rond gewasopkomst een mestsoort aan te wenden die rijk is aan direct opneembare stikstof.  
(dit proefschrift)
5. Voor de relevantie van nutriëntenonderzoek voor de biologische landbouw is het niet nodig dat het onderzoek uitsluitend in een biologisch landbouwsysteem wordt uitgevoerd.
6. Statistische programma's waarbij de gebruiker de stappen in de analyse niet hoeft te programmeren vergroten de kans op het trekken van onjuiste conclusies.
7. Mensen in de huidige maatschappij zijn omgekeerde utopisten: terwijl utopisten niet kunnen maken wat zij zich voorstellen, kunnen wij ons niet voorstellen wat er technisch al mogelijk is.  
(Günter Anders in: P. van Dijk, 1998. Günter Anders Antropologie in het tijdperk van de techniek, Damon).

8. Mensen die sektarisch denken en daarbij gewelddadige termen gebruiken, leveren de munitie voor hen die terreur plegen.
9. AIO's zullen aantoonbaar minder uitlopen na het tijdig volgen van een cursus projectmatig werken.
10. Je moet op vakantie gaan als je er geen tijd voor hebt.
11. Iemand met twee linkerhanden is slechts onhandig als hij rechtshandig is.

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## Abstract

Van Delden, A., 2001. Yielding ability and weed suppression of potato and wheat under organic nitrogen management. PhD Thesis. Wageningen University, The Netherlands. English and Dutch summaries.

Understanding how to obtain good yields and farm profits in arable organic farming systems is useful for conventional and integrated farming to decrease the current reliance on pesticides and mineral fertilisers. Two issues are of particular importance for organic farming: organic nitrogen (N) management and weed management.

Optimisation of organic N management is complex because N directly affects crop growth and yield, and indirectly affects pests, diseases and weeds. Yields in organic farming are known to be 0–50% lower than in conventional farming, but it is unclear to what extent this is due to direct effects of N on growth. N management may also influence growth and reproduction of late-emerging weeds. Although they do not directly damage the crop, they may cause long-term weed management problems due to replenishment of the seed bank.

The direct effects of N management on crop growth and yield of the target crops potato and wheat, and on establishment and reproduction of late-emerging weeds were investigated in a series of field experiments. Yield under organic N management strategies was explored with a model for crop growth and N dynamics in crop and soil. Nitrogen applied by slurry in amounts currently used in organic farming was found to limit growth of potato and wheat from emergence onwards. Early N limitations caused a linear decrease in the rate of early foliar expansion, while the light use efficiencies of the crops were hardly affected. Early foliar expansion rates with sufficient N were studied in more detail because they are an important base to calculate N-limited expansion rates. A combination of experiments and simulations showed that early foliar expansion rates with sufficient N could best be predicted when driven by temperature from emergence onwards up to a leaf area index of 1 for potato and 1.5 for wheat, after which they were driven by radiation. Model explorations showed that potato tuber yields under organic N management varied considerably with timing of slurry application, weather conditions and crop maturity class, and that low yields were associated with early N shortages. Increased N supply decreased reproduction of late-emerging *Stellaria media* in potato, but increased that in wheat. It is concluded that a basic dressing of an organic N source with a large proportion of mineral N could improve crop yields in organic farming, while row application of such manure may favour the crop relative to the weed.

*Keywords:* chickweed, early growth, leaf area expansion, light interception, light use efficiency, manure, mineralisation, modelling, organic farming, organic matter, soil nitrogen content, *Solanum tuberosum* L., specific leaf area, *Stellaria media* (L.) Vill., *Triticum aestivum* L., weed suppression.

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## Table of contents

	Page
Chapter 1    General introduction	1
Chapter 2    Yield and growth components of potato and wheat under organic nitrogen management	9
Chapter 3    Temperature response of early foliar expansion of potato and wheat	39
Chapter 4    Modelling temperature- and radiation-driven leaf area expansion in the contrasting crops potato and wheat	65
Chapter 5    Simulation of attainable potato yield under different organic nitrogen management strategies: model development and explorations	97
Chapter 6    The influence of nitrogen supply on the ability of wheat and potato to suppress <i>Stellaria media</i> growth and reproduction in organic farming systems	129
Chapter 7    General discussion	153
References	167
Summary	183
Samenvatting	189
Curriculum vitae	195
Dankwoord	197

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# 1

## General introduction

## ***External inputs***

After 1945, crop yields increased as a result of the increased use of mineral fertilisers, the introduction of herbicides and pesticides, irrigation, mechanisation and improved crop varieties (De Wit, 1992; Evans, 1998). The intensification of agricultural production not only led to the necessary production increase, but also had a number of unintended consequences. The cultivation of a limited number of genotypes raised concern about the maintenance of genetic diversity of arable crops. The widespread use of pesticides resulted in resistance to pesticides, outbreaks of secondary pests, rapid resurgence of target pest populations, undesirable environmental effects, hazards to pesticide handlers and concerns about food safety (Stern et al., 1959; Smith et al., 1976). Overuse of nitrogen (N) and phosphorus (P) in agriculture contributes to acidification, eutrofication of aquatic ecosystems, and contamination of groundwater that is used for drinking water.

Agricultural production is particularly intensive in The Netherlands, with specialised arable and livestock production systems. Dutch agricultural production is among the highest in Europe, and is efficient in terms of input per kg of product and has a low emission per kg of product (Rabbinge and De Wilt, 1998). Due to the intensity, size and concentration of agricultural activity in The Netherlands, its contribution to environmental pressure is large. Nation-wide, the yearly agricultural input of N and P exceeds the removal by harvested products by 324 kg N ha<sup>-1</sup> and 31 kg P ha<sup>-1</sup> (Fong, 1999). This N and P surplus is one of the largest in Europe (Van Bruchem, 1997). Since the 1980s, the Dutch government has initiated regulations on the use of animal manure and mineral fertilisers (Henkens, 2001). During 1987–1998, those regulations aimed to restrict the application rates of manure. In 1998, the mineral accounting system (MINAS) was introduced, which only allows a maximum surplus of N and P at the farm level (Smit, 2001). Furthermore, regulations are initiated to restrict the production of manure (Henkens, 2001).

Also the agricultural inputs of pesticides in The Netherlands are among the highest in Europe (Van Bruchem, 1997). In 1984–1986, average pesticide use was 20 kg active ingredients ha<sup>-1</sup> (Anonymous, 1990). In 1992, the Dutch government adopted a policy plan which aimed to reduce the annual pesticide use by about 50% in 2000 (Anonymous, 1990), down from the 1984–1986 reference period. By 1998, the average pesticide use was reduced by 43%, which was mainly achieved because of a reduction in the use of soil disinfectants (Anonymous, 2000a). Since 2000, a new policy plan has been adopted that aims to further reduce the average pesticide use (Buurma et al., 2000).

### ***The importance of increased insight in ecological processes***

From an agricultural point of view, the challenge is to reduce the negative side effects of farming and still obtain good crop yields. Different strategies exist to reduce nutrient and pesticide losses to the environment (Rabbinge and De Wilt, 1998). Two of those strategies involve the use of measures to improve the resource use efficiency of inputs: 1) by taking measures integrated within the current production systems, and 2) by taking measures that go beyond the farming systems level.

The first strategy can be achieved by a more judicious use of external inputs, e.g. by using techniques for fine-tuning in space and time of mineral fertilisers (Schröder et al., 2000b) and biocides (Lotz et al., 2000b). The first strategy includes a decreased reliance on mineral fertilisers and pesticides. That requires an increased understanding of ecological processes underlying the interactions between soil, crops and pests (including diseases and weeds). An example of the latter is that insight into the mechanisms of interplant competition, have been used to improve the suppression of weeds by crops (Baumann et al., 2001a).

The second strategy involves the exchange of inputs, resources and waste materials between agricultural sectors. A well-known example is the export of manure from dairy to arable farming, and the export of fodder crops (grains, lucerne) from arable to dairy farming. This exchange contributes to a reduction in the national N and P surplus when accompanied by a reduced use of mineral fertilisers, because the current large production of nutrients (manure) on dairy farms is accompanied by a lack of farmland area to apply the manure on (Smit, 2001). The use of manure on arable land requires insight into the effects of organic N management on crop growth in order to optimise N supply with crop demand.

Research on organic arable farming, that prohibits the use of biocides and mineral fertilisers, is especially useful for understanding effects of organic N management on crop growth, and to improve understanding of ecological processes underlying the interactions between soil, crops, and pests, diseases and weeds. In the present thesis, two topics were addressed that have been identified as important issues for organic farming: the effect of N management on crop growth, and its effect on weed growth and reproduction (Vereijken et al., 1994; David, 1998; Vereijken, 1998).

### ***Challenges of organic farming***

Optimisation of N management in organic farming is a complex matter. Nitrogen management is not only a question of optimising crop yields and minimising N losses, but also of considering the effects of N on the occurrence of pests. Several studies showed that arable crop yields in organic farming are often smaller than in conventional (including integrated) farming (e.g. Eltun, 1996), with yield reductions

ranging from 0–50% for potato and wheat (Stanhill, 1990; Tamis and Van den Brink, 1999). It is unclear, however, to what extent the yields in organic farming are limited by nutrients, or reduced by pests (Möller et al., 1997; Haraldsen et al., 2000). When properly fertilised, yields in Dutch arable organic farming are not often limited by K or P, as Dutch soils generally have soil K and P contents that are sufficient for optimal growth (Pothoven, 1995). Nitrogen, however, which is more mobile than P and K, is expected to be most limiting nutrient in organic farming.

The first challenge for organic farming is to match soil N supply with crop N demand. Using a simulation study, Pang and Letey (2000) found that the dynamics of soil N supply did not match well with the dynamics N uptake of maize under conditions of sufficient N. They concluded that it would be difficult to fertilise the crop with only organic N to meet peak N demands mid-way the crop growth cycle, without an excessive N in the soil before and after crop growth. Field measurements on organic farms by Poutala et al. (1993), however, suggest that N limits wheat growth from emergence onwards.

Understanding of crop response to organic N supply requires the quantification of crop N demand and deficiency, in order to determine the timing of N deficiency and to establish relationships between N deficiency and major crop growth processes.

Understanding of early leaf area expansion is especially important for organic farming. Leaf area expansion is an important determinant of crop growth. Nitrogen-limited crops generally have smaller leaf area indices (Grindlay, 1997), resulting in smaller light interceptions and lower crop growth rates. Because the increase in light interception with leaf area index is largest at small leaf area indices, quantification of early leaf area expansion is important. The dynamics of early leaf area expansion are also important for crop–weed competition, because differences in the rate of are often decisive for the establishment and growth of the crop and the weed (Kropff et al., 1992). Although canopy leaf area dynamics are important, they remain difficult to predict in new environments; a better understanding of the main factors affecting leaf area development, temperature and radiation is therefore needed.

A second challenge of organic farming is to reduce the many hours of hand weeding that are needed on organic farms at present (Peacock and Norton, 1990; Vereijken, 1998; Lotz et al., 2000a). Optimisation of weed management requires the use of long-term approaches that account for the dynamics of weed populations over a rotation (Wallinga and Van Oijen, 1997; Jones and Medd, 2000), and that consider the seed set of (uncontrolled) weeds (Wallinga and Van Oijen, 1997). In a survey in The Netherlands, many reproducing weeds were found in potato and wheat crops (Vereijken, 1998). Chickweed, *Stellaria media* (L.) Vill., was the main weed with densities up to 8 plants per m<sup>2</sup>. In potato and wheat, weeds are mechanically controlled mainly in the early part of the growing season when the crop is still small and soil cover is not yet complete. As mechanical control in potato and wheat can kill up to 80% of the *S. media* plants (Darwinkel et al., 1993; Hoffmann, 1994), it seems

likely that the uncontrolled late-emerging *S. media* plants contribute significantly to the seed bank.

It can be assumed that the effect of increased soil N supply on growth and reproduction of late-emerging weeds largely depends on the outcome of the crop–weed competition for light and N. We hypothesised that increased soil N supply reduces the growth and reproduction of late-emerging weeds in wheat and potato, as a result of a larger leaf area index and light interception by the crop at time of weed emergence.

In the present thesis, potato and wheat crops were selected as target species, for various reasons. Firstly, both species are important in a rotation of organic arable farming: potato mainly because it is an economically high value crop, and wheat because it reduces the intensity of soil-borne diseases and pests, and because it improves the soil structure of heavily textured soils. Secondly, both crops may exhibit different types of responses to N. Wheat has a larger N recovery than potato, because its roots penetrate the soil faster and reach a greater final depth, and because wheat has a larger root length density than potato (Vos and Groenwold, 1986). Wheat is therefore expected to be less sensitive to small soil N supplies than potato. Thirdly, the response of crop growth processes to N deficiency is expected to differ between the dicot potato and the monocot wheat (see Radin 1983; Vos and Van der Putten, 1998).

### ***Research objectives***

The main objectives of the study were to quantify and understand:

1. The response of major crop growth processes to N;
2. Early foliar expansion as driven by temperature and radiation;
3. The integrated effects of organic N management on crop growth and yield; and
4. Growth and reproduction of late-emerging weeds under organic N supply to crops.

Based on the understanding of the effects of organic N management on crop growth processes and yield, recommendations for improvement of organic N management can be given. Furthermore, an understanding of interacting effects of N on crop and late-emerging weeds, will be used for recommendations to reduce seed setting of late-emerging weeds in organic farming.

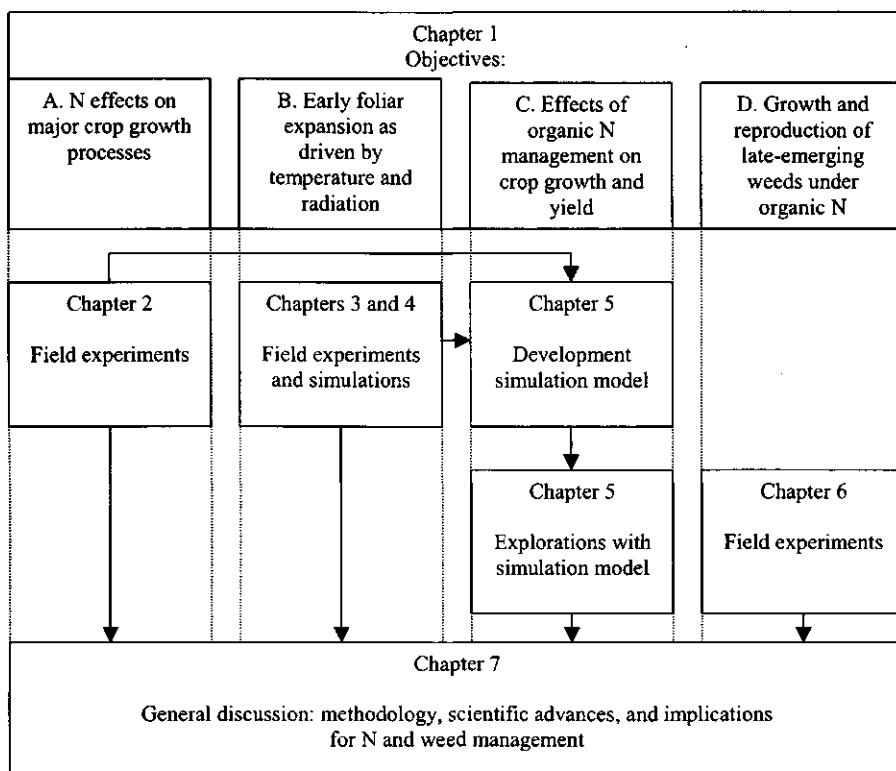


Figure 1. Schematic representation of the thesis. Arrows indicate flow of information.

### *Approach and outline of the thesis*

Research objectives were studied by combining field experiments with simulation models, as illustrated in Fig. 1. A series of field experiments was conducted to establish relationships between the rate of N supply, as supplied by organic sources, and crop growth processes of potato and wheat, particularly leaf area development and light use efficiency (Chapter 2). Pests and diseases were controlled chemically to avoid crop growth reductions. A particular growth process, early foliar expansion, was quantified in relation to temperature using additional field experiments (Chapter 3). Simulation procedures for leaf area expansion based on temperature and radiation was developed and tested in Chapter 4. The relationships obtained in Chapters 2–4 were integrated in a model that simulates soil and crop N dynamics (Chapter 5). That model was then used to obtain a better understanding of the complex and contrasting effects of organic N-management (sources, levels, timing) on dry matter production and yield

formation under different weather conditions (Chapter 5). Field experiments were used to understand the influence of organic N supply on weed growth and reproduction in a crop canopy, from its effects on soil N supply and crop light interception (Chapter 6). The thesis concludes with a general discussion (Chapter 7) in which the methodology of the study, the scientific achievements and their implications for organic N management are evaluated.



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# 2

## **Yield and growth components of potato and wheat under organic nitrogen management**

A. van Delden

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## Abstract

In order to optimise N management in organic farming systems, knowledge of crop growth processes in relation to N limitation is necessary. The present chapter 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. Potato and wheat cultivars were grown in field experiments (1997, 1998) at three N levels: no N (N1), cattle (*Bos taurus*) slurry (N2), and cattle slurry supplemented by mineral N fertiliser (N3). Estimated available N ( $\text{kg ha}^{-1}$ ) (0–0.9 m soil) was 80 (N1), 150 (N2), and 320 (N3) (potato) and 115 (N1), 160 (N2), and 230 (N3) (wheat). N deficiency was quantified by an N nutrition index (NNI) (1=hardly limited, 0=severely limited). N deficiency increased in the N1 and N2 treatments up to 20 (potato) and 50 (wheat) days 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, a linear increase in 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 concentration. In conclusion, both crops respond to N limitation by reducing light interception while maximising the LUE and leaf N concentration.

## Introduction

Nitrogen (N, list of abbreviations in Appendix 1) management in organic farming systems is complex. The supply of N from organic sources is difficult to synchronise 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 to 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 available N requires more effective distribution among the various crops in order to optimise farm results.

Optimisation 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 photosynthetic active radiation (PAR) by the canopy, in the light use efficiency (LUE), and harvest index (Charles-Edwards, 1982). Depletion and/or shortage of N indicate 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 ( $N_{LA}$ :  $g\ m^{-2}$ ).

Plant species differ in their degree of these two plant responses. Two extreme types of responses are: (1) maintenance of the  $N_{LA}$  necessary for unrestricted productivity per unit leaf area (i.e. maintain LUE at the cost of a reduced rate of leaf area expansion), (2) maximisation of the leaf area expansion and intercepted PAR at the cost of a reduced  $N_{LA}$  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 ground area are achieved when a crop maintains an optimal  $N_{LA}$  necessary for unrestricted productivity per unit leaf area, which corresponds to the first type of response. Goudriaan (1995) also showed that maintaining a smaller  $N_{LA}$  increased the light interception but decreased the daily gross photosynthesis. The second strategy, i.e. maximisation of leaf area expansion with smaller values of  $N_{LA}$ , may be useful for maximising 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 in order to achieve a competitive advantage in large canopy (Grindlay, 1997).

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  $C_3$  crops (Booij et al., 1996). For wheat, a  $C_3$  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  $C_3$  and  $C_4$  species, to be less responsive to N than that of dicotyledons. The LUE of the  $C_4$  cereals maize (*Zea mays* L.) and sorghum (*Sorghum bicolor* L.) responded to the N supply (Muchow and Sinclair, 1994).

Comparison of crop responses to N deficiency requires quantification. To that end, Lemaire et al. (1989) proposed a nitrogen nutrition index (NNI), defined as the ratio of actual/ critical crop [N]:

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

where the critical crop [N] barely limits the growth rate of the crop. For calculation of mean values for NNI over time, a maximum value of 1 is used because crop growth rates are at their maximum for  $NNI \geq 1$ , and  $NNI > 1$  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; Booiij 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 1) to establish relationships between N uptake and dry matter production for potato and spring wheat cultivars, 2) to use these relationships to quantify crop N demand and deficiency, 3) to establish relationships between N deficiency and growth characteristics, and 4) to 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 Dr. H.J. Lovinkhoeve experimental farm, at Marknesse (52°42'N 5°53'E), The Netherlands. The soil was a silt loam soil, with 12 vol% sand (>50 µm), 68 vol% silt (2–50 µm), 20 vol% clay (< 2 µm), 0.023 (g g<sup>-1</sup>) organic matter (Lebbink et al., 1994) and pH-KCl of 7.4 (sampling December 1998). Soil phosphorus and potassium 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 value in the rhizosphere was below 2.85 for potato and below 3.0 for wheat at all sample times.

### ***Treatments***

For each year and crop, N was supplied at three rates (Tables 2 and 3): 1) unfertilised or only garden compost (N1), 2) fertilisations with cattle slurry, conform usage in organic farming systems in The Netherlands (N2), and 3) 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 fertiliser was applied as calcium ammonium nitrate (Table 3) and corrected for expected net N mineralisation from organic sources (Table 2) during the growing season, as explained in Appendix 2.

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

	Potato		Spring wheat
Year	1997		1997
Planting/sowing date	18 April 1997		14 April 1997
Previous crop	Winter wheat		Fodder beet
Green manure crop	Mustard		-
Sampling date $P_w^a$ , K-HCl <sup>a</sup>	30 March 1998		24 Sept. 1998
$P_w$ (mg $P_2O_5$ l <sup>-1</sup> H <sub>2</sub> O)	44		30
K-HCl (mg $K_2O$ 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	Agria	Baldus, Axona
Emergence date	01 June	31 May	27 April
Sampling (DAE)	3,8,15,36,50, 58(N1),65(N2,N3),99	4,9,16,23,39,53 59(N1),75(N2),79(N3),100	9,23,30,45,67,81, 102,114
Year	1998		1998
Planting/sowing date	13 May 1998		9 May 1998
Previous crop	Spring wheat		Fodder beet
Green manure crop	Mustard		-
Sampling date $P_w^a$ , K-HCl <sup>a</sup>	24 September 1998		14 September 1998
$P_w$ (mg $P_2O_5$ l <sup>-1</sup> H <sub>2</sub> O)	30		30
K-HCl (mg $K_2O$ / 100 g dm)	21		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	Agria	Baldus, Axona
Emergence date	28 May	30 May	17 May
Sampling (DAE)	7,18,27,46,63,94	5,16,25,47,82,117	5,15,32,53,86,117

a  $P_w = P_{\text{water}}$  soil phosphorus content  $\geq 21$  and K: soil potassium content  $\geq 21$  is sufficient for a good crop growth of potato and wheat (dm = dry matter)

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

Table 2. Dates and rates of N application, actual total N content in organic N sources and expected net N mineralisation during the growing season for potato and spring wheat, at three N treatments (N1, N2, and N3)<sup>a</sup> in 1997 and 1998.

Crop/ Year	Date manure/ Treatment	Application rate		N rate		Expected net N mineralisation <sup>b</sup>			
		Com- post	Cattle slurry	Com- post	Cattle slurry	Com- post	Cattle slurry	Previous crop	Sum
		Mg fresh matter ha <sup>-1</sup>			kg N ha <sup>-1</sup>				
Potato	02-Sep-96								
1997	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
	30-Sep-97								
1998	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	10-Apr-97								
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
	08-May-98								
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

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

b Calculation of expected net N mineralisation during the growing season is explained in Appendix 2 and presented values of Table 2 are based on measured total and organic N contents of slurry and garden compost. Calculated amount of supplied mineral fertiliser N was based on standard values for organic N contents, as manure samplings were not available at the time.

### Design and plot size

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

Table 3. Sampling date and soil mineral N content just after planting/sowing and expected net N mineralisation from organic sources (expected net N mineralisation (ENM), from Table 2). Dates and rates of mineral N application just after planting/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 (depth: 0–0.9m), ENM and mineral fertiliser N. Crops and treatments are as in Table 2.

Crop/ Year	N Treatment <sup>a</sup>	Soil mineral N		Total ENM	Mineral fertiliser N		Total N
		0–0.6m	0–0.9m		First	Second	
kg N ha <sup>-1</sup>							
Potato		21-Apr-97			26-May-97		
1997	N1	50	61	12	0	0	72
	N2	80	101	28	0	0	129
	N3	112	148	55	110	0	313
		18-May-98			20-May-98		
1998	N1	65	89	6	0	0	94
	N2	84	121	43	0	0	164
	N3	94	127	83	120	0	330
Wheat		21-Apr-97			5-Jun-97		
1997	N1	67	79	30	0	0	109
	N2	90	101	35	0	0	136
	N3	84	94	41	0	75	210
		19-May-98			20-May-98	26-Jun-98	
1998	N1	66	88	30	0	0	118
	N2	107	139	43	0	0	182
	N3	82	108	55	15	75	253

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

### Crop husbandry

Potato tubers were pre-sprouted and planted by machine. Pests and diseases (notably late blight, *Phytophthora infestans*) on potato and wheat were controlled using standard farming practices for the area to avoid interaction of N with biotic factors. In 1998, tubers were disinfected with validamycin (Solacol, H.S.A. bv, The Netherlands) against *Rhizoctonia solani*. By omission, tubers were not disinfected in 1997 and about 5% of the tubers of cultivar Junior were infected by *Rhizoctonia solani* but hardly any tubers of cultivar Agria were infected. Weeds were mechanically controlled by harrowing and hoeing.

Table 4. 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	Potato			Spring wheat					
		treatment <sup>a</sup>	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 g g <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
	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
	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. Year (Y) <sup>b</sup>			n.s.	n.s.		*	**	n.s.	n.s.	
Sig. Nitrogen (N)			**	***		*	*	n.s.	*	
Sig. Cultivar (C)			***	***		n.s.	**	***	n.s.	
Sig. Interactions.			YxNxN	YxNxN		YxN (*)	YxN *	n.s.	n.s.	
			(*)	(*)		NxC *	NxC (*)			
LSD (P=0.05) N				1.67	18.6		1.46	0.54	0.012	28.8
LSD (P=0.05) N within YxC				2.54	29.9		2.17	0.84	0.023	42.1

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

b \*\*\*=P<0.001, \*\*=P<0.01, \*=P<0.05, (\*)=P<0.1, n.s. = non-significant (P≥0.1).

## Measurements

At regular intervals, growth was analysed 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. Potatoes were harvested on 8 September 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, 24 h) and weighed. Total N was determined using the Dumas-method (Macro N; Foss Heraus Analysensysteme, Hanau, Germany). Nitrate in green leaves and stems was extracted with water and determined using a continuous flow analyser (TRAACS 800, Bran & Luebbe, De Meern, The Netherlands). Previous studies showed that nitrate 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 nitrate concentration was determined in one replicate and was found to be very small. The nitrate 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 present chapter, N concentrations refer to organic N only as they were calculated as total N minus nitrate-N. Ammonium concentrations in the plants were assumed to be small because soil-derived ammonium 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 ammonium taken from atmospheric deposition results in low leaf ammonium concentrations. Yin et al. (1996) found ammonium concentrations in leaves of *Pelargonium zonale* L. to be about  $0.3 \mu\text{g N-NH}_4 \text{ g}^{-1}$  leaf fresh weight, with hardly any increase by ammonia fumigation.

Soil inorganic N was analysed (ammonium-N, and nitrate-N) after combining four cores of all plots per treatment, using a 30-mm diameter probe. Exchangeable  $\text{N-NH}_4^+$ , and  $\text{N-NO}_3^-$  were determined in 1M KCL, with a continuous flow analyser (TRAACS 800, Bran & Luebbe).

### *Interception of PAR and LUE*

Intercepted PAR was measured once or twice a week for wheat, ten times per recording, with a portable line sensor (TFDL, Wageningen, The Netherlands). Recordings were taken within one hour 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 a day (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 non-linear relationship with thermal time (modified from Spitters (1990a), see Appendix 3). Less frequently, intercepted PAR was also measured for potato and both methods correlated well. Daily soil cover values were transformed into the fraction of intercepted PAR, according to a relationship similar that published by Van der Zaag (1984).

Table 5. Means and effects of year (Y), nitrogen (N) and cultivar (C) on average nitrogen nutrition index (NNI), crop biomass, tuber dry weight, harvest index, light use efficiency (LUE) and cumulative intercepted photosynthetic active radiation (PAR) of potato at about 52 DAE in 1997 and 47 DAE in 1998. *Actual* = measured biomass, *Critical* = 95% of maximum biomass (just barely N-limited), *Total* = total biomass production, including shed leaves.

Y	C	N	NNI	Crop dry weight			Tubers <sup>a</sup> Harvest index <sup>a</sup>		LUE	Cum. interc. PAR <sup>b</sup>	
				Actual	Critical	Total	Total	g g <sup>-1</sup>		g MJ <sup>-1</sup>	Actual
									Mg ha <sup>-1</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	N1	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. Year (Y) <sup>c</sup>			n.s.	**		**	***	*	n.s.	***	
Sig. Nitrogen (N)			***	**		**	(*)	**	*	***	
Sig. Cultivar (C)			***	n.s.		n.s.	*	***	n.s.	n.s.	
Sig. interactions			NxC (*)	n.s.		n.s.	NxC (*)	*	YxC *	YxN (*)	YxC***
LSD P=0.05 N			0.065	1.23		1.15	0.62	0.044	0.34	14.7	
LSD P=0.05 N, within YxC			0.086 <sup>d</sup>	1.81		1.69	0.92	0.063	0.51	24.2	

a Excluding two units that were initially waterlogged. Critical crop dry weight (W) was derived from Fig. 1. Harvest index, and LUE based on total W.

b 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.

c \*\*\* =P<0.001, \*\*=P<0.01, \*=P<0.05, (\*)=P<0.1, n.s. = non-significant (P≥0.1).

d Upper value 1997, lower value 1998

Table 6. Means and effects of year (Y), nitrogen (N) and cultivar (C) on average nitrogen nutrition index (NNI), crop biomass, grain dry weight, harvest index, light use efficiency (LUE) and cumulative intercepted photosynthetic active radiation (PAR) of wheat at 102 DAE in 1997 and 86 DAE in 1998. *Actual* = measured biomass, *Critical* = 95% of maximum biomass (just barely N-limited), *Total* = total biomass production, including shed leaves.

Y	C	N	NNI	Crop dry weight			Grains Harvest index <sup>a</sup>		LUE <sup>a</sup>	Cum. interc. PAR <sup>a</sup>	
				Actual	Critical	Total	Actual	Total		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) <sup>b</sup>			*	(*)	*	***	***	***	***	
	Sig. Nitrogen(N)			*	(*)	(*)	n.s.	(*)	n.s.	**	
	Sig. Cultivar(C)			n.s.	n.s.	n.s.	***	***	n.s.	n.s.	
	Sig. interactions			n.s.	n.s.	n.s.	n.s.	YxC (*)	n.s.	n.s.	
	LSD (P=0.05) N			0.098	1.6	1.6	0.27	0.008	0.23	32.2	
	LSD (P=0.05) N, within YxC			0.062	2.4	1.2	0.98	0.017	0.18	30.2	

a Harvest index, and LUE based on total W. Critical cum. interc. PAR explained in Table 5, note b.

b \*\*\*=P<0.001, \*\*=P<0.01, \*=P<0.05, (\*)=P<0.1, n.s. = non-significant (P≥0.1).

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 leaf dry weight production for subsequent periodic harvests. Crop biomass production and growth components were compared well before the final harvest (see Results and discussion), 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 Booi (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 ( $k_{NU}$ ,  $W_m$ ) were subjected to analysis of variance using REML (see Section Statistical analysis), after a log<sub>10</sub> transformation.

At each fertiliser 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, parameters ( $A$ ,  $B$ ) were subjected to analysis of variance (see Section Statistical analysis), after a log<sub>10</sub> transformation.

### ***Calculation of nitrogen nutrition index and leaf area duration***

NNI was calculated according to Eq. 1. For calculation of mean values for NNI over time, a maximum value of 1 was used (see Introduction). 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 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 versus DAE, where LAI was linearly interpolated between successive sampling times. Throughout the present chapter, 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, cultivar) and variates (e.g. NNI, DAE) were analysed with a linear mixed model, using the residual maximum likelihood (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 refer to significant effects at a 5% significance level unless otherwise stated.

## **Results and discussion**

### ***Final crop yields, harvest index, and nitrogen uptake***

For potato at final harvest, higher rates of N increased tuber dry weight and tuber N uptake independent of year and cultivar (Table 4). 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 4). The increase of dry weight with N was larger for Axona than for Baldus. Total N uptake increased with N supply, from 124 kg N ha<sup>-1</sup> in N1 to 180 kg N ha<sup>-1</sup> in N3, 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 cultivar Baldus than for Axona, which was associated with the higher (9.5%) harvest index of Baldus (Table 4).

### ***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 ( $k_{\text{NU}}$  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  $k_{\text{NU}}$  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 fertiliser 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 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] in potato and wheat smaller than  $1 \text{ Mg ha}^{-1}$  were not included because the initial effects of N were small, which resulted in strong over-estimations of the critical [N], namely [N] above 7 %.

Calculated critical [N] for potato (Fig. 2A) was clearly larger than those found by Greenwood et al. (1990); whereas calculated critical [N] values for spring wheat (Fig. 2B) were consistent with data from Justes et al. (1994), also after anthesis. Our relationship for potato probably overestimated critical [N] because crop dry matter production at a given date as a function of N supplies (Figs. 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, as explained below. The ratio of actual / near-maximum crop dry weight was found to be 1 at an  $\text{NNI}=1$  (Figs. 4A, B) as expected from the definition of NNI (Eq. 1, Lemaire et al., 1989), whereas an over-estimation of crop N content at the near-maximum crop dry weight would have resulted in under-estimations of NNI.

### ***Nitrogen nutrition index (NNI)***

In both years, the NNI (see Eq. 1) for potato cultivars decreased in the N1 and N2 treatments from 0.8–0.9 at emergence until 0.6–0.7 at about 15 DAE in 1997 and

0.4–0.5 at about 25 DAE (1998), from then on changes in NNI were much smaller (Figs. 3A and 3B). The NNI for potato cultivars at high N (N3) in 1997 also decreased, but after 20 DAE 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 (emergence–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) for 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 20–30 DAE. Thereafter, the NNI remained about 0.8 in N3, but decreased in N1 and N2 until about 0.6 at 50 DAE, and hardly changed thereafter. Averaged over years and cultivars, higher N levels increased the average NNI (emergence–maturity) for wheat by 2% (N2) and 20% (N3) (Figs. 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 NNI***

Throughout the current section, crop biomass production (actual weight corrected for leaf shedding) and their components (Tables 5 and 6) 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 5). 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 by 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 6), and average temperature and daily PAR during growth were higher (see above). The LUE for wheat was smaller in 1997 than in 1998, associated with a larger average daily PAR from emergence until harvest in 1997 (8.9 MJ m<sup>-2</sup> d<sup>-1</sup> 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 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.

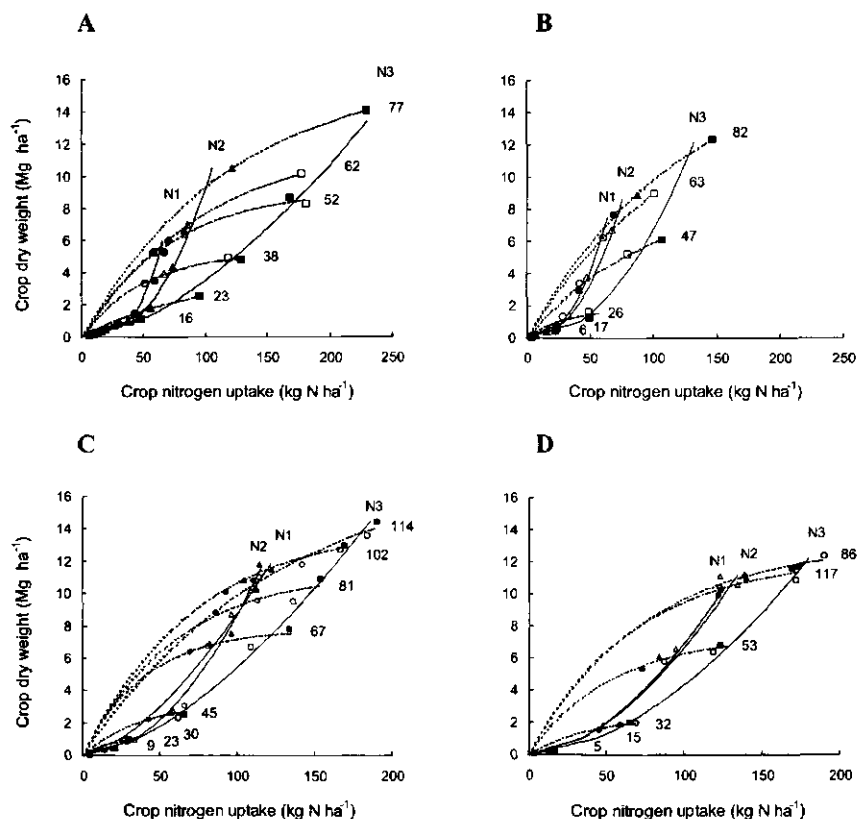


Figure 1. Relationship between N uptake and total dry matter production of potato (A, B) and wheat (C, D) in 1997 (A, C) and 1998 (B, D). For each DAE, the line was fitted according to Eq. 2 (broken lines) and at each N level rate according to Eq. 3 (solid lines). Data values are DAE of periodic samplings. N1 (○,●), N2 (△,▲) and N3 (□,■), potato cv. Junior and wheat cv. Axona (open symbols), potato cv. Agria and wheat cv. Baldus (closed symbols).



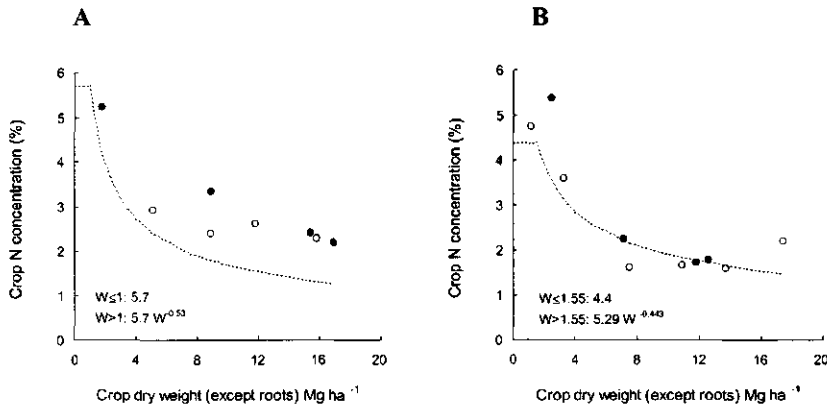


Figure 2. Relationship between crop dry matter production ( $W$ , Mg ha<sup>-1</sup>), and critical [N] (100 g N g dm<sup>-1</sup>) in (A) potato, Greenwood et al. (1990), and (B) wheat, Justes et al. (1994). Symbols are [N] at 95% of the calculated maximum crop dry weight (Eq. 2 in text), as derived from Fig. 1, 1997 (○), 1998 (●).

The response of crop dry weight and growth components to the average NNI, across years and cultivars, is shown in Figures 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 (Figs. 4A and 4B). REML analysis 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 was no longer affected by average NNI 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 (Figs. 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 (Figs. 5C and 5D).

Other studies also found potato and wheat harvest index near crop maturity to be unaffected by nitrogen depletion (Millard and Marshall, 1986; Green, 1987; Duchenne et al., 1997). 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).

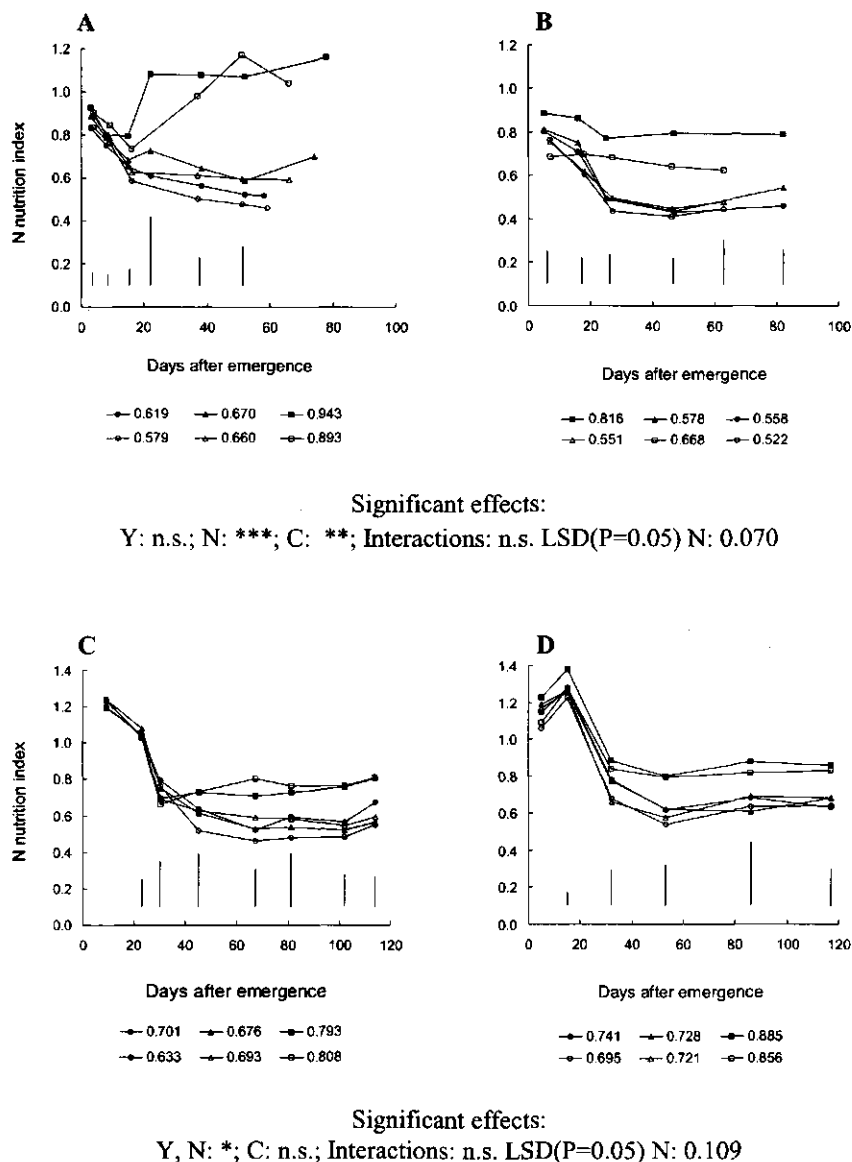


Figure 3. Course of the N nutrition index (NNI) (see Eq. 1) with days after emergence (DAE) of potato (A,B) and wheat (C,D) in 1997 (A,C) and 1998 (B,D). Bars represent the LSD ( $P=0.05$ ) at each sampling date. Data values are average NNI values from emergence until the largest possible DAE that cultivars could be compared [58 DAE(A), 63 DAE (B), 114 DAE(C), 117 DAE(D)]. N1 (○,●), N2 (△,▲) and N3 (□,■), potato cv. Junior and wheat cv. Axona (open symbols), potato cv. Agria and wheat cv. Baldus (closed symbols).

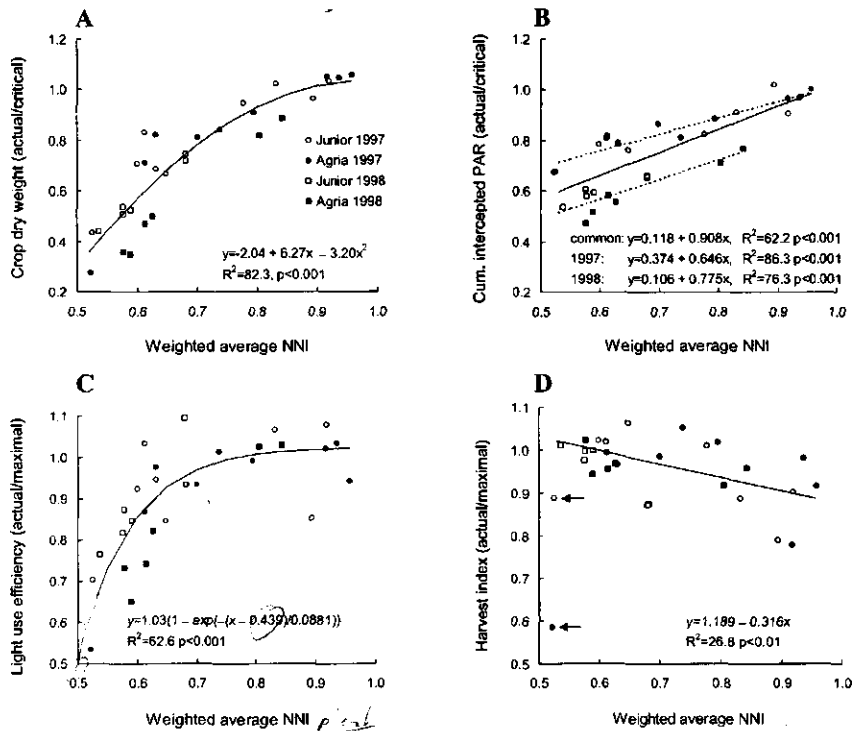


Figure 4. Influence of average N nutrition index (NNI) on the relative values of crop dry weight (A), cumulative intercepted PAR (B), light use efficiency (C), and harvest index (D) of potato at about 52 DAE in 1997 and 47 DAE in 1998. The values are relative to maximum or critical values as given in Table 5. Points represent individual replicates. Solid regression lines include all points, except those indicated by arrows. Dotted lines represent separate years.

Results in Fig. 4 corroborate the hypothesis by Vos and Van der Putten (1998) that in response to N limitation potato maximises LUE but reduces light interception, as explained below. For NNI 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 unfertilised treatment to be reduced from their other N rates of 50–250 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 from 1 to 0.7. The results of the present study agreed with those of Meinke et al. (1997) but contrasted with other studies (cf. Green, 1987). 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> and higher.

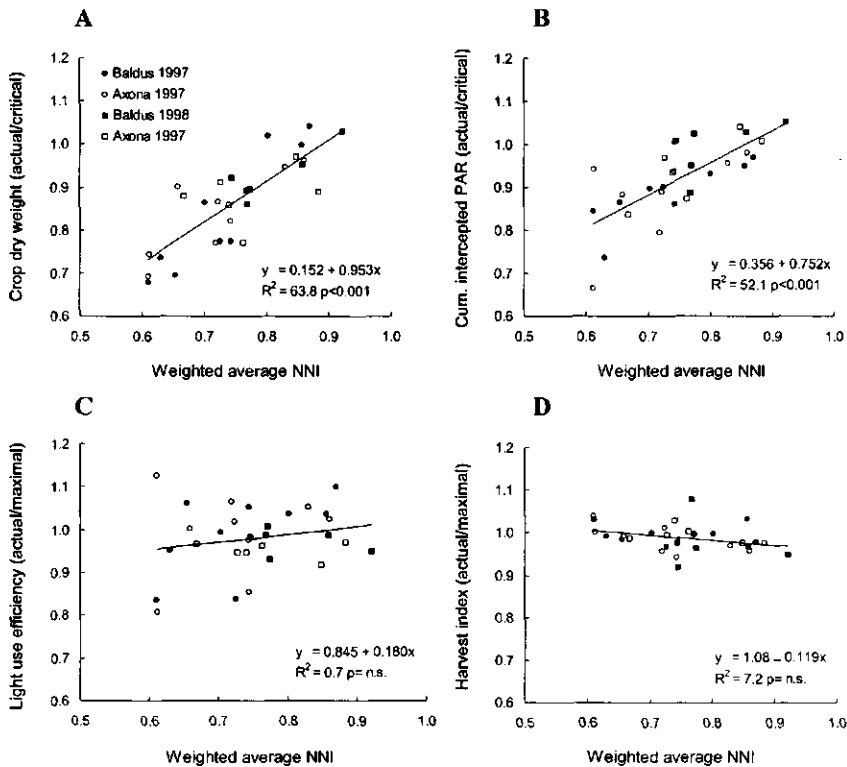


Figure 5. Influence of average N nutrition index (NNI) on relative values of crop dry weight (A), cumulative intercepted PAR (B), light use efficiency (C), and harvest index (D) for wheat at 102 DAE in 1997 and 86 DAE in 1998. The values are relative to maximum or critical values as given in Table 6. Points are for individual replicates. Solid regression lines include all points.

The contrasting results in previous wheat studies might have resulted from differences in crop N deficiency, from cultivar differences and from timing of N deficiency. Sivasankar et al. (1998) recently reported a differential response in leaf area of two wheat genotypes to N supply. One genotype reduced leaf area expansion and maintained leaf [N] per unit dry weight with reduced N supply, but leaf area expansion for the other genotype was hardly reduced. According to Grindlay (1997), all cultivated  $C_3$  species adjust their leaf area expansion rate and maintain their  $N_{LA}$  with decreasing N. Grindlay (1997) suggested that the variation of cultivated species in response of LUE and photosynthesis to  $N_{LA}$  has been decreased as a result of selection. Photosynthesis decreases much faster with decreasing N per unit 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 post-anthesis 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 NNI***

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 7). The slope of these relationships did not vary with year or cultivar, but the intercept did (Table 7). 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 to the later cultivar Agria (Table 7).

For wheat, a smaller N deficiency increased the leaf [N] based both on dry weight (Fig. 7B) and on leaf area (Fig. 7A). The slopes did not vary with year or cultivar (Table 8). 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, Table 8).

For potato and wheat, the present study (Figs. 6 and 7) showed that the response of  $N_{LA}$  to average NNI 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 maximising  $N_{LA}$  and LUE. Potato leaf [N] ( $g\ g^{-1}$ ) increased more with increased N supply than  $N_{LA}$  ( $g\ m^{-2}$ ) 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 in specific leaf area for wheat was found in the present study, which support earlier results of Meinke et al. (1997).

Table 7. 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: d) of potato at about 52 days after emergence (DAE) in 1997 and 47 DAE in 1998. Regressions also are given for NNI and thermal time from emergence till 50% intercepted PAR (t50: °Cd) and maximum leaf area index (LAI<sub>m</sub>). REML analysis for effects of year (Y) and cultivar (C) on regression parameters.

	Y	C	Intercept		Slope		Regression		Slope		Among	Among	LSD
			mean	s.e.	Mean	s.e.	R <sup>2</sup>	P <sup>a</sup>	P	slopes	lines	(P=0.05)	
N <sub>LA</sub>	1997	Junior	1.74	0.32	0.34	0.43	-	n.s.	n.s.	n.s.	Y x C		a
	1997	Agria	2.19	0.27	0.06	0.28	-	n.s.			***		b
	1998	Junior	2.47	0.88	-0.48	1.44	-	n.s.					ab
	1998	Agria	3.30	0.34	-0.63	0.50	10.4	n.s.					c
[N <sub>L</sub> ]	1997	Junior	16.8	3.9	38.0	5.3	86.1	***	***	n.s.	Y x 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	n.s.					b
	1998	Agria	34.4	1.8	23.9	2.7	94.1	***					c
LAD	1997	Junior	-77.1	26.5	223	36.5	82.0	***	***	Y	C		
	1997	Agria	-65.2	17.7	204	23.0	90.7	***		***	***		
	1998	Junior	-92.0	26.0	230	42.7	84.9	**					
	1998	Agria	-56.3	7.1	146	10.4	97.5	***					
t50	1997	Junior	450	90	-307	114	44.0	*	***	n.s.	Y x C		a
	1997	Agria	511	65	-373	79	72.7	**			***		a
	1998	Junior	312	73	-95	103	-	n.s.					a
	1998	Agria	862	145	-701	181	73.6	*					b
LAI <sub>m</sub>	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	***					

a \*\*\*=P<0.001, \*\*=P<0.01, \*=P<0.05, (\*)=P<0.1, n.s. = non-significant (P≥0.1).

Observed patterns of LUE with NNI (Figs. 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 decreased leaf N concentration with increased canopy depth, which has been found in wheat (Dreccer et al., 2000b) 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).

Table 8. 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: d) of wheat at 102 days after emergence (DAE) in 1997 and 86 DAE in 1998. Linear regressions also are given for NNI and thermal time until 50% intercepted PAR (t50: °Cd) and maximum leaf area index (LAI<sub>m</sub>). REML analysis for effects of year (Y) and cultivar (C) on regression parameters is given.

	Y	C	Intercept		Slope		Regression		Slope		Among	
			mean	s.e.	mean	s.e.	R <sup>2</sup>	P <sup>a</sup>	P	Among	lines	
$N_{LA}$	1997	Axona	0.73	0.16	1.29	0.22	80.1	***	***	n.s.	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	***	***	n.s.	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	**	***	n.s.	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	n.s.				
t50	1997	Axona	1553	367	-1225	390	52.5	*	***	n.s.	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 <sub>m</sub>	1997	Axona	-3.62	3.29	7.65	3.96	25.5	(*)	***	Y x 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	n.s.				

a \*\*\*=P<0.001, \*\*=P<0.01, \*=P<0.05, (\*)=P<0.1, n.s. = non-significant (P≥0.1).

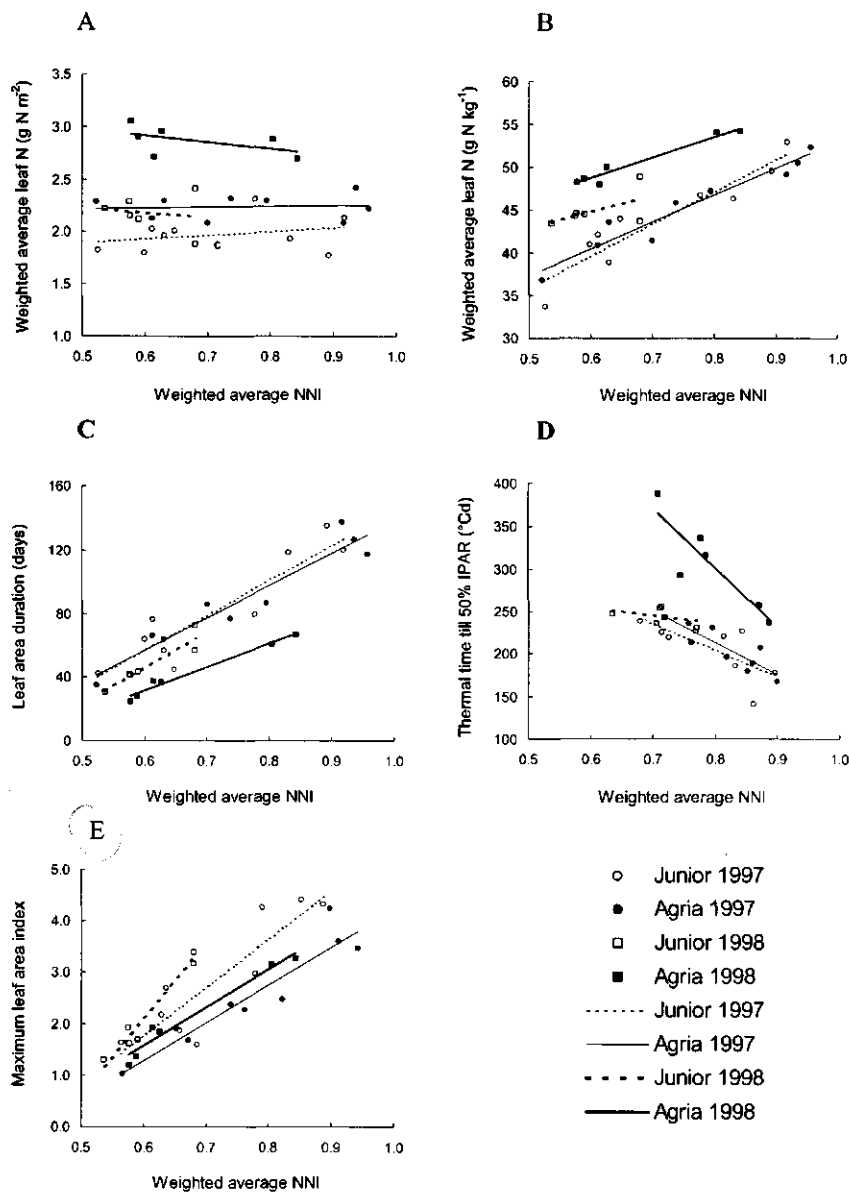


Figure 6. Influence of average N nutrition index (NNI) on average areal leaf N content ( $\text{g m}^{-2}$ ) (A), leaf [N] ( $\text{g kg}^{-1}$ ) (B), and leaf area duration (C) of potato at about 52 DAE in 1997 and 47 DAE in 1998. Influence of NNI on thermal time till 50% intercepted PAR at start of the season (D) and maximum leaf area index (E) of potato. Points are for individual replicates. Lines are regressions for each cultivar and year separately. Parameter estimates of lines are in Table 7.



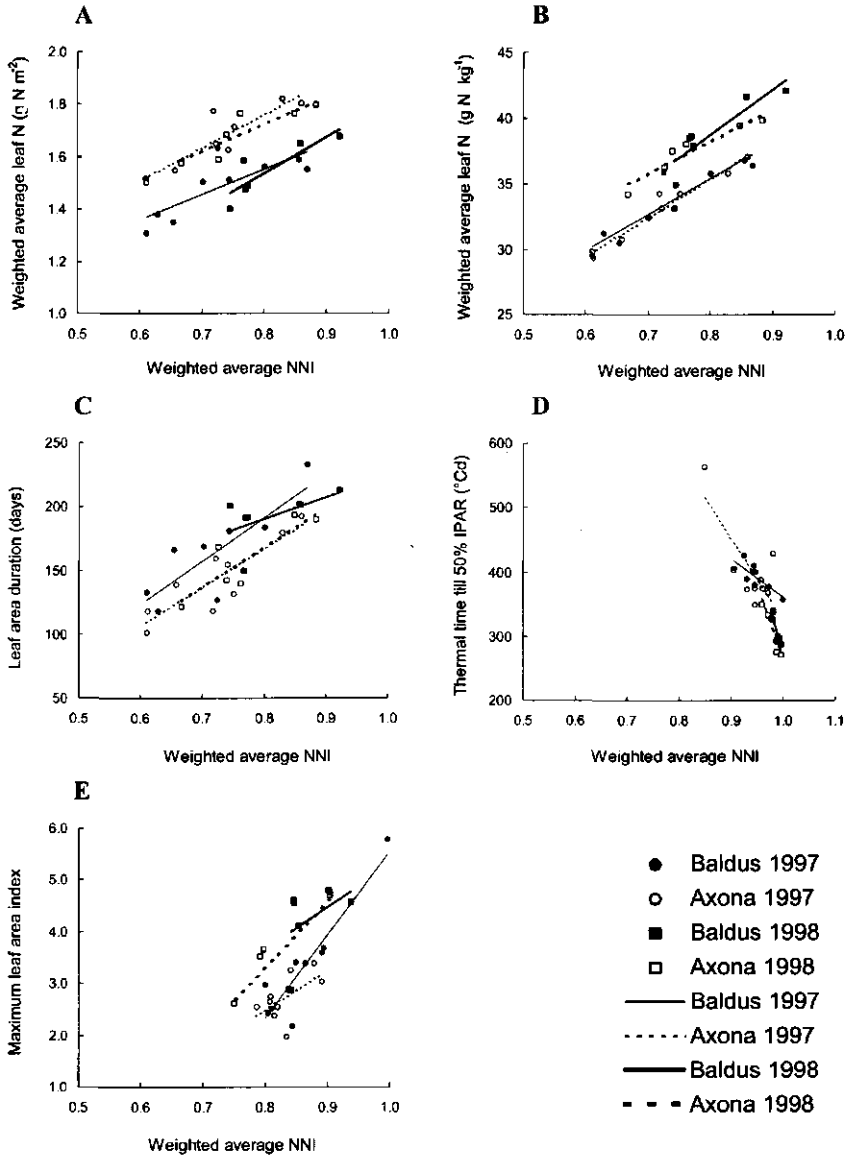


Figure 7. Influence of average N nutrition index (NNI) on average areal leaf N content ( $\text{g m}^{-2}$ ) (A), leaf N ( $\text{g kg}^{-1}$ ) (B), and leaf area duration (C) of wheat at 102 DAE in 1997 and 86 DAE in 1998. Influence of NNI on thermal time till 50% intercepted PAR at start of the season (D) and maximum leaf area index of wheat (E). Points are for individual replicates. Solid lines are regression lines for each cultivar and year separately. Parameter estimates of lines are in Table 8.

### ***Towards optimisation of organic N management***

The present study was conducted to improve our knowledge on the responses of light interception, LUE and harvest index to N. Ultimately these findings are to be used to improve organic N management. Increased yields with increased N supply were found to be mainly caused by a longer leaf area duration and thus an increased light interception. Shortage of N in the N1 and N2 treatments developed early in the season and resulted in a reduced rate of early leaf area expansion (Figs. 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 mineralisation from manure. The  $N_{min}$  content of  $82 \text{ kg N ha}^{-1}$  (0–0.6 m, Table 3) at planting of potato and subsequent expected net mineralisation of  $30\text{--}50 \text{ kg N ha}^{-1}$  (Table 3) totalled about  $120 \text{ kg N ha}^{-1}$ . Such N contents are well below the recommended values in regular farming (Van Dijk, 1999) of  $265 - 1.1 * N_{min}$ .  $N_{min}$  at planting ( $99 \text{ kg N ha}^{-1}$ , Table 3) for wheat plus the expected net N mineralisation during the first half of the season ( $20 \text{ kg N ha}^{-1}$ , half values of Table 3), totalled about  $120 \text{ kg N ha}^{-1}$ . Such values were close to recommended rates in regular farming until stem extension, being  $120 - N_{min}$  (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 soil mineral N contents plus released N were too small to meet crop demands. Early N limitation by crops may depend both on weather conditions determining N leaching during winter and rates of N mineralisation, and on 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 with an organic N source that contains a large proportion of mineral N (e.g. a slurry compared to a farmyard manure). Further research is required on: 1) matching crop N supply with demand while subjecting the crop to a range of organic N sources, and 2) comparing the LUE and leaf area dynamics among  $C_3$  and  $C_4$  crops under a range of mineral N fertiliser levels. Once established, this should be followed by a comparison of their yield response under organic N management.

## Appendix 1

### List of abbreviations

Abbreviation	Characteristic	Unit
DAE	Days after emergence	d
LAI	Leaf area index	-
LUE	Light use efficiency	g dm MJ <sup>-1</sup>
[N]	Nitrogen concentration	g N kg <sup>-1</sup>
N1	Unfertilised	kg N ha <sup>-1</sup>
N2	Fertilisations with cattle slurry at a rate corresponding to current organic farming systems in The Netherlands	kg N ha <sup>-1</sup>
N3	Fertilisations with cattle slurry supplemented with mineral N according to recommended rates in conventional farming	kg N ha <sup>-1</sup>
N <sub>LA</sub>	Areal leaf N content	g N m <sup>-2</sup>
NNI	Nitrogen nutrition index	-
N <sub>min</sub>	Soil mineral N content	kg N ha <sup>-1</sup>
pF	Log10 of cm water pressure	-
REML	Residual maximum likelihood	-
W	Crop dry weight	Mg ha <sup>-1</sup>

## Appendix 2

### *Calculation of expected nitrogen mineralisation from organic sources*

#### *Cattle slurry*

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

$$\text{ENM} = S \cdot N_{\text{tot}} \cdot \left( \frac{N_{\text{org}}}{N_{\text{tot}}} \right) \cdot \left( \frac{N_e}{N_{\text{org}}} \right) \cdot \left( \frac{N_{\text{season}}}{N_e} \right)$$

$$= S \times 4.9 \times 0.5 \times 0.5 \times \{0.60 \text{ potato}, 0.66 \text{ wheat}\},$$

where  $S$  ( $\text{Mg ha}^{-1}$ ) is, the amount of applied cattle slurry,  $N_{\text{tot}}$  ( $\text{kg N Mg}^{-1}$ ) is the N content of the slurry,  $N_{\text{org}}$  is the organic N content,  $N_e$  is the organic N content that is released within the first year after application, and  $N_{\text{season}}$  is the proportion of mineralised N which becomes available during the months of the growing season.  $N_{\text{tot}}$  of cattle slurry is, on average,  $4.9 \text{ kg N Mg}^{-1}$  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 mineralisation from garden compost was estimated to be 10% from total N content (Van Dijk, 1999), with a N content of  $10.7 \text{ kg N Mg}^{-1}$  fresh matter (Schröder, unpublished 1996).

#### *Leaves of sugar beet*

Nitrogen mineralisation from leaves of sugar beets was estimated to be  $30 \text{ kg N ha}^{-1}$  (Van Dijk, 1999).

## Appendix 3

### *Calculation of daily intercepted PAR*

Spitters (1990a) 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,  $R_0$  ( $^{\circ}\text{Cd}^{-1}$ ) is the relative increase rate for light interception and  $t$  ( $^{\circ}\text{Cd}$ ) is the thermal time with a base temperature of  $2^{\circ}\text{C}$  (potato) and  $0^{\circ}\text{C}$  (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,  $t$  ( $^{\circ}\text{Cd}$ ) is the thermal time, and  $a$  is ( $^{\circ}\text{Cd}$ ) $^{-1}$  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, Eqs. A1 and A2 were combined:

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

## Abstract

We studied the course of early leaf area expansion and specific leaf area ( $S_{LA}$ ) in potato (*Solanum tuberosum* L.) and wheat (*Triticum aestivum* L.) genotypes and tested whether air temperature explains differences in these courses within different environments. That knowledge can be used to improve crop growth modelling.

The relative rate of leaf area expansion ( $R_L$ ) of potato and wheat decreased with thermal time, but was nearly linear up to a leaf area index ( $L$ ): of 1.0. The  $R_L$  ( $L < 1$ ; mean:  $17.9 \cdot 10^{-3} (\text{°Cd})^{-1}$ ) of potato showed interaction between genotype and environment and varied with year. The  $R_L$  ( $L < 1$ ; mean:  $7.1 \cdot 10^{-3} (\text{°Cd})^{-1}$ ) of winter wheat was lower than that of spring wheat (mean:  $10.9 \cdot 10^{-3} (\text{°Cd})^{-1}$ ) and both varied with year.

$S_{LA}$  of potato increased nearly linearly with thermal time from 5 to  $15 \text{ m}^2 \text{ kg}^{-1}$  at 50% emergence to 20 to  $25 \text{ m}^2 \text{ kg}^{-1}$  at  $155 \text{ °Cd}$  and then decreased slightly. The  $S_{LA}$  of both winter and spring wheat began at 16 to  $23 \text{ m}^2 \text{ kg}^{-1}$  and in most cases increased slightly with thermal time. In potato, regression parameters of  $S_{LA}$  with thermal time were affected by environment (management conditions and year) and genotype; in wheat they were affected by environment (year and site). Treatment effects on  $R_L$  of potato were not correlated to those on  $S_{LA}$ , and only partly so for wheat. Therefore we conclude that the early foliar expansion of potato is associated with a strong increase in  $S_{LA}$ , not so for wheat, and that for both crops the course of early leaf area expansion and of  $S_{LA}$  with air temperature are not robust over environments and genotypes. The consequences of these results for modelling are discussed.

## Introduction

Leaf area expansion is an important determinant of crop growth rate (Goudriaan and Van Laar, 1994). Crop growth rate increases with leaf area index ( $L$ , a list of abbreviations is given in the Appendix) particularly at early growth stages because the relative increases in the interception of photosynthetically active radiation ( $I_{PAR}$ ) are largest when  $L$  is small (Jamieson et al., 1998). The dynamics of early leaf area expansion are important for the crop-weed competition, because differentials in rate of leaf area expansion just after emergence are often decisive for the establishment and growth of the crop and of the competitive weed (Kropff et al., 1992).

Although canopy leaf area dynamics are important, they remain difficult to model among different environments (Asseng et al., 1988). A better understanding of the environmental effect on canopy leaf area dynamics is therefore needed. When management practices are such that water and nutrients do not limit crop growth and when crop growth is not reduced by pests, diseases or by competition with weeds, the leaf area expansion of a canopy mainly depends on temperature, photoperiod, leaf assimilate availability and genotype. Other factors affecting leaf area dynamics are relative humidity, light quality (Dale, 1988) and soil physics (Masle, 1992). Genotype

is known to affect potato leaf area dynamics mainly at the end of the growing season. Genotypic differences during early growth stages of potato are less distinct (Spitters, 1987). Recently, Rebetzke and Richards (1999) demonstrated that the early L of a wheat canopy (five main stem leaves per plant) differs considerably among genotypes.

For crops grown in the field without weeds, temperature is often most influential (Horie et al., 1979). Individual leaf area expansion rates as well as the appearance rates of new leaves are related to thermal time ( $T_i$ ) in potato (e.g. Firman et al., 1995) and wheat (e.g. Jamieson et al., 1995). As a result of temperature effects on the expansion of individual leaves and appearance rates of new leaves, the total plant leaf area of small plants often increases exponentially (Hunt, 1982) at a relative rate of leaf area expansion ( $R_L$ ) which is constant with  $T_i$  for a given species (e.g. MacKerron and Waister, 1985). This initial  $R_L$  is not usually maintained beyond a given leaf area index (L) and the decline thereafter may be linear (Hunt, 1982).

The  $T_i$  from the first leaf till ear appearance of wheat, decreased clearly when photoperiod increased from 9 h to 21 h, because the final number of leaves on the main stem was fewer, the extent depending on genotype (Brooking et al., 1995). It is unclear whether photoperiod also affects canopy leaf area expansion rates (Dale, 1988). Nevertheless, photoperiod effects are of importance to explain differences in the duration of canopy leaf area expansion of wheat caused by differences in sowing times (Brooking et al., 1995).

An increase in  $I_{PAR}$ ,  $CO_2$  or seed reserves accelerates the rate of leaf area expansion when leaf area expansion is limited by assimilate availability (Dale, 1988). Under these conditions, L can be calculated as the product of the rate of increase in leaf dry matter and the specific leaf area of new leaves ( $S_{LA}$ : the ratio between leaf area and leaf weight). For many crops, the  $S_{LA}$  of a canopy tends to change with the developmental stages of a crop (Penning de Vries et al., 1989). The  $S_{LA}$  dynamics may be a reflection of the change in carbohydrate supply to the growing tissue (Johnson and Thornley, 1983). The developmental stage of a crop is often expressed in terms of  $T_i$ . When the change of  $S_{LA}$  with crop developmental stage is robust in a certain region, then the change in  $S_{LA}$  with  $T_i$ , together with leaf weight, can be used to calculate L.

Few experimental field studies have characterised early leaf area expansion and  $S_{LA}$  of potato and wheat. Moreover, it has not been tested whether relationships of L and  $S_{LA}$  with  $T_i$  are affected by genotype and are robust when measured in different environments. We therefore collected data on early leaf area dynamics of potato and spring wheat genotypes at different sites in The Netherlands. We also used data on winter wheat that were collected by Groot and Verberne (1991). Our study had two objectives: (1) to ascertain the relationship between early leaf area expansion and  $S_{LA}$  with  $T_i$  for potato and wheat, and (2) to study whether these relationships are affected by genotype and are robust when determined in different environments. Because the sowing dates within the set of winter wheat experiments and the set of spring wheat experiments were close together, we did not consider photoperiod effects within each set.

## Materials and methods

Data on early leaf area and leaf dry matter dynamics were collected in the Netherlands for potato (two sites: Table 1A) and wheat (three sites: Table 1B). At each site data were collected during two consecutive years. Data from different environments (sites, years, management conditions) but with the same genotypes were pooled, resulting in five data sets (Table 2).

Table 1A. Description of the experimental sites and experimental methods of potato.

	Droeendaal	Lovinkhoeve
Site	Wageningen 51°58'N 5°40'E	Marknesse 52°42'N 5°53'E
Soil type	Sandy humus	Silty loam
Weather station	Wageningen	Marknesse
Distance from site (km)	2	0
Genotype	Eersteling Bintje	Junior Agria
Planting pattern (m x m)	0.75 x 0.30	0.75 x 0.30
Planting method	by hand	by machine
No of replicates	3	3
Water supply	irrigated	rain fed
Reference	present study	present study
Data set number	1	3
Year	1996	1997
Planting date	15 April	18 April
Emergence date	see Table 1B	1 June (Junior) 31 May (Agria)
Previous crop	spring barley	winter wheat
Green manure crop	oil-seed radish	mustard
Gross plot size (m <sup>2</sup> )	1.07	19.8
Net plot size (m <sup>2</sup> )	0.9	9.45
Data set number	2	3
Year	1997	1998
Planting date	17 April	13 May
Emergence date	16 May (Eersteling) 17 May (Bintje)	28 May (Junior) 30 May (Agria)
Previous crop	winter wheat	spring wheat
Green manure crop	none	mustard
Gross plot size (m <sup>2</sup> )	7.2	23.4
Net plot size (m <sup>2</sup> )	2.7	9.45



### Data sets

In the first data set (potato Droevendaal 1996), we studied the effect of genotype (early cultivar Eersteling and late cultivar Bintje), planting depth (8 or 18 cm from middle of tuber to top of ridge at planting), plastic mulch (yes/no) and presprouting (yes/no) of the tubers. Treatments were applied in a split-split-split plot design with three blocks. Cultivar was the main plot, and plastic, presprouting and planting depth were subsequent subplot levels. Non-presprouted tubers were kept at 4°C in darkness until the day before planting. Tubers for presprouting were initially kept in darkness at 4°C,

Table 1B. Description of the experimental sites and experimental methods of wheat.

	The Eest	The Bouwing	Lovinkhoeve
Site	Nagele 52°37'N 5°45'E	Randwijk 51°57'N 5°45'E	Marknesse 52°42'N 5°53'E
Soil type	Silty loam	Silty clay loam	Silty loam
Crop	winter wheat	winter wheat	spring wheat
Weather station	Swifterband	Wageningen	Marknesse
Distance from site (km)	15	7	0
Genotype	Arminda	Arminda	Baldus
Row spacing (m)	0.15	0.25	0.3
No of replicates	8	8	3
Water supply	rain-fed	rain-fed	rain-fed
Reference	Groot and Verberne (1991)	Groot and Verberne (1991)	present study
Data set number	4	4	5
Year	1982, 1983	1982, 1983	1997
Planting date	19 October	21 October	14 April
Emergence date	not recorded	not recorded	27 April
Previous crop	potatoes	potatoes	fodder beet
Plant density (pl m <sup>-2</sup> )	218	214	260
Gross plot size (m <sup>2</sup> )	3.75	3.75	6
Net plot size (m <sup>2</sup> )	0.45	0.5	1.05
Data set number	4	4	5
Year	1983, 1984	1983, 1984	1998
Planting date	21 October	27 October	9 May
Emergence date	not recorded	not recorded	17 May
Previous crop	potatoes	potatoes	fodder beet
Plant density (pl m <sup>-2</sup> )	256	223	230
Gross plot size (m <sup>2</sup> )	3.75	3.75	10
Net plot size (m <sup>2</sup> )	0.45	0.5	1.2

Table 2. Environments (year, sites and management conditions) and genotypes per data set, for both potato and wheat.

Data set	Crop	Environment			Genotypes
		Years	Sites	Management	
1	Potato	1996	Droevendaal	plastic mulch (yes/no) x presprouting (yes/no) x planting depth (8 cm/18 cm)	Eersteling Bintje
2	Potato	1997	Droevendaal	no plastic mulch, presprouted, planting depth 12 cm	Eersteling Bintje
3	Potato	1997	Lovinkhoeve	no mulch, presprouted,	Junior
		1998		planting depth 12 cm	Agria
4	Winter wheat	1983	The Eest	no treatments	Arminda
		1984	The Bouwing		
5	Spring wheat	1997	Lovinkhoeve	No treatments	Baldus
		1998			Axona

and then at 20°C for 12 days in darkness followed by 20°C for 7 days, under ambient light/dark rhythm. Before planting, all tubers were disinfected chemically against *Rhizoctonia*. The tubers were planted by hand on small ridges in 8 or 18 cm deep holes. Before emergence, ridges were earthed up resulting in a final planting depth of 12 or 22 cm. The plastic mulch was in situ from planting (15 April 1996) until first sampling (30% emergence). Fertiliser was applied just before planting at a rate of 150 kg N ha<sup>-1</sup>, 95 kg P<sub>2</sub>O<sub>5</sub> ha<sup>-1</sup> and 130 kg K<sub>2</sub>O ha<sup>-1</sup>. Fields were irrigated when needed.

In the second data set on potato (Droevendaal 1997), we studied the effect of genotype (cultivars Eersteling and Bintje). Two cultivars were grown in three blocks, each in a separate experiment, therefore genotype was not an experimental treatment. The tubers were presprouted in the dark until small sprouts were visible, then placed outdoors for 7 days. They were disinfected chemically against *Rhizoctonia*. The tubers were planted by hand on small ridges in holes 12 cm deep. Before emergence, ridges were earthed up once, resulting in a final planting depth of 16 cm. Fertiliser was applied at a rate of 300 kg N ha<sup>-1</sup>, 115 kg P<sub>2</sub>O<sub>5</sub> ha<sup>-1</sup> and 120 kg K<sub>2</sub>O ha<sup>-1</sup>. Fields were irrigated when needed.

In the third (potato) and the fifth (spring wheat) data sets (both at Lovinkhoeve in 1997 and 1998) we studied the effects of year and genotype (early potato cultivar Junior and late cultivar Agria; spring wheat cultivar Baldus with abundant foliage and cultivar Axona with poor foliage). In each set, both cultivars were grown in three replicates. The potato tubers were presprouted and planted by machine. In 1997, tubers were not disinfected, but in 1998 they were disinfected chemically against *Rhizoctonia*. Nitrogen was applied at recommended commercial rates (Sieling, 1992). Soil potassium and phosphorus content were sufficiently high.

In the fourth data set (The Eest and The Bouwing, in 1983 and 1984) we studied the effect of environment (site, year) on the leaf area dynamics of winter wheat cultivar Arminda. Eight replicates were used for each year and site. For details on management and nutrients see Groot and Verberne (1991). Nitrogen (in  $\text{kg N ha}^{-1}$ ) was applied at a rate of 120 (stem extension) and 40 (anthesis) in 1983 at The Bouwing and The Eest site. In 1984, nitrogen was applied at a rate of 70 (tillering), 120 (stem extension) and 40 (anthesis) at The Bouwing site and at a rate of 50 (tillering), 60 (stem extension) and 40 (anthesis) at The Eest site.

The plants in data sets three, four and five were all rain-fed. Water was not considered to limit crop growth in these data sets because at all sample times the pF value until rooting depth was below 2.85 for potato and below 3.0 for wheat.

### **Crop data**

Plants were sampled periodically, varying from once a week (Droevendaal 1996) to once a month (winter wheat). Sample sizes for potato were 4 plants (Droevendaal 1996), 12 plants (Droevendaal 1997) and 42 plants (Lovinkhoeve) (follows from Table 1A). The samples taken at Droevendaal were smaller because potatoes had been planted by hand, whereas those at Lovinkhoeve had been planted by machine. Sample sizes for wheat were about 100 plants (winter wheat) and 270 plants (spring wheat) (follows from Table 1B). Each wheat and potato sample was subsampled to collect green leaves.

For potato and spring wheat at Lovinkhoeve, the first sample was taken near the time of maximum emergence, for the potato set 1 at 30% emergence, whereas for winter wheat the first sample was taken in early February, close to start of tillering [decimal code 21 of Zadoks et al. (1974)]. The number of emerged potato plants was counted daily. Day of 50% emergence of potato was defined as the day on which the median of the final percentage of emerged potato plants occurred. Spring wheat was sown very late (end April, early May) and emerged within two days. The day of 50% emergence of spring wheat was estimated visually.

To assure accurate measurements of leaf area increments, we did not include samples beyond the time when a maximum of 5% of total leaf dry weight consisted of yellow leaves because dead leaves could not possibly be sampled accurately. At that stage L varied from 1.3 to 3.3 for potato set 2 and 3, from 0.5 to 2.6 for spring wheat and from 4.0 to 5.2 for winter wheat. In Droevendaal 1996 (set 1), data were collected until 4 weeks after emergence, which corresponded to a L of 0.3 to 3.0. Samples of potato leaves included the petiole as the compound leaf was cut at the last leaflet near the stem. Samples of wheat leaves consisted solely of leaf blades. The leaf area of each sample was measured with an electronic planimeter (Li-Cor model 3100, LI-COR Inc., Lincoln Nebraska, USA). Samples were oven-dried at 70°C for 48 h and weighed.

### ***Weather data***

Daily minimum and maximum air temperatures at 1.5 m height were obtained from official meteorological stations (Tables 1A and B). In the first two data sets (potato) we measured daily minimum and maximum air temperatures at 0.3 m height, and in the first set we also measured soil temperature at the level of the mother tuber. Both air and soil temperature in the first data set were measured at 10-min intervals using a data-logger (Grant Squirrel sq32-16u, Catec, Rijswijk, The Netherlands). Average daily air temperatures calculated from data-logger measurements (11.9°C in 1996 and 14.3°C in 1997) corresponded well with those calculated from the official meteorological station 2 km away (12.1 in 1997 and 14.7 in 1998). Thus the  $T_i$  calculations based on the air temperatures of the data-logger corresponded well with those of the official station.

### ***Thermal time calculation***

Thermal time ( $T_i$ , °Cd) was calculated as the cumulative daily effective air temperature ( $T_e$ , °C). The daily effective temperature was calculated as the average daily air temperature ( $T_a$ ) minus the base temperature ( $T_b$ ) below which leaves do not expand.  $T_a$  was calculated as the mean of daily minimum and maximum temperature. We used generally accepted  $T_b$  values of 2°C for potato (MacKerron and Waister, 1985) and of 0°C for wheat (e.g. Jamieson et al., 1995).

For potato and spring wheat the  $T_i$  was calculated from the day of 50% emergence onwards. For the winter wheat data,  $T_i$  was calculated from start of tillering, because the effects of vernalisation and photoperiod on leaf area dynamics are unclear. The winter wheat was fully vernalised at start of tillering, as calculated from our weather data using the adapted vernalisation equation in Reinink et al. (1986).

### ***Data analysis***

Leaf area indices were transformed using the natural logarithm, because  $L$  of potato and wheat increased exponentially with  $T_i$  ( $P < 0.001$  for a constant exponential increase, pooled F-test over all treatments, with  $L < 1$ ). The transformation yielded homogeneity of variances with  $T_i$ , and it enabled us to show the change of  $R_L$  (°Cd)<sup>-1</sup> against  $T_i$ .  $R_L$  is the slope of  $\ln(L)$  against  $T_i$ :

$$d \ln(L) / dT_i = R_L \quad (1)$$

It can be seen that  $R_L$  is the relative rate of leaf area expansion by back-transforming and integrating Eq.1:

$$L = L_0 \exp \left( \int R_L T_e dt \right) \quad (2)$$

In which  $L_0$  is the estimated apparent  $L$  at zero  $T_i$ . At a constant  $R_L$ , Eq. 2 simplifies to

$$L = L_0 \exp (R_L T_i) \quad (3)$$

There was no need to transform the data on  $S_{LA}$ . The patterns of the  $\ln$ -transformed  $L$  and of  $S_{LA}$  with  $T_i$  were described by regression analysis (Genstat 5 Committee, 1993), the model depending on the observed pattern (see results). Regression parameters were calculated for each replicate and were subjected to analysis of variance to detect treatment effects. When interaction effects were significant ( $P < 0.05$ ) based on analysis of variance, the differences between individual treatments were tested by least significant difference. The effects of environment (year, site) and of genotype when used in different experiments (data set 2) were also tested by analysis of variance, using the pooled residual variance as the estimate for the within-treatment variance. This means that a significant test result on year, site and genotype in data set 2, shows only whether variation in a parameter between years, sites and genotypes is significantly higher than that within them, and does not prove what factor caused that difference.

## Results

At Droevendaal in 1996 emergence times of potato plants ranged from 25 April for the presprouted shallow-planted mulched Eersteling plants to 19 May for the non-presprouted deep-planted non-mulched Bintje plants (Table 3). As the potatoes of the different treatments emerged at different dates, their foliage expanded under different weather conditions.

### *Leaf area index versus thermal time*

The  $R_L$  of potato decreased with  $T_i$  in the data sets of Droevendaal 1996 and 1997 (Fig. 1A and B). Figure 1A shows only the data for Droevendaal 1996 for non-presprouted tubers and a planting depth of 8 cm. The other treatments showed the same pattern (data for presprouted tubers can be seen in Fig. 1B). The decrease in  $R_L$  was especially clear just after the final potato sprouts had emerged at Droevendaal 1997 (right of the vertical broken lines in Fig. 1). At Lovinkhoeve, where  $L$  was sampled only three times and after full emergence of the potato sprouts,  $R_L$  declined slightly (Fig. 1C). The  $R_L$  of winter wheat and that of spring wheat in 1997 was nearly linear up to a  $L$  of 1 and then clearly decreased with  $T_i$  (Figs. 2A and 2B). For spring wheat in 1998 leaf senescence occurred so early that only two sampling points were available (Fig. 2B).

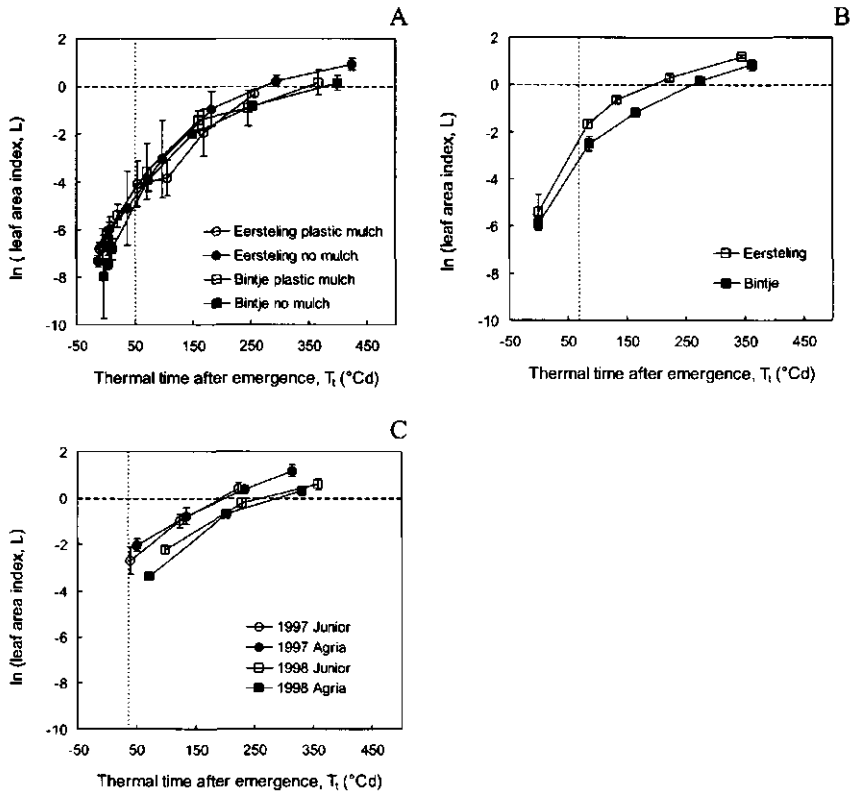


Figure 1. Natural-logarithm transformed leaf area index of potato ( $\ln(L)$ ) as a function of thermal time ( $^{\circ}\text{Cd}$ ) after 50% emergence for data set 1 (A), 2 (B) and 3 (C). Plants in data set 1 were non-presprouted tubers and had a planting depth of 8 cm. Data sets are described in Table 1A. Data points are means per treatment. Error bars represent standard deviation. Horizontal broken line indicates a leaf area index of 1. Points left of the vertical broken line were collected before the last sprout had emerged.

To compare differences in the  $R_L$  across genotypes and environments, we fitted a straight line to the relationship between  $\ln$ -transformed  $L$  and  $T_t$  (see equation 3), using only  $L$  values smaller than 1. For potato,  $L$  values sampled before final sprout density were not included, because the increment in  $L$  during that period partly depends on the sprout emergence rate, which depends on soil temperature and is not dealt with in the present paper. We did not fit a decreasing  $R_L$  with  $T_t$  (a second order exponential polynomial, see Hunt (1982)), because we wanted to apply the same model to all data sets and the decrease in  $R_L$  could not be estimated accurately from the Lovinkhoeve data sets. The reason we only included  $L$  values smaller than one was because  $R_L$  was nearly linear up to that point and, therefore, by so doing we avoided systematic errors arising from the fall in the  $R_L$ .

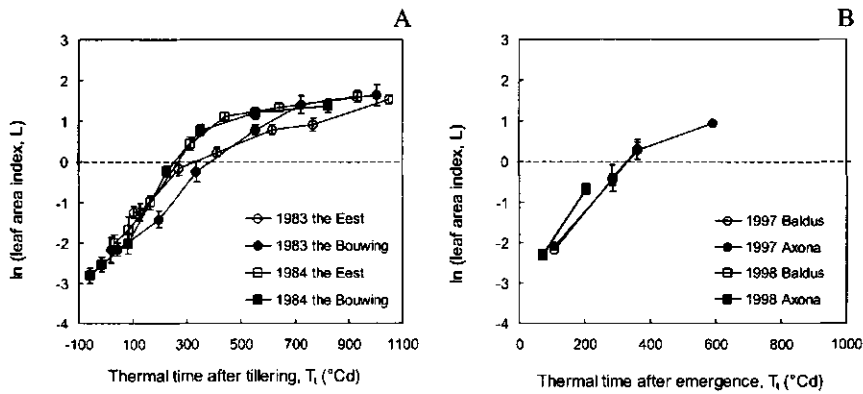


Figure 2. Natural-logarithm transformed leaf area index of wheat ( $\ln(L)$ ) as a function of thermal time ( $^{\circ}\text{Cd}$ ) after tillering (A, data set 4 winter wheat) and after 50% emergence (B, data set 5 spring wheat). Data sets are described in Table 1B. Data points are means per treatment. Error bars represent standard deviation. Horizontal broken line indicates a leaf area index of 1.

Table 3. Soil thermal time at planting depth after date of planting (mean values with standard errors in brackets) and emergence dates of potato under different treatments in Droevendaal 1996 (data set 1).

Treatment	Soil thermal time ( $^{\circ}\text{Cd}$ )	Emergence
	Planting till emergence	Date
Eersteling	249 (16.1)	5 May
Bintje	264 (14.2)	6 May
Plastic mulch	211 (9.7)	2 May
No plastic mulch	303 (13.8)	9 May
Presprouted	211 (10.4)	1 May
Not presprouted	302 (13.4)	10 May
Depth 8 cm	227 (15.0)	3 May
Depth 18 cm	286 (12.9)	8 May
<i>earliest emergence</i>		
Eersteling, plastic mulch, presprouted, depth 8 cm	129 (0.0)	25 Apr
<i>latest emergence</i>		
Bintje, no plastic mulch, non-presprouted, depth 18 cm	388 (0.0)	19 May

### *Specific leaf area versus thermal time*

The  $S_{LA}$  of potato increased linearly from 5 to 15 m<sup>2</sup> kg<sup>-1</sup> at 50% emergence till a maximum of 20 to 25 m<sup>2</sup> kg<sup>-1</sup> at a  $T_i$  of about 150 °Cd after 50% emergence (Fig. 3). Thereafter,  $S_{LA}$  remained more or less constant (Figs. 3B, 3C 1997) or decreased slightly (Fig. 3A Bintje). Figure 3A shows only data for non-presprouted tubers and a planting depth of 8 cm at Droeendaal in 1996. The other treatments showed the same pattern. Only at Lovinkhoeve in 1998, did  $S_{LA}$  of potato clearly continue to increase up to the last sampling (Fig. 3C). Throughout the sampling period, the  $S_{LA}$  of winter wheat increased slightly with  $T_i$  (Fig. 4A) except at The Eest in 1983, where it decreased slightly. For spring wheat (Fig. 4B), the  $S_{LA}$  either increased slightly (1998), decreased slightly (1997 Axona) or remained stable (1997 Baldus).

To compare  $S_{LA}$  patterns across environments and genotypes, the relationship between  $S_{LA}$  of potato and  $T_i$  was described by a segmented model with two straight lines (Fig. 5). In that model,  $S_{LA}$  increases linearly with  $T_i$ , from an initial value  $S_{LA,0,p}$  (m<sup>2</sup> kg<sup>-1</sup>) at zero  $T_i$  at a rate of  $R_{SLA,p}$  (m<sup>2</sup> kg<sup>-1</sup> (°Cd)<sup>-1</sup>), up to maximum value  $S_{LA,max,p}$  at the  $T_i$  value  $T_{i,Smax}$  (°Cd), after which the  $S_{LA,p}$  remains constant:

$$\begin{aligned} S_{LA,p} &= S_{LA,0,p} + R_{SLA,p} T_i \text{ if } T_i < T_{i,Smax} \\ &= S_{LA,0,p} + R_{SLA,p} T_{i,Smax} = S_{LA,max,p} \text{ if } T_i \geq T_{i,Smax} \end{aligned} \quad (4)$$

All values ( $S_{LA,0,p}$ ;  $R_{SLA,p}$ ;  $S_{LA,max,p}$ ;  $T_{i,Smax}$ ) are estimated by regression analysis.

Other functions, such as a polynomial, would have described the course of  $S_{LA}$  with  $T_i$  for potato more precisely, but the segmented model shows the main pattern with parameters that are easy to interpret. It was not possible to estimate  $T_{i,Smax}$  in genotype by environment combinations in which  $S_{LA}$  continued to increase with  $T_{i,Smax}$  (e.g. for cultivars Junior and Agria in 1998, Fig. 3C). We assumed that in these genotype by environment combinations  $S_{LA}$  would have reached a maximum at a  $T_i$  greater than 350 °Cd. Because in most genotype by environment combinations the fast increase in  $S_{LA}$  with  $T_i$  ceased at about the same  $T_i$  value (150 °Cd, Fig. 3), we used one common  $T_{i,Smax}$  value across all genotype by environment combinations. To find that common  $T_{i,Smax}$  value, Eq. 4 was fitted to all potato data sets simultaneously, allowing the parameters  $S_{LA,0}$ ,  $S_{LA,max}$  and  $R_{SLA}$  to vary with genotype and environment. The estimated  $T_{i,Smax}$  was 154.5 °Cd (adjusted  $R^2=84.6$ ;  $n=390$ ) and was further used in regression analysis.

The changes in  $S_{LA}$  of spring and winter wheat with  $T_i$  were small compared to those of potato and they did not show a consistent pattern with  $T_i$ . Therefore, the relationship between  $S_{LA}$  of spring and winter wheat with  $T_i$  was described by a linear model as shown in Fig. 5B. In this model  $S_{LA}$  starts at an initial value of



$S_{LA,1,ww}$  (winter wheat) or  $S_{LA,0,sw}$  (spring wheat) at zero  $T_i$ , and either increases or decreases with  $T_i$  at an average rate  $R_{SLA}$ :

$$S_{LA,ww} = S_{LA,1,ww} + R_{SLA,ww} T_i \quad (5a: \text{winter wheat})$$

$$S_{LA,sw} = S_{LA,0,sw} + R_{SLA,sw} T_i \quad (5b: \text{spring wheat})$$

### *Fitted parameter values for leaf area index*

The back-transformed apparent  $L$  of potato at 50% emergence ( $L_{0,p}$ ) varied from 0.0038 to 0.0400 for individual treatments at Droevendaal 1996 (Table 4A), from 0.0162 to 0.0334 at Droevendaal 1997 (Table 4B) and from 0.0086 to 0.0646 at the Lovinkhoeve (Table 4C). The  $R_L$  of potato varied from  $11.9 \cdot 10^{-3}$  to  $21.9 \cdot 10^{-3} (\text{°Cd})^{-1}$  for the individual treatments at Droevendaal 1996 (Table 4A). The  $R_L$  of potato at Droevendaal 1997 (Table 4B) and at Lovinkhoeve (Table 4C) were within the range of Droevendaal 1996. The  $R_L$  of potato showed interaction between genotype and presprouting at Droevendaal 1996 (Table 4A). For non-presprouted tubers,  $R_L$  of Eersteling ( $20.6 \cdot 10^{-3} (\text{°Cd})^{-1}$ ) was significantly higher than of that Bintje ( $13.9 \cdot 10^{-3} (\text{°Cd})^{-1}$ ) but for presprouted tubers no genotypic effect was found ( $R_{L,p}$ :  $15.8 \cdot 10^{-3} (\text{°Cd})^{-1}$ ). Genotype did not affect the  $R_L$  nor the apparent  $L$  at 50% emergence of potato in Droevendaal 1997. At Lovinkhoeve, the  $R_L$  was not affected by any treatment, but the apparent  $L$  of potato at 50% emergence was significantly higher in 1997 (0.0450) than in 1998 (0.0147).

The back-transformed apparent  $L$  of winter wheat at start of tillering ( $L_{1,ww}$ ) (0.0898 to 0.147, Table 5A) was lower than that of spring wheat at the same growth stage (0.195 to 0.331, calculated from Table 5B with start of spring wheat tillering at  $164 \text{ °Cd}$ ). Leaf area per plant was also lower for winter wheat ( $4.0$  to  $6.7 \text{ cm}^2 \text{ plant}^{-1}$ ) than for spring wheat ( $7.6$  to  $13.7 \text{ cm}^2 \text{ plant}^{-1}$ ) (plant densities in Table 1B). The relative rates of leaf area expansion of winter wheat ( $R_{L,ww}$ :  $5.8 \cdot 10^{-3}$  to  $9.1 \cdot 10^{-3} (\text{°Cd})^{-1}$ ) were lower than those of spring wheat ( $R_{L,sw}$ :  $9.4 \cdot 10^{-3}$  to  $12.1 \cdot 10^{-3} (\text{°Cd})^{-1}$ ) and both were lower than those of potato (Table 4). Leaf area indices of spring wheat were always higher than those of winter wheat, when compared in terms of  $T_i$  after tillering. The difference in the  $R_L$  of winter and spring wheat (significant at  $P < 0.05$ ), was much smaller when  $R_L$  was expressed per developmental unit (du) rather than per  $T_i$ . If we define one development unit as the  $T_i$  from tillering till anthesis (mean:  $1080 \text{ °Cd}$  for winter wheat and  $663 \text{ °Cd}$  for spring wheat), then the  $R_L$  of winter wheat was  $7.7 (\text{du})^{-1}$  and was not significantly different from that of spring wheat  $7.3 (\text{du})^{-1}$  ( $P = 0.74$ ) (not shown in tables).

The  $R_L$  of both winter and spring wheat depended on year. The  $R_L$  of winter wheat was higher in 1984 ( $8.2 \cdot 10^{-3} (\text{°Cd})^{-1}$ ) than in 1983 ( $6.0 \cdot 10^{-3} (\text{°Cd})^{-1}$ ), and that of spring wheat was higher in 1998 ( $12.1 \cdot 10^{-3} (\text{°Cd})^{-1}$ ) than in 1997 ( $9.7 \cdot 10^{-3} (\text{°Cd})^{-1}$ ).

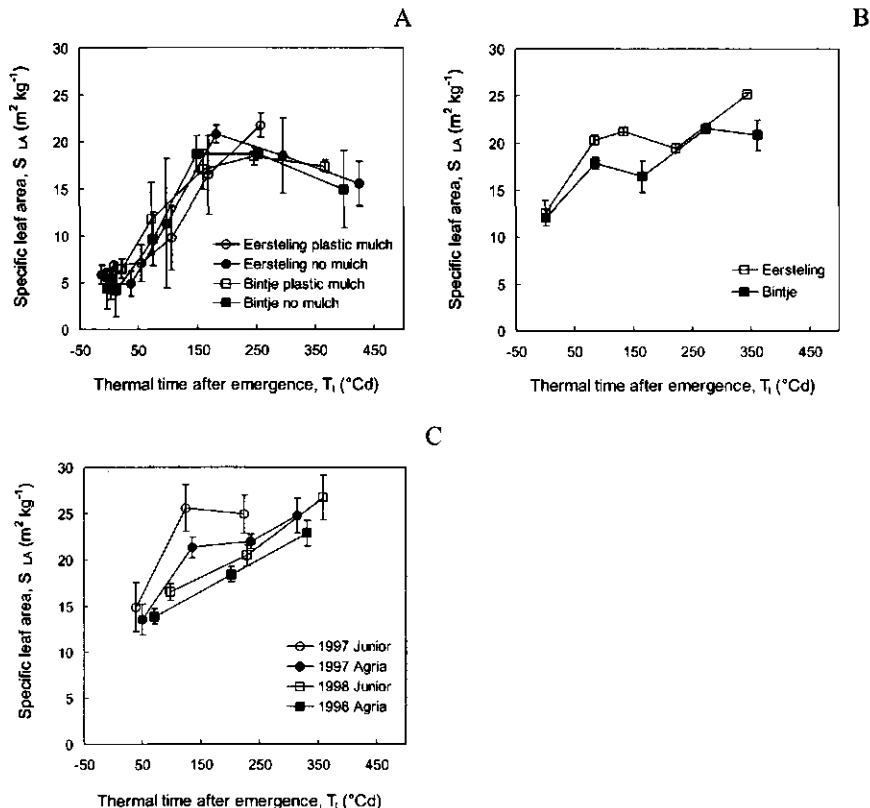


Figure 3. Specific leaf area of potato ( $S_{LA,p}$ ) as a function of thermal time ( $T_i$ ,  $^{\circ}Cd$ ) after 50% emergence for data set 1 (A), 2 (B) and 3 (C). Plants in data set 1 were non-presprouted tubers and had a planting depth of 8 cm. Data points are means per treatment. Error bars represent standard deviation. Data sets are described in Table 1A.

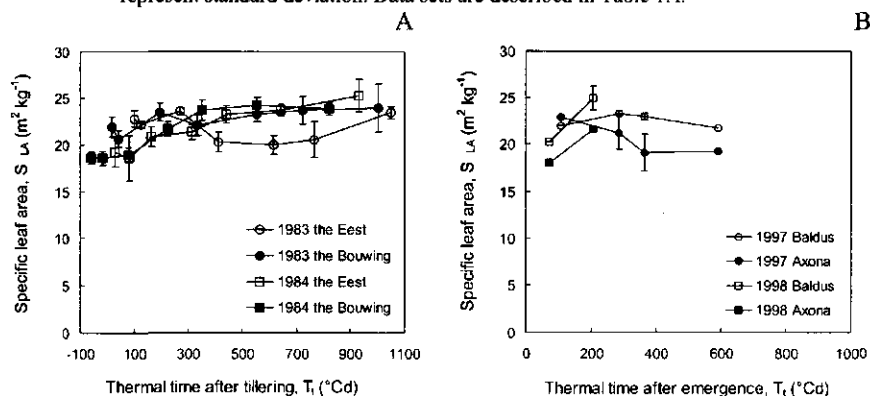


Figure 4. A. Specific leaf area of winter wheat ( $S_{LA,ww}$ ; data set 4) as a function of thermal time ( $T_i$ ,  $^{\circ}Cd$ ) after tillering. B. Specific leaf area of spring wheat ( $S_{LA,sw}$ ; data set 5) as a function of  $T_i$  after 50% emergence. Data points are means per treatment. Error bars represents standard deviation. Data sets are described in Table 1B.

*Fitted parameters values for specific leaf area*

For all individual treatments in the three data sets, the variation in the three parameters that described the course of the  $S_{LA}$  of potato with  $T_t$  was least for the maximum value ( $S_{LA,max,p}$  13.2 to 26.4  $m^2 kg^{-1}$ ) and largest for the value at 50% emergence ( $S_{LA,0,p}$  3.51 to 13.67  $m^2 kg^{-1}$ ) (Table 4). Contrary to the parameters of the leaf area expansion, all management conditions significantly affected the increase  $S_{LA}$  with  $T_t$  ( $R_{SLA}$ ) and the maximum  $S_{LA}$  at Droevendaal 1996, but genotype did not affect them (Table 4A). Presprouting with shallow planting without mulching significantly reduced the increase of  $S_{LA}$  per unit of  $T_t$  ( $R_{SLA,0,p}$ : 56.6  $10^{-3} m^2 kg^{-1} (^{\circ}Cd)^{-1}$ ) compared to the other treatments (84.2  $10^{-3} m^2 kg^{-1} (^{\circ}Cd)^{-1}$ ) except presprouted shallow-planted tubers and it had a smaller maximum  $S_{LA}$  ( $S_{LA,max,p}$ : 14.8  $m^2 kg^{-1}$ ) compared to the other treatments (17.6  $m^2 kg^{-1}$ ). Presprouting with deep planting with mulching increased  $S_{LA,max,p}$  (20.1  $m^2 kg^{-1}$ ) compared to the other treatments (17.6  $m^2 kg^{-1}$ ).

Table 4. Calculated mean values, standard errors (in brackets) and significant effects in analysis of variance ( $P < 0.05$ ) of the parameters that relate leaf area expansion and specific leaf area to thermal time. Data are for Droevendaal, 1996 (4A), Droevendaal, 1997 (4B) and the Lovinkhoeve, 1997 and 1998 (4C). Parameters refer to Eqs. 3 and 4; see also appendix.

## 4A.

Treatments	$\ln(L_{0,p})$	$R_{L,p}$ $10^{-3} (^{\circ}Cd)^{-1}$	$S_{LA,0,p}$ $m^2 kg^{-1}$	$R_{SLA,p}$ $10^{-3} m^2 kg^{-1} (^{\circ}Cd)^{-1}$	$S_{LA,max,p}$ $m^2 kg^{-1}$
Eersteling (G)	-4.38 (0.20)	18.4 (1.0)	5.79 (0.27)	77.3 (3.4)	17.7 (0.4)
Bintje	-4.50 (0.18)	14.7 (0.8)	5.01 (0.27)	80.6 (3.4)	17.5 (0.5)
Plastic mulch (M)	-4.41 (0.21)	16.5 (0.8)	5.80 (0.25)	80.0 (3.2)	18.1 (0.4)
No plastic mulch	-4.47 (0.17)	16.6 (1.1)	5.00 (0.30)	77.9 (3.7)	17.0 (0.4)
Presprouting (P)	-4.46 (0.19)	15.8 (0.8)	5.82 (0.26)	72.7 (3.5)	17.0 (0.5)
No Presprouting	-4.42 (0.19)	17.3 (1.2)	4.98 (0.28)	85.2 (2.9)	18.1 (0.4)
Depth 8 cm (D)	-4.50 (0.23)	16.0 (1.0)	5.53 (0.32)	73.5 (3.5)	16.9 (0.4)
Depth 18 cm	-4.38 (0.14)	17.1 (1.0)	5.27 (0.25)	84.3 (3.0)	18.3 (0.4)
Lowest value	-5.56(0.30)	11.9(1.8)	3.51(0.71)	49.9(13.9)	13.2(1.3)
Highest value	-3.22(0.22)	21.9(3.0)	7.38(0.26)	92.1(14.7)	20.6(1.5)
Number of points per regression	3.3	3.3	7.0	7.0	7.0
Significant main effects	-	-	M	P,D	P,D
Significant interactions	n.t. <sup>1</sup>	GxP	n.t. <sup>1</sup>	MxPxP	MxPxP

<sup>1</sup> Intercepts ( $\ln(L_{0,p})$  and  $S_{LA,0,p}$ ) were not tested because the slopes were affected.

## 4B.

Genotype (G)	$\ln(L_{0,p})$	$R_{L,p}$ $10^{-3} (^{\circ}\text{Cd})^{-1}$	$S_{LA,0,p}$ $\text{m}^2 \text{kg}^{-1}$	$R_{SLA,p}$ $10^{-3} \text{m}^2 \text{kg}^{-1}$ $(^{\circ}\text{Cd})^{-1}$	$S_{LA,max,p}$ $\text{m}^2 \text{kg}^{-1}$
Eersteling	-3.40 (0.16)	20.6 (0.7)	13.43 (0.71)	60.0 (5.9)	22.7 (0.21)
Bintje	-4.12 (0.40)	18.8 (2.5)	13.67 (1.08)	39.4 (11.4)	19.8 (0.73)
Number of points per regression	2.0	2.0	4.8	4.8	4.8
Significant main effects	-	-	-	-	G

## 4C.

Year (Y) Genotype (G)	$\ln(L_{0,p})$	$R_{L,p}$ $10^{-3} (^{\circ}\text{Cd})^{-1}$	$S_{LA,0,p}$ $\text{m}^2 \text{kg}^{-1}$	$R_{SLA,p}$ $10^{-3} \text{m}^2 \text{kg}^{-1}$ $(^{\circ}\text{Cd})^{-1}$	$S_{LA,max,p}$ $\text{m}^2 \text{kg}^{-1}$
1997 Junior	-3.46 (0.43)	20.1 (2.2)	11.80 (2.20)	94.7 (15.6)	26.4 (1.19)
Agria	-2.74 (0.35)	14.6 (4.1)	8.87 (1.30)	93.5 (8.4)	23.3 (0.72)
1998 Junior	-3.67 (0.20)	15.1 (1.3)	4.33 (1.49)	124.9 (14.6)	23.6 (1.02)
Agria	-4.76 (0.15)	20.1 (0.9)	8.12 (0.60)	81.1 (4.7)	20.7 (0.59)
Number of points per regression	2.0	2.0	3.3	3.3	3.3
Significant main effects	Y	-	Y	-	Y,G
Significant interactions	-	-	-	-	-

At Droevendaal 1997, the maximum  $S_{LA}$  of Eersteling ( $22.7 \text{ m}^2 \text{kg}^{-1}$ ) was higher than of Bintje ( $19.8 \text{ m}^2 \text{kg}^{-1}$ ) (Table 4B). At the Lovinkhoeve site, maximum  $S_{LA}$  was higher for genotype Junior ( $25.0 \text{ m}^2 \text{kg}^{-1}$ ) than for Agria ( $22.0 \text{ m}^2 \text{kg}^{-1}$ ) (Table 4C). Both the  $S_{LA}$  at 50% emergence and the maximum  $S_{LA}$ , but not the slope ( $R_{SLA}$ ), were higher in 1997 ( $10.3$  and  $24.9 \text{ m}^2 \text{kg}^{-1}$ ) than in 1998 ( $6.2$  and  $22.1 \text{ m}^2 \text{kg}^{-1}$ ).

The variation in the  $S_{LA}$  at tillering of winter wheat ( $S_{LA,1,ww}$   $19$  to  $22 \text{ m}^2 \text{kg}^{-1}$ , Table 5A) and in the  $S_{LA}$  at 50% emergence of spring wheat ( $S_{LA,0,sw}$   $16$  to  $23 \text{ m}^2 \text{kg}^{-1}$ , Table 5B) was much less than that for  $S_{LA}$  at 50% emergence of potato ( $S_{LA,0,p}$ ). In contrast to potato, the  $S_{LA}$  of wheat changed only slightly per unit of  $T_i$ , the change being 10 till 100 times smaller than that of potato (see difference in  $R_{SLA}$  in Fig. 5A and Fig. 5B). The only exception was the large  $R_{SLA}$  of spring wheat in 1998, but that was based on two sampling points only.

Table 5. Calculated mean values, standard errors (in brackets) and significant effects in analysis of variance ( $P < 0.05$ ) of the parameters that relate leaf area expansion and specific leaf area to thermal time. Data are for winter wheat (5A) and spring wheat (5B). Parameters refer to Eqs. 2 and 5. See appendix for abbreviations.

## 5A.

Year (Y)	Site (S)	$\ln(L_{1,ww})$	$R_{L,ww}$ ( $10^{-3} (^{\circ}\text{Cd})^{-1}$ )	$S_{LA,1,ww}$ ( $\text{m}^2 \text{kg}^{-1}$ )	$R_{SLA,ww}$ ( $10^{-3} \text{m}^2 \text{kg}^{-1} (^{\circ}\text{Cd})^{-1}$ )
1983	The Eest	-1.92 (0.08)	6.19 (0.44)	22.1 (0.2)	-0.59 (0.21)
	The Bouwing	-2.38 (0.06)	5.83 (0.21)	21.7 (0.2)	2.58 (0.73)
1984	The Eest	-2.23 (0.11)	7.44 (0.89)	19.1 (0.3)	7.20 (0.59)
	The Bouwing	-2.41 (0.05)	9.05 (0.25)	19.3 (0.2)	7.39 (0.25)
Number of points per regression		3.5	3.5	7	7
Significant effects		n.t. <sup>1</sup>	Y	n.t. <sup>1</sup>	Y, S, YxS

<sup>1</sup> Intercepts ( $\ln(L_{1,ww})$  and  $S_{LA,1,ww}$ ) were not tested because the slopes were affected.

## 5B.

Year (Y)	Genotype (G)	$\ln(L_{0,sw})$ <sup>1</sup>	$R_{L,sw}$ ( $10^{-3} (^{\circ}\text{Cd})^{-1}$ )	$S_{LA,0,sw}$ <sup>1</sup> ( $\text{m}^2 \text{kg}^{-1}$ )	$R_{SLA,sw}$ ( $10^{-3} \text{m}^2 \text{kg}^{-1} (^{\circ}\text{Cd})^{-1}$ )
1997	Baldus	-3.27 (0.11)	10.0 (1.1)	22.7 (0.3)	-0.7 (1.2)
	Axona	-3.12 (0.05)	9.4 (0.5)	23.2 (0.8)	-7.8 (2.2)
1998	Baldus	-3.16 (0.03)	12.1 (0.5)	17.8 (0.4)	35.0 (5.6)
	Axona	-3.15 (0.03)	12.1 (0.4)	16.1 (0.0)	26.5 (0.6)
Number of points per regression		2	2	3	3
Significant effects		n.t. <sup>1</sup>	Y	n.t. <sup>1</sup>	Y

<sup>1</sup> Intercepts ( $\ln(L_{0,sw})$  and  $S_{LA,0,sw}$ ) were not tested because the slopes were affected.

The change in the  $S_{LA}$  of winter wheat per unit of  $T_i$  was affected by an interaction between year and site (Table 5A). In 1983, the change in  $S_{LA}$  of winter wheat per unit of  $T_i$  was significantly higher at The Bouwing ( $2.58 \cdot 10^{-3} \text{m}^2 \text{kg}^{-1} (^{\circ}\text{Cd})^{-1}$ ) than at The Eest ( $-0.59 \cdot 10^{-3} \text{m}^2 \text{kg}^{-1} (^{\circ}\text{Cd})^{-1}$ ) whereas in 1984 the two sites were not significantly different (mean  $7.29 \cdot 10^{-3} \text{m}^2 \text{kg}^{-1} (^{\circ}\text{Cd})^{-1}$ ) but both were higher than in 1997 (see also Fig. 4A). The  $S_{LA}$  of spring wheat per unit of  $T_i$  increased in 1998 ( $30.8 \cdot 10^{-3} \text{m}^2 \text{kg}^{-1} (^{\circ}\text{Cd})^{-1}$ ) whereas it decreased in 1997 ( $-4.2 \cdot 10^{-3} \text{m}^2 \text{kg}^{-1} (^{\circ}\text{Cd})^{-1}$ ) (Table 5B). In conclusion, the course  $S_{LA}$  of potato, spring and winter wheat was not solely explained by  $T_i$ .

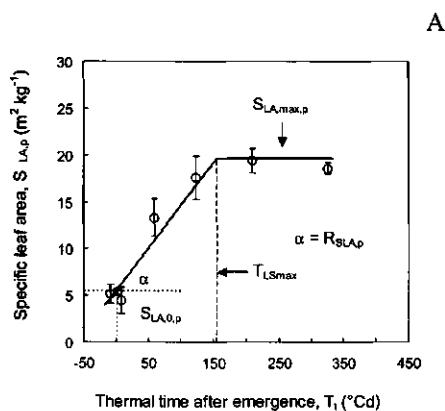


Figure 5A. The line shows the estimation of the course of the specific leaf area of potato ( $S_{LA,p}$ ) as a function of thermal time ( $T_t$ ) (°Cd) after 50% emergence with a segmented model of two straight lines. Parameters of the model were  $S_{LA,p}$  at 50% emergence ( $S_{LA,0,p}$ ), the rate of increase of  $S_{LA,p}$  per unit of  $T_t$  ( $R_{SLA,p}$ ), the maximum  $S_{LA,p}$  ( $S_{LA,max,p}$ ) and the  $T_t$  at  $S_{LA,p}$  is just at its maximum ( $T_{t,Smax}$ ).  $T_{t,Smax}$  was estimated for all treatments simultaneously, the other parameters were estimated per treatment. The solution with the least residual sum of squares was chosen. Data points are of a representative treatment of data set 1 (see Table 1A). Bintje with plastic mulch until emergence, non-presprouted tubers and had a planting depth of 18 cm. Error bars represent standard deviation.

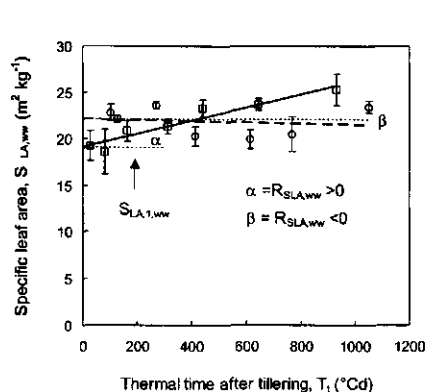


Figure 5B. The line shows the estimation of the course of the  $S_{LA}$  of winter wheat as a function of  $T_t$  (°Cd) after tillering, using a linear regression model. Parameters of the model were the  $S_{LA}$  at tillering ( $S_{LA,1,ww}$ ) and the slope of the regression line  $R_{SLA,ww}$ . Symbols represent the same treatments as in Figure 4A. Error bars represent standard deviation.

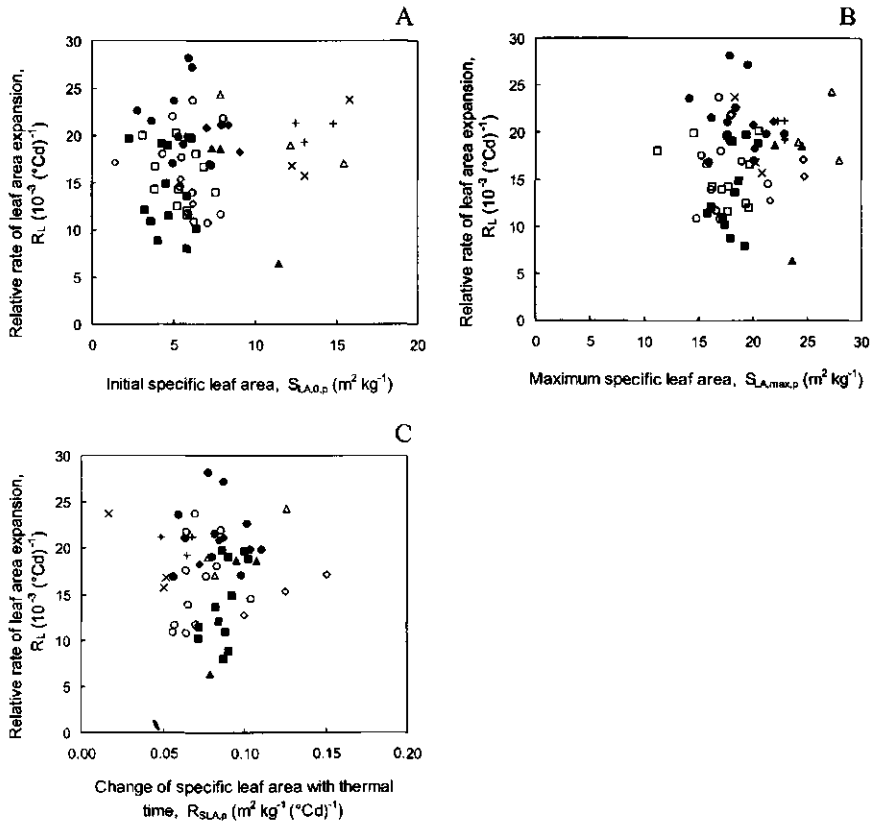


Figure 6. Relationship between the estimated relative rate of leaf area expansion of potato and (A) the initial  $S_{LA}$  at 50% emergence, (B) the maximum  $S_{LA}$  and (C) slope of  $S_{LA}$  with  $T_i$ . Each point represents an individual replicate. Treatments were: Eersteling presprouted tubers 1996 (○, data set 1), Eersteling non-presprouted tubers 1996 (●, data set 1), Bintje presprouted tubers 1996 (□, data set 1), Bintje non-presprouted tubers 1996 (■, data set 1), Eersteling 1997 (+, data set 2), Bintje 1997 (x, data set 2), Junior 1997 (Δ, data set 3), Agria 1997 (▲, data set 3), Junior 1998 (◇, data set 3) and Agria 1998 (◆, data set 3). Data sets are described in Table 1A.

### Correlation between $R_L$ and $S_{LA}$

In studies comparing relative growth rates across species, part of those differences were explained by interspecific differences in  $S_{LA}$  (e.g. McKenna and Shipley, 1999). To investigate whether treatment effects on  $S_{LA}$  and  $R_L$  were correlated in our study, we plotted the  $R_L$  as a function of the  $S_{LA}$  parameters of potato (Fig. 6), and of the  $R_{SLA}$  and the average  $S_{LA}$  wheat, for all replicates (Fig. 7). The  $R_L$  of potato, as affected by

treatments, did not show any relationship with the corresponding  $S_{LA}$  parameters. Thus in our study, the differences in  $R_L$  and in  $S_{LA}$  between treatments of potato were not linked. For winter wheat,  $R_L$  per treatment mean tended to increase with  $R_{SLA}$  ( $R^2_{adjusted}=48.5$ ,  $P=0.19$ ) but to decrease with the average  $S_{LA}$  ( $R^2_{adjusted}=52.8$ ,  $P=0.17$ ). Regressions of treatment means were not significant, but they were only based on four treatments. For spring wheat, a higher  $R_L$  per treatment mean was associated with a larger change of  $S_{LA}$  with  $T_t$  ( $R_{SLA}$ ) ( $R^2_{adjusted}=95.6$ ,  $P<0.05$ ,  $n=4$  treatments) but the  $R_L$  did not show a relationship with the average  $S_{LA}$  value ( $P=0.9$ ).

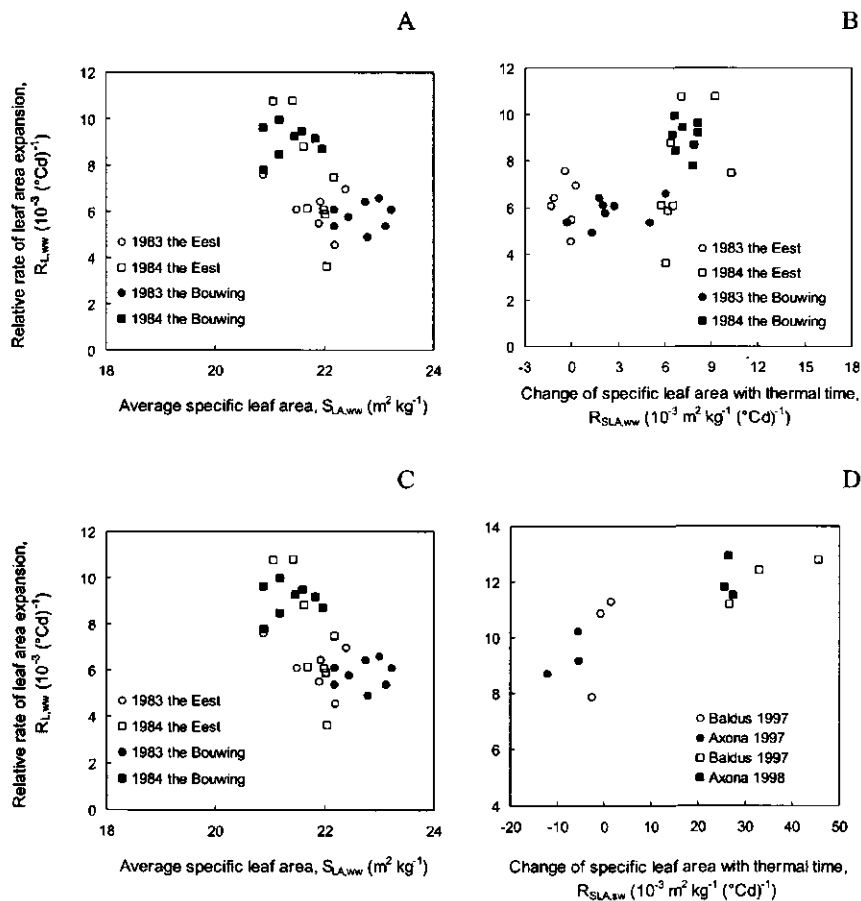


Figure 7. Relationship between the estimated relative rate of leaf area expansion of winter and: (A) the average specific leaf area ( $S_{LA}$ ) (B) slope of  $S_{LA}$  with thermal time ( $T_t$ ). Likewise for spring wheat (C and D). Each point represents an individual replicate per treatment.



## Discussion

### *Pattern of leaf area index versus thermal time*

Our finding that the  $R_L$  of potato and wheat decreased gradually with  $T_t$  corroborated earlier findings at constant temperatures in which  $R_L$  decreased with time (Friend et al., 1965; Horie et al. 1979; Hunt, 1982).  $R_L$  decreases with time, because plants invest more in structural tissues as they become larger (Hunt, 1982). The simplest way to describe the decrease in  $R_L$  is to use a function in which  $R_L$  decreases linearly with  $T_t$ :  $R_L = dL / L dT_t = b_1 + 2 b_2 T_t$  and  $\ln(L) = L_0 + b_1 T_t + b_2 T_t^2$  (second order polynomial), which is why the second order polynomial is preferred by some (see Hunt, 1982) above the use of a constant  $R_L$ . Our data sets with more than four sampling points of  $L$  (potato in 1996 at Droevendaal and winter wheat) indicate that such a linear decrease of  $R_L$  is appropriate indeed (see Figs. 1A and 1B). The application of such a model requires enough sampling points at higher  $L$  values so that the decrease can be accurately estimated. Because our data sets varied much in the final  $L$  that was sampled and because some data sets had only three (early) sampling points, we restricted our data to  $L$  for which  $R_L$  was nearly constant. The environmental and genotypic effects of our study on  $R_L$  therefore only refer to part of our data ( $L < 1$ ).

$L$ -values of potato collected near 50% emergence were not included in the calculation of the  $R_L$ , because the initial  $R_L$  is also a function of sprout emergence. The actual  $L$  values collected near 50% emergence at Droevendaal 1996 were therefore much lower (mean: 0.0025) than the estimated ones at 50% emergence (mean: 0.0118). When differences in the  $R_L$  of different potato genotypes by environment combinations are compared, e.g. to improve crop competitiveness against weeds in breeding programmes (Rebetzke and Richards, 1999), it is important to recognise that the initial  $L$  of potato increases because new sprouts emergence and the leaf area on already emerged sprouts expands. An early indicator of  $L$  should be collected when a fixed proportion of sprouts has emerged.

### *Pattern of specific leaf area versus thermal time*

$S_{LA}$  of potato increased from 5 to 15 m<sup>2</sup> kg<sup>-1</sup> at 50% emergence till an maximum of 20 to 25 m<sup>2</sup> kg<sup>-1</sup> at a common value of 155 °Cd and decreased slightly thereafter. We analysed the course of  $S_{LA}$  with  $T_t$  by the same simple model applied to all genotype by environment combinations. We realise that the course of  $S_{LA}$  with  $T_t$  would have been better described by fitting another model (e.g. a straight line) to those combinations for which it was not possible to fit a maximum. Nonetheless, it would no longer be possible to do a good statistical test for genotype and environment effects on the parameters of the model. First of all, the maximum  $S_{LA}$  and  $T_{t, S_{max}}$  would have

a number of missing values and secondly, the fitted value for the change of  $S_{LA}$  with  $T_i$  ( $R_{S_{LA},p}$ ) of a single straight line would have the tendency to be lower than that of the model with two straight lines. The  $R_L$  value of a single straight line is lower, because it is fitted to points for which the slope decreases with  $T_i$ , but the model does not account for that decrease.

The consequence of our simplified description of potato is two fold. Firstly, the value of 155 °Cd at which  $S_{LA}$  is at its maximum indicates an approximate value because we could not test the parameter on genotype by environment effects. When such a study as ours is repeated more sampling points should be included near that maximum  $S_{LA}$  value to enable estimation of that maximum in all genotype by environment combinations. Secondly, in the present study it is best to look at the effect of genotype and environment on the group of parameters describing  $S_{LA}$  with  $T_i$ , because individual parameters could have been affected by the use of a common  $T_{i,Smax}$  value. Nevertheless, the conclusion will hold that genotype and environment affects the course of  $S_{LA}$  with  $T_i$  as becomes visually apparent in Fig. 3, especially in 3B and 3C.

We know of no published studies on early  $S_{LA}$  development of potato. However, Horie et al. (1979) found an initial sharp increase in  $S_{LA}$  with time for cucumber seedlings at constant temperatures. For cucumber, that low initial  $S_{LA}$  was caused by the inclusion of the thick cotyledons in the calculation of the  $S_{LA}$  of cucumber. The thick leaves of potato at emergence (low  $S_{LA}$ ) are likely to reflect a high level of stored non-structural carbohydrates, as has been found before for both monocot species (e.g. Van Loo, 1992) and for potato (Cao and Tibbitts, 1997), as explained below. During potato sprout growth, a hormonal stimulus triggers the breakdown of tuber starch into sucrose which is subsequently hydrolysed into glucose and fructose. Sugars are amply available for sprout growth, as during sprouting large amounts of starch are stored in the sprouts (Moorby and Milthorpe, 1975). The primary leaves of the dark-grown sprouts expand hardly because leaf cell enlargement of dicots needs high fluence white light (Van Volkenbrugh, 1987). The starch storage combined with a small leaf area expansion of dark-grown sprouts probably explains the low  $S_{LA}$  of potato leaves at emergence. In contrast to potato, the expansion of the first wheat leaves is not restricted by light as the leaf extension zone is always enclosed by leaf sheaths and is not directly exposed to light (e.g. Kemp, 1980). At emergence, the seed reserves of wheat are not so amply available as in potato, and many studies showed that seed reserves limit wheat seedling growth (Peterson et al., 1989).

After emergence  $S_{LA}$  increases with  $T_i$ , probably because leaf carbohydrate supply per unit of leaf area decreases. Carbohydrate supply decreases because seed reserve levels decrease, whereas the number of expanding leaves (sinks) increases and daily  $I_{PAR}$  decreases relative to the daily effective temperature for leaf area expansion from 1.0 ( $\text{MJ m}^{-2} \text{d}^{-1} \text{°C}^{-1}$ ) in February to 0.55 in June ( $T_b=0\text{°C}$ , average 1961–1990 De Bilt, the Netherlands). The leaf carbohydrate supply from photosynthesis during

early growth stages is also higher for potato than for wheat, because potato has a larger extinction coefficient ( $k$ ) for PAR (Spitters et al., 1989), whereas light use efficiency ( $E_{LU}$ ) (Spitters, 1987; Van Keulen and Stol, 1991) and dry matter partitioning to leaves ( $P_L$ ) are similar for both crops (Spitters et al., 1989).

In conclusion, we hypothesise that the general pattern of  $S_{LA}$  with  $T_i$  (Fig. 5) of both potato and wheat is mainly caused by variation in the ratio of leaf area expansion rate over carbohydrate supply to leaves, conform Johnson and Thornley (1983). Therefore,  $S_{LA}$  not only varies with temperature, as shown by Hotsonyame and Hunt (1998), but also by radiation interception and seed reserve levels.

### ***Thermal time calculations***

In our study, leaf area development was related to temperature, expressed as  $T_i$ . For wheat,  $T_i$  equally affects both leaf area development and crop development stage because temperature affects leaf appearance rates (Jamieson et al., 1995), which is then related to both leaf area expansion as well as to crop development stage. For potato however, leaf appearance rates are not strictly related to crop development, and up to the appearance of the first branch (end of leaf appearance on main stem), leaf appearance rates for various maturity classes are almost the same (Firman et al., 1995). For wheat, the smaller  $R_L$  of the winter type compared to the spring type when expressed per  $^{\circ}\text{Cd}$  was explained by the shorter  $T_i$  from tillering till anthesis for the spring type. We probably found a higher  $R_L$  ( $^{\circ}\text{Cd}$ )<sup>-1</sup> for the spring type, because we based our  $T_i$  calculations on air temperature, rather than on apex temperature. The use of air temperatures causes leaf appearance rates per  $T_i$  of spring sowings to be faster than those of winter sowings, as explained in Jamieson et al. (1995).

### ***Differences between treatments in parameter values***

The second objective of our study was to determine whether the relationships of leaf area expansion and of  $S_{LA}$  with  $T_i$  are robust over environments. Such a robustness indicates that either relationship can be used to predict leaf area development in new environments. Neither the parameters of leaf area expansion, nor those of  $S_{LA}$  were robust, but both were affected by genotype and environment (site, year and management conditions). Still, we believe that the set of results indicates what approach should be taken to predict leaf area development of potato and wheat. For potato, leaf area expansion up to a  $L$  of 1 was not likely to be determined by the product of  $S_{LA}$  times leaf dry weight for two reasons. Firstly, the effects of genotype and environment on the  $S_{LA}$ , did not show any relationship with the  $R_L$  of potato (Fig. 6). Secondly, the initial  $S_{LA}$  of potato is very low (Fig. 5A) indicating a high level of stored carbohydrates rather than a source limitation.

Thus, for  $L$  of potato smaller than 1, the  $S_{LA}$  is likely to be mainly a resultant of leaf area expansion and leaf dry matter increase and effects of the environment on that parameter (Table 4) may be a reflection of difference in temperature and radiation conditions in those environments. The interactive effects of genotype and presprouting on the  $R_L$  (Table 4A) may be caused by differentials in sink-strength, which in turn may be caused by differences in physiological age of the tuber (Van der Zaag and Van Loon, 1987). We have no full explanation for the higher in  $L$  at 50% emergence at the Lovinkhoeve site in 1997 than in 1998 (Table 4C). Part of that difference may be explained by the higher total number of emerged tubers in 1997 (4.3 tubers  $m^{-2}$ ) than in 1998 (3.9 tubers  $m^{-2}$ ).

In contrast to potato,  $S_{LA}$  of wheat hardly changed with  $T_L$ . It was not so clear whether the effects of year and site on the  $S_{LA}$  of wheat (Table 5) were related to those on  $R_L$  (Fig. 7), because the number of treatments were small. We discussed that the leaf dry matter supply of wheat is expected to be smaller than that of potato, especially during early growth stages. Besides temperature as a main factor, early leaf area expansion of wheat may have been affected by radiation levels (Fig. 7 D) which then partly explains the reported year effect on  $R_L$  of spring wheat. Also leaf appearance rates of wheat have been reported to increase with  $CO_2$  and leaf carbohydrates (McMaster et al., 1999). During later growth stages, radiation is also expected to affect leaf area development of potato, because the tuber sink increases whereas daily radiation levels decrease relative to the daily effective temperatures for foliar expansion.

We therefore conclude that leaf area dynamics should not be modelled as a direct function of temperature only, nor should it solely be based on the use of a fixed  $S_{LA}$  development. Instead, we hypothesise that leaf area dynamics should be described as a function of both temperature and radiation. We will test that hypothesis in a next paper. Source-sink models of this type have been developed for simulation purposes, for example for grasslands (Schapendonk et al., 1998). After inclusion of a source component, it is important to re-test whether the parameters of the equations are affected by different genotypes and environments. The equations could also be extended to account for vernalisation and photoperiodic effects and, by using apex temperatures (Jamieson et al., 1995) to explain the leaf area dynamics of crops with different sowing dates. If the parameters of these equations are no longer affected by environment and are able to predict the dynamics in new environments, they could be applied in simulation models in which leaf area dynamics are crucial.

## Appendix

### List of abbreviations

Abbreviation	Characteristic	Unit
$E_{LU}$	Light utilisation efficiency	$\text{g MJ}^{-1}$
pF	$\log_{10}$ of cm water pressure	-
$S_{LA}$	Specific leaf area	$\text{m}^2 \text{kg}^{-1}$
$S_{LA,0,x}$	$S_{LA}$ at 50% emergence of potato (x=p) and spring wheat (x=sw) ( $\text{m}^2 \text{kg}^{-1}$ )	
$S_{LA,1,ww}$	$S_{LA}$ of winter wheat at start tillering (GS 21)	$\text{m}^2 \text{kg}^{-1}$
$S_{LA,max,p}$	Fitted maximum $S_{LA}$ of potato	$\text{m}^2 \text{kg}^{-1}$
K	Extinction coefficient for PAR	
L	Leaf area index	-
$L_{0,x}$	L at 50% emergence of potato (x=p) and spring wheat (x=sw)	-
$L_{1,ww}$	L at start tillering of winter wheat	-
$I_{PAR}$	Incoming photosynthetically active radiation	$\text{MJ m}^{-2} \text{d}^{-1}$
$R_L$	Relative rate of leaf area expansion	$^{\circ}\text{C}^{-1} \text{d}^{-1}$
$R_{L,x}$	$R_L$ of potato (x=p), spring wheat (x=sw), winter wheat (x=ww)	$^{\circ}\text{C}^{-1} \text{d}^{-1}$
$R_{SLA}$	Change of $S_{LA}$ per unit of thermal time	$\text{m}^2 \text{kg}^{-1} (^{\circ}\text{Cd})^{-1}$
$R_{SLA,x}$	$R_{SLA}$ of potato (x=p), spring wheat (x=sw), winter wheat (x=ww)	$\text{m}^2 \text{kg}^{-1} (^{\circ}\text{Cd})^{-1}$
$T_a$	Daily average air temperature	$^{\circ}\text{C}$
$T_{bs}$	Base temperature	$^{\circ}\text{C}$
$T_e$	Effective temperature	$^{\circ}\text{C}$
$T_t$	Thermal time	$^{\circ}\text{Cd}$
$T_{t,Smax}$	$T_t$ at which $S_{LA}$ of potato is just at its maximum	$^{\circ}\text{Cd}$

**Modelling temperature- and radiation-  
driven leaf area expansion in the  
contrasting crops potato and wheat**

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## Abstract

The performance of a model for simulating increase in leaf area index ( $L$ ) was evaluated for potato (*Solanum tuberosum* L.) and wheat (*Triticum aestivum* L.) cultivars across environments (years and sites). Rate of  $L$  expansion just after emergence was assumed to depend on temperature. After a pre-defined  $L$ ,  $L_S$ , expansion was assumed to increase in proportion to leaf dry weight increase that depended on intercepted radiation, henceforward: radiation-limited expansion. The  $L_S$  value at which the model performed best was considered to be the most realistic  $L$  at which expansion shifts from temperature to radiation-limitation. An  $L_S$  value of zero leads to solely radiation-limited expansion, whereas a value larger than maximum  $L$  leads to solely temperature-limited expansion. The criteria used to evaluate the model were constancy of calibrated model parameters across environments, and predictive ability. For potato and wheat, parameters were most robust across environments, when  $L_S$  was neither zero nor at maximum  $L$ . Model parameters did not vary with genotype. The model's predictions were best at an  $L_S$  of 1.0 for potato and 1.5 for wheat. Using these  $L_S$  values, the coefficient of determination between observed and predicted values was 91% for potato and 88% for wheat. Sensitivity analysis revealed that smaller  $L_S$  values led to larger changes in rate of leaf area expansion and crop dry weight than larger values did. Crop dry weight was hardly affected by an increase in  $L_S$ . Implications of the results for modelling are discussed.

## Introduction

Light interception and crop growth rate are largely determined by leaf area index ( $L$ , abbreviations are given in Table 1) (Monteith, 1977). Thus an accurate prediction of  $L$  is important to calculate light interception. It is especially important for small  $L$  values to be predicted accurately because errors in light interception resulting from errors in  $L$  are largest when  $L$  is small (Jamieson et al., 1998). Accurate prediction of  $L$  is also important in crop-weed competition where initial differences in light interception between crop and weed enlarge over time (Spitters, 1990b). Understanding leaf area expansion is also crucial for correct predictions of crop nitrogen uptake when nitrogen does not limit growth, as this uptake often increases linearly with  $L$  (Booij et al., 1996; Grindlay, 1997; Lemaire and Gastal, 1997).

When crops are supplied sufficiently with water and nutrients and their growth is not reduced by pests and diseases, the main factors affecting the rate of  $L$  increase are temperature (Horie et al., 1979) and assimilate supply (Milthorpe and Newton, 1963; Dale, 1988). Other factors affecting the rate of  $L$  increase are relative humidity, light quality (Dale, 1988) and root impedance (Masle, 1992). Photoperiod also

Table 1. Description of symbols and acronyms, their units and the equation number in which they were used for the first time.

Acronym	Units	Eqn.	Description
$D_L$	$d^{-1}$	—	Mean daily rate of L increase
$E_{LU}$	$g\ MJ^{-1}$	9	Average light use efficiency
$I$	$MJ\ m^{-2}\ d^{-1}$	8	Daily incident PAR
$J$	$MJ\ m^{-2}\ d^{-1}$	8	Daily intercepted PAR
$k$	—	8	Extinction coefficient for light
$L$	—	1	Leaf area index
$L_0$	—	3	L at $T_i=0$
$L_d$	—	1	L of dead leaves
$L_g$	—	1	L of green leaves
$L_S$	—	—	L at switch from temperature- to radiation-limited L expansion
MD	—	12	Mean deviation between predictions and observations
$O_i$	—	12	Observed value for "ith" observation
$P_i$	—	12	Predicted value for "ith" observation
PAR	$MJ\ m^{-2}\ d^{-1}$	—	Daily incident photosynthetic active radiation
$P_{L,t}$	$g\ g^{-1}$	10	Fraction of total crop dry matter partitioned to leaves, at time t
$Q_p$	$MJ\ m^{-2}\ d^{-1}\ ^\circ C^{-1}$	—	Photothermal coefficient
$R_L$	$(^\circ Cd)^{-1}$	2	Relative rate of leaf area expansion
$R_{L,0}$	$(^\circ Cd)^{-1}$	4	$R_L$ at $T_i=0$
$R_{L,t}$	$(^\circ Cd)^{-2}$	4	Linear change of $R_L$ with $T_i$
RMSE	—	13	Root mean square for error
RSS	—	11	Residual sums of squares
$S_{LA,max}$	$m^2\ g^{-1}$	7	Specific leaf area of newly formed leaves
$\Delta t$	d	1	Time step of integration
$T_{av}$	$^\circ C$	2	Daily average temperature
$T_b$	$^\circ C$	2	Base temperature
$T_e$	$^\circ C$	2	Effective temperature
$T_{min}$	$^\circ C$	6	Daily minimum temperature
$T_{max}$	$^\circ C$	6	Daily maximum temperature
$T_t$	$^\circ Cd$	6	Thermal time of leaf area expansion
$W$	$g\ m^{-2}$	9	Total crop dry weight
$W_L$	$g\ m^{-2}$	7	Leaf dry weight

influences leaf area dynamics, but it is unclear whether photoperiod influences the rate of L increase (Dale, 1988). It certainly influences the time of emergence of the flag leaf of wheat and thus maximum L (Brooking et al., 1995).

In models, L has been simulated based on leaf assimilate availability, on temperature and on a combination of both approaches. Some models (e.g. De Wit et al., 1970; Van Keulen and Seligman, 1987) assume that leaf area expansion is



proportional to leaf weight increase so that the leaf area expansion may be found from the leaf weight increase times a specific leaf area ( $S_{LA}$ ), i.e. the amount of leaf area per unit of dry matter. The value of the  $S_{LA}$  was allowed to vary with the rate of leaf dry weight increase (De Wit et al., 1970), or with crop development stage (Van Keulen and Seligman, 1987). The assumption underlying this approach was that during use of a  $S_{LA}$ , leaf area expansion is limited by assimilate supply (Spitters et al., 1989). Such models were extremely sensitive to the partitioning of dry matter to leaves, and to the  $S_{LA}$  (Spitters, 1984). The approach requires that the  $S_{LA}$  or its change with e.g. crop development stage (see Penning de Vries et al., 1989) varies little with environment. Chapter 2 showed that the increase of  $S_{LA}$  of potato and wheat cultivars with crop development stage was not constant but varied with year and site.

Other models simulate  $L$ , based on temperature. The underlying assumption is that rates of leaf appearance and final leaf size are constrained by temperature through its effect on cell division and extension, rather than by the supply of assimilates (Horie et al., 1979; Spitters et al., 1989). Daily increase in  $L$  may then be calculated as a single function of temperature, as is done in models developed by Jones and Kiniry (1986), Hammer et al. (1993) and Jamieson et al. (1998). Meinke et al. (1998b) found that predictions of  $L$  with two of such models (SA and BA in Meinke et al. (1998b)) were poor in a new environment. Results of experimental studies have shown that radiation also affects  $L$  increment. In those studies, the rate of  $L$  increment of both monocot and dicot species increased with incident photosynthetic active radiation (PAR) (Tardieu et al. 1999), with the  $L$  increase peaking at about  $6 \text{ MJ PAR m}^{-2}\text{d}^{-1}$  or above (Friend et al., 1965).

A third group of models combines effects of temperature and assimilate supply on  $L$  expansion. Comprehensive models, such as SUBGOL and ALFALFA (Loomis et al., 1976; 1990), calculate leaf area expansion based on temperatures and available assimilates using an hourly time step. Leaf expansion was found to switch from temperature to substrate limitation both within a day (Loomis and Ng, 1977), as well as a gradually during the growing season (Loomis et al., 1976). Based on those findings, summary models for  $L$  expansion with a daily time step were developed (Kropff, 1988; Spitters et al., 1989) that calculate  $L$  increment as a function of temperature from emergence onwards till a given  $L$ ,  $L_s$ , after which  $L$  expands in proportion to leaf dry weight increase. Henceforward, that summary approach is referred to as temperature-limited and radiation-limited  $L$  expansion. The  $L_s$  was estimated roughly from  $L$  expansion curves (Kropff and Spitters, 1992) and set between 0.75 (Spitters et al., 1989) and 1.0 (Kropff et al., 1994).

Summary models have been developed for practical applications such as agro-ecological zonation and yield predictions, based on previously developed comprehensive models. Comprehensive models were less suitable for that purpose as they require input data of great detail (Bouman et al., 1996). Prediction of  $L$  in summary models have been based on the above-described temperature- and radiation-limited  $L$  expansion using both factors (e.g. Kropff and Spitters, 1992), or solely

temperature (e.g. Jamieson et al., 1998) or solely radiation (e.g. Van Keulen and Seligman, 1987), but these approaches have never been formally compared using experimental data sets. To make this comparison, data from contrasting crops such as potato and wheat would be useful. If leaf expansion becomes increasingly limited by assimilates due to increased competition for assimilates with other sinks (cf. Loomis et al., 1976), then potato is expected to switch earlier than wheat, as explained below. Partitioning of assimilates to potato leaves decreases from the onset of linear tuber bulking onwards (e.g. Spitters et al., 1989), and start of tuber bulking as calculated according to Spitters and Schapendonk (1990) coincided with a  $L$  of about 0.7 in the data described in Chapter 3. Partitioning of assimilates to wheat leaves decreases onwards from the onset of stem extension (Spitters et al., 1989), which coincides with a  $L$  value of about 2 in data by Groot and Verberne (1991) and data of the present paper.

In the present chapter, we estimated  $L_s$  for potato and wheat cultivars and hypothesised that its value was neither zero, indicating solely radiation-limited expansion, nor equal to the maximum  $L$  of a crop, which would imply solely temperature-limited expansion. The relationships underlying  $L$  expansion were described in a summary model and tested against experimental data collected in different environments in The Netherlands. Environment represents a combination of year and site (Chapter 3). It was assumed that the model described the temperature and radiation effects on leaf area expansion most realistically at the  $L_s$  value at which model parameters were least affected by environment (year, site).

## **Materials and methods**

The rate of  $L$  increase was described in a summary model in which the rate of  $L$  increase was assumed to be temperature-limited from emergence onwards until a set  $L$  value,  $L_s$ , after which the rate was proportional to the increase in leaf dry weight. To estimate  $L_s$ , the model was tested against field data on the  $L$  expansion of potato and wheat cultivars in different environments. The experimental  $L$  data, ranging from emergence until maximum  $L$ , are described below (Section 'Experimental data'). As a first step to estimate  $L_s$ , model parameters were calibrated using the observed  $L$  values, with  $L_s$  being (1) estimated or (2) set at zero (implying only radiation-limited expansion), or (3) set at maximum  $L$  (implying only temperature-limited expansion). We tested effects of cultivar and environment on parameter values for these three situations of  $L_s$  (see Section 'Statistical analysis of model parameters'). We then assessed the predictive ability of the model by comparing model's output with the field data, with  $L_s$  varying from 0 to maximum  $L$  in steps of about 0.5  $L$  units. Finally, we tested the sensitivity of  $L$  expansion to  $L_s$  (see Section 'Sensitivity analysis of  $L_s$ ').

### Model

The daily net rate of L increase ( $\Delta L/\Delta t$ ,  $d^{-1}$ ) is the daily leaf expansion rate ( $\Delta L_g/\Delta t$ ) minus the daily leaf senescence rate ( $\Delta L_d/\Delta t$ ):

$$\Delta L/\Delta t = \Delta L_g/\Delta t - \Delta L_d/\Delta t \quad (1)$$

Leaf expansion rate is assumed to be temperature-limited from emergence onwards up to a given leaf area index  $L_s$  and is assumed to be radiation-limited thereafter. Calculation of leaf dry weight increase was done according to LINTUL (Spitters and Schapendonk, 1990).

#### *Temperature-limited leaf expansion rate*

The relative increase in L each day, was described as a linear function of daily average air temperature ( $T_{av}$ ) as was done in previous summary models (e.g. Spitters and Schapendonk, 1990; Kropff and Spitters, 1992; Jamieson et al., 1995; see Fig 1A):

$$(dL_g/dt) / L = R_L (T_{av} - T_b) = R_L T_e \quad (2)$$

where  $L_g$  is the new leaf area, and  $R_L$  with units  $(^{\circ}\text{Cd})^{-1}$  is the relative increase of L and  $T_b$  is a base temperature for leaf area expansion, being  $2^{\circ}\text{C}$  for potato (MacKerron and Waister, 1985) and  $0^{\circ}\text{C}$  for wheat (Jamieson et al., 1995).  $T_e$  is the effective temperature for leaf expansion. Hence, during this phase, L can be calculated as an exponential function of thermal time ( $T_t$ ,  $^{\circ}\text{Cd}$ , see Section 'Thermal time calculation') (see Fig 1C):

$$L_{g,t} = L_0 \exp(R_L T_t) \quad (3)$$

where  $L_0$  is the L at zero thermal time (for starting point of  $T_t$  see below). A common plant response is that  $R_L$  declines more or less linearly as a plant grows (Hunt, 1982), which has also been found for potato and wheat in Chapter 3. To account for the whole increase of L from emergence to maximum L,  $R_L$  was, therefore, described to decrease linearly with thermal time:

$$R_L = R_{L,0} + R_{L,t} T_t \quad (4)$$

where  $R_{L,0}$  ( $^{\circ}\text{Cd})^{-1}$  is the  $R_L$  at zero  $T_t$ , and  $R_{L,t}$  ( $^{\circ}\text{Cd})^{-2}$  the linear rate of change of  $R_L$  with  $T_t$ , with  $R_{L,t}$  below zero. Using a discrete time step ( $\Delta t$ , d),  $\Delta L_g/\Delta t$  can be derived from Eqs. 2 and 4 as:

$$\Delta L_g/\Delta t = L_t (e^x - 1) / \Delta t \quad (5a)$$

with:

$$x = R_{L,0} T_e \Delta t + (R_{L,t} T_e \Delta t)(T_t + 0.5 T_e \Delta t) \quad (5b)$$

Examples of  $R_L$ , the rate of expansion, and  $L$  against  $T_t$  are given in Figs. 1A–C. Values of  $R_{L,0}$  and  $R_{L,t}$  were calibrated using actual field data (see Section ‘Calibration procedure’).

#### *Thermal time calculation*

$T_t$  for leaf area expansion was calculated as in Spitters and Schapendonk (1990) as the average ( $T_{av}$ ) of daily maximum ( $T_{max}$ ) and minimum temperature ( $T_{min}$ ), minus the base temperature ( $T_b$ ) as given above:

$$T_t = \Sigma(T_{max} + T_{min})/2 - T_b \quad (6)$$

Reduction in  $L$  expansion at temperatures above the optimum of about 25°C (Kooman and Haverkort, 1995; Jamieson et al., 1998) was not considered, as  $T_{max}$  was occasionally and hardly above 25°C. For potato and spring wheat,  $T_t$  was calculated from the day of 50% emergence onwards. For winter wheat,  $T_t$  was calculated from the start of tillering (about mid-February) onwards, because the effects of vernalisation on leaf area dynamics are unclear. The winter wheat was fully vernalized at start of tillering (see Chapter 3).

#### *Radiation-limited leaf expansion rate*

Daily leaf expansion rate in proportion to daily rate of leaf dry matter increase ( $\Delta W_L/\Delta t$ , g leaf  $m^{-2}$  ground area  $d^{-1}$ ) was described as:

$$\Delta L_g/\Delta t = \Delta W_L/\Delta t S_{LA,max} \quad (7)$$

in which  $S_{LA,max}$  ( $m^2$  leaf  $g^{-1}$  leaf) is the specific leaf area of newly formed leaves.  $S_{LA,max}$  was assumed to be conservative across environments and crop development stage, because it describes the *maximum* area of new leaves that can be produced per unit of leaf dry matter. Variation in actual measured  $S_{LA}$  values is assumed to result from conditions where leaf expansion is limited by temperature and not by leaf dry weight increase (Horie et al., 1979; Johnson and Thornley, 1983).  $S_{LA,max}$  was calibrated using actual field data (see Section ‘Calibration procedure’).

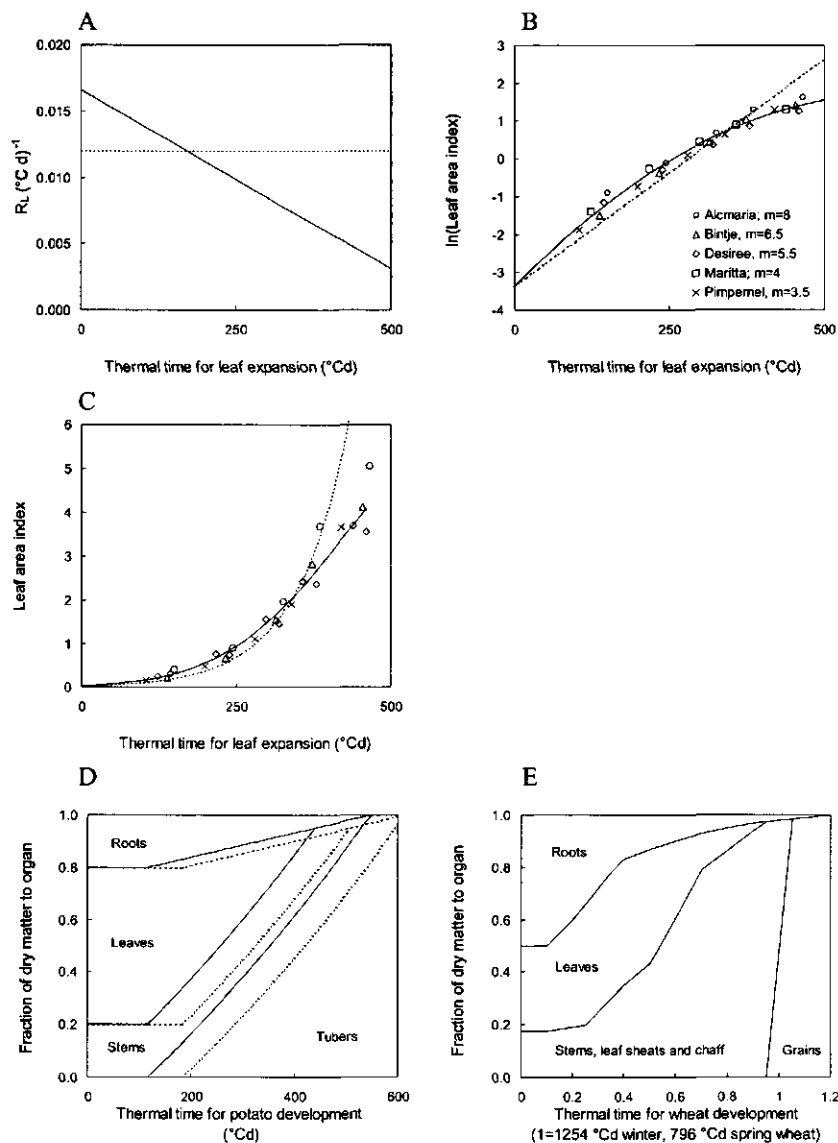


Figure 1. Illustration for parts of the model. Relative leaf expansion rate,  $R_L$ , (A), the  $\ln$ -transformed leaf area index (B), and the leaf area index (C) as a function of thermal time illustrated for potato. Solid line for a constant  $R_L$ , broken line for a linearly decreasing  $R_L$ , symbols in Fig 1B, and 1C for potato cultivars varying from early (maturity,  $m=8$ ) to late ( $m=3.5$ ) grown in Lelystad, The Netherlands in 1985 (unpublished data from Spitters, 1987). Partitioning of dry matter to leaves, stems, roots and storage organs for potato (D) and wheat (E) as a function of thermal time as used in the model. Solid line in Fig. 1D for an early cultivar (Junior,  $m=9$ ), broken line for a mid-late cultivar (Agria,  $m=5$ ).

### Leaf senescence

Although only data up to the maximum  $L$  were used, senescence had to be described for both potato and spring wheat because in those crops leaf senescence in the field started just before  $L$  reached its maximum. For winter wheat, leaf senescence began at maximum  $L$ . For potato, leaf senescence was described according to the SUCROS87 model (Spitters et al., 1989). For spring wheat, rates and start of leaf senescence matched those described for the crop winter wheat in SUCROS87 (Spitters et al., 1989).

### Calculation of leaf dry weight increase

Daily leaf dry weight increase ( $\Delta W_L/\Delta t$ ) was calculated according to LINTUL (Spitters and Schapendonk, 1990). First, the amount of intercepted PAR ( $J$ ,  $\text{MJ m}^{-2} \text{d}^{-1}$ ) was calculated from the daily sum of PAR above the canopy ( $I$ ,  $\text{MJ m}^{-2} \text{d}^{-1}$ ) and the actual  $L$  (Monsi and Saeki, 1953):

$$J = I (1 - e^{-kL}) \quad (8)$$

where  $k$  ( $\text{m}^2 \text{m}^{-2}$ ) is the extinction coefficient for  $I$ , taken as 1.0 for potato (Spitters and Schapendonk, 1990) and 0.44 for wheat (Gallagher and Biscoe, 1978). Daily total dry matter production ( $\Delta W/\Delta t$ ,  $\text{g m}^{-2} \text{d}^{-1}$ ) was calculated from the product of ' $J$ ' and the conversion efficiency for dry matter production ( $E_{LU}$ ,  $\text{g MJ}^{-1}$ ):

$$\Delta W/\Delta t = J E_{LU} \quad (9)$$

$E_{LU}$  was calibrated on the data, see below. Next,  $\Delta W_L/\Delta t$  was calculated as the product of daily total dry matter production and the actual partitioning coefficient ( $P_{L,t}$ ,  $\text{g g}^{-1}$ ) of leaves for dry matter:

$$\Delta W_L/\Delta t = \Delta W/\Delta t P_{L,t} \quad (10)$$

$P_{L,t}$  of potato (see Fig. 1D) is a function of the maturity class of the potato cultivar and of the thermal time for potato development ( $T_b=2^\circ\text{C}$ , optimal temperature  $13^\circ\text{C}$  till  $18^\circ\text{C}$ , and upper temperature  $29^\circ\text{C}$ ), as given in Spitters and Schapendonk (1990). The maturity classes of the potato cultivars according the Dutch variety list (Anonymous, 1999) were, from early to mid-late: 9 for Junior, 8.5 for Eersteling, 6.5 for Bintje and 5 for Agria.  $P_L$  of wheat (see Fig. 1E) is a function of the thermal time for wheat development with a base temperature of  $0^\circ\text{C}$  and was taken from SUCROS87 (Spitters et al., 1989).

During the calibration of model parameters, errors in simulated  $\Delta W_L/\Delta t$  based on daily radiation should be as small as possible to ensure that estimates of  $S_{LA,\max}$  and

other model parameters ( $R_{L,0}$ ,  $R_{L,t}$  and  $L_S$ ), are accurate. Therefore, in the first step, simulated  $W_L$  values were matched with actual  $W_L$  values by calibrating  $E_{LU}$  for each cultivar by environment combination while using observed  $L$  values as input. The calibration procedure is described in Section 'Calibration procedure.'

Carbon supply from tubers to organ growth (stems, leaves, roots) was not considered because Ritchie et al. (1995) showed that played a role only up to  $L$  of 0.2–0.3, whereas most of our smallest predicted  $L$  values were above 0.3. This was confirmed in a preliminary analysis, which showed that not more than 1.5 g leaf dry matter per  $m^2$  of ground area could not be attributed to current photosynthesis.

#### *Inputs and initial conditions of the model*

Daily  $T_{min}$ ,  $T_{max}$  and daily global radiation were input into the model. Incident PAR was considered to be half the incident daily global radiation. Weather data for the field experiments were obtained from a meteorological station nearby the sites of the experiments, as described in Chapter 3.

The  $L$  and  $W_L$  values were obtained by Euler integration of their rates, using a time step of 1 day.  $L$  was simulated from the first experimental sampling date (see Section 'Experimental data sets') onwards, using observed  $L$  and  $W_L$  values at first sampling date as input into the model.

#### *Calibration procedure*

Parameters  $S_{LA,max}$ ,  $R_{L,0}$ ,  $R_{L,t}$  and  $L_S$  were calibrated, with  $S_{LA,max}$  representing the average  $S_{LA}$  between  $L_S$  and maximum  $L$ , and  $R_{L,t}$  the average value up to  $L_S$ . Parameters were calibrated by minimising the residual sum of squares (RSS) between fitted and observed  $L$  values using controlled random search (Price, 1977). Controlled random search started with 200 checkpoints for parameter values. From a random sample of those checkpoints, equal to the number of estimated parameters + 1, a new point is chosen which replaces the worst of the previous 200 checkpoints if it leads to an improved fit.

Because the residuals were a function of the mean, data were ln-transformed, which resulted in homogeneity of variances. Price's method could not be used to obtain standard errors for the parameters.

#### *Experimental data*

Data on leaf area and leaf dry matter dynamics were collected in The Netherlands for potato (three sites), winter wheat (two sites) and spring wheat (one site) (Tables 2 and 3). At each site, data were collected for two consecutive years. The experimental data

sets used in the present analysis are described in Tables 2 and 3 and with the exception of Droevendaal 1996, have been described in detail in Chapter 3. The materials and methods for Droevendaal 1996 were identical to Droevendaal 1997 as described in Chapter 3, except that fertilisers were applied at a rate of 200 kg N ha<sup>-1</sup>, 41 kg P ha<sup>-1</sup> and 108 kg K ha<sup>-1</sup>, with winter wheat as previous crop followed by fodder radish (*Raphanus sativus* L. var. *oleiformis* Pers.) as green manure crop. The winter wheat data of 1983 and 1984 were collected and described by Groot and Verberne (1991). Area and dry matter of leaves up to maximum L were sampled periodically, varying from once in 2 weeks (potato, spring wheat), to once a month (winter wheat). Samples of potato leaves included the petiole as the compound leaf was cut at the last leaflet near the stem. Samples of wheat leaves consisted solely of leaf blades. Sample sizes and dates are given in Tables 2 and 3.

Table 2. Description of the experimental sites and experimental methods for potato.

	Data set P1	Data set P2
Farm	Droevendaal	Lovinkhoeve
Years	1996, 1997	1997, 1998
Site	Wageningen	Marknesse
	51°58'N 5°40'E	52°42'N 5°53'E
Cultivars	Eersteling	Junior
	Bintje	Agria
Soil type	Sandy	Silty loam
Planting pattern (m x m)	0.75 x 0.30	0.75 x 0.30
Year	1996	1997
Planting date	15 April	18 April
Emergence date	17 May (Eersteling)	1 June (Junior)
	19 May (Bintje)	31 May (Agria)
Sampling dates	24 May; 3,7,14 June, 3 July (Eersteling)	4,9,16 June; 7 July (Junior)
	24 May; 7,11,18 June;4 July (Bintje)	4,9,16,23 June (Agria)
Gross plot size (m <sup>2</sup> )	7.2	19.8
Net plot size (m <sup>2</sup> )	2.7	9.45
Year	1997	1998
Planting date	17 April	13 May
Emergence date	16 May (Eersteling)	28 May (Junior)
	17 May (Bintje)	30 May (Agria)
Sampling dates	21,26 May; 2,9,17,30 June (Eersteling)	4,15,24 June; 13 July (Junior)
	23,30 May; 6,11,24 June (Bintje)	4,15,24 June; 16 July (Agria)
Gross plot size (m <sup>2</sup> )	7.2	23.4
Net plot size (m <sup>2</sup> )	2.7	9.45



Further details can be found in Chapter 3. For potato and spring wheat, the first sample used in the present study was taken at full emergence. For winter wheat the first sample was taken near tillering in late February. Data on the same cultivars from different environments (site, years) were analysed as a group, resulting in four data sets (Tables 2 and 3). Within each year and site, three replicates were used, except for the winter wheat data, where eight replicates were used. Water and nutrients, as described in detail in Chapter 3, were supplied sufficiently, so as not to limit yield. Pests, diseases and weeds were fully controlled.

Table 3. Description of the experimental sites and experimental methods for wheat.

	Data set winter wheat (WW)	Data set WW (continued)	Data set spring wheat (SW)
Farm	The Eest	The Bouwing	Lovinkhoeve
Years	1982–1983, 1983–1984	1982–1983, 1983–1984	1997, 1998
Sites	Nagele 52°37'N 5°45'E	Randwijk 51°57'N 5°45'E	Marknesse 52°42'N 5°53'E
Cultivars	Arminda	Arminda	Baldus, Axona
Soil type	Silty loam	Silty clay loam	Silty loam
Row spacing (m)	0.15	0.25	0.30
Year	1982–1983	1982–1983	1997
Sowing date	19 October	21 October	14 April
Emergence date	Not recorded	Not recorded	27 April
Sampling dates	9 Feb; 2, 30 Mar; 20 Apr; 11, 25 May, 15 June 1983	7, 28 Feb; 28 Mar; 18 Apr; 5, 24 May, 13 June 1983	6, 20, 27 May; 11 June; 3 July 1997
Plant density (pl m <sup>-2</sup> )	218	214	260
Gross plot size (m <sup>2</sup> )	3.75	3.75	6
Net plot size (m <sup>2</sup> )	0.45	0.50	1.05
Year	1983–1984	1983–1984	1998
Sowing date	21 October	27 October	9 May
Emergence date	Not recorded	Not recorded	17 May
Sampling dates	13 Feb; 12 Mar; 2, 24 Apr; 7, 28 May, 18 June 1984	15 Feb; 14 Mar; 4, 25 Apr; 9, 29 May, 20 June 1984	22 May, 1, 18 June; 9 July 1998
Plant density (pl m <sup>-2</sup> )	256	223	230
Gross plot size (m <sup>2</sup> )	3.75	3.75	10
Net plot size (m <sup>2</sup> )	0.45	0.50	1.2

### ***Photothermal coefficient***

For all years and sites, the monthly average for the ratio of daily incident PAR to daily effective temperature ( $T_e$ , see Section 'Temperature-limited leaf expansion rate') for leaf area increment was calculated. This ratio, also referred to as photothermal coefficient ( $Q_P$ ) of Nix (1976), is a rough indicator of the ratio between the supply (incident PAR) and demand ( $T_e$ ) for assimilates for leaf expansion. A decrease of  $Q_P$  is a rough indicator that radiation increasingly limits expansion. The actual  $Q_P$  values per site and year were compared with the variation in  $Q_P$ , calculated over 30 years for De Bilt (Tables 4 and 5), as a representative site for The Netherlands. Given the different effects of temperature and radiation on leaf area expansion accounted for by the model, tests of the model's performance across environments must include variation in temperature and radiation between these environments, i.e. variation in  $Q_P$ .

### ***Statistical analysis of model parameters***

The hypothesis ( $L_S \neq 0$  and  $L_S \neq \text{maximum } L$ , see Introduction) was tested by studying the constancy of estimated parameters of the model across environments at different  $L_S$  values: (1) 0, (2) maximum  $L$  and (3) estimated by fitting the model. Using these three options for  $L_S$ , the  $L_S$  value at which model parameters were least affected by environment (year, site), was assumed correspond with the most realistic description of temperature and radiation effects on leaf area expansion. In addition, we tested whether results were the same for different cultivars. The effects of cultivar and environment on the calibrated model parameter values  $S_{LA, \max}$ ,  $R_{L,0}$ ,  $R_{L,t}$  and  $L_S$  were tested using analysis of variance, according to a procedure explained in detail by Neter et al. (1996). In that procedure, an F test determines whether the RSS of a model (C) with parameters calibrated on individual treatments is significantly smaller than the RSS of a restricted model (R) with parameters calibrated against combined treatments:

$$F = \left( \frac{RSS(R) - RSS(C)}{df_R - df_C} \right) / \left( \frac{RSS(C)}{df_C} \right) \quad (11)$$

which follows an F-distribution when the reduced model holds. The degrees of freedom  $df_R$  and  $df_C$  are those associated with the RSS of the reduced and complete model respectively. Parameters could not be calibrated on individual replicates because the number of samples over time was often too small (see Table 2). Therefore, means per sampling date were used and in the restricted model the parameters were fitted either per cultivar (environments pooled) or per environment (cultivars pooled) resulting in a sufficiently large number of points to estimate values of the four parameters. With winter wheat, however, the larger number of data points allowed that parameters could be fitted for each cultivar and environment.

### ***Evaluation of model predictions***

In addition to the statistical analysis, the hypothesis was tested by studying model predictions for a range of different  $L_s$  values across cultivars and environments. The value of  $L_s$  at which model predictions were best (evaluation criteria are explained below) was assumed to be the most realistic value at which  $L$  increment shifts from temperature- to radiation-limited  $L$  increment. To obtain those model predictions and compare them with the experimental data, the parameters  $R_{L,0}$  and the  $S_{LA,max}$ , were first calibrated using independent published and unpublished data (see Results). To investigate the effect of the switching point,  $L_s$ , on model predictions, its value was not calibrated but was fixed at values between 0 and 6.5, using steps between 0.2 and 0.5. The smaller steps were used in the most sensitive part of the response variable (Figs. 3 and 4). The value of value of 6.5 corresponds with the maximum  $L$  in the data set. In separate runs, for each fixed value of  $L_s$ , parameter  $R_{L,t}$  was calibrated for each cultivar on year  $x$  and that calibration was then used to predict the  $L$  of year  $y$ . For example, for potato cultivar Junior, at each fixed value of  $L_s$  the calibration of  $R_{L,t}$  on year 1997 was used to predict the  $L$  of 1998, and the calibration of  $R_{L,t}$  on 1998 was used to predict the  $L$  of 1997. The predictive capacities of the models were analysed with three statistical properties, the first two calculated according to McMaster and Simka (1988): (1) the mean deviation (MD) between predictions ( $P$ ) and observations ( $O$ ) (MD, or bias):

$$MD = \frac{1}{n} \sum_{i=1}^n (P_i - O_i) \quad (12)$$

where 'i' is the i'th observation and 'n' is the total number of evaluation instances; and (2) the root mean square for error (RMSE):

$$RMSE = \left( \frac{1}{n} \sum_{i=1}^n (P_i - O_i)^2 \right)^{\frac{1}{2}} \quad (13)$$

The bias shows to what extent data are over- or under-predicted, while RMSE is equivalent to the standard error of the mean as used in experimental data, but now the error term is caused by prediction error and not by measurement error. A small RMSE means a high prediction accuracy. The third method (3) examined the randomness of residuals, with a residual calculated as  $P_i - O_i$ .

To obtain homogeneity of variance with  $L$ , similar to the calibration of parameters, the MD, RMSE and residuals were calculated for  $\ln$ -transformed  $L$  values. By doing so, values of RMSE and MD could be examined relative to their means, after applying a back-transformation as explained below. For RMSE, the value relative to the means can be found as follows: when predicted  $\ln(L)$  values are between ' $\ln(L) - RMSE$ ' and ' $\ln(L) + RMSE$ ' then, on a back-transformed scale,

predicted  $L$  values are between ' $L [e^{-RMSE} - 1]$ ' and ' $L [e^{RMSE} - 1]$ .' Relative values for MD were found as follows: from  $MD = \overline{\ln(P_i/O_i)}$  (Eq. 12 with  $\ln$  values), follows that the back-transformed  $P/O = e^{MD}$ .

### ***Sensitivity analysis of $L_S$***

Model sensitivity to a change in  $L_S$  was tested, using the model with the optimum  $L_S$  as reference value. The changes in mean rate leaf area increase ( $D_L$ ,  $d^{-1}$ ) and of total crop dry weight ( $W$ ) triggered by a change in  $L_S$ , were analysed using 30 years of weather data for De Bilt. Response variables  $D_L$  and  $W$  were calculated from emergence until the average day of maximum  $L$  for a given crop cultivar. That day was found from simulations with the 30 years of weather data. The  $R_{L,0}$  and  $S_{LA,max}$  values were those also used for predictions. The  $R_{L,b}$ ,  $E_{LU}$  and initial conditions per crop type were the average of the two years of predictions at the reference  $L_S$  values.

## **Results**

### ***Weather conditions***

Monthly values for temperature and global radiation differed more between years than between sites within a year (Tables 4 and 5). At all sites,  $Q_p$  as defined in the Section 'Materials and methods', decreased with month of the year. For potato ( $T_b=2^\circ\text{C}$ ), the monthly  $Q_p$  at the experimental sites varied between 0.55 and 0.98, for spring wheat ( $T_b=0^\circ\text{C}$ ) between 0.49 and 0.74 (Table 4), and for winter wheat ( $T_b=0^\circ\text{C}$ ) between 0.58 and 1.41 (Table 5).

### ***Calibration of $E_{LU}$***

Using  $L$  as a forcing function, observed  $W_L$  values of potato (Fig. 2A) and wheat (Fig. 2B) were simulated well after  $E_{LU}$  had been calibrated for each cultivar by environment combination. The regressions between fitted and observed values were close to the 1:1 line, with an  $R^2$  of 0.97 (d.f.=27) for potato and 0.98 (d.f.=36) for wheat. Thus there was no need to change the partitioning coefficients of dry matter to leaves. Based on a ' $k$ ' of 1 (cf. Spitters and Schapendonk, 1990), the calibrated  $E_{LU}$  values for potato, all given as mean  $\pm$  s.e.m. in  $\text{g MJ}^{-1}$  PAR with  $n=4$ , were  $1.99 \pm 0.11$  (Droevendaal) and  $1.91 \pm 0.06$  (Lovinkhoeve). Based on a  $k$  of 0.72 (cf. Khurana and McLaren, 1982), which corresponds better with our experiments, and when increasing the  $E_{LU}$  in proportion to the fraction dry matter proportioned to tubers

(cf. Spitters and Schapendonk, 1990), the calibrated  $E_{LU}$  values were  $2.73 \pm 0.17$  and  $2.66 \pm 0.09$  at the point where all dry matter is partitioned to the tuber. The latter value corresponds well with the tuber- $E_{LU}$  for well-fertilised potato of 2.75 (Spitters and Schapendonk, 1990). Based on a  $k$  of 0.44 (Gallagher and Biscoe, 1978), the calibrated  $E_{LU}$  of winter wheat was  $2.06 \pm 0.17$  and for spring wheat it was  $3.48 \pm 0.31$ . Based on a  $k$  of 0.51 (own data) for spring wheat, the calibrated  $E_{LU}$  was  $3.15 \pm 0.27$ , which corresponds well with the value of 3.0 well-fertilised wheat (Gallagher and Biscoe, 1978). Low value for the calibrated  $E_{LU}$  of winter wheat was associated with average daily temperatures below  $10^{\circ}\text{C}$  in February till April (Table 5). At temperatures below  $10^{\circ}\text{C}$ , the  $E_{LU}$  of wheat is reduced (cf. Eckersten and Jansson, 1991).

Table 4. Average daily global radiation ( $I$ :  $\text{MJ m}^{-2}\text{d}^{-1}$ ), average daily temperature ( $T_{av}$ :  $^{\circ}\text{C}$ ) and average daily photothermal coefficient ( $Q_p$ :  $\text{MJ m}^{-2}\text{d}^{-1} ^{\circ}\text{C}^{-1}$ ).  $Q_p$  is calculated daily as 0.51 divided by  $T_e$ . Data were recorded for potato and wheat during the months and years of measurements. Normal values are from De Bilt, The Netherlands, 1959–1988, with 5, 50 and 95% as percentiles of normal values.

	Month	Normal			Droevendaal (potato)		De Lovinkhoeve (potato and wheat)	
		5%	50%	95%	1996	1997	1997	1998
I	May	13.4	16.2	19.5	14.0	18.0	17.3	17.7
	June	14.2	17.4	21.7	18.6	18.7	18.8	15.2
	July	14.2	16.5	19.4	17.4	16.8	17.9	15.1
$T_{av}$	May	10.3	12.0	13.8	10.3	12.3	12.2	14.4
	June	13.4	15.0	16.9	15.1	15.8	15.3	15.6
	July	15.0	16.4	18.9	15.9	17.2	17.5	15.5
$Q_p$ ( $T_e=2^{\circ}\text{C}$ ) (potato)	May	0.73	0.90	1.09	0.98	0.98	0.92	0.72
	June	0.58	0.72	0.86	0.73	0.69	0.73	0.57
	July	0.51	0.57	0.65	0.65	0.55	0.58	0.56
$Q_p$ ( $T_e=0^{\circ}\text{C}$ ) (wheat)	May	0.60	0.72	0.83	— <sup>a</sup>	—	0.74	0.61
	June	0.49	0.61	0.74	—	—	0.63	0.49
	July	0.44	0.50	0.57	—	—	0.51	0.49

a Not determined because of a division by zero.

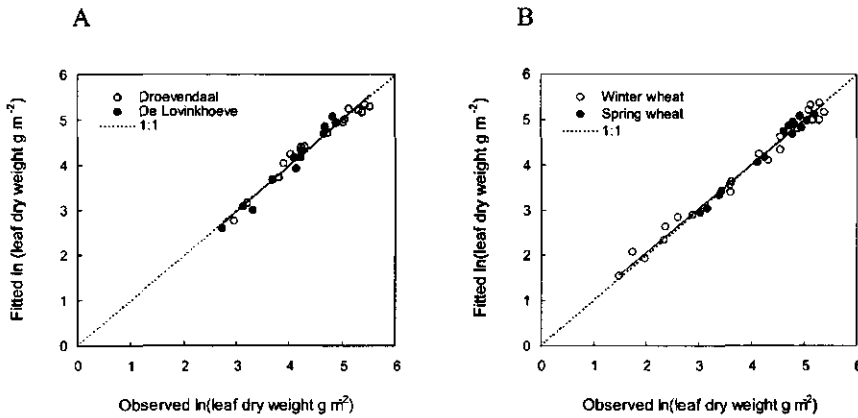


Figure 2. Fitted versus observed ln-transformed leaf dry weight for potato (A), winter wheat and spring wheat (B). Fitted values were calculated after calibration of  $E_{LU}$  per cultivar by environment combination (values in Section 'Results').

The Section 'Results' used standard values for  $k$  of potato ( $k=1$ ), and wheat ( $k=0.44$ ). Model calculations showed that the use of other  $k$  values hardly changed the relationship between fitted and observed  $W_L$ , and likewise hardly changed results of the statistical analysis (Section 'Constancy of model parameters') or the predictions (Section 'Evaluation of model predictions') (data not shown).

### Constancy of model parameters

Because of the strong correlation among the parameters related to temperature-limited L increment ( $R_{L,0}$ ,  $R_{L,t}$ ), constancy of their values with environment was not tested for  $R_{L,0}$  and  $R_{L,t}$  individually, but was tested simultaneously for both parameters, according to the procedure given in Section 'Statistical analysis of model parameters'. Constancy of  $S_{LA,max}$  and of  $L_S$  was also tested simultaneously for both parameters.

Tables 6–9 present the estimated parameter values of the model based on the experimental data. The parameter values for potato did not differ between cultivars (Tables 6 and 7). When  $L_S$  was set at zero (radiation-limited only), estimated  $S_{LA,max}$  at Droeendaal was clearly smaller in 1997 ( $21.2 \text{ m}^2 \text{ kg}^{-1}$ ) than in 1996 ( $25.3 \text{ m}^2 \text{ kg}^{-1}$ ) (Table 6). When  $L_S$  was set at maximum L (temperature-dependence only), parameter values at Lovinkhoeve were 8.2% ( $R_{L,0}$ ) and 6.2% ( $R_{L,t}$ ) larger in 1998 than in 1997 (Table 7). When  $L_S$  was estimated freely, the parameter values for potato did not vary with year.

Table 5. Average daily global radiation ( $I$ ,  $\text{MJ m}^{-2}\text{d}^{-1}$ ), average daily temperature ( $T_{\text{av}}$ ,  $^{\circ}\text{C}$ ) and average daily photothermal coefficient ( $Q_p$ ,  $\text{MJ m}^{-2}\text{d}^{-1}\text{ }^{\circ}\text{C}^{-1}$ ).  $Q_p$  is calculated daily as 0.51 divided by  $T_e$ . Data were recorded for winter wheat during the months and years of measurements. Normal values are from De Bilt, The Netherlands, 1959–1988, with 5, 50 and 95% as percentiles of normal values.

	Month	Normal			The Bouwing		The Eest	
		5%	50%	95%	1983	1984	1983	1984
I	February	4.0	4.8	5.9	5.0	3.9	4.9	3.9
	March	6.7	8.0	9.5	6.9	8.1	7.5	8.2
	April	10.7	12.5	15.4	11.3	14.3	11.3	14.2
	May	13.4	16.2	19.5	11.6	11.9	11.8	11.9
	June	14.2	17.4	21.7	19.3	15.6	20.2	15.9
$T_{\text{av}}$	February	-1.0	2.8	5.1	0.7	2.1	0.3	1.7
	March	2.5	4.9	7.2	5.5	3.8	5.2	3.7
	April	6.1	8.0	10.1	8.5	7.2	7.8	7.1
	May	10.3	12.0	13.8	10.9	10.1	10.4	10.2
	June	13.4	15.0	16.9	15.9	13.3	15.6	13.0
$Q_p(T_b=0^{\circ}\text{C})$	February	- <sup>a</sup>						
	March	0.58	0.93	1.88	0.78	–	0.89	1.41
	April	0.67	0.92	1.26	0.74	1.10	0.83	1.06
	May	0.60	0.72	0.83	0.54	0.62	0.58	0.61
	June	0.49	0.61	0.74	0.63	0.58	0.67	0.61

a Not determined because of a division by zero.

For all three methods of determining  $L_S$ , parameter values for winter wheat varied with environment (Table 8). When  $L_S$  was set at zero or at maximum  $L$ , parameter values were affected by an interaction between year and site. When  $L_S$  was set at zero,  $S_{LA,\text{max}}$  was larger in 1984 ( $24.1 \text{ m}^2 \text{ kg}^{-1}$ ) than in 1983 ( $19.8 \text{ m}^2 \text{ kg}^{-1}$ ) whereas differences between sites for the 2 years were small, and  $S_{LA,\text{max}}$  at The Eest was larger than at The Bouwing in 1983 but was smaller in 1984. When  $L_S$  was set at maximum  $L$ , differences in parameter values varied more between years than between sites and differences in  $R_{L,0}$  were opposite for the 2 years. When  $L_S$  was estimated by the model, the parameter values for winter wheat varied between years. The main differences were a larger  $R_{L,0}$  in 1984 ( $8.45 \cdot 10^{-3} ({}^{\circ}\text{Cd})^{-1}$ ) than in 1983 ( $4.90 \cdot 10^{-3} ({}^{\circ}\text{Cd})^{-1}$ ) and a larger  $L_S$  in 1984 (2.28; corresponding to 4 May) compared to 1983 (0.29; corresponding to 6 March). For spring wheat, no significant effects of cultivar or of environment on parameter values were found, except when  $L_S$  was set at zero (Table 9). Then estimated  $S_{LA,\text{max}}$  was clearly larger in 1998 ( $33.3 \text{ m}^2 \text{ kg}^{-1}$ ) than in 1997 ( $25.8 \text{ m}^2 \text{ kg}^{-1}$ ).

Table 6. Fitted parameter values and effects of year (Y), and cultivar (C) for  $L_S$  set at zero, at maximum L or when fitted. Parameter values are given per treatment when significance levels are  $<0.1$ , with significance level between brackets. Note that parameter values did not vary with cultivar, so values are obtained by pooling cultivars. Average day of year at which L equals the fitted  $L_S$  is given between brackets. Parameters and model are explained in Section Materials and Methods. Data sets are given in Table 2.

$L_S$	$R_a^{2a}$	Parameter	Units	Common value	Effects <sup>b</sup>	Treatment	Values per treatment
<i>Potato, set P1</i>							
0	91.6	$S_{LA,max}$	$m^2 kg^{-1}$	23.5	Y ( $P=0.021$ )	1996	25.3
						1997	21.2
Maximum L 89.4		$R_{L,0}$	$10^{-3} (^{\circ}C d)^{-1}$	21.0	-		
		$R_{L,t}$	$10^{-6} (^{\circ}C d)^{-2}$	-38.3			
Fitted	95.1	$R_{L,0}$	$10^{-3} (^{\circ}C d)^{-1}$	27.1	-		
		$R_{L,t}$	$10^{-6} (^{\circ}C d)^{-2}$	-67.7			
		$S_{LA,max}$	$m^2 kg^{-1}$	25.3			
		$L_S$	-	1.41			
				(day nr =158)			

a Total of 17 sampling dates.

b Only main effects tested.

In conclusion, the results reveal that when  $L_S$  was estimated freely by the model and was larger than zero and smaller than maximum L, parameter values did not vary with environment (potato and spring wheat) or varied only with year (winter wheat) and not with year and site as was the case at an  $L_S$  of 0 or at maximum L for winter wheat. Thus, when  $L_S$  was estimated freely, parameter values were affected less by environment than when set at the extremes, despite substantial variation in the between-year parameter estimates for winter wheat (Table 8).

### Evaluation of model predictions

The  $R_{L,0}$  and  $S_{LA,max}$  values of potato and wheat as calibrated on independent data are presented in Table 10. Experimental data were predicted with  $L_S$  set at a given value starting at 0 and increasing by steps of 0.2–0.5 L units until maximum L. The accuracy of prediction was quantified as RMSE based on ln-transformed L values, where the RMSE is equivalent to the standard error of the mean of experimental data. A small RMSE indicates a high accuracy. In Sections 'Predictions for potato' and



'Predictions for wheat', the absolute RMSE values based on  $\ln(L)$  values are given, as well as the RMSE values relative to the mean  $L$ , as obtained from back-transformation (see Section 'Evaluation of model predictions'). The results for MD are presented as relative over- and under-predictions and refer to the back-transformed  $P/O = e^{MD}$  (see Section 'Evaluation of model predictions').

### Predictions for potato

Fig. 3A reveals that RMSE was smallest (0.27; back-transformed:  $-0.24L$ ,  $+0.31L$ ) at an  $L_S$  of 1 and increased to 0.34 (back-transformed:  $-0.29L$ ,  $0.40L$ ) when  $L_S$  decreased to zero (radiation-limited only) and increased to 0.39 (back-transformed:  $-0.32L$ ,  $0.48L$ ) when  $L_S$  increased to 6.5, which was above maximum  $L$  (temperature-

Table 7. Fitted parameter values and effects of year (Y), and cultivar (C) for  $L_S$  set at zero, at maximum  $L$  or when fitted. Parameter values are given per treatment when significance levels are  $<0.1$ , with significance level between brackets. Note that parameter values did *not* vary with cultivar, so values are obtained by pooling cultivars. Average day of year at which  $L$  equals the fitted  $L_S$  is given between brackets. Parameters and model are explained in materials and methods, data sets are given in Table 2.

$L_S$	$R_a^{2a}$	Parameter	Units	Common value	Effects <sup>b</sup>	Treatment	Values per treatment
<i>Potato, set P2</i>							
0	88.7	$S_{LA,max}$	$m^2 kg^{-1}$	31.6	—		
Maximum L	79.6	$R_{L,0}$	$10^{-3} (^{\circ}Cd)^{-1}$	19.7	Y	1997	20.5
					( $P=0.090$ )		
						1998	22.1
		$R_{L,1}$	$10^{-6} (^{\circ}Cd)^{-2}$	-35.0		1997	-44.2
						1998	-41.5
Fitted	96.8	$R_{L,0}$	$10^{-3} (^{\circ}Cd)^{-1}$	22.4			
		$R_{L,1}$	$10^{-12} (^{\circ}Cd)^{-2}$	-4.43	—		
		$S_{LA,max}$	$m^2 kg^{-1}$	25.5			
		$L_S$	—	0.26			
				(day nr.=159)			

a Total of 12 sampling dates.

b Only main effects tested.

limited only). The standard error of the mean of the experimental  $\ln(L)$  data that are predicted can be considered as an accuracy that is achieved when the model provides very good predictions. The average standard error of the mean for the eight cultivar by environment combinations was 0.12 (back-transformed: -0.12L, 0.13L) which was smaller than the highest accuracy that was found with the model (at an  $L_S$  of 1).

Table 8. Fitted parameter values and effects of year (Y) and site (S) for  $L_S$  set at zero, at maximum L or when fitted, applied to winter wheat. Parameter values are given per treatment when significance levels are  $<0.1$ , with significance level between brackets. Average day of year at which L equals the fitted  $L_S$  is given between brackets. Parameters and model are explained in Section 'Materials and methods', data sets are given in Table 3.

$L_S$	$R_a^{2a}$	Para-meter	Units	Common value	Effects <sup>b</sup>	Treatment	Value per treatment
<i>Winter wheat</i>							
0	94.4	$S_{L,A,max}$	$m^2 kg^{-1}$	22.1	Y x S (P=0.037)	1983 The Eest 1983 The Bouwing 1984 The Eest 1984 The Bouwing	20.0 19.5 23.8 24.4
Maximum L	92.8	$R_{L,0}$	$10^{-3} (^{\circ}Cd)^{-1}$	8.7	Y x S (P=0.006)	1983 The Eest 1983 The Bouwing 1984 The Eest 1984 The Bouwing	5.88 7.00 10.04 9.87
		$R_{L,t}$	$10^{-6} (^{\circ}Cd)^{-2}$	-10.2		1983 The Eest 1983 The Bouwing 1984 The Eest 1984 The Bouwing	-5.30 -5.97 -12.75 -13.35
Fitted	96.1	$R_{L,0}$	$10^{-3} (^{\circ}Cd)^{-1}$	7.75	Y (P=0.011)	1983 1984	4.90 8.45
		$R_{L,t}$	$10^{-6} (^{\circ}Cd)^{-2}$	-102.2		1983 1984	$-2.99 \cdot 10^{-6}$ $-2.57 \cdot 10^{-6}$
		$S_{L,A,max}$	$m^2 kg^{-1}$	22.9		1983 1984	23.87 16.28
		$L_S$		0.12 (day nr.=53)		1983  1984	0.29  2.28 (day nr.=125)

a Total of 24 sampling dates.

b Main and interaction effects tested.

Table 9. Fitted parameter values and effects of year (Y), and cultivar (C) for  $L_S$  set at zero, at maximum L or when fitted. Parameter values are given per treatment when significance levels are  $<0.1$ , with significance level between brackets. Note that parameter values did *not* vary with cultivar, so values are obtained by pooling cultivars. Average day of year at which L equals the fitted  $L_S$  is given between brackets. Parameters and model are explained in materials and methods, data sets are given in Table 3.

$L_S$	$R_a^{2a}$	Parameter	Units	Common value	Effects <sup>b</sup>	Treatment	Value per treatment
<i>Spring wheat</i>							
0	74.5	$S_{LA,max}$	$m^2 kg^{-1}$	29.2	Y ( $P=0.046$ )	1997	25.8
						1998	33.3
Maximum L	93.5	$R_{L,0}$	$10^{-3} (^{\circ}C d)^{-1}$	13.0	–		
		$R_{L,t}$	$10^{-6} (^{\circ}C d)^{-2}$	–16.9			
Fitted	95.6	$R_{L,0}$	$10^{-3} (^{\circ}C d)^{-1}$	14.8	–		
		$R_{L,t}$	$10^{-6} (^{\circ}C d)^{-2}$	–23.5			
		$S_{LA,max}$	$m^2 kg^{-1}$	50.6			
		$L_S$		2.54 (day=164)			

a Total of 14 sampling dates.

b Only main effects tested.

The average MD (Fig. 3B) revealed a minimum plateau at an  $L_S$  between 1 and 4, where observed L values were underestimated by 4–10% (after back-transformation, P/O was 0.96–0.90). Observed L values were overestimated by 12% when  $L_S$  was set at zero and they were underestimated by 18% when  $L_S$  was set at 6.5.

The randomness of residuals (i.e. predicted minus observed  $\ln(L)$  values) was better at the  $L_S$  value with the smallest RMSE ( $L_S=1$ ) than when  $L_S$  was set either at zero or at maximum L (Figs. 3C–E). The variance of residuals tended to decrease with the observed mean  $\ln(L)$  values (Fig. 3C) when  $L_S$  was set at zero. When  $L_S$  was set at maximum L, the observed L values tended to be underestimated at small L values and overestimated at large L values (Fig. 3D). To a lesser extent, this residual pattern was also found at an  $L_S$  of 1 (Fig. 3E).

Table 10. Calibration against independent data of the relative rate of leaf area expansion at zero thermal time ( $R_{L,0}$   $10^{-3}$  ( $^{\circ}\text{Cd}^{-1}$ ) and the specific leaf area ( $S_{LA,max}$ ,  $\text{m}^2 \text{kg}^{-1}$ ) of newly formed leaves of potato (P), winter wheat (WW) and spring wheat (SW).

Crop	Parameter	Method of estimation	mean	s.e.m	R <sup>2</sup>	Cultivar(s)	Reference
P	$R_{L,0}$	Regression	16.5	5.0	99.0	5, different maturity classes	Spitters (1987)
	$S_{LA,max}$	Regression	29.5	3.0	87.2	5, different maturity classes	Spitters (1987), with $L > 1$
SW	$R_{L,0}$	Regression	11.9	1.1	98.3	Baldus, Axona	Unpublished field data of 1999, first value from Spitters and Kramer (1986), year 1985
	$S_{LA,max}$	No change	20.2		95.1	4 cultivars	Aase (1978); Van Keulen and Seligman (1987)
WW	$R_{L,0}$	Regression	6.88	0.90	94.1	Arminda	Groot and Verberne (1991), site Lelystad
	$S_{LA,max}$	No change	20.2		95.1	4 cultivars	Aase (1978)

In conclusion, the observed  $L$  of potato was best predicted at an  $L_S$  of 1. At this value, the accuracy was optimal, the bias had a minimum plateau value and residuals were distributed most randomly. For  $L_S=1$ , the  $R^2$  between predicted and observed values was 0.911 (d.f.=27; Fig. 3F). The average date reaching an  $L_S$  of 1 was 12 June (day 163, not shown).

#### *Predictions for wheat*

Over almost the whole range of  $L_S$  values, namely  $L_S \geq 0.5$ , the RMSE of wheat ranged between 0.33 (back-transformed:  $-0.28L$ ,  $0.39L$ ) and 0.37 (back-transformed:  $-0.31L$ ,  $0.45L$ ) (Fig. 4A). Only when  $L_S$  was set at zero (radiation-limited only) was prediction accuracy decreased, with an RMSE of 0.53 (back-transformed:  $-0.41L$ ,  $0.70L$ ). The average standard error in the predicted experimental data, 0.074 (back-transformed:  $-0.071L$ ,  $0.077L$ ), was smaller than the best model predictions.

MDs of the predictions for wheat are illustrated in Fig. 4B. The average MD passed an optimum at  $L_S=1.5$ , where  $L$  was underestimated by only 1.7% (after back-transformation, see Section 'Evaluation of model predictions'). Underestimation of  $L$  increased with lower  $L_S$  values, up to 32% at an  $L_S$  of zero, but it increased only gradually with higher  $L_S$  values, up to 7.0% at an  $L_S$  of 6.

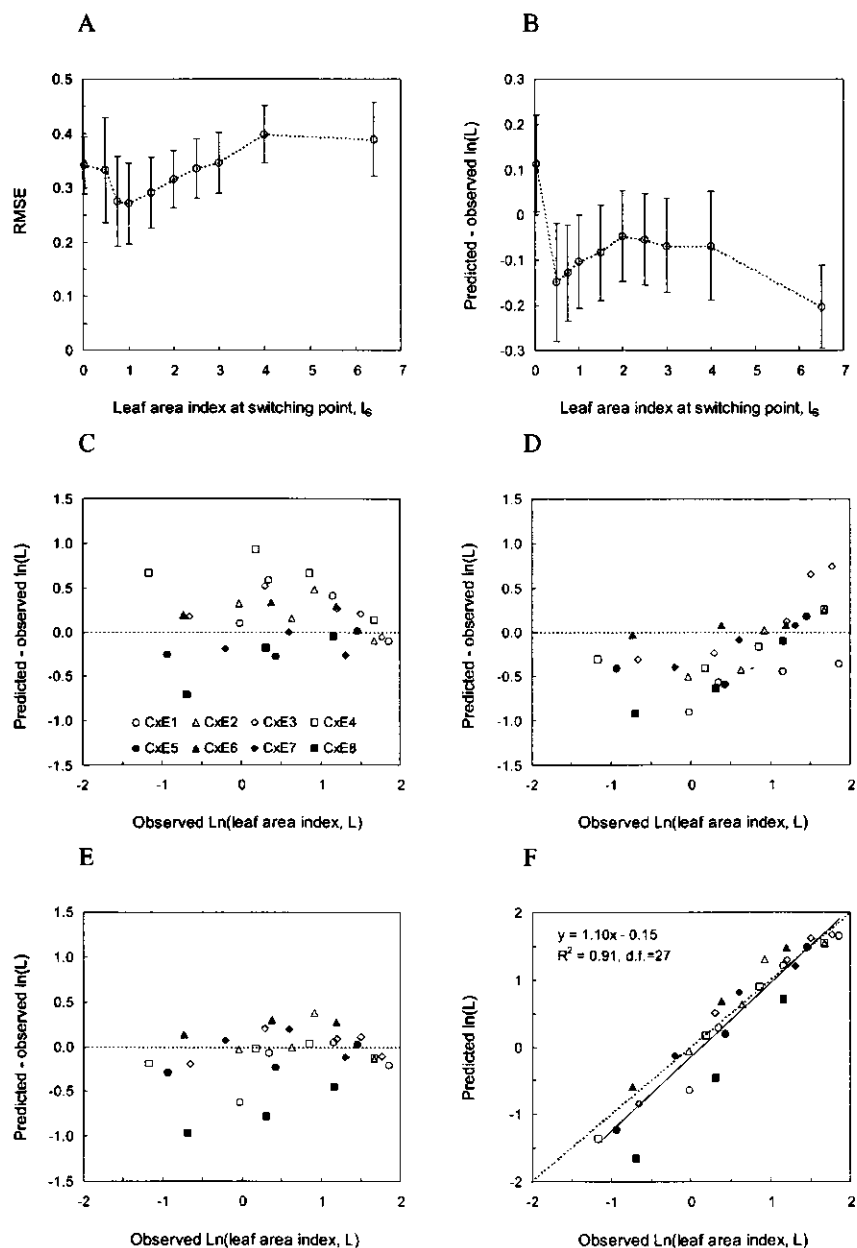


Figure 3. Predictions of  $L$  for potato at a range of  $L_s$  values with  $\ln$ -transformed  $L$  values. RMSE (A); MD (B) (mean  $\pm$  standard error); residuals versus observations at  $L_s = 0$  (C),  $L_s$  at maximum  $L$  (D) and  $L_s = 1$  (E) and predictions versus observations at  $L_s = 1$  (F) for eight cultivar by environment combinations (CxE): 1 Eersteling 1996, 2 Bintje 1996, 3 Eersteling 1997, 4 Bintje 1997, 5 Junior 1997, 6 Agria 1997, 7 Junior 1998, 8 Agria 1998.

When  $L_S$  was set at zero (Fig. 4C) or at maximum  $L$  (Fig. 4D), residuals varied systematically with observed  $\ln(L)$  values. When  $L_S$  was set at zero,  $L$  was overestimated at small  $L$  values but underestimated at large values (Fig. 4C). When  $L_S$  was at maximum  $L$ , the variance of residuals increased as mean  $\ln(L)$  increased. This effect was greater for winter wheat predictions than for spring wheat predictions (Fig. 4D). For the  $L_S$  value 1.5, which had the smallest RMSE and MD, residual variance also increased with mean  $L$  value, but less so than when  $L_S$  was at maximum  $L$  (Fig. 4E).

In conclusion, wheat  $L$  predictions were the poorest with  $L_S=0$ . Predictions with  $L_S=1.5$  were somewhat better than for  $L_S$  at maximum  $L$ , as inferred from the randomness of residuals and a slightly smaller bias, but the prediction accuracy hardly differed. For  $L_S=1.5$ , the  $R^2$  between predicted and observed values was 0.886 (d.f.=36; Fig. 4F). The average date reaching an  $L_S$  of 1.5 was 1 May for winter wheat (day 121) and 2 June for spring wheat (day 153, not shown).

### ***Sensitivity analysis***

For each cultivar, sensitivity of  $D_L$  and  $W$  to a change in  $L_S$  was calculated. The reference value for  $L_S$  was the  $L_S$  value with which the model best predicted  $L$  expansions: an  $L_S$  of 1 for potato and of 1.5 for wheat.

#### ***Sensitivity analysis for potato***

The sensitivities of  $D_L$  and  $W$  for potato are illustrated for cultivar Junior, over 30 years at De Bilt (lines in Figs. 5A and 5B). For comparison, the years 1997 and 1998 at Lovinkhoeve are shown (symbols in Figs. 5A and 5B). The sensitivities of the later-maturing cultivar Agria, were consistently 61% ( $D_L$ ) and 66% ( $W$ ) as great as for Junior (data not shown). Junior is in nearly the same maturity class as Eersteling, and Agria in nearly the same maturity class as Bintje. The sensitivity of the cultivar Eersteling is therefore expected to be similar to that of Junior, and the sensitivity of Bintje similar to Agria.

The median value of  $D_L$  and  $W$  of potato cultivar Junior over 30 years at the Bilt (thick solid line in Figs. 5A and 5B) increased when  $L_S$  was both smaller or larger than 1. The  $D_L$  increased with an  $L_S$  smaller than 1 (an earlier start of radiation-limitation), because the estimated  $S_{LA,max}$  of potato ( $29.5 \text{ m}^2 \text{ kg}^{-1}$ , Table 10) was much larger than the actual  $S_{LA}$  at low  $L$  values ( $10 \text{ m}^2 \text{ kg}^{-1}$ ; Chapter 3). The  $D_L$  also increased with  $L_S$  larger than 1 (longer period of temperature-dependence), because the underlying  $R_L$  was overestimated when extrapolating to thermal times longer than those against which the parameters were calibrated.

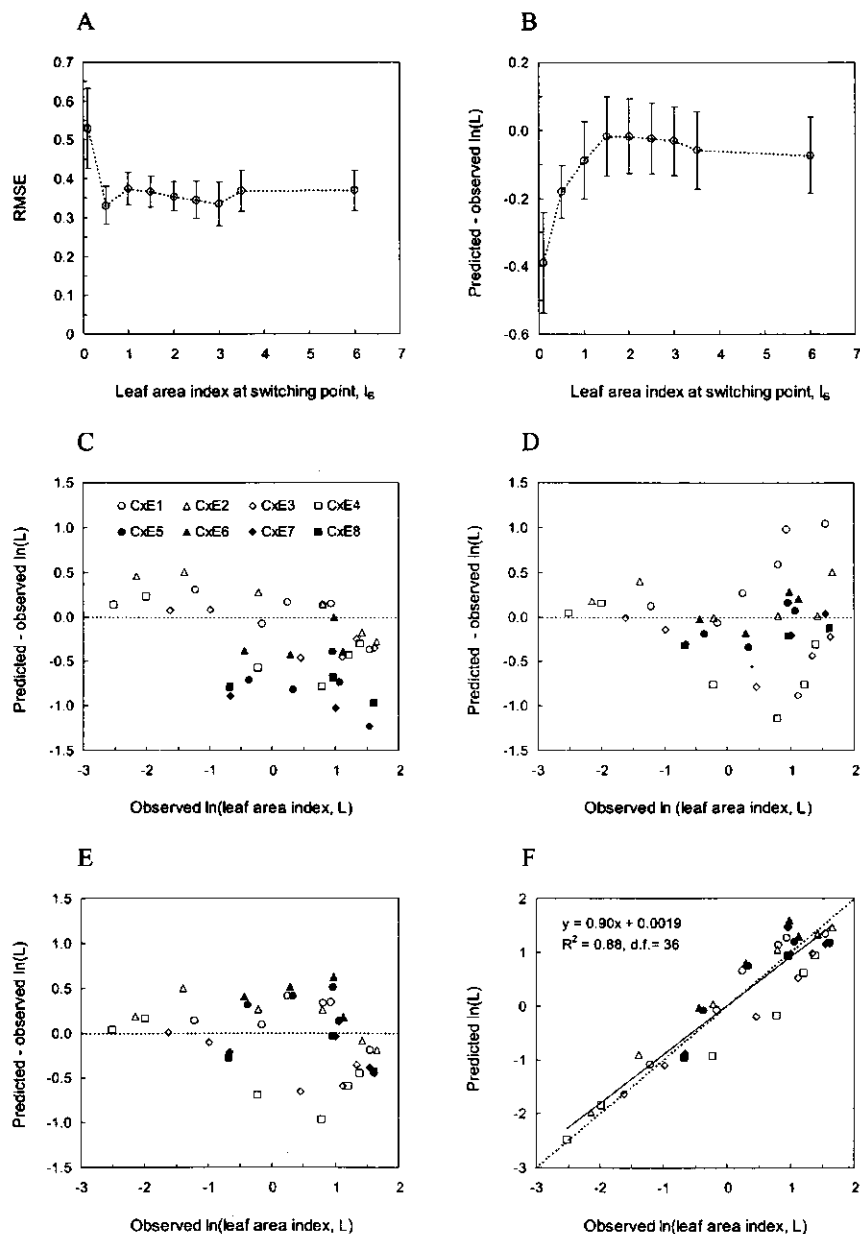


Figure 4. Predictions of L for wheat at a range of values with  $\ln$ -transformed L values. RMSE (A); MD (B) (mean  $\pm$  standard error); residuals versus observations at  $L_s = 0$  (C),  $L_s$  at maximum L (D) and  $L_s = 1.5$  (E) and predictions versus observations at  $L_s = 1.5$  (F) for eight cultivar by environment combinations (CxE): 1 The Eest 1983, 2 The Bouwing 1983, 3 The Eest 1984, 4 The Bouwing 1984, 5 Baldus 1997, 6 Axona 1997, 7 Baldus 1998, 8 Axona 1998.

Median values of  $D_L$  and  $W$  of potato cultivar Junior increased faster when  $L_S$  was reduced below 1 than when  $L_S$  was increased above 1.  $W$  was less sensitive to  $L_S$  than  $D_L$ , especially at higher  $L_S$  values. The explanation is that the fraction of intercepted light saturates at higher  $L$  values. For potato cultivar Junior, an increase in  $L_S$  up to maximum  $L$  increased the median value of  $W$  by only 3%.

Considerable variation in the sensitivity of  $D_L$  and  $W$  of potato cultivar Junior between years (Figs. 5A and B) was associated with yearly differences in  $Q_p$  (Figs. 5C and D). At an  $L_S$  below the optimum of 1 (see Fig. 5C,  $L_S=0$ ), i.e. longer radiation-limited expansion, sensitivity increased with increased  $Q_p$  ( $0.5I$  divided by  $T_c$ ), whereas at an  $L_S$  above the optimum (see Fig. 5D,  $L_S=2$ ), i.e. longer temperature-limited expansion, sensitivity increased with decreasing  $Q_p$ .

#### *Sensitivity analysis for wheat*

The sensitivities of  $D_L$  and  $W$  of winter wheat are illustrated over 30 years at De Bilt (thick solid line in Figs. 6A and 6B). For comparison, results for 1983 and 1984 at The Eest and The Bouwing are shown (symbols as explained in captions for Figs. 6A and 6B). The sensitivities of spring wheat cultivars were similar to those of winter wheat.

Contrary to potato, the  $D_L$  of wheat decreased with an  $L_S$  smaller than the reference value.  $D_L$  decreased because the sensitivity analysis used the  $E_{LU}$  from the experimental data but the estimated  $S_{LA,max}$  from published data ( $20.2 \text{ m}^2 \text{ kg}^{-1}$ , Table 10) was smaller than the one found in the predicted experimental data ( $22.1 \text{ m}^2 \text{ kg}^{-1}$ , Table 8).  $D_L$  increased with a longer duration of temperature-dependent expansion for the same reason as indicated for potato.

The decrease in the median  $D_L$  and  $W$  of winter wheat with a reduction in  $L_S$  below 1.5 was larger than its increase above 1.5. As with potato,  $W$  was less sensitive to  $L_S$  than  $D_L$ . When  $L_S$  increased from 1.5 to 3, median  $W$  increased by only 6% (Fig. 6B).  $W$  in wheat was more sensitive to  $L_S$  than in potato, because the extinction coefficient for light was smaller for wheat than for potato. Variation in the sensitivities of  $D_L$  and  $W$  between years was associated with  $Q_p$  in the same way as for potato (Figs. 6C and 6D).

In conclusion, the rates of  $L$  increase and crop weight of potato and wheat, as described by the model, were less sensitive to a radiation-dependency starting later than the optimum value (1 for potato and 1.5 for wheat), than to radiation-dependency starting earlier. Sensitivities of  $L$  increase and crop weight to an earlier switch increased with  $Q_p$ , whereas sensitivities to a later switch decreased with  $Q_p$ .



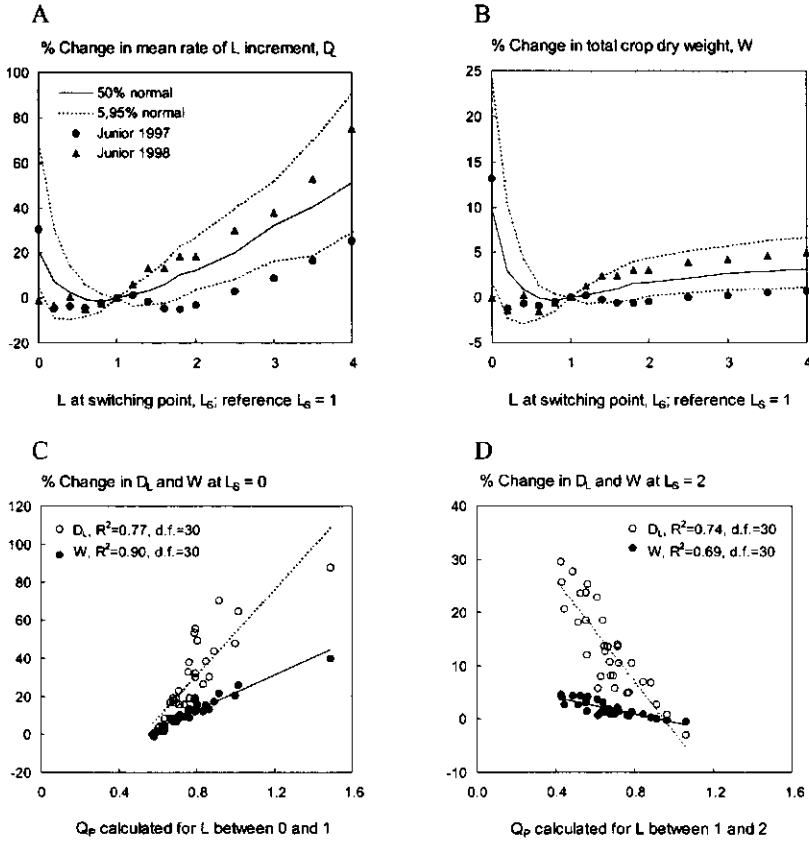


Figure 5. Sensitivity of the mean rate of leaf area increment (A) and of crop dry weight (B) to a change in  $L_s$ , with an  $L_s=1$  as reference value, for potato cultivar Junior from emergence until mean day of maximum  $L$ . Symbols are for Lovinkhoeve, in 1997 and 1998. Lines are 5, 50 and 95 percentiles of 30 years (1959–1988) of weather data from the De Bilt site, The Netherlands. Correlation between sensitivity and the photothermal coefficient ( $Q_p$ ) at  $L_s=0$  (C) and  $L_s=2$  (D).

## Discussion

Above we described how the  $L_s$  value at which  $L$  expansion switches from temperature- to radiation-dependency was determined analysing experimental data with a simple simulation model. Below, we first discuss the methodology as used in the present study, and then the conclusions and their implications for modelling  $L$  expansion. Finally we will suggest how the current model could be improved on the basis of an understanding of physiological processes underlying leaf area expansion.

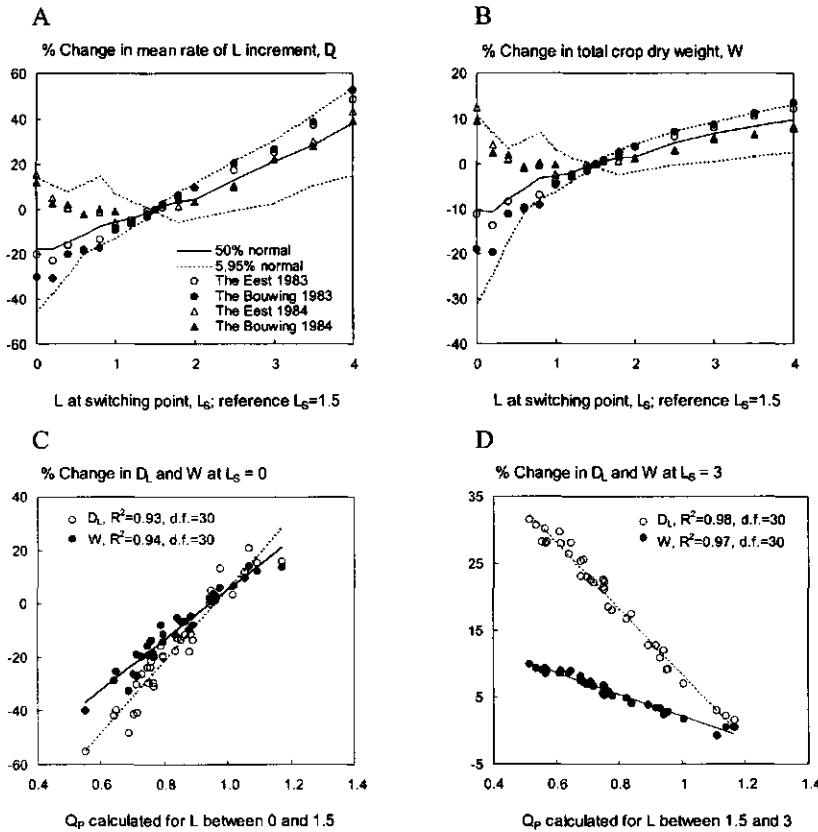


Figure 6. Sensitivity of the mean rate of L increment (A) and of crop dry weight (B) to a change in  $L_s$ , with an  $L_s=1.5$  as reference value, for winter wheat cultivar Arminda from emergence until mean day of maximum L. Symbols are for The Eest and The Bouwing, in 1983 and 1984. Lines are 5, 50 and 95 percentiles of 30 years (1959–1988) of weather data from the De Bilt site, the Netherlands. Correlation between sensitivity and the photothermal coefficient ( $Q_p$ ) at  $L_s=0$  (C) and  $L_s=3$  (D).

## Methodology

Robust models often rely on summary relationships provided the relationships are based on a range of experimental experience and on a sound theoretical derivation from the next lower level (Sinclair and Seligman, 2000). In modelling L expansion, different summary relationships were used, based on a temperature- and radiation-limitation, which have been shown to perform well in certain environments (see Introduction). However, testing of the models over environments and genotypes was relevant, since previous studies revealed predictions with those approaches could be

poor when tested in new environments. To our knowledge, differences in prediction of  $L$  among the three approaches have not been evaluated before. Testing of existing approaches of whole model behaviour (Meinke et al., 1998b) or of a sub-process of crop growth is a sound method, which has been done previously, e.g. by Kage et al. (2001).

Temperature-limited  $L$  expansion was based on an exponential expansion, and thus on relative rather than on absolute rates. Use of relative thermal rates is supported by experimental studies that have shown that after a period of stress the relative thermal rates of leaf area expansion were re-attained whereas absolute rates were not. This was found both for monocot rice after transplanting (Kropff et al., 1994) and for dicot sunflower after a period of shading (Tardieu et al., 1999). Because relative rates were used in the present study, the model outcome was sensitive to the errors in initial input values of  $L$ . The relative error in predicted  $L$  due to  $L_0$  was highest for temperature-limited expansion that maintains the initial relative errors (see Eq. 3). These were about 0.12 for potato and 0.08 for wheat (see Results).

The calibrated  $S_{LA,max}$  values that were further used for predictions and sensitivity analyses (Table 10) were based on cultivars other than those in the actual field trials. These values seem reasonable, however, because cultivar variation in  $S_{LA}$  has been reported to be small for wheat (Spitters and Kramer, 1986). The present study focused on the effect of environment on the value of various parameters, including  $S_{LA,max}$ , because it is known that  $S_{LA}$  varies greatly with environment (e.g. Tardieu et al., 1999).

### ***Constancy of parameters and predictions***

Both the constancy of the calibrated parameter values and the model's predictive ability across environments supported use of a switch from temperature- to radiation-limited  $L$  expansion. For both potato and wheat, the calibrated parameter values within a data set varied least with years and sites when  $L_S$  was neither zero nor at maximum  $L$ . Fitted  $L_S$  values varied across data sets of potato (0.26 or 1.41) and across years of winter wheat (0.29 and 2.28) (Tables 6–9). The model's predictive ability was poorest when  $L_S$  was zero and best when  $L_S$  was near 1 for potato and near 1.5 for wheat, and decreased slightly beyond these values.

Differences in  $L_S$  values obtained by the different methods of the present study may be partly attributable to the methods themselves and partly to differences in environmental conditions in the data sets, as explained below. In the prediction procedure, values of  $L_S$  varied independently of other parameters, whereas in the statistical analysis (Tables 6–9) all parameter values were fitted vary simultaneously. For this reason, the statistical analysis was less useful for finding the optimum  $L_S$  than the predictions were, so we used it mainly to find environmental effects within a data set. Environmental conditions might also account for the differences in fitted and

predicted values of  $L_S$ . An environment with a smaller  $Q_P$  has a relatively smaller radiation level, which is a rough indicator for conditions with higher limitation of L expansion by radiation. Smaller fitted  $L_S$  values (earlier start of radiation-limited expansion) were associated with smaller  $Q_P$  values among winter wheat years and among potato sites (Tables 6–9).

The optimum  $L_S$  values for potato and wheat as estimated in the present study were slightly larger than the published value of 0.75 (Spitters et al., 1989) who estimated it from leaf area expansion curves. The optimum values of  $L_S$  were close to the L values where partitioning of dry matter to leaves decreased relative to that of the potato tuber (L about 0.7) and the stem (L about 2.0) of wheat. That supports the hypothesis by Loomis et al. (1976) that leaf expansion becomes limited by assimilate supply due to increased competition for assimilates with other sinks. However, because the predictive ability of our model was hardly sensitive to  $L_S$ , the findings of the present study should be validated, possibly by using a wider range of environmental conditions.

In modelling L, it is important account for both temperature- and radiation-limited leaf area expansion especially under conditions of competition (Kropff and Spitters, 1991), and also in monocrops in order to correctly predict crop nitrogen uptake when nitrogen does not limit crop growth (Booij et al., 1996; Grindlay, 1997; Lemaire and Gastal, 1997). Some models for monocrops use temperature only to predict L expansion, e.g. Jones and Kiniry (1986), Hammer et al. (1993) and Jamieson et al. (1998). That approach can be used successfully to predict crop growth rates, as radiation in the open often correlates with temperature (Marcelis et al., 1998) and because L is predicted reasonably well up to  $L=3$  (Jamieson et al., 1998; also in our study). Errors in L, with L above 3 result in only small errors in PAR interception. However, L expansion is expected to be overestimated under low-light environments.

### *Need for refinements of the model*

With the summary approach as tested in the present study, large differences remained between the prediction accuracy (RMSE of about 0.3) and experimental accuracy (s.e.m. about 0.12 for potato and 0.07 for wheat) of L values at the optimal  $L_S$ . Also at the optimal  $L_S$ , the bias in the predicted values for wheat still varied between 1.64 and 0.60 times those observed at L values of 0.4 and higher (Fig. 4E). The small prediction accuracy, combined with the large bias reveals the need to improve the structure of the model.

To improve the model, it is especially important to improve the description of temperature and radiation-limitations on L expansion (see next Section). The present summary approach is based on a single switch from temperature to radiation-limitation, whereas other studies indicated that switches may occur more than once

during a growing season and even within a day (Loomis and Rapoport, 1977), and switches may occur gradually rather than suddenly (cf. Loomis et al., 1976).

### ***Towards a new model***

Multiple switches between temperature- and radiation-limited L expansion within a growing season may be accounted for in summary models with daily time advance by simulating L expansion as the minimum of daily calculated temperature- and radiation-limited expansion rates. That approach has been used successfully to simulate re-growth of grass after cutting (Schapendonk et al., 1998). A preliminary analysis with the current experimental data (not shown), showed no improvement of predictive ability with multiple switches.

A next step would be to investigate the simulation of canopy leaf area expansion from the processes of the next lower level: leaf emergence rate, rate and duration of expansion of individual leaves and longevity of leaves, as done by Porter (1984). Each of these processes may show a different response to temperature and radiation. If so, then responses to temperature and radiation described directly at the next higher level, the leaf area index, are not necessarily robust over environments.

Eventually, even more comprehensive models could be used e.g. with hourly time advance, such as ELCROS (De Wit et al., 1970) and BACROS (De Wit et al., 1978), to investigate effects of daily fluctuations in assimilate reserve levels, (leaf) temperature, and transpiration on the processes underlying leaf area expansion. Such comprehensive models could then be used to study the importance of different physiological processes on leaf area dynamics over a season. Results of those studies, together with experimental studies, could form the basis for development of improved summary approaches, that are robust over a wide range of environments and account for gradual changes in temperature and radiation limitations.

## **Conclusions**

We have demonstrated that leaf area expansion of potato and wheat in response to temperature and radiation conditions in the field is more realistically described with a switch from temperature- to radiation-limited expansion, than when based solely on one factor or the other. Averaged over experimental sites and years in The Netherlands, the optimum L value at the switch was estimated from predictions to be 1 for potato and 1.5 for wheat. The large difference in accuracy and bias between predictions and observations at the optimal switching point, reveals the need for improvement of the model structure.

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# 5

## **Simulation of attainable potato yield under different organic nitrogen management strategies: model development and explorations**

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(submitted to Agriculture, Ecosystems and Environment)

## Abstract

In order to improve crop yields in organic farming systems, insight into the effects of organic nitrogen (N) management on crop yield is required. A model for potato growth, crop and soil N dynamics was adapted to account for the release of N from crop residues and manure, for effects of N on leaf area dynamics and on light use efficiency. The model accurately predicted tuber dry matter yield, N uptake and soil mineral N residues at harvest, in response to 0–200 kg mineral N ha<sup>-1</sup> yr<sup>-1</sup>, to applications of up to 480 kg slurry N ha<sup>-1</sup> yr<sup>-1</sup> and green manure applications. Subsequently, the model was used to explore tuber yield and residual soil mineral N at harvest under a range of weather conditions influenced by: 1) the time of application, 2) the lateness of the potato cultivar, 3) the N/P<sub>2</sub>O<sub>5</sub> ratio of the manure, and 4) soil N content as a result of the historical fertiliser use. Using 30 years of weather data, the model simulated an increased tuber yield from 8.0 Mg ha<sup>-1</sup> to 11.2 Mg ha<sup>-1</sup> for 490 kg slurry N ha<sup>-1</sup> when spring-applied and up to 10.0 Mg ha<sup>-1</sup> when autumn-applied. Depending on the year, autumn-applied slurry resulted in 77 to 100% of tuber yields compared to that for spring-applied slurry. Tuber yields without slurry varied with year from 57 to 83% of the yield at 490 kg spring-applied slurry N ha<sup>-1</sup>. Tuber yields for a mid-late cultivar were larger than for an early cultivar when harvested on September 1, but were generally smaller when harvested on 1 August. Tuber yield when using a rate of slurry N equal to the average rate used over the whole rotation, was only 5% smaller with an N/P<sub>2</sub>O<sub>5</sub> ratio of 1.7 than with a ratio of 2.7. On farms recently converted from conventional farming, yields were maximally 12% larger on farms with large historical N fertiliser inputs than on farms with small inputs. We conclude that a spring-applied slurry is to be preferred over autumn-applied slurry in order to avoid winter losses of N. Patterns of N uptake suggest that organic N with a large proportion of mineral N applied shortly after emergence could improve potato yields in organic farming.

## Introduction

Optimisation of nitrogen (N) management in organic farming systems is complex. In addition to the direct effect of N on leaf area development and crop growth (Grindlay, 1997), N also has an indirect effect on crop damage by pests (including diseases and weeds) (Jørnsgård et al., 1996; Möller et al., 1998). This occurs especially in organic farming systems where the use of pesticides is prohibited. Several studies have reported smaller crop yields in organic farming systems compared to conventional farming systems, ranging from 0–50% for potato and wheat (e.g. Stanhill, 1990; Van Delden, 1997; Tamis and Van der Brink, 1999). The direct effect of N management is difficult to assess, because the direct effect of N on yield, the indirect effect of N on yield through pests, and the effect of pests on yield regardless of N are confounded.

To improve crop yields in organic farming systems, a quantitative understanding of these confounding yield effects is necessary.

The direct effect of N management on yield and on environmental N losses in organic farming cannot fully be quantified from the surveys (e.g. Stanhill, 1990) that have been performed to date. This is due to the fact that yields were (partly) affected by pests, and because the decomposition and accumulation of soil organic N are often not yet in equilibrium on organic farms. Such a disequilibrium will affect the long-term N supply capacity of the soils (Haraldsen et al., 2000).

Two kinds of disequilibria may exist on organic farms:

(1) Accumulation of organic N may exceed decomposition. This situation applies to organic farms that have recently converted from a conventional farming system in which only limited amounts of mineral N were applied. Soil organic N content increases on such recently converted farms, because the N in manure has not been fully decomposed in a single year.

(2) On most organic farms that are in disequilibrium, however, decomposition of organic N exceeds accumulation. This occurs in two historical situations. Firstly, when farms have recently been converted from conventional farming in which large amounts of mineral N were applied. Part of that N is immobilised in organic matter (Motavalli et al., 1992). The second situation where decomposition of organic N exceeds accumulation occurs when past applications of manure were high (Whitmore and Schröder, 1996), as occurring on Dutch organic farms at present (see below). Current rates of manure applications result in soil P accumulation (Water, 1999). This occurs because under current legislation, manure is a cheaper N source than leguminous crops are, whereas the amount of slurry given to meet the crop's N demand is associated with an over-use of P. To avoid P leaching, smaller rates of manure are required at the farm level, which will reduce future manure N inputs and may decrease the soil organic N content.

Experiments can be used to study differences in yield of crops supplied with organic or mineral N fertilisers (e.g. Wadman et al., 1989), and to study the effects of changes in soil N content (Motavalli et al., 1992). However, the number of experiments under the relevant range of soil and weather conditions with the necessary treatments is limited as studies on soil N supply are expensive and time-consuming. Simulation models can be used to obtain a better understanding of the complex and contrasting effects of organic N-management (manure types, rates, timing) on dry matter production and yield formation. Such models have been successfully used in the past, for example to study changes in soil C and N content in relation to applications of manure (Whitmore and Schröder, 1996) or to compare soil N supply with crop requirements (Pang and Letey, 2000).

In the present study, potato was used as a target crop to quantify tuber yield in relation to organic N management. Potato was chosen because it is an economically important crop in organic farming and because the crop has a low N recovery compared to cereals (Smit and Van der Werf, 1992). Potato recovers less N, probably



it has less root proliferation than in cereals and because parts of the soil are hardly exploited by roots, as a result of the use of ridges (Vos and Groenwold, 1986). Potato crops require a relatively large N input, and leave much mineral N (up to 110 kg ha<sup>-1</sup>) in the soil after crop harvest at optimal N management. This residual N is a potential risk for over-winter N losses to the environment (Wadman et al., 1989; Neeteson, 1995).

Several instruments are available to match N mineralisation dynamics from manure with the crop N requirements during the growing season. The first instrument is the timing of manure application. An autumn application may result in larger N losses during winter than a spring application (Wadman et al., 1989; Schröder et al., 1993). However, a spring application of manure may not always be possible on heavily textured soils, as this may damage the soil structure. A second instrument is the selection of a cultivar with an N requirement that matches the N mineralisation dynamics. In Chapter 4 was found that a late potato cultivar shows a larger N recovery than an early cultivar because it has a longer growth cycle. A critical selection of manure types in terms of their N/P<sub>2</sub>O<sub>5</sub> ratio is another instrument. In order to avoid P accumulation and depletion and yet match crop N requirements, manures with a N/P<sub>2</sub>O<sub>5</sub> ratio close to 2.5, the ratio of harvested arable products (Schröder et al., 1996b; Vos and Van der Putten, 2000), may be selected. The use of manure with a N/P<sub>2</sub>O<sub>5</sub> ratio below 2.5 is also possible, but requires leguminous crops in the rotation to meet the crop's N demand. The economic return of leguminous crops is low. Furthermore, it is important to quantify the effect of weather variation on the effectiveness of those instruments.

The objectives of the present study were to quantify tuber yield and residual soil mineral N at harvest under a range of weather conditions, as influenced by: 1) the time of application, 2) the lateness of the potato cultivar, 3) the N/P<sub>2</sub>O<sub>5</sub> ratio of the manure, and 4) soil N content as a result of the historic fertiliser use.

## Materials and methods

### *Model description*

The model for potato growth (LINTUL-NPOTATO) used in the simulation study was modified from NPOTATO (Wolf, 2000). LINTUL (*Light INTerception and Utilization of Light*) calculates dry matter production from intercepted radiation and the Light Use Efficiency parameter (see Section 'Crop submodel'). NPOTATO was derived from a simulation model for winter wheat NWHEAT (Groot and De Willigen, 1991). Brief descriptions of the major processes are given here, and the major changes and extensions to NPOTATO are described in detail. For more details, see the included references, especially Groot and De Willigen (1991) and Wolf (2000).

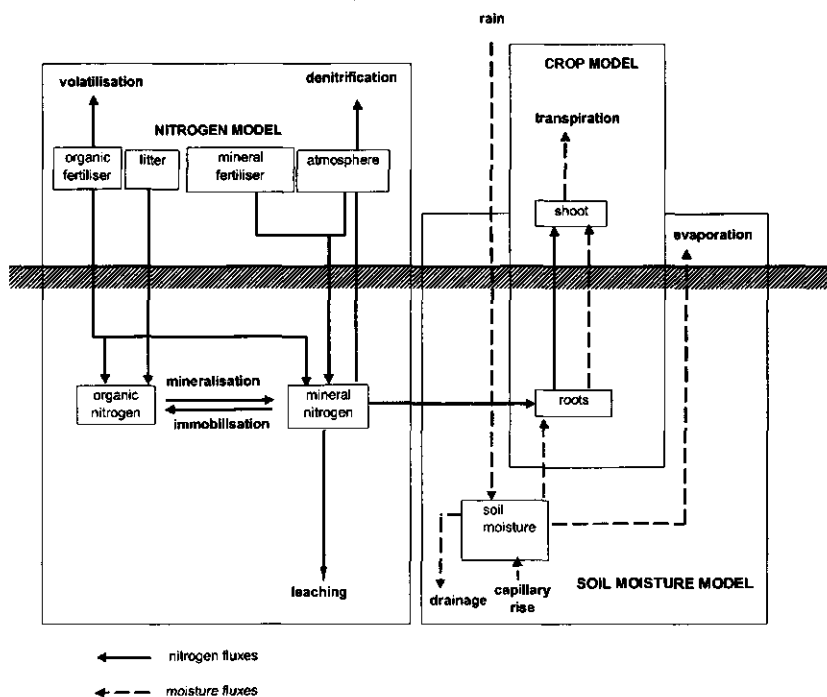


Figure 1. Schematic representation of the model structure (redrawn after Groot and De Willigen, 1991).

The model consists of three submodels (Fig. 1): one for soil N dynamics, one for crop and soil moisture dynamics, and one for crop growth and N uptake.

#### Soil moisture submodel

The soil is treated as a multi-layered system with a fixed number of compartments. Changes in moisture content of a compartment are calculated from the balance between water infiltration, extraction due to soil surface evaporation, extraction by the roots and downward movement of water through the compartments (Groot and De Willigen, 1991).

The model was adapted to account for capillary action of soil water, which rises up to 3 mm per day in a silty loam soil (De Vos, 1997). Capillary rise action was approximated by introducing a maximum pF value of 2.7, except for the soil in the potato ridge, because De Vos et al. (1994) showed for a number of years that the soil did not become dryer. At pF values above 2.8, the growth of the potato crop was assumed to be reduced.

### *Soil nitrogen submodel*

According to the original model version of Groot and De Willigen (1991), soil N content is the result of N input through mineral N fertiliser, decomposition of crop residues, and N output through crop uptake and leaching to deeper soil compartments. The model used in the present study was extended to account for  $\text{NH}_4\text{-N}$  input from manure, decomposition of manure, and for denitrification and volatilisation.

In order to describe the decomposition of manure and crop residues, the fundamental structure of the organic matter model by Verberne et al. (1995) was used. In that model, carbon (C) and N from plant residues (and manure) decompose in soil to produce soil organic matter, using two pools of plant residues (decomposable and resistant) and two soil organic matter pools (labile, stable). A proportion of the C and N becomes soil organic matter, the remainder of C is lost as  $\text{CO}_2$ , and the remainder of N is available for N uptake. Intermittent steps of microbial biomass are not included. In the model, release of C and N depends on the rate of decomposition of a pool, on the C/N ratio of that pool (fixed), and on the proportion of C and N incorporated into soil organic matter.

Soil N uptake is assumed to equal crop N demand (c.f. Wolf, 2000), as long as the transport rate of N from bulk soil to the root exceeds the demand. Nitrogen is initially taken up by mass flow and if N demand exceeds the N taken up by mass flow, the remaining portion is taken up by diffusion. The highest transport rate of N by diffusion occurs when the N concentration at the root surface is zero, the root behaving as a zero sink. The zero-sink uptake rate is proportional to the average N concentration in the soil, the flow of water towards the roots and the diffusion coefficient of N in the soil, which in turn depends on soil moisture content (Groot and De Willigen, 1991).

### *Crop submodel*

Crop growth was calculated according to NPOTATO (Wolf, 2000) with a number of important adjustments and extensions in the calculation of biomass increment and in the effect of N on biomass increment. Furthermore a direct effect of N on leaf area dynamics was included.

Crop growth was calculated as the product of intercepted photosynthetic active radiation (PAR) and the light use efficiency (LUE), in contrast with the original version of NPOTATO (Wolf, 2000). Light interception is related to leaf area index (LAI) via Beer's law. Leaf senescence was calculated according to Spitters et al. (1989) as a relative death rate, the rate depending on the earliness of the cultivar. Dry matter is partitioned as a function of thermal time after emergence, according to Spitters et al. (1989).

In the present model, the LUE is calculated according to Rodriguez et al. (1999) as a function of PAR and crop physiological parameters (Appendix 4) to

account for the reduction of LUE at higher levels of PAR (Kooman, 1995) and for the effect of N on LUE (see below).

In the present model, N affects the LUE through its effect on the photosynthesis rate of upper leaves at light saturation ( $P_{\max}$ ).  $P_{\max}$  increases non-linearly with leaf N concentration ([N]) at the top of the canopy; the shape of the curve was reported by Marshall and Vos (1991), using a maximum leaf [N] of  $0.06 \text{ kg kg}^{-1}$ . Other effects of N on parameters underlying LUE (see Table 1, and Appendix 1) were not accounted for, because sensitivity analysis showed that equal relative changes in those parameters ( $\gamma$  increases,  $\alpha$  decreases, and  $k$  decreases) hardly affected the LUE. Leaf [N] at the top of the canopy was calculated according to Yin et al. (2000). Calculation of LUE and leaf [N] of upper leaves, assumed that PAR, leaf [N], and  $P_{\max}$  decline at the same rate with depth of the canopy.  $\kappa = \kappa$

Also new in the model is the direct effect of N on LAI increase, whereas in Wolf (2000), N affected LAI expansion only indirectly through a reduction in crop photosynthesis. That description was changed because experiments showed that LAI expansion can be reduced while the LUE of the crop is not affected (Chapter 2). In the present model, rate of LAI expansion is first calculated as a function of temperature and radiation. LAI is assumed to expand exponentially with temperature up to a LAI of 1.0, after which it is calculated as the product of leaf dry matter increase and the specific leaf area ( $\text{m}^2 \text{g}^{-1}$ ) (cf. Chapter 4). Next, the rate of expansion is adjusted as a function of the relative [N] in the crop, the nitrogen nutrition index (NNI) proposed previously for tall fescue (Belanger et al., 1992). The NNI is defined as the ratio of actual/critical crop [N], with a maximum of 1. Below the critical crop [N], crop growth rate is reduced, with critical crop [N] calculated according to Greenwood et al. (1990). Maximum [N] of organs was modified from Wolf (2000), to allow for a maximum crop [N] of 20% above the critical [N].

A final adjustment in the model was the description of leaf senescence as a function of N. In the present model leaf senescence was adapted from an "N-stress factor" (Wolf, 2000) into the effect of N on two processes. In the present model, leaf senescence was initially calculated as a function of leaf ageing and shading of leaves (cf. Spitters et al., 1989). Next, that rate of senescence was compared with N-limited rate of senescence of which the maximum rate was used. According to the first process, leaves were assumed to senesce when their leaf [N] below a minimum value, accounting for a profile in leaf [N] as described in Yin et al. (2000). Secondly, N translocation from leaves, stems and roots is increased to meet tuber N demand when the tuber [N] is close to a minimum value of 0.5% (Wolf, 2000). This second process is based on the self-destruction hypothesis introduced by Sinclair and De Wit (1976). Preliminary model explorations showed that the minimum leaf [N] caused enhanced leaf senescence under conditions of moderate N limitations and the minimum tuber [N] caused enhanced leaf senescence mainly under strong N limitations.

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Table 1. Model parameters and their values for those parameters that were changed compared to NPOTATO (Wolf, 2000) or are new.

Name	Description	Value	Units	Reference
<i>Crop</i>				
$\alpha$	Leaf quantum yield	12.5	$\text{g CO}_2 \text{ MJ}^{-1}$	Spitters et al., 1989
$\gamma$	New biomass per gross assimilated $\text{CO}_2$	Fig. 2A	$\text{g dm g}^{-1} \text{ CO}_2$	Output of NPOTATO
$P_{\max} = f(N)$	Relative effect of leaf [N] on $P_{\max}$			Marshall and Vos, 1991
$N_b$	Minimum leaf [N] below which leaves senesce	0.2	$\text{g N m}^{-2}$ <i>leaf</i>	Calibrated (see text)
$N_{\min, \text{tu}}$	Minimum tuber [N]	0.005	$\text{g N g}^{-1} \text{ dm}$	Wolf, 2000
$N_{\text{opt}}$	Optimal crop [N] except roots			Greenwood et al., 1990
SLA	Specific leaf area	23	$\text{m}^2 \text{ kg}^{-1}$	Kooman, 1995
K	Extinction coefficient for PAR and for [N]	0.72	$\text{m}^2 \text{ m}^{-2}$	Khurana and McLaren, 1982
LUE	Light use efficiency at optimal temperature and [N]	3.0	$\text{g dm MJ}^{-1}$	Wolf, 2000
$R_L$	Relative leaf area expansion rate	0.0197	$\text{m}^2 \text{ m}^{-2} \text{ d}^{-1}$	Chapter 3 (Sandy soil site, 1997)
Root d	Maximum effective rooting depth	0.50 0.45	m	Sandy soil site, 1997 De Vos and Heinen, 1999
LAIS	Leaf area index at start use of SLA	1	$\text{m}^2 \text{ m}^{-2}$	Chapter 4
RGM	Maximum rate of root extension	1.4	$\text{cm d}^{-1}$	Calibrated (see text)
<i>Soil</i>				
KCDPM	Relative decomposition rate of DPM	$2.90 \cdot 10^{-2} \text{ d}^{-1}$		Whitmore and Groot, 1994
KCRPM	Relative decomposition rate of RPM	$4.40 \cdot 10^{-3} \text{ d}^{-1}$		Parton et al., 1987
KCLOM	Relative decomposition rate of LOM, sandy soil	$8.00 \cdot 10^{-4} \text{ d}^{-1}$		Calibrated (see text)
KCLOM	idem, silty loam soil	$8.49 \cdot 10^{-4} \text{ d}^{-1}$		Van Faassen and Lebbink, 1994
KCSOM	Relative decomposition rate SOM, sandy soil	$8.80 \cdot 10^{-6} \text{ d}^{-1}$		depends on KCLOM, see text
KCSOM	idem, silty loam soil	$4.11 \cdot 10^{-6} \text{ d}^{-1}$		depends on KCLOM, see text
ERPM	Proportion of C-RPM incorporated into LOM	0.7	$\text{g g}^{-1}$	Parton et al., 1987
ELOM	Proportion of C-LOM incorporated into SOM	0.02	$\text{g g}^{-1}$	Parton et al., 1987, see text
ESOM	Proportion of C-SOM incorporated into LOM	0.016	$\text{g g}^{-1}$	Parton et al., 1987, see text

DPM = decomposable plant material, RPM = resistant plant material, LOM = labile organic matter, SOM = stable organic matter.

Partitioning of dry matter between organs was described according to Spitters et al. (1989) as a function of thermal time, with later-maturing cultivars having a larger thermal time till start of linear tuber bulking. Nitrogen limitation shifts the dry matter partitioning from leaves to roots and tubers. The partitioning of dry matter to leaves with sufficient N, is compared with the (smaller) partitioning of dry matter to leaves under N limitation (see below). The resulting difference in dry matter is partitioned for 20% to roots, and for 80% to tubers (if present), as calculated from Vos and Groenwold (unpublished, Plant Research International). Partitioning of dry matter to leaves under N limitation, is calculated from the assumption that the specific leaf area ( $\text{m}^2 \text{g}^{-1}$ ) of the newly formed potato leaves is not changed by N limitation, as found by Vos (1995). The start of linear tuber bulking was assumed to be unaffected by N supply.

### ***Parameterisation***

The model was calibrated and validated against data sets conducted in The Netherlands on a sandy and silty loam soils (see Section "Data sets"). Model parameters were obtained from Wolf (2000), except for site-specific parameters, for newly introduced processes, and for some other values listed below. Table 1 provides an overview of the changed and newly introduced parameters.

#### *Soil moisture and soil nitrogen submodel*

Soil water retention curves for the two soils had been previously determined at both sites. Data for soil organic matter dynamics were obtained from Verberne et al. (1995), except for the decomposition rates, efficiency factors, and sizes of soil organic matter pools and the effect of soil moisture which were obtained from literature (Table 1). Values for decomposition of organic inputs were adjusted in order to match reported values for 1) the proportion of C being left-over after one year (0.39 for green manure and 0.58 for animal manure, Wolf and Janssen, 1991), and 2) the proportion of organic N released during the first year of decomposition (50%, Beijer et al., 1996; Schröder et al., 1996a).

Decomposition rates of labile and stable soil organic matter, and their pool sizes were obtained by combining measurements of organic matter contents with estimates on N release, assuming that accumulation and decomposition of soil organic matter input was in equilibrium. The latter seems reasonable for the top 25 cm of the silty loam soil "Lovinkhoeve" (Kooistra et al., 1989). For the silty loam soil, decomposition of organic matter in the subsoil was not considered, as it consists mainly of old material (Kooistra et al., 1989) with low rates of decomposition. Moreover, the subsoil is very wet, so a significant part of released N may be denitrified.

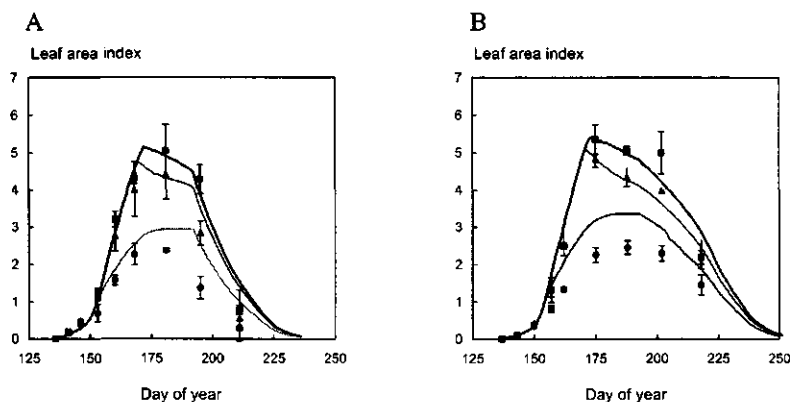


Figure 3. Leaf area index dynamics of potato as affected by N supply [ $0 \text{ kg N ha}^{-1}$  (●),  $100 \text{ kg N ha}^{-1}$  (▲) and  $200 \text{ kg N ha}^{-1}$  (■)] for cultivar Eersteling (A), and Bintje (B). (Sandy soil site, 1997).

The minimum leaf [N] below which leaves senesce ( $N_b$   $0.2 \text{ g N m}^{-2}$ ) was calibrated against observations at the sandy soil site (Droevendaal) in 1997 for cultivar Eersteling with no N input (N1), and resulted in a reasonable description of the leaf senescence (Fig. 3A and 3B).

## Model explorations

### Sensitivity analysis

Sensitivity of tuber yield of an early (Junior) and a mid-late (Agria) cultivar to a number of crop and soil parameters was tested by varying parameter values by  $-2.5\%$  and  $+2.5\%$ . The used weather data were the 30 year daily averages from De Bilt ( $52^{\circ}06'N$   $5^{\circ}11'E$ ) of radiation, minimum and maximum temperature, wind speed and precipitation.

### Scenario studies

Tuber dry weight, tuber N uptake and soil mineral N content after harvest was calculated for eight scenarios (Table 2). Each scenario was calculated for different rates of applied slurry N, ranging from  $0$ – $490 \text{ kg slurry N ha}^{-1}$ , and for 30 separate years of historical weather data from De Bilt (1959–1988). In each scenario, the crop

Table 2. Overview of the scenarios used in the present study. Each scenario was calculated over a range of slurry N rates (0–490 kg slurry N ha<sup>-1</sup> yr<sup>-1</sup>) and 30 years of historical weather data.

Name		Timing of slurry application	Harvest time	Maturity class	N/P <sub>2</sub> O <sub>5</sub> kg kg <sup>-1</sup>	Organic matter g g <sup>-1</sup>
Spring application	SA	1 April	1 Sept.	9	2.7	0.028
Autumn application	AA	1 Sept.	1 Sept.	9	2.7	0.028
Mid-late cultivar, late harvest	LL	1 April	1 Sept.	5	2.7	0.028
Early cultivar, early harvest	EE	1 April	1 Aug.	9	2.7	0.028
Late cultivar, early harvest	LE	1 April	1 Aug.	5	2.7	0.028
Low N/P <sub>2</sub> O <sub>5</sub> ratio	NP	1 April	1 Sept.	9	1.7	0.024
Large past N inputs	LN	1 April	1 Sept.	9	2.7	0.022
Small past N inputs	SN	1 April	1 Sept.	9	2.7	0.034

was set to emerge on 15 May and soil mineral N content (in kg N ha<sup>-1</sup>) at start of the manure application was 20 (depth: 0–0.25m), 10 (depth: 0.25–0.60m), and 10 (depth: 0.6–1.0m). Simulations started with the manure application.

Five variables (see Introduction) were varied in the scenarios (Table 2): timing of slurry application (1 April, 1 September), maturity class of the potato cultivar (early, mid-late), effects of maturity class at different harvest times (1 Aug., 1 Sept.), N/P<sub>2</sub>O<sub>5</sub> ratio (2.7, 1.7), and past N inputs (small, large).

The autumn application of manure application (1 September) is followed by yellow mustard (*Sinapis alba* L.) which is ploughed on 1 November. The N uptake by yellow mustard was calculated from the average availability of soil mineral N to 0.6 m depth between 1 September and 1 November. N uptake by yellow mustard was calculated, assuming a 70% N recovery and a maximum uptake of 80 kg N ha<sup>-1</sup> (Schröder et al., 1997).

For most scenarios, soil N decomposition and accumulation were taken to be in equilibrium at the level of a complete crop rotation, which depends on the average rate of slurry N that is applied in a rotation (see below). The equilibrium influences the release of N by soil organic matter and is thus important for tuber yield, but a range of slurry N can still be applied to the potatoes (as has been done in the scenarios), because crops in the rotation do not all require the same amounts of manure.

The average rate of slurry N at the level of a complete rotation, was calculated from the average P<sub>2</sub>O<sub>5</sub> exported via harvested products, and from the N/P<sub>2</sub>O<sub>5</sub> ratio of the manure. This export, estimated from the Lovinkhoeve organic system at 47 kg P<sub>2</sub>O<sub>5</sub>, was calculated from measurements during 1996–2000. Application rate of slurry



Table 3. Calculation of increase of organic matter (OM, mg g<sup>-1</sup> soil) under steady state conditions by a yearly input of cattle and pig slurry respectively, given P withdrawal by crop products equals P input by manure. Based on model equations, the fraction of organic N released within one year was 58% for cattle slurry and 71% for pig slurry.

Slurry type	Yearly input of N,C in slurry		Left after 1 year		C pools steady state						Released by RPM,LOM,SOM	
	N	C	N	C	DPM	RPM	LOM	SOM	Total	OM	N	C
	kg ha <sup>-1</sup>										mg g <sup>-1</sup>	
Cattle	128	858	25.2	384	344	401	6162	5057	13770	5.7	23.9	399
Pig	81	330	9.7	148	132	154	2370	1945	5296	2.2	9.2	154

Table 4. Slurry composition in kg per Mg fresh product.

Slurry type	Application date	Dry matter	Organic matter	N	NH <sub>4</sub> -N	P <sub>2</sub> O <sub>5</sub>	K <sub>2</sub> O	C/N-org <sup>a</sup>
<i>Experiment</i>								
Cattle	02-Sep-96	74	57	4.7	2.4	1.5	7.4	12.3
	30-Sep-97	97	73	6.0	2.8	2.5	6.4	11.4
<i>Average<sup>b</sup></i>								
Cattle		90	66	4.9	2.6	1.8	6.8	14.3
Pig		90	60	7.2	4.2	4.2	7.2	10.0

a C/N ratio, using only the organic N fraction in manure, and assuming 0.5 g C g<sup>-1</sup> organic matter.

b Van Dijk, 1999.

was thus limited to avoid P accumulation or depletion and resulted in an average application of 128 kg slurry N ha<sup>-1</sup> yr<sup>-1</sup> (N/P<sub>2</sub>O<sub>5</sub>=2.7, cattle slurry) and 81 kg slurry N ha<sup>-1</sup> yr<sup>-1</sup> (N/P<sub>2</sub>O<sub>5</sub>=1.7, pig slurry) (Tables 3, 4).

The historical N fertiliser use affects the soil N supply (see Introduction), resulting in an increased (rich past, RP) or a decreased (poor past, PP) N supply compared to a soil in which N decomposition is in equilibrium (EQ) with N accumulation. The yearly N mineralisation for PP in long-term rotation experiments was estimated at 120 kg N ha<sup>-1</sup> (Van Faassen and Lebbink, 1994), corresponding to 0.022 g organic matter g<sup>-1</sup> soil (Kooistra et al., 1989). The yearly N mineralisation from soil organic matter was calculated to increase by 24 kg N ha<sup>-1</sup> due to long-term applications of 128 kg slurry N ha<sup>-1</sup> yr<sup>-1</sup> (Table 3), according to formula described in Verberne et al. (1990). The yearly N mineralisation in EQ was, therefore, 120 plus 24 kg N ha<sup>-1</sup>, corresponding to 0.028 g organic matter g<sup>-1</sup> soil. The yearly N mineralisation in RP was taken to be 120 plus 48 kg N ha<sup>-1</sup>, corresponding to 0.033 g organic matter g<sup>-1</sup> soil.

## Calculations

Apparent N recovery (ANR, %) of tubers was calculated as

$$\text{ANR} = (N_t - N_{t0}) / \text{slurry N}, \quad (1)$$

where  $N_t$  ( $\text{kg N ha}^{-1}$ ) is tuber N uptake at a given amount of slurry N,  $N_{t0}$  ( $\text{kg N ha}^{-1}$ ) is tuber N uptake when no slurry is applied, and 'slurry N' ( $\text{kg N ha}^{-1}$ ) is the amount of N as applied with slurry.

## Data sets

The two data sets used consisted of experiments in which potatoes were grown under a range of N supplies, planted on ridges, with 0.75 m distance between ridges and 0.3 m within a ridge ( $4.44 \text{ plants m}^{-2}$ ). In both sets, dry weight of plant organs and soil mineral N content were sampled 6–10 times during the growing season. One set of experiments was conducted on a sandy soil at Wageningen from 1996 to 1999, the other on a silty loam soil at Marknesse from 1997 to 1998. In both sets, potatoes were grown in a 1:6 (sandy soil) or a 1:7-year rotation (silty loam soil). Soil characteristics of the two sites are given in Table 5. Pests, diseases, and weeds did not affect yields, and water did not limiting yields (Chapters 2 and 3), except for *Verticillium* spp., which infected the potatoes on the sandy soil in 1999 (after 9 August), and on the silty loam soil in 1997 (after 1 July).

In the sandy soil, early cultivar Eersteling was grown in 1996 and 1997 and mid-late cultivar Bintje from 1996 to 1999. Cultivars were grown at three rates of mineral N fertiliser: 0, 100 and  $200 \text{ kg N ha}^{-1}$ . Fodder radish (*Raphanus sativus* L. var *oleiformis* Pers.) was planted 30 August, 1995 in the field preceding the potato crop and ploughed on 6 March 1996. P and K were supplied according to recommended rates set by Van Dijk (1999) for optimal crop growth. Lay-out and sampling procedures are described in Chapter 3.

On the silty loam soil, the early cultivar Junior and mid-late cultivar Agria were grown at three N rates: no N, about  $230 \text{ kg slurry N ha}^{-1}$ , and  $420 \text{ kg slurry N ha}^{-1}$  supplemented with mineral N fertiliser, according to recommended rates (Van Dijk, 1999). Cattle slurry was applied in autumn after the harvest of wheat (around 15 August) followed by yellow mustard, which was ploughed around 15 November. Slurry composition is given in Table 4. Soil P- and K-status were sufficient for optimal crop growth (Van Dijk, 1999). The experiments on the silty loam soil have been described in detail in Chapter 2.

Table 5. Some properties of the two soils of the data sets.

Site	Depth m	Organic matter g g <sup>-1</sup> soil	Bulk density g cm <sup>-3</sup>	Total N (%) mg g <sup>-1</sup> soil
Sandy soil (Droevendaal)	0.0–0.2	0.03	1.40	1.2 <sup>a</sup>
	0.2–0.4	0.02	1.40	0.8 <sup>a</sup>
	0.4–0.6	0.01	1.40	0.4 <sup>a</sup>
Silty loam soil (Lovinkhoeve)	0.0–0.25	0.022	1.35	1.3
	0.25–0.60	– <sup>b</sup>	1.35	–
	0.60–1.0	–	1.25	–

a Based on a C/N ratio of 15 (Verberne et al., 1990).

b Only N release from top 0–0.25 m was considered.

## Results and discussion

### *Comparison of model predictions with independent data*

Before validating the model on independent data, some adjustments to the model were made for simulation of potato growth at the Lovinkhoeve site 1998, as predictions with the original model strongly overestimated crop N uptake (not shown). Measurements by De Vos and Heinen (1999) during that experiment showed that shortly after crop emergence (day 162–172) and during three other periods in 1998 (days 179–184; 193–198; 207–214) the soil was saturated with water. Observed crop plus soil N (0–0.90 m) at sequential harvests combined with simulated N leaching and deposition showed that additional N was lost at rates of up to 1.6 kg N ha<sup>-1</sup> d<sup>-1</sup> following intensive rains, probably due to denitrification from the vulnerable upper soil (0–0.3 m) (De Vos, 1997). The present model does not account for soil moisture contents above field capacity and for peaks in denitrification. For 1998, crop growth was therefore simulated using the calculated denitrification rates as input. It was additionally assumed that crop N uptake was zero and N mineralisation inhibited during the periods of water saturation. After these adjustments, performance crop N uptake was simulated well (Fig. 4).

The performance of the model compared with observations is shown in Fig. 4, and statistics showing the goodness of fit are given in Table 6. In two cases senescence of the potato crop was hastened due the occurrence of 'potato early dying disease' (*Verticillium* spp.), namely on the sandy soil in 1999 (after 9 August), and on the silty loam soil in 1997 (after 1 July). In those two cases, predicted values were compared with observed ones up to the occurrence of that disease. Predictions of crop

N uptake by leaves, stems and tubers were good ( $R^2=0.87$ ), although N uptake was somewhat underestimated for the sandy soil (Fig. 4A). Tuber N uptake was also well simulated, both for N uptake throughout crop development ( $R^2=0.94$  for all data points), as well as for the final N uptake ( $R^2=0.86$ ) (Fig. 4B). LAI was less well predicted than of other crop components (Fig. 4C), with an accuracy as measured by the RMSE of  $0.57 \text{ m}^2 \text{ m}^{-2}$ , and an  $R^2=0.83$ , but the average bias was zero (Table 6). Predictions of crop dry weight ( $R^2=0.94$ ) and tuber dry weight ( $R^2=0.93$ ) were accurate, but tuber dry weight before the completion of crop development was underestimated for the sandy soil (Fig. 4D). Nonetheless, prediction of final tuber dry weight was good at both the sandy and the silty loam soil ( $R^2=0.87$ ) (Fig. 4D), with a slope for simulated versus observed values of 1.03 (Table 6). Predictions were least accurate for the soil mineral N content (0–0.6m) (Fig. 4E), with an overall accuracy (RMSE) of  $33 \text{ kg N ha}^{-1}$  for all data. However, the average deviation between observed and predicted values was small, when taking all sampling times into consideration, as well as for the values at harvest ( $-2.7 \text{ kg N ha}^{-1}$ ).

Predictions of crop and tuber N uptake, and of crop and tuber dry matter yield explained 86–94% of the data variation. The newly introduced description for LAI expansion (Fig. 2D) was identical the one found previously by Belanger et al. (1992) for a tall fescue sward. Together with the description for leaf senescence, it explained 83% of the observed variation in LAI. The original data by Biemond and Vos (1992) could be used to verify whether the relationship as derived from tomato, is also found in experimental data for potato. In three cases, the model under-estimated the maximum LAI during the growing season on the sandy soil, where the observed LAI was about 6.5, while predicted LAI was 4.2–4.8 (Fig. 4C). In those cases, the model overestimated shading-related leaf senescence. Prediction of LAI was less accurate than for crop dry matter or crop N uptake, as was the case in studies with other crop growth models (e.g. Asseng et al., 1998).

The newly introduced description for LUE gave good predictions for crop dry matter (Table 6). The non-linear relationship between leaf [N] and LUE used in the present model (Fig. 2C), corroborated experimental results by Dreccer et al. (2000a), who found a similar non-linear relationship between LUE and [N] of light intercepting organs in oilseed rape and wheat.

Some parameter values underlying the calculation of the LUE deviated from previously reported values. The values for  $\gamma$  found in the present study generally exceeded  $0.36 \text{ g g}^{-1}$ , the value of as found for wheat by Rodriguez et al. (1999). This is due to the overall lower [N] in the potato crop than in the wheat crop, with particularly tubers having a low [N], and the predicted smaller costs for growth and maintenance (cf. Amthor, 2000). The actual value for  $\gamma$  deserves further quantification, as Ewing and Struik (1992) reviewed that starch in part of the initiated tubers is broken-down during potato growth, e.g. with resorption of small tubers, which will be associated with  $\text{CO}_2$  respiration.

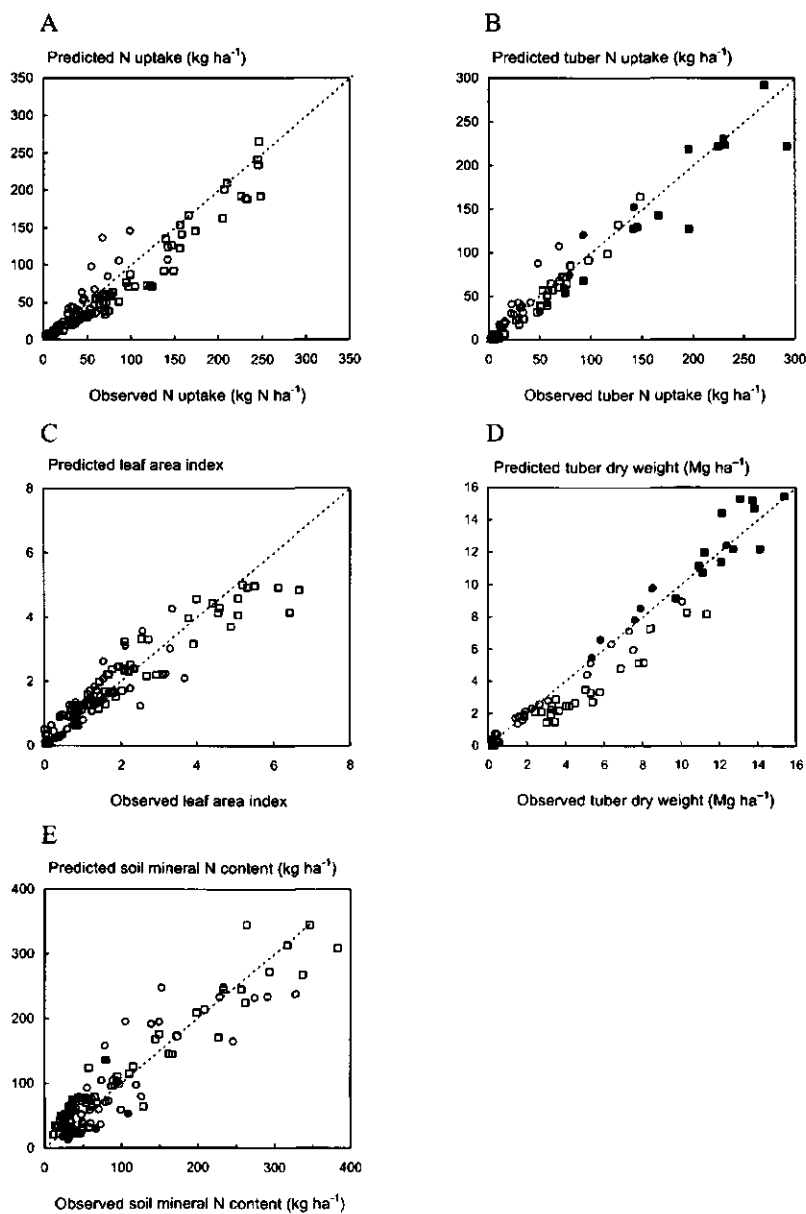


Figure 4. Predicted versus observed potato crop characteristics before crop maturity (open symbols) and at crop maturity (solid symbols), at sandy soil site ( $\square$ ,  $\blacksquare$ ) and at the silty loam soil site ( $\circ$ ,  $\bullet$ ). (A) N uptake by tubers, green leaves and green stems together; (B) N uptake of tubers; (C) leaf area index; (D) tuber dry weight, and (E) soil mineral N content (0–0.6m).

Table 6. Statistics showing the goodness of fit to the data of the sandy soil and the sitly loam soil.

Variable	Units <sup>a</sup>	n	RMSEP <sup>b</sup>	Bias <sup>c</sup>	R <sup>2</sup> (1:1)	Slope <sup>d</sup>
<i>All harvests</i>						
Crop weight <sup>e</sup>	Mg ha <sup>-1</sup>	117	0.79	0.298	0.940	0.878
Tuber weight	Mg ha <sup>-1</sup>	75	1.19	0.049	0.931	0.943
Leaf area index		126	0.567	0	0.826	0.903
Crop N uptake <sup>e</sup>	kg ha <sup>-1</sup>	117	21.6	9.56	0.870	0.868
Tuber N uptake	kg ha <sup>-1</sup>	75	16.8	-3.18	0.935	0.944
Soil mineral N content 0-0.6m	kg ha <sup>-1</sup>	106	33.5	-2.72	0.839	0.951
<i>Final harvest</i>						
Tuber weight	Mg ha <sup>-1</sup>	18	1.08	0.353	0.865	1.03
Tuber N uptake	kg ha <sup>-1</sup>	18	28.4	12.1	0.860	0.928
Soil mineral N content 0-0.6m	kg ha <sup>-1</sup>	18	27.6	-2.7	0.813	0.986

a Units for RMSEP and Bias.

b Accuracy of simulation (S). Root mean squared error of prediction =  $(1/n \sum (O - S))^2$ ,  
with O = observations

c Mean difference between S and O:  $1/n \sum (O - S)$ .

d Slope of S against O, forced through the origin.

e For non-senesced stems, leaves and tubers.

The values calculated for  $P_{\max}$  exceeded  $0.9 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , the value of reported for young potato leaves under field conditions (Vos and Van der Putten, 1998). The value for  $N_b$  is below those reported for the areal leaf N content at which photosynthesis is just zero:  $0.5 \text{ g N m}^{-2}$  for potato (Vos and Van der Putten, 1998) and rice (Yin et al., 2000). The reason for the large  $P_{\max}$  and small  $N_b$  values may be that N declines less strongly with depth of the potato canopy that light does. Measurements by Biemond and Vos (1992) and by Osaki (1995) suggest a small decline of N at the top of the potato canopy, but to our knowledge the N decline as a function of LAI has not been quantified to date for potato. If the declines of light and N deviate strongly, the calculation of LUE may be adapted to better represent the underlying processes.

The maximum daily rate of vertical root extension (at 16–24°C) for potato was calibrated to  $1.4 \text{ cm d}^{-1}$  at the sandy soil site 1997, whereas Groot and De Willigen (1991) used  $2.0 \text{ cm d}^{-1}$  for wheat. A.L. Smit and J. Groenwold (Plant Research International, unpublished), also found a larger root extension for wheat ( $0.3 \text{ cm (}^\circ\text{Cd)}^{-1}$ ) than for potato ( $0.1 \text{ cm (}^\circ\text{Cd)}^{-1}$  with base temperature 0°C).

The soil water balance of the model, as based on the tipping bucket principle has been validated before (Groot and De Willigen, 1991). The tipping bucket approach does not allow for soil moisture contents to become above field capacity. As a result, the present model does not accurately describe the N dynamics in years with

intensive precipitation, as occurred on the silty loam soil in 1998. For an accurate simulation of such conditions, more detailed descriptions of soil water and N dynamics may be needed, such as the model by De Vos et al. (2000). Such model approaches, however, are difficult to parameterise, and were, therefore, not used for the present study.

Decomposition of crop residues and manure was not explicitly validated in the present study, but is expected to be acceptable for several reasons. Firstly, in the present study the simulation of the C and N decomposition of green manure crops had been taken from Whitmore and Groot (1994), who validated their model and found acceptable predictions. Secondly, simulation of C and N decomposition of animal manure was nearly identical to Whitmore and Schröder (1996), who validated their model and successfully estimated changes in soil C and N content after applications of slurry manure. Finally, predictions for crop N uptake and the overall result of the soil N dynamics, the soil N content explained more than 80% of the data variation, and the bias was small.

Validation of soil N dynamics included N inputs from green manure, and from slurry N up to 480 kg slurry N ha<sup>-1</sup>. Based on the good predictions for crop growth, tuber dry matter yield and soil N content, we concluded that the model is suitable for exploring tuber yields under organic N inputs with green manure crops and animal manure. The N inputs used in the explorations do not go beyond 490 kg slurry N ha<sup>-1</sup>, so largely remaining within the range of inputs for which the model was validated.

### ***Sensitivity analysis***

Simulated tuber yield of the early variety Junior was most sensitive to the crop parameters  $R_L$ , which determines the rate of leaf area expansion up to an LAI of 1 in dependence of temperature, and to the maximum rate of vertical root extension (RGM) (Fig. 5). Early N uptake increases with RGM, because N at greater depths is reached more quickly. Simulated tuber yield of early variety Agria was less sensitive to  $R_L$  than Junior because its maximum LAI was much larger than that of Junior. Agria was also less sensitive to RGM than Junior because of its longer growth cycle. Instead, simulated tuber yield of mid-late cultivar Agria was most sensitive to  $\gamma$ , because it determines the leaf area production above an LAI of 1. Increased soil N availability decreased the sensitivity to  $R_L$  of early cultivar Junior, because LAI and leaf area duration increased with N whereas  $R_L$  only affects the LAI up to a value of 1. For cultivar Agria, sensitivity to  $R_L$  was small when no slurry was applied because soil N content was so small that N, and not  $R_L$ , determined the (maximum) LAI.

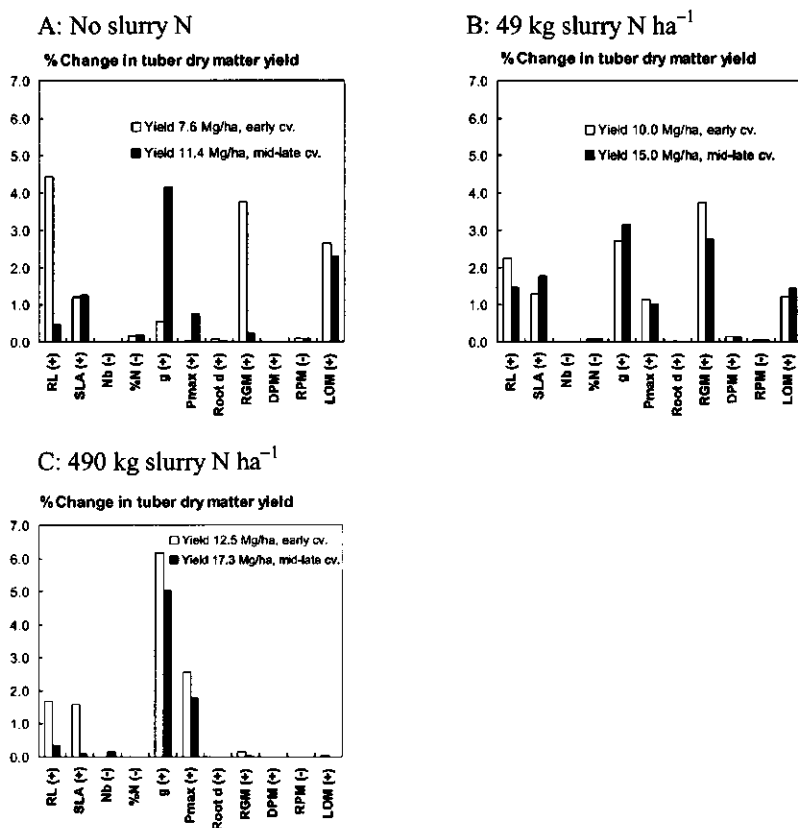


Figure 5. Model sensitivity of tuber dry matter to a 5% (i.e.  $-2.5, +2.5\%$ ) change in parameter values for an early potato cultivar (Junior) and mid-late potato cultivar (Agria) at three rates of slurry N at the silty loam soil site. A positive sign indicates a tuber yield increase with a change in parameter from  $-2.5$  to  $+2.5\%$ , a negative sign indicates the opposite. Parameters are in Table 1, '%N' =  $N_{min,tu}$ , 'g' =  $\gamma$ , other parameters see Table 1.

Simulated tuber yield of both varieties was more sensitive to the decomposition rate of LOM (labile organic matter) than to the decomposition rate of manure (DPM and RPM) with an application of  $49 \text{ kg slurry N ha}^{-1}$  (Fig. 5). The reason for this is that the absolute amount of N available to the crop during the growing season from the soil organic matter ( $80\text{--}90 \text{ kg N ha}^{-1}$ ) was much larger than that from slurry (about  $15 \text{ kg N ha}^{-1}$ ). Differences in sensitivities between the two cultivars were not related to differences in harvest index, as the harvest indices of both cultivars at maturity were nearly identical (about 0.8, not shown). Differences in sensitivities across N supply rates were also little related to the harvest index, as predicted harvest index decreased only slightly with increased N supply, from 0.84 at no slurry to 0.80 (early cultivar)



and 0.79 (mid-late) at 490 kg slurry N ha<sup>-1</sup>. Biemond and Vos (1992) also found hardly any change in harvest index with N supply.

## Scenarios

In the present section, first the effects of variation within the different variables (timing, cultivar maturity, harvest date, N/P<sub>2</sub>O<sub>5</sub> ratio of manure and fertilisation history) on N uptake, tuber yield and residual soil mineral N at harvest are given and discussed. Next, an overview of the scenarios is given, together with implications for organic N management.

### Timing of N application

Slurry increased the crop N uptake of potato from 95 kg N ha<sup>-1</sup> (no slurry) to 300 kg N ha<sup>-1</sup> when spring-applied (SA) at a rate 490 kg slurry N ha<sup>-1</sup> (Fig. 6A). This increase was limited to 160 kg N ha<sup>-1</sup>, when a similar slurry rate was applied in autumn (AA). The corresponding tuber dry matter yield increase amounted to 3.2 Mg ha<sup>-1</sup> (SA) and 2.0 Mg ha<sup>-1</sup> (AA). Crop N uptake was smaller in AA than in SA, because soil mineral N content at emergence was smaller (see Fig. 7C). The proportion of N in the tubers remained nearly constant at about 0.8 up to a tuber N uptake of about 192 kg N ha<sup>-1</sup> as achieved with 245 kg slurry N ha<sup>-1</sup> in SA (Fig. 6A).

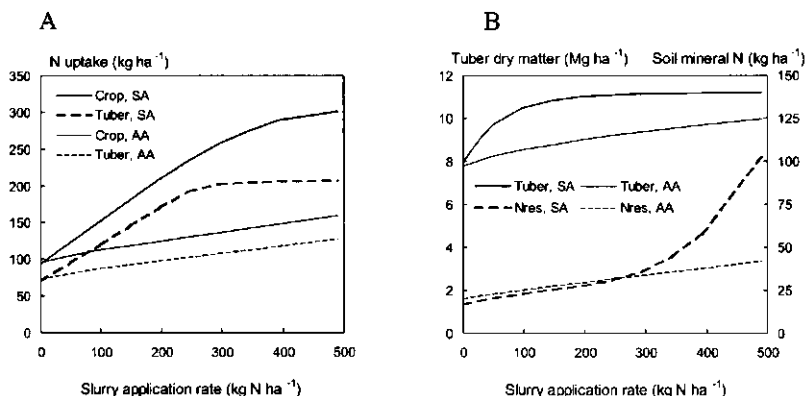


Figure 6. Relationship between slurry application rate and (A) simulated N uptake in the crop (roots excluded) and in tubers only, (B) simulated tuber dry matter yield and residual soil mineral N content at harvest (0–0.6m), as affected by slurry application date (spring-applied, SA; autumn-applied, AA) (cultivar Junior, averaged over 30 years of historic weather).

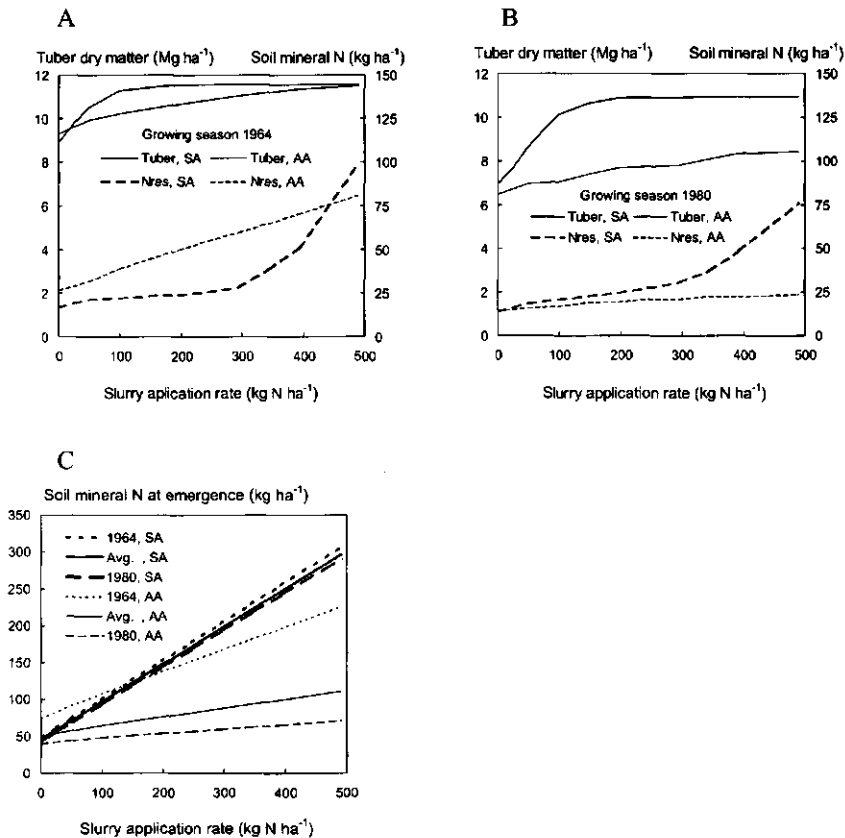


Figure 7. (A,B) Same relationship as shown in Fig. 6, but now for the two most extreme growing seasons. (C) Relationship between slurry application rate and soil mineral N content at crop emergence.

This is in agreement with Biemond and Vos (1992), who also found not change in the proportion of N in tuber at crop maturity. Only applications above 245 kg slurry N ha<sup>-1</sup> resulted in a reduction of the proportion of N in the tubers, N uptake by the crop as a total still increased, due to N uptake by the shoot, whereas N uptake by the tuber hardly increased (Fig. 6A).

The residual soil mineral N content at harvest (0–0.6m), remained smaller in AA than in SA, and was at most 42 kg N ha<sup>-1</sup> (AA) and 102 kg N ha<sup>-1</sup> (SA). However, following autumn application more N was lost from the upper 60 cm of soil (potato rhizosphere) in the winter preceding the growing season.

The difference in tuber dry matter yield between AA and SA depended strongly on weather conditions. For the 30 years of simulations using historical weather data, the yield reduction in AA compared to SA for tuber dry matter at 490 kg

slurry N ha<sup>-1</sup> varied from nil (1964) to 77% (1980) (Fig. 7A). The smaller yield difference between AA and SA simulated for the 1964 growing season, was associated with a relatively small precipitation surplus in the preceeding winter (1 November–15 May), smaller N losses in the preceeding winter and, hence, little difference between the soil mineral N content at emergence between AA and SA (Fig. 7C).

The relative tuber yield response for the early cultivar Junior to spring-applied slurry N varied from year to year (Fig. 8A; Table 7). Without slurry, tuber yield ranged from 57% (1983) to 83% (1981) of the yield at 490 kg slurry N ha<sup>-1</sup>. These differences in relative tuber yield could not be explained by differences in N release from soil organic matter during the growing season. This release was 83 kg N ha<sup>-1</sup> in 1983 and 96 kg N ha<sup>-1</sup> in 1981 whereas tuber N uptake was 77 kg N ha<sup>-1</sup> in 1983 and 103 kg N ha<sup>-1</sup> in 1981. The tuber yield differences between those two years were mainly caused by differences in early LAI expansion (see below). The simulated harvest index at maturity did not vary with N, and neither did the proportion of N in the tubers (see above). Tuber yield differences between years were associated with differences in the maximum LAI obtained in that year (Fig. 8B). In 1983, uptake of N during the first 30 days after emergence was about half that in 1981, and the relative N shortage in 1983 was larger (NNI of 0.2) than in 1981 (NNI of 0.4), which after 30 days led to an LAI of 1.2 in 1983 and 2.2 in 1981.

Recovery of slurry N in tubers for the SA and AA treatments were both constant up to a slurry N application of about 250 kg N ha<sup>-1</sup>, and declined thereafter in the SA treatment (Fig. 6A). Up to 250 kg slurry N ha<sup>-1</sup>, N recovery in the SA treatment (49%) was much larger than in the AA treatment (12%). This is in agreement with observations reported by e.g. Schröder et al. (1993; 1997), despite the use of cover crops. The use of a cover crop did not result in a full transfer of the N applied in autumn to the following growing season, for two reasons. Firstly, the uptake capacity of cover crops (1 September to 1 November) was limited in our study to 80 kg N ha<sup>-1</sup> (0–0.6 m), whereas a total amount of mineral N up to 0.6 m depth at 1 November as a result of the soil N dynamics was 344 kg N ha<sup>-1</sup> when 490 kg slurry N ha<sup>-1</sup> was applied. Secondly, N mineralisation from cover crops is not fully synchronized with N uptake dynamics of potato. Variation in tuber yield differences between AA and SA with years, may explain why Wadman et al. (1989) found only small differences in tuber yield between autumn and spring-applied slurry. The results suggest that a spring application of slurry should be preferred over an autumn application, if this can be realised without damaging the soil structure.

The prediction that years with relatively strong yield responses to cattle slurry N, also had relatively small maximum LAI (Fig. 8) confirmed experimental findings that N limitation to crop growth affects the maximum LAI (Chapter 2). The sensitivity of LAI to N shortage are well documented (Belanger et al., 1992; Booiij et al., 1996; Grindlay, 1997). Model predictions as analysed during specific years also

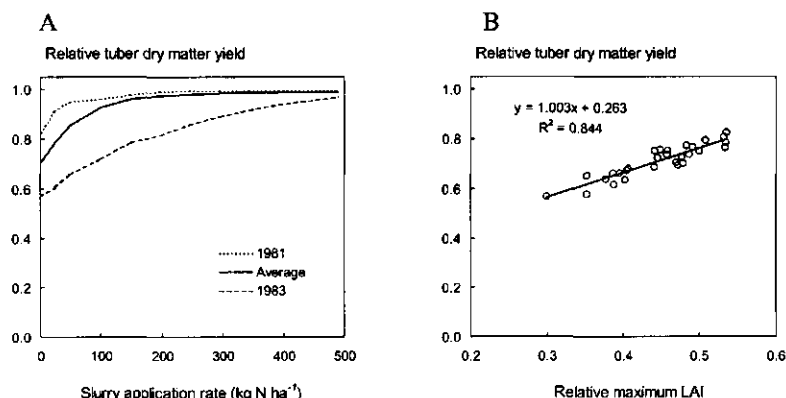


Figure 8. (A) Relationship between slurry application rate and relative tuber dry matter yield for the two most extreme growing seasons. Relative yield at 490 kg slurry N ha<sup>-1</sup> was set at 100%. (B) relationship between simulated relative tuber yield and simulated relative maximum LAI, with no applied slurry using 30 individual years of historical weather data (spring-applied slurry, early cultivar).

suggest that nearly two-fold differences in LAI were already established during the first 30 days of growth due to early N shortages, confirming previous findings in Chapter 2. A study on cereal growth in Norway under organic N management also reported poor early crop growth, which was suggested to be due to early N shortage (Eltun, 1996). Findings of the present study and of Eltun (1996) suggest that early growth and crop yields in organic N management could be improved by applying organic N that contains a large proportion of mineral N (e.g. urine) shortly after emergence. The occurrence of early N limitations as found in the present study, underline the importance of the inclusion of a direct effect of N on simulation of LAI expansion.

#### *Effect of cultivar maturity*

Using a mid-late (LL) rather than an early cultivar (EL) at the standard harvest date of 1 September, increased the simulated crop N uptake and tuber dry matter yield at the whole range of applied slurry N (Fig. 9B). Difference in crop N uptake between LL and EL was 14 kg N ha<sup>-1</sup> at no N input, and increased up to 97 kg N ha<sup>-1</sup> at 490 kg slurry N ha<sup>-1</sup> (Fig. 9A; Table 7). The corresponding difference in tuber dry matter yield amounted to 3.6 Mg ha<sup>-1</sup> at no N input and 3.9 Mg ha<sup>-1</sup> at 490 kg slurry N ha<sup>-1</sup>. The apparent recovery of slurry N in the tuber was larger in LL than in EL, being 46% and 27% respectively at 490 kg slurry N ha<sup>-1</sup>. The larger N recovery in LL resulted in a smaller residual mineral soil N content at harvest in LL than in EL when more than 300 kg slurry N ha<sup>-1</sup> was applied (Fig. 9B).

Table 7. Simulated mean and standard deviation (between brackets) of total N uptake, tuber yield (dry matter) and residual mineral N (0–0.6m) at harvest for eight scenarios (see Table 2), at three rates of slurry N. Means and standard deviations were calculated from simulations with 30 separate years of historical weather from De Bilt, The Netherlands.

Scenario	Total N uptake kg N ha <sup>-1</sup>	Tuber yield Mg ha <sup>-1</sup>	Residual mineral N kg N ha <sup>-1</sup>
<i>No slurry N</i>			
Spring application	93.5 (6.7)	8.0 (1.1)	16.9 (1.7)
Autumn application	95.5 (11.4)	7.8 (1.2)	20.5 (4.2)
Mid-late cultivar, late harvest	107.1 (6.2)	11.6 (1.2)	10.6 (2.3)
Early cultivar, early harvest	83.8 (5.7)	7.0 (0.9)	11.0 (1.6)
Late cultivar, early harvest	81.6 (5.5)	7.5 (0.9)	10.5 (1.4)
Low N/P <sub>2</sub> O <sub>5</sub> ratio	86.8 (6.2)	7.7 (1.1)	15.2 (1.6)
Large past N inputs	82.7 (6.0)	7.5 (1.0)	14.2 (1.6)
Small past N inputs	103.9 (7.4)	8.4 (1.2)	19.7 (1.8)
<i>Slurry N at the average rate over rotation</i>			
Spring application	169 (14)	10.7 (1.2)	24.5 (4.0)
Autumn application	117 (18)	8.7 (1.3)	27.1 (7.8)
Mid-late cultivar, late harvest	185 (13)	14.4 (0.9)	12.9 (4.5)
Early cultivar, early harvest	157 (14)	9.1 (0.9)	13.9 (4.4)
Late cultivar, early harvest	155 (13)	8.7 (0.7)	13.4 (4.3)
Low N/P <sub>2</sub> O <sub>5</sub> ratio	139 (11)	10.2 (1.3)	20.7 (3.0)
Poor past N application	158 (13)	10.6 (1.2)	21.5 (3.8)
Rich past N application	180 (14)	10.8 (1.1)	27.5 (4.1)
<i>490 kg slurry N</i>			
Spring application	301 (23)	11.2 (1.0)	102.1 (22.6)
Autumn application	161 (37)	10.0 (1.3)	42.8 (18.1)
Mid-late cultivar, late harvest	389 (35)	15.1 (0.8)	25.6 (12.7)
Early cultivar, early harvest	298 (24)	9.4 (0.7)	77.3 (22.6)
Late cultivar, early harvest	340 (34)	8.7 (0.6)	29.9 (12.0)
Low N/P <sub>2</sub> O <sub>5</sub> ratio	303 (20)	11.2 (1.0)	121.7 (27.3)
Poor past N application	300 (24)	11.2 (1.0)	89.7 (20.6)
Rich past N application	302 (21)	11.2 (1.0)	114.4 (24.5)

Advancement of the harvest date from 1 September to 1 August, lowered the simulated crop N uptake and tuber yield of the mid-late cultivar to a larger extent than that of the early cultivar (compare Fig. 9A–D). On 1 August, crop N uptake was larger for mid-late cultivar than for the early one (Fig. 9C). In contrast, tuber N uptake was slightly smaller for the mid-late than for the early cultivar (Fig. 9C), because a

smaller proportion of total N was transferred to the tubers. On 1 August, the mid-late cultivar tuber yield was smaller than that of the early one at applications of 75 kg slurry N ha<sup>-1</sup>, but was larger at smaller slurry N applications (Fig. 9D). Tuber yield of the mid-late cultivar was generally smaller, because by 1 August, a smaller proportion of total dry matter was partitioned to the tubers. At very low rates of applied slurry N, tuber yield was slightly greater for a mid-late cultivar than for an early one, because of changes in partitioning as explained below. When N is limiting, an increased proportion of crop dry matter is partitioned to tubers (see Section Model description). At small rates of N, N was more limiting to the mid-late cultivar than to the early one (already discussed in Section Sensitivity analysis), because the mid-late cultivar had a greater proportion of leaf material than the early cultivar when compared at 1 August. The stronger N-limitation in the mid-late cultivar than in early one, resulted in an overall increased partitioning of dry matter to the tubers at the premature harvest date, that its tuber yield was larger than of the early cultivar. The larger total N uptake of the mid-late cultivar, resulted in a smaller residual soil N content at 1 August with the mid-late cultivar than with the early cultivar, especially at rates above 300 kg slurry N ha<sup>-1</sup> (Fig. 9D).

In current organic farming, the occurrence of *Phytophthora infestans* may result in a premature crop harvest. At premature crop harvests, the tuber yield of a mid-late cultivar may be smaller than that of an early one (Fig. 9), and its tuber quality may be reduced because of a small dry matter content. The growth of a (mid-)late potato cultivar in organic farming therefore requires development of plant protection measures to reduce the risk of late blight.

#### *Effect of N/P<sub>2</sub>O<sub>5</sub> ratio of manure*

The average rates of applied slurry over the rotation were calculated to result in an increase in N of 9 kg N ha<sup>-1</sup> (N/P<sub>2</sub>O<sub>5</sub>=1.7) and 25 kg N ha<sup>-1</sup> (N/P<sub>2</sub>O<sub>5</sub>=2.7) released from soil organic matter (Table 3). That is only a small increase relative to the 120 kg N ha<sup>-1</sup> released by soil organic matter in a rotation in which no manure was applied (see Materials and methods). Decreasing the N/P<sub>2</sub>O<sub>5</sub> ratio of the slurry from 2.7 to 1.7 only resulted in a small reduction in crop N uptake (7 kg N ha<sup>-1</sup>) and in tuber dry matter yield (3.7%) when no slurry N was applied to the potato (Table 7). The response of crop yield to slurry N hardly changed with decreasing the N/P<sub>2</sub>O<sub>5</sub> ratio (not shown).

Nonetheless, the total amount of slurry N that can be applied at a potato field is reduced, because, averaged over the rotation 40 kg N ha<sup>-1</sup> less is available. When tuber yields are compared at the average rate of slurry N over the rotation, yields were reduced from 10.7 to 10.2 Mg ha<sup>-1</sup> when the N/P<sub>2</sub>O<sub>5</sub> ratio decreased 2.7 to 1.7 (Table 7). Although dry weight differences in tuber yield appear to be small, such a yield reduction of 5% may be important in terms of financial income.

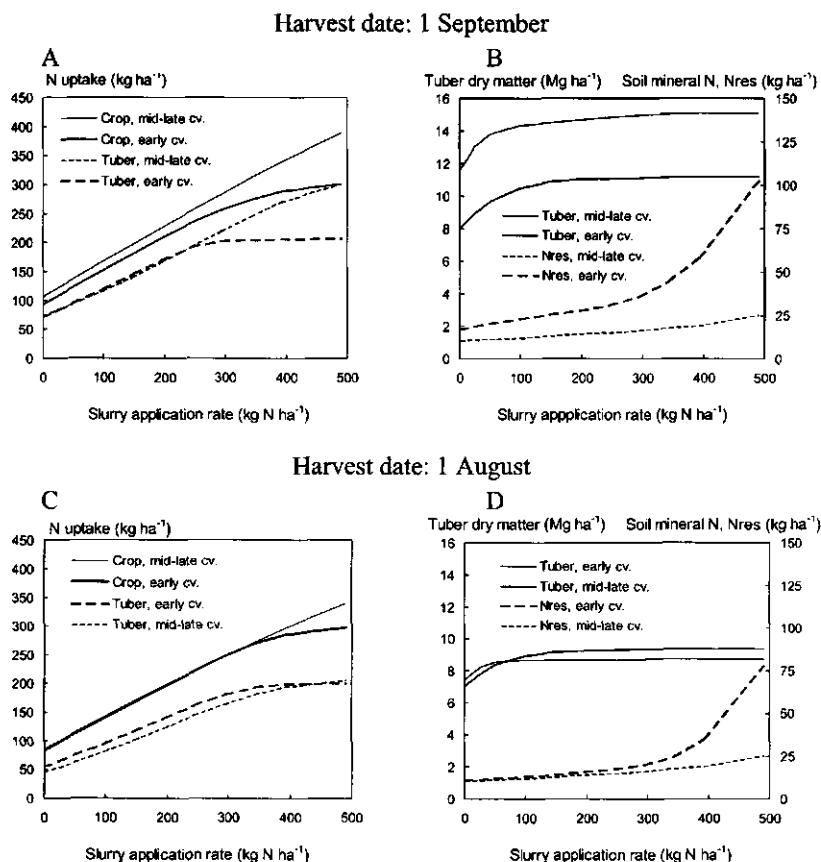


Figure 9. Relationship between slurry application rate and (A, C) simulated N uptake in the crop (roots excluded) and in tubers only, (B, D) simulated tuber dry matter yield and residual soil mineral N content at harvest (0–0.6m), as affected by maturity class of the cultivar at two harvest dates (spring-applied slurry, averaged over 30 years of historic weather).

### Effect of past N management

The simulated response of total and tuber N uptake to past N fertiliser use for early cultivar Junior with a spring-applied slurry is shown in Fig. 10A. Differences in total N uptake between PP (poor past, see Section Scenario studies), EQ and RP were largest when no slurry was applied, and decreased to zero at 490  $\text{kg slurry N ha}^{-1}$ . Total crop N uptake increased with past N fertilisation from 83  $\text{kg N ha}^{-1}$  (PP) to 104  $\text{kg N ha}^{-1}$  (RP) when no slurry was applied (Fig. 10A; Table 7). The yearly N mineralisation from soil organic matter increased by 48  $\text{kg N ha}^{-1}$  with past N fertilisation (from PP to RP), of which about 29  $\text{kg N ha}^{-1}$  was released during the growing season. Thus it appears that 72% of the additionally released soil N was

recovered in the crop (exclusive roots) when no slurry was applied. When no slurry was applied, the simulated tuber dry matter yield increased from PP to EQ by  $0.5 \text{ Mg ha}^{-1}$  (6.6%), and from EQ to RP by  $0.4 \text{ Mg ha}^{-1}$  (5.0%) (Fig. 10B; Table 7). Differences in tuber yield with past N fertilisation were negligible with applications above  $200 \text{ kg slurry N ha}^{-1}$ . Contrastingly, differences between PP, EQ and RP in residual soil N content at crop harvest increased with applications above  $200 \text{ kg slurry N ha}^{-1}$  (Fig. 10B), because not all of the additional N was recovered in the crop (Fig. 10A).

The predicted yield increase of 5% from PP to EQ, represents the expected yield increase which results from the *additional* soil N release of  $24 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  due to long-term application of  $128 \text{ kg slurry N ha}^{-1}$ . This situation represents organic farms that have been recently converted from conventional farms on which excessive amounts of N were not used. To mimic RP, we decided to increase the soil N release by another  $24 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ . Of course, differences in tuber yields between EQ and RP will likely be larger than calculated in the present study, when the difference in past N fertilisation is larger. For example, Motavalli et al. (1992) found a yield increase of 66% in experiments when past long-term N fertilisation rates increased from  $12 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  to  $224 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ .

### ***Implications for organic nitrogen management***

Mean values and variability for tuber dry matter yield, crop N uptake, and residual soil mineral N content at crop harvest simulated for the eight scenarios over 30 years of weather data are summarised in Table 7. Tuber yields for a potato crop receiving no slurry, could be as low as 66% of yields with spring-applied slurry at a rate of  $490 \text{ kg slurry N ha}^{-1}$  (Table 7). The influence of weather, however, was considerable: with a coefficient of variation for crop N uptake of 8.8%, for tuber yield of 11%, and for residual soil N content at harvest of 23.0%, averaged across scenarios and the three N inputs (Table 7). Consequently, the effect of a scenario varied from year to year (Figs. 7 and 8). For a specific year, tuber yields in potato receiving no slurry could be as low as 57% of maximum yields and close to the maximum at only  $110 \text{ kg slurry N ha}^{-1}$  (Fig. 8). This illustrates that N management can at least partly explain the yield differences (0–50%) found between organic and conventionally grown potatoes (see Introduction). Möller et al. (1998) also found tuber yields in organic farming, to be N limited, even with early occurrence of potato late blight. In the N-limited fields, only up to  $40 \text{ kg farmyard N ha}^{-1}$  was used. Thus N management should be optimised to improve tuber yields, as discussed below.

Two instruments were found to be especially useful to match soil N supply with crop N demand: timing of N application and cultivar maturity. Postponement of the application of slurry from autumn to spring increased N uptake and tuber yield (Table 7), and decreased over-winter losses of N. Soil mineral N at harvest, however, was larger. A spring application of N should therefore be preferred over an autumn



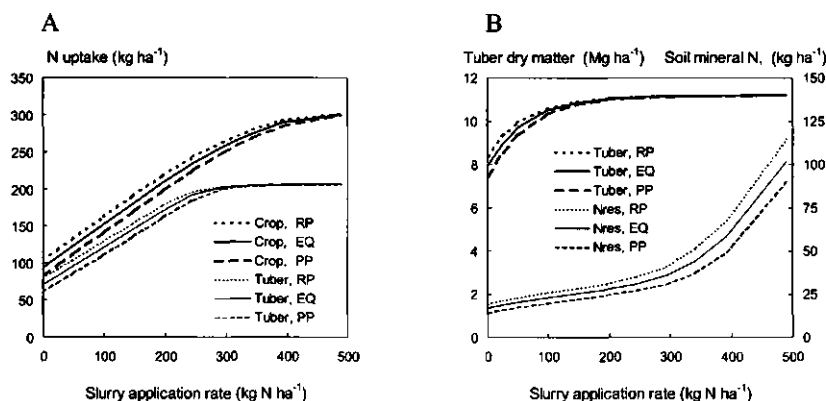


Figure 10. Relationship between slurry application rate and (A) simulated N uptake in the crop (roots excluded) and in tubers only, (B) simulated tuber dry matter yield and residual soil mineral N content at harvest (0–0.6m), as affected by past N inputs [large past N inputs (RP, small past N inputs PP, same inputs applied on long-term basis, EQ) (spring-applied slurry, averaged over 30 years of historic weather).

application, even when the latter is combined with a cover crop. Results in Figs. 7C and 8 further suggest that potato yields were N limited from emergence onwards in years with a small mineral soil N content (0–0.6m) in spring. Crop N uptake might therefore be further increased by a basic N dressing in the ridges, using a form of organic N containing a large proportion of mineral N, e.g. urine. The rate of N required for such a basic dressing may be derived from experiments and simulation models to calculate the effect of N placement on potato N uptake (e.g. De Vos and Heinen, 1999). However, the use of spring-applied slurry requires special equipment to avoid damage to the soil structure on heavily textured soils.

Timing and placement of N are expected to be especially effective for potatoes as they have a poor N recovery compared to other arable crops such as sugar beet and cereals (Neeteson, 1995). Roots of cereals penetrate the soil faster than those of potato (A.L. Smit and J. Groenwold, Plant Research International unpublished) they have larger root length densities and grow deeper than potato (Vos and Groenwold, 1986). Cereals are, therefore, expected to be less sensitive to early N limitations than potato. Hence, cereals may be less responsive to the postponement of a slurry application from autumn to spring.

The use of a later-maturing potato cultivar is another effective instrument to improve tuber yields, crop N uptake and in reducing residual soil N content at harvest (Table 7). The tuber yields, however, are only improved when premature harvests, e.g. due to potato late blight, can be prevented.

Reduction of the  $N/P_2O_5$  ratio of the slurry from 2.7 to 1.7 decreased the average rate of supplied N over the rotation by one-third. Selection of a slurry type with an  $N/P_2O_5$  ratio below 1.7 would decrease it even further, and would clearly limit the tuber yield (Fig. 6B). To avoid those N limitations, leguminous crops would be needed in the rotation, but they are currently unattractive in terms of financial returns. The choice in the present study to use a slurry type of manure rather than a farmyard manure, resulted in a large amount of available N to the crops. Some organic farmers, however, prefer the use of farmyard manure, but crop growth is then expected to be even more limited by N, as it contains less mineral N per unit of P (Beijer et al., 1996).

The variation in crop N uptake, tuber yield, and residual soil mineral N at harvest with past N fertilisation, as found in the present study was not greater than the year-to-year variation (Table 7), suggesting that a sufficient number of experimental years are needed to quantify effects of long-term applications of manure.

## Appendix 1

$$\text{LUE} = \frac{\gamma \cdot \alpha}{1 + \frac{\alpha \cdot k \cdot I_0}{P_{\max} \cdot \delta}}, \quad (1)$$

where

$k$  = extinction coefficient for light ( $\text{m}^2 \text{m}^{-2}$ ), 0.72

$I_0$  = incoming PAR ( $\text{MJ m}^{-2} \text{d}^{-1}$ ),

$\gamma$  = efficiency of conversion of gross assimilated  $\text{CO}_2$  into biomass ( $\text{g dm g}^{-1} \text{CO}_2$ ), 0.34

$\alpha$  = the leaf quantum yield ( $\text{g CO}_2 \text{ MJ}^{-1}$ ), 12.5

$\delta$  = photoperiod duration ( $\text{d d}^{-1}$ ), and

$P_{\max}$  = photosynthesis rate of upper leaves at light saturation ( $\text{g CO}_2 \text{ m}^{-2} \text{d}^{-1}$ ).

Marshall + 10% (1966)

$$P_{\max} = 200 \text{ g CO}_2 \text{ m}^{-2} \text{d}^{-1} \rightarrow 200 \text{ g m}^{-2} \text{d}^{-1}$$

$$0.34 \text{ g dm g}^{-1} \cdot 12.5 \text{ g CO}_2 \text{ MJ}^{-1}$$

$$1 + \frac{12.5 \text{ g CO}_2 \text{ MJ}^{-1} \cdot 0.72 \text{ m}^2 \text{m}^{-2}}{0.24/1000 \cdot 3600 \cdot 24 \text{ g CO}_2 \text{ m}^{-2} \text{d}^{-1}}$$

$$0.24/1000 \cdot 3600 \cdot 24 \text{ g CO}_2 \text{ m}^{-2} \text{d}^{-1}$$

**The influence of nitrogen supply on the  
ability of wheat and potato to suppress  
*Stellaria media* growth and reproduction  
in organic farming systems**

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## Abstract

Quantitative insight into the effect of nitrogen supply on weed growth and reproduction facilitates effective weed management in organic farming. We tested the hypothesis that increased soil nitrogen supply reduces the growth of late emerging weeds in wheat and potato by enhancing canopy leaf area development and thereby reducing the availability of light for weed growth. From 1997 to 1999, two series of experiments were conducted: one in spring wheat with *Stellaria media* (L.) Vill. sown at stem extension, and one in potato with naturally emerged weeds, including *S. media*. Each crop was grown during two separate years at three levels of nitrogen supply with two cultivars per crop. In wheat, the total dry weight and seed dry weight, and seed number per cluster (4–6 plants per cluster) of *S. media* increased with soil nitrogen supply. Increased soil nitrogen supply increased the nitrogen uptake of *S. media*, despite the reduced light availability to this weed; it was concluded that the growth of *S. media* in wheat was limited by nitrogen. Contrary to wheat, in potato the total dry weight and number of seed capsules per plant of *S. media* decreased with increased soil nitrogen supply. In potato, the growth of *S. media* was limited by light at the soil surface which decreased with increased soil nitrogen supply. In the early potato cultivar Junior, the biomass of *S. media* was larger than in mid-late cultivar Agria at the same soil nitrogen supply. Reproduction of *S. media* in the potato crop (estimated as up to 1400 seeds per plant) was much greater than in wheat (up to 8 seeds per cluster, with about 6 plants per cluster). The densities of reproductive weeds in potato, including *S. media*, decreased with increased soil nitrogen supply. We conclude that the differences between wheat and potato in the influence of soil nitrogen supply on growth and reproduction of *S. media* are attributable to higher soil nitrogen levels in the potato crop, and that differences between potato cultivars were caused by soil nitrogen levels in Junior than in Agria at the same radiation levels under the canopy.

## Introduction

The certification standards of most countries prohibit the use of synthetic fertilisers or pesticides in organic farming. Consequently, nitrogen management in organic farming is not only a question of optimising crop yield and minimising nitrogen losses (Haraldsen et al., 2000; Pang and Letey, 2000), but also of considering the effects of the nitrogen strategy on the occurrence of pests, diseases and weeds. The impact on weed management requires particular attention, because the many hours of hand-weeding needed in organic farming systems (Peacock and Norton, 1990; Vereijken, 1998; Lotz et al., 2000a) mean that weeds are a major labour constraint. Weed growth and weed densities in crops are known to respond to soil nitrogen supply (e.g. Jørnsgård et al. (1996). Moreover, the composition of weed species on organic farms

in Sweden has been found to differ from that on conventional farms, and tended to be less nitrophilous (Rydberg and Milberg, 2000).

To optimise weed management at the farm level, there is a need for long-term management of weed populations rather than a short-term approach looking at single-season economic thresholds (Wallinga and Van Oijen, 1997; Jones and Medd, 2000). The latter approach fails to consider the seed set of uncontrolled weeds (Wallinga and Van Oijen, 1997), whereas seed densities in the soil have to be low in order to reduce management costs when herbicides are not used (Kropff et al., 1996). In a survey in The Netherlands, many reproducing weeds were found in potato and wheat crops (Vereijken, 1998). Chickweed, *Stellaria media* (L.) Vill. was the main weed with densities up to 8 plants per m<sup>-2</sup>. The large number of hours of hand-weeding needed to control this weed in subsequent crops (Vereijken, 1998) could be reduced if the seed setting of *S. media* could be reduced.

*S. media* is a cosmopolitan species, common in cereal and broad-leaved arable crops (Lotz et al., 2000a; Lutman et al., 2000; Rydberg and Milberg 2000). It emerges throughout the year (Sobey, 1981), with time of emergence being closely associated with time of soil cultivation (Tørresen, 1998). When potato and wheat crops are grown organically, weeds are mechanically controlled mainly in the early part of the growing season, because both crops rapidly cover the soil and when the soil is completely covered their canopies shade out weeds (Altieri, 1995; Vereijken, 1998, Liebman and Davis, 2000). The weeding techniques for wheat and potato differ: in wheat, control is mostly done by hoeing and/or harrowing up to stem extension, whereas in potato weed control is mostly done by earthing up the ridge several times until canopy closure. As mechanical control in potato and wheat can kill up to 80% of *S. media* plants (Darwinkel et al., 1993; Hoffmann, 1994), it seems likely that the uncontrolled late-emerging *S. media* plants contribute significantly to the seed bank.

It can be assumed that the effect of increased soil nitrogen supply on growth and reproduction of late-emerging weeds largely depends on competition for light and nitrogen between crop and weeds. Increased nitrogen supply enhances the leaf area development of potato and wheat (Chapter 2), thus reducing light levels at the soil at the time of establishment of late-emerging weeds. Competition for light has been shown to be asymmetrical, i.e. larger plants are able to obtain a share of the resources that is disproportionate to their relative size and to suppress the growth of smaller individuals (Weiner et al., 1997). Crop plants that are large when the weeds emerge are better able to suppress the weeds by shading them out. There is evidence that below-ground competition is more symmetrical, i.e. if the resources are distributed homogeneously, initial differences in size between crop and weed plants will not be magnified (Weiner et al., 1997). Competition for nutrients is then determined by the relative size of the root system, which in the case of late-emerging weeds will be larger for the crop. Our hypothesis was, therefore, that increased soil nitrogen supply reduces the growth of late-emerging weeds in wheat and potato, as a result of a larger leaf area index and light interception by the crop. As seed number and dry weight of

weeds are often linearly related to vegetative biomass (Thompson et al., 1991), we also expected increased nitrogen supply to reduce the reproductive effort of *S. media*.

The objectives of the study were: 1) to determine the influence of nitrogen application rate in wheat and potato on crop performance, particular light interception and yield, and soil N content, 2) to use this information to analyse the relationship between nitrogen application rate and growth and seed production of *S. media* in these two crops, and 3) to determine the effect of soil nitrogen supply on the establishment of *S. media* and other weeds.

## Materials and methods

Two series of field experiments were conducted on the experimental farm Lovinkhoeve, at Marknesse (52°42'N 5°53'E), The Netherlands: one in spring wheat with detailed measurements on *S. media* growth, and one in potato, for which weed data obtained near final harvest. Wheat was grown in 1997 and 1999 and potato in 1997 and 1998. Each crop was grown at three levels of soil nitrogen supply, with two cultivars. In spring wheat, weeds were controlled by harrowing and hoeing until mid-stem extension, when the height of the crop was about 0.5 m. At that time, pre-germinated seeds of *S. media* were sown in the spring wheat crop and in adjacent monoculture plots at 0.60 m distance within each row, resulting in an average density of 5.6 groups of seeds per m<sup>2</sup>. The dry weight of *S. media* was determined by periodic sampling until wheat maturity. At wheat maturity the total dry weight, seed weight and seed number of *S. media* were determined. In the potato experiment, weeds were controlled once, by earthing up the ridge when the potato crop emerged. At the end of the growing season, the number of reproductive weeds (i.e. weeds bearing flowers and/or seeds) were counted once. In 1997, a sample was also taken to determine total dry weight and number of seed capsules per *S. media* plant. In both wheat and potato, light interception by the crop was determined once or twice a week, and soil mineral nitrogen content was determined once every two to three weeks.

### *Soil type, crop husbandry, treatments and design in wheat and potato*

The experiments were done on a silty loam soil, with 30% < 16  $\mu$ , 10% CaCO<sub>3</sub>, 2.3% organic matter (sampling October 1995) and a pH-KCl of 7.4 (sampling October 1995; and December 1998). The soil phosphorus and potassium contents (Table 1) met the criteria set by Van Dijk (1999) to enable unrestricted growth of potato and wheat. Water was not considered to limit crop growth, because at all soil samplings (about once a month, see Fig. 3), the pF value throughout the rhizosphere was below 2.85 for potato and below 3.0 for wheat.

Table 1. Description of the experimental farm Lovinkhoeve and experimental methods for spring wheat, potato and *S. media* in the wheat experiment, with *S. media* grown under two wheat cultivars (mix) and in monoculture (mono).

	Spring wheat	<i>S. media</i> in wheat	Potato
Year	1997		1997
Planting/sowing date	14 April, 1997	16 June, 1997	18 April, 1997
Previous crop	Fodder beet		Winter wheat
Green manure crop	—		Mustard
Sampling date $P_w$ , K-HCl <sup>a</sup>	24 Sep, 1998		30 March, 1998
$P_w$ (mg $P_2O_5$ l <sup>-1</sup> H <sub>2</sub> O)	30		44
K-HCl (mg $K_2O$ 100 g dm <sup>-1</sup> )	21		27
Plant density (pl m <sup>-2</sup> )	260	5.7	4.44
Row spacing (m)	0.3	0.3 x 0.6	0.75
Gross plot size (m <sup>2</sup> )	6	6	19.8
Net plot size (m <sup>2</sup> )	1.05	20 (mix) 10 (mono) clusters <sup>b</sup>	9.45
Cultivars	Baldus, Axona		Junior, Agria
Re-earthing potato ridge	—	—	26 May
Emergence date	27 April, 1997	23 June, 1997	01 June (Junior), 31 May (Agria)
Plant samplings dates	19 Aug	3, 11, 17, 23, 31 July, 19 Aug	8 Sept (Junior, Agria)
Weed counting potato			26 Aug
Year	1999		1998
Planting/sowing date	29 April, 1999	1 July, 1999	13 May, 1998
Previous crop	Carrots		Spring wheat
Green manure crop	—		Mustard
Sampling date $P_w$ , K-HCl <sup>a</sup>	Dec, 1998		24 Sep, 1998
$P_w$ (mg $P_2O_5$ l <sup>-1</sup> H <sub>2</sub> O)	27		30
K-HCl (mg $K_2O$ 100 g dm <sup>-1</sup> )	15		21
Plant density (pl m <sup>-2</sup> )	264 (Bal.), 293 (Ax.)	5.7	4.44
Row spacing (m)	0.3	0.3 x 0.6	0.75
Gross plot size (m <sup>2</sup> )	48	48	23.4
Net plot size (m <sup>2</sup> )	1.05	15 (mix) 19 (mono) clusters <sup>b</sup>	9.45
Cultivars	Baldus, Axona		Junior, Agria
Re-earthing potato ridge			19 May
Emergence date	5 May 1999	July 4, 1999	28 May (Junior) 30 May (Agria)
Plant sampling dates	24 Aug	13, 20, 27 July, 3, 17, 24 Aug	30 Aug (Junior), 24 Sept (Agria)
Date weed counts in potato			11 Aug

a,b  $P_w = P_{water}$ , explanation of  $P_{water}$  and K in Chapter 2, Table 1.  $P_{water} \geq 21$  and  $K \geq 15$  is sufficient for optimal crop growth of arable crops (Van Dijk, 1999) b For cluster see Figure 1.



The studies described here were not intended to investigate interactions between nitrogen supply and damage by pests and diseases. Pests and diseases on potato (notably late blight) and wheat were controlled using standard procedures used in regular arable farming in the area. Potato tubers were presprouted and planted by machine. In 1997, tubers were not disinfected and in 1998 they were disinfected with Solacol against *Rhizoctonia solani*.

For each year and crop, nitrogen was supplied at three levels (levels in kg N ha<sup>-1</sup> given in Table 2), N1: no fertilisation or only city compost, N2: cattle slurry applied at an intermediate fertilisation rate, based on nutrient management practices current in Dutch organic farming, and N3: about twice the rates of cattle slurry of N2, supplemented by artificial fertilisers according to recommended rates (Van Dijk, 1999) for potato and wheat based on soil analysis. Artificial nitrogen fertiliser was applied as calcium ammonium nitrate (Table 2). Supplementary rates of artificial fertiliser were corrected for expected net mineralisation from organic sources (values in Table 2) during the growing season, as explained in detail in Chapter 2. For each crop, two genotypes differing in leaf area dynamics were used: potato cultivars Junior (early) and Agria (mid-late) and wheat cultivars Axona (relatively small maximum leaf area index) and Baldus (larger maximum leaf area index). Each experiment was laid out as a split-plot design with three replicates, with nitrogen as main plots (blocks) and cultivar as subplots. In the spring wheat experiment, monocultures of *S. media* were randomly assigned to plots adjacent to one of the two subplots. Periodic samplings of *S. media* in the spring wheat experiment were randomised within each plot. Border plants were not sampled. The sowing, planting and sampling dates, sampling areas, plant densities and row distances for both experiments are given in Table 1.

Soil samples for inorganic N analysis (ammonium-N, and nitrate-N), and for volumetric soil water content were taken 3–5 times (see Fig. 2) using a 30 mm diameter probe, and combining four cores per plot and the three replicates per treatment. Samples were taken at depths of 0–0.3 m in the wheat experiment and 0–0.3 and 0.3–0.6 m in the potato experiment, and for crop fertilisation also at 0.6–0.9 m depth. Exchangeable NH<sub>4</sub><sup>+</sup>-N, and NO<sub>3</sub><sup>-</sup>-N were determined in 1M KCL, using a continuous flow analyser (TRAACS 800, Bran and Luebbe). Because the replicates were pooled during soil sampling, treatment differences in inorganic soil nitrogen and in volumetric soil moisture content could not be tested statistically.

### **Spring wheat experiment**

The yield and total nitrogen uptake of spring wheat were determined at crop maturity. Nitrogen concentration (nitrate + organic nitrogen) in dry matter was determined using the Dumas-method (Macro N, Foss Heraeus Analysensysteme, Hanau, Germany). During crop growth, interception of photosynthetically active radiation (PAR) by the

Table 2. Mineral soil nitrogen content (depth: 0–0.9 m) near sowing of wheat and planting of potato, dates of nitrogen application and their rates, actual nitrogen content in cattle slurry, expected net mineralisation from organic nitrogen during the growing season, and total expected available nitrogen (total N) in 1997, 1998 and 1999 for wheat and potato. Total N is the sum of Nmin, expected net N mineralisation and mineral N fertiliser.

Crop/ Year	Date manure/ Treat- ment	Date/ Nmin 0–0.9m	Application rate		Expected net N mineralisation			Date/ Rate mineral N fertiliser		Total N
			Com- post	Cattle slurry	Com- post	Cattle slurry	Previous crop	First date	Second date	
			kg N ha <sup>-1</sup>	Mg fresh matter ha <sup>-1</sup>				kg N ha <sup>-1</sup>		
Wheat	10-Apr 1997	21-Apr 1997					Sugar beet		05-Jun 1997	
1997	N1	79	0	0	0	0	30 <sup>a</sup>	0	0	109
	N2	101	0	15	0	5	30	0	0	136
	N3	94	0	30	0	11	30	0	75	210
Wheat	28-Apr 1999	19-May 1999					Winter carrot	19-May 1999	07-Jul 1999	
1999	N1	51	0	0	0	0	36 <sup>b</sup>	0	0	87
	N2	60	0	15	0	13	36	0	0	105
	N3	61	0	30	0	25	36	58	75	231
Potato	2-Sep- 1996	21-Apr 1997						26-May 1997		
1997	N1	61	10	0	12	0	0	0	0	72
	N2	101	0	40	0	28	0	0	0	129
	N3	148	0	80	0	55	0	110	75	314
Potato	30-Sep- 1997	18-May 1998						20-May 1998		
1998	N1	89	5	0	6	0	0	0	0	94
	N2	121	5	45	6	43	0	0	0	170
	N3	127	5	80	6	77	0	120	0	330

a Van Dijk (1999).

b The carrot crop was ploughed into the soil, because the crop had been damaged by frost before harvest. N delivery was estimated using an estimated 60 Mg ha<sup>-1</sup> tuber fresh matter yield, using 10% dm, 15 kg N Mg<sup>-1</sup> dm (Smit and Van der Werf, 1992), and 40% of N available for next crop. It is assumed that leaves had decomposed by May (frost in autumn).

canopy was measured once or twice a week with a portable line sensor (TFDL, Wageningen, The Netherlands). Recordings were taken within one hour of solar noon. There were at least 10 sets of measurements of PAR above and below the canopy, taken in rapid succession while moving the sensor across the experimental plot. The average intercepted PAR based on all measurements within a plot was used for further calculations. Global radiation data were obtained from a weather station on the farm; the PAR was taken as half of global radiation.

The seeds of *S. media* that were sown in spring wheat in 1997 had been collected from plants on 'Droevendaal' experimental farm near Wageningen in 1991, whereas the seeds that were sown in spring wheat in 1999 had been collected from plants on the experimental farm 'Lovinkhoeve' in 1997. They had been pre-germinated in 2% water agar with 0.1% KNO<sub>3</sub> (Kempenaar and Schnieders, 1995) in a growth chamber with 14 hours light per day at temperatures of 15°C in dark and 25 °C in light, to promote germination (Sobey, 1981). The seed spacing was 0.6 m (within wheat rows) by 0.3 m (wheat row distance) (Fig. 1), resulting in a density of 5.6 seed clusters (patches) per m<sup>2</sup>, corresponding with natural *S. media* densities found on organic farms in the region (P.H. Vereijken, Plant Research Int., pers. comm.). We defined a cluster as the groups of plants that were sown together at a single sowing station (4 mm in diameter)(see Fig. 1).

The dry weight of *S. media* was determined once every ten days (on average) until wheat reached maturity. At each sampling, *S. media* was collected from two wheat rows, using 10–20 clusters. At wheat maturity, total dry weight, dry weight of seeds per plant and seed weight were measured. Plant organs were dried at 80°C for two days. Plant nitrogen content was determined at final harvest, using the Dumas method (Macro N, Foss Heraeus Analysensysteme, Hanau, Germany). Results were presented 'per cluster' rather than 'per plant,' as intra-specific competition within a cluster was expected to be high. Final percentages of clusters with one or more emerged plants, and number of emerged plants per cluster were determined 24 days after emergence of *S. media*.

### **Potato experiment**

Tuber fresh yield and tuber nitrogen uptake of potato were determined at crop maturity, as described previously in Chapter 2. Total nitrogen uptake at maturity could not be determined, as, by then, the stems were rotting. Near potato maturity the weeds were counted in rectangles placed randomly in each plot; three rectangles (0.5 x 0.75 m) per plot were used in 1997 and two rectangles (1.0 x 0.75 m) per plot in 1998. Mean plot counts were used for further calculations. In 1997, three *S. media* plants per plot were taken to determine their dry weight, and their seed capsules were counted.

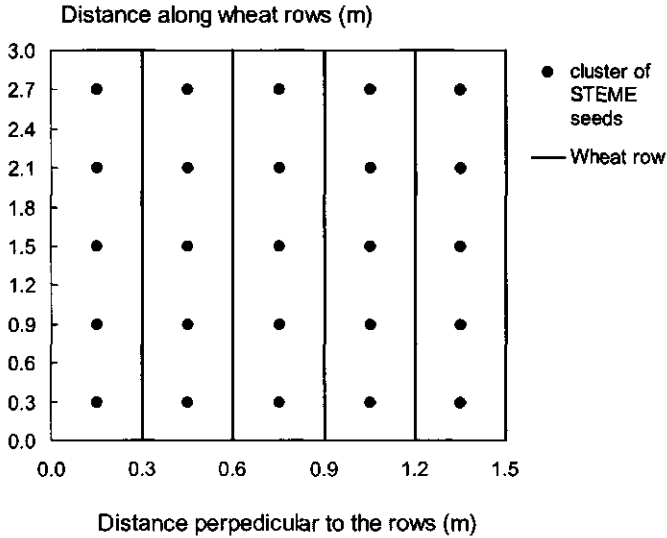


Figure 1. Illustration of the sowing pattern of *S. media* in the wheat canopy. Each dot is a cluster of about 10 sown seeds, which resulted in 4–6 emerged plants.

### Statistical analysis

All statistical analyses were done using Genstat (Genstat 5 Committee, 1993). Treatment effects were analysed by analysis of variance. In accordance with the procedure of Paolini et al. (1999), the variation between years was also tested by analysis of variance, with year taken as the hierarchically highest main effect and the pooled residual variance being used as the estimate for within treatment variance. After analysis of treatment effects, differences between individual treatment means were tested by least significant difference (LSD). The LSD procedure was only used for a limited number of comparisons. Data for analysis of variance were transformed to obtain homogeneity of variances, except when the range in data values was small (Gomez and Gomez, 1982). The type of transformation used is reported in the relevant tables and was based on Gomez and Gomez (1982) and on inspection of residual patterns. In the tables, original data are presented, because the transformations did not affect their interpretation. Linear and non-linear regression analysis was applied to study relationships between variables. In regression analysis, residuals were weighted to obtain homogeneity of variances, with weighting factors derived from the transformations needed in analysis of variance. Unless stated otherwise, henceforth all effects mentioned in the results and discussion are statistically significant effects with a 5% significance level.

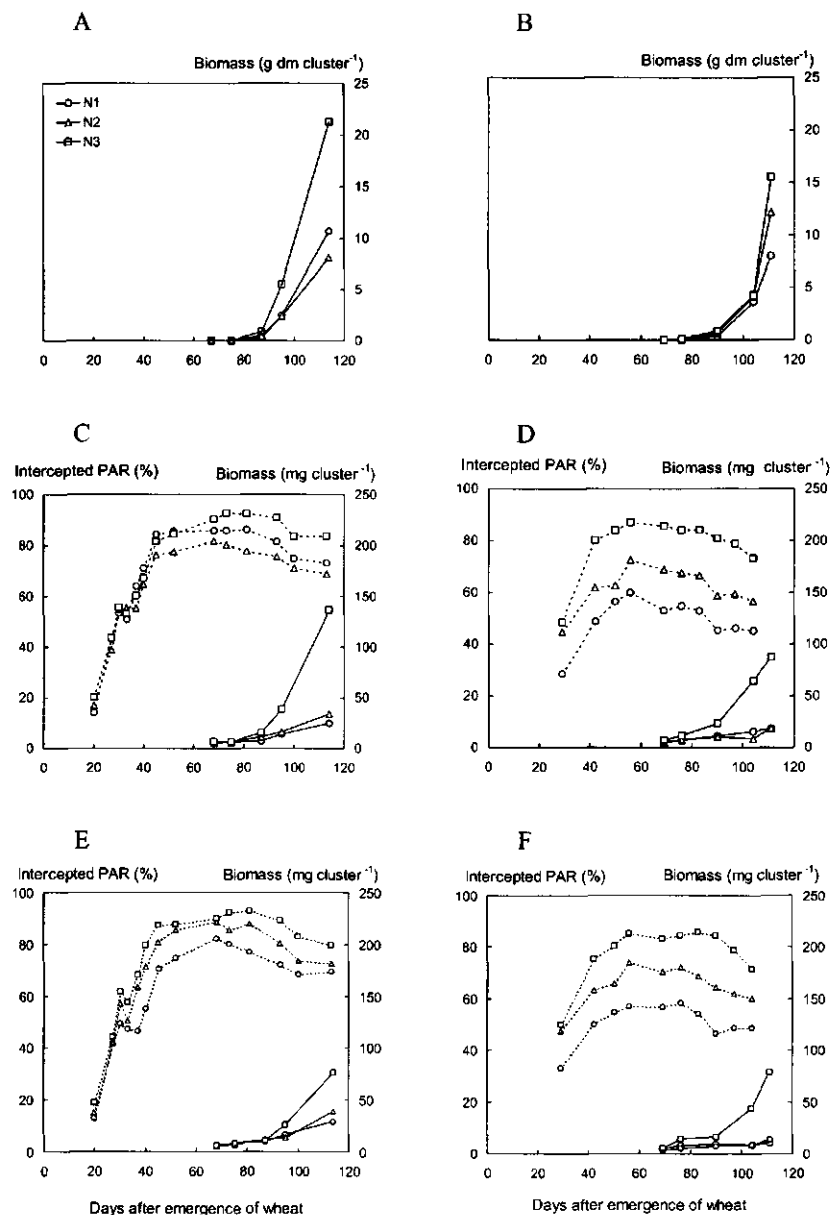


Figure 2. Solid line represents the dry weight (right abscissa) of *S. media* per cluster as a function of days after emergence of spring wheat, in monoculture of *S. media* (A, B) and in wheat cultivar Baldus (C, D), and Axona (E, F) in 1997 (A, C, E) and in 1999 (B, D, F) at three nitrogen levels. A cluster (see Fig. 1, and Materials and methods) contains 4–6 plants. Broken line represents the percentage of intercepted PAR (left abscissa) by the wheat canopy (C–F). Each point is the average of three replicates.

## Results

### *Wheat production, nitrogen uptake and light interception*

Averaged over years and cultivars, wheat biomass (in  $\text{Mg ha}^{-1}$ ) increased concomitantly with nitrogen supply from 9.15 in N1 to 10.2 in N2 and 13.2 in N3, the increase being larger for cultivar Axona than for Baldus (Table 3). Biomass was larger in 1997 than in 1999. Averaged over years and cultivars, grain yield (at 84% dm,  $\text{Mg ha}^{-1}$ ) increased with nitrogen supply, from 5.11 in N1, to 5.60 in N2 and 7.39 in N3, with a larger increase in 1999 than in 1997. Averaged over years and nitrogen supply, grain yield was larger for cultivar Baldus ( $6.22 \text{ Mg ha}^{-1}$ ) than for Axona ( $5.85 \text{ Mg ha}^{-1}$ ). Wheat nitrogen uptake ( $\text{kg ha}^{-1}$ ) increased with nitrogen supply from 107 in N1 and N2 to 184 in N3 (averaged over years and cultivars), was larger in 1997 than in 1999, but was not affected by cultivar.

In both years, intercepted PAR (%) by the wheat canopy peaked near anthesis, and then it decreased somewhat until wheat maturity (Figs. 2C–F). Differences in intercepted PAR(%) between nitrogen treatments gradually increased until about 40 days after emergence, but remained small throughout the growth period of the weeds. Nonetheless, differences between nitrogen treatments in terms of the light available to the weeds (% transmitted PAR) were considerable. In 1997, the average transmitted PAR (from *S. media* emergence till wheat maturity) decreased with increased nitrogen supply: from 21.3% in N1 and N2 to 11.6% in N3 (not shown). In 1999, the transmitted PAR decreased more sharply with nitrogen supply than in 1997, being 48.7% in N1, 35.0% in N2 and 18.9% in N3. The two cultivars did not differ in transmitted PAR.

The variation in volumetric soil moisture content ( $\theta$ ,  $\text{m}^3 \text{ m}^{-3}$ ; 0–30 cm depth) in plots of wheat and *S. media* was only 3% between wheat cultivars in both 1997 and 1999 and just 1% with nitrogen treatment in 1997 (data not shown). Averaged over cultivar and nitrogen and from emergence till harvest of *S. media*,  $\theta$  was 0.24 (range 0.21–0.28) in 1997 and 0.20 (range 0.17–0.25) in 1999. On two dates in 1999,  $\theta$  decreased with increased nitrogen supply: on 13 July from 0.22 (N1) to 0.18 (N3), and on 3 August from 0.20 (N1) to 0.15 (N3). In 1999, the average  $\theta$  was larger in monoculture of *S. media* (0.24, range 0.22–0.26) than in wheat.

### *Growth of S. media in the wheat experiment*

More of the clusters (see Fig. 1) of *S. media* seeds emerged in 1997 ( $90.0\% \pm 8.2$ , mean  $\pm$  st.dev.) than in 1999 ( $78.0\% \pm 9.7$ ) and fewer plants emerged per cluster in 1997 ( $3.95 \pm 1.3$ ) than in 1999 ( $5.36 \pm 1.3$ ). The emergence and plants per cluster did not differ between *S. media* sown in monoculture or sown among the wheat cultivars.

Table 3. Means, standard error of the mean (within brackets), and effects of year (Y), nitrogen (N) and cultivar (C) on total crop biomass, grains, total N uptake of spring wheat at maturity and of tuber fresh yield of potato. Data were not transformed for analysis.

Spring wheat						Potato				
Y	N	C	Biomass	Grains	N uptake	Y	N	C	Tuber	Tuber N uptake
				(84% dm)	(total)				(fresh)	
			Mg ha <sup>-1</sup>	Mg ha <sup>-1</sup>	kg N ha <sup>-1</sup>				Mg ha <sup>-1</sup>	kg N ha <sup>-1</sup>
1997	N1	Baldus	11.8 (0.9)	6.48 (0.27)	142 (21)	1997	N1	Junior	22.5 (5.4)	44.4 (9.8)
	N2		10.2 (0.6)	5.70 (0.35)	109 (8)		N2		26.1 (3.9)	58.2 (10.4)
	N3		13.6 (0.6)	7.60 (0.25)	184 (19)		N3		47.0 (2.3)	145.2 (8.3)
	N1	Axona	10.8 (1.1)	5.47 (0.47)	111 (16)		N1	Agria	28.7 (7.4)	60.8 (14.2)
	N2		11.5 (0.7)	5.81 (0.36)	123 (7)		N2		38.7 (2.9)	89.3 (11.8)
	N3		14.5 (0.4)	7.16 (0.21)	190 (4)		N3		48.4 (2.5)	142.8 (10.8)
1999	N1	Baldus	6.9 (0.2)	4.49 (0.16)	83 (4)	1998	N1	Junior	24.9 (2.5)	50.3 (2.7)
	N2		8.6 (0.5)	5.31 (0.33)	97 (6)		N2		27.6 (1.4)	57.2 (5.8)
	N3		12.0 (0.2)	7.73 (0.29)	175 (11)		N3		36.4 (4.0)	92.5 (10.7)
	N1	Axona	7.0 (0.4)	3.99 (0.15)	87 (6)		N1	Agria	26.7 (3.4)	73.6 (11.9)
	N2		10.4 (0.2)	5.59 (0.13)	103 (0)		N2		30.8 (2.1)	78.9 (12.6)
	N3		12.8 (0.5)	7.08 (0.38)	196 (13)		N3		48.6 (4.5)	141.8 (9.2)
Sig. Y*			***	***	**				n.s.	n.s.
Sig. N			***	***	***				***	***
Sig. C			*	*	n.s.				***	***
Sig. Interactions			NxC *	YxN *	n.s.				YxNxC *	n.s.

A      \*: P<0.05, \*\*: P<0.01, \*\*\*: P<0.001, n.s.: P>0.05

Both the average soil nitrogen content ( $N_{\min}$  kg N ha<sup>-1</sup> 0–0.3 m, Figs. 3A, B), and the biomass (g cluster<sup>-1</sup>) in the monoculture of *S. media* (Figs. 2A, B) increased with nitrogen supply and were larger in N3 than in N1 and N2. The final biomass in the monoculture of *S. media* increased non-linearly with nitrogen uptake (Fig. 5A), and was almost twice as high in N3 (18.4 g cluster<sup>-1</sup>) than in N1 (9.4 g cluster<sup>-1</sup>) (Table 4A), when averaged over years. Final biomass did not differ between years.

Average soil nitrogen content ( $N_{\min}$  0–0.3 m) was smaller in wheat than in monoculture (see Figs. 3A–D) and differences between cultivars were small (not shown). Soil nitrogen content decreased quickly after crop emergence and was about 5 kg N ha<sup>-1</sup> in N1 and N2 at the time of emergence of *S. media* (Figs 3C, D). Average soil nitrogen content (kg N ha<sup>-1</sup>) increased strongly with nitrogen supply in 1999, but hardly at all in 1997. The biomass of *S. media* in wheat was about 200 to 300 times

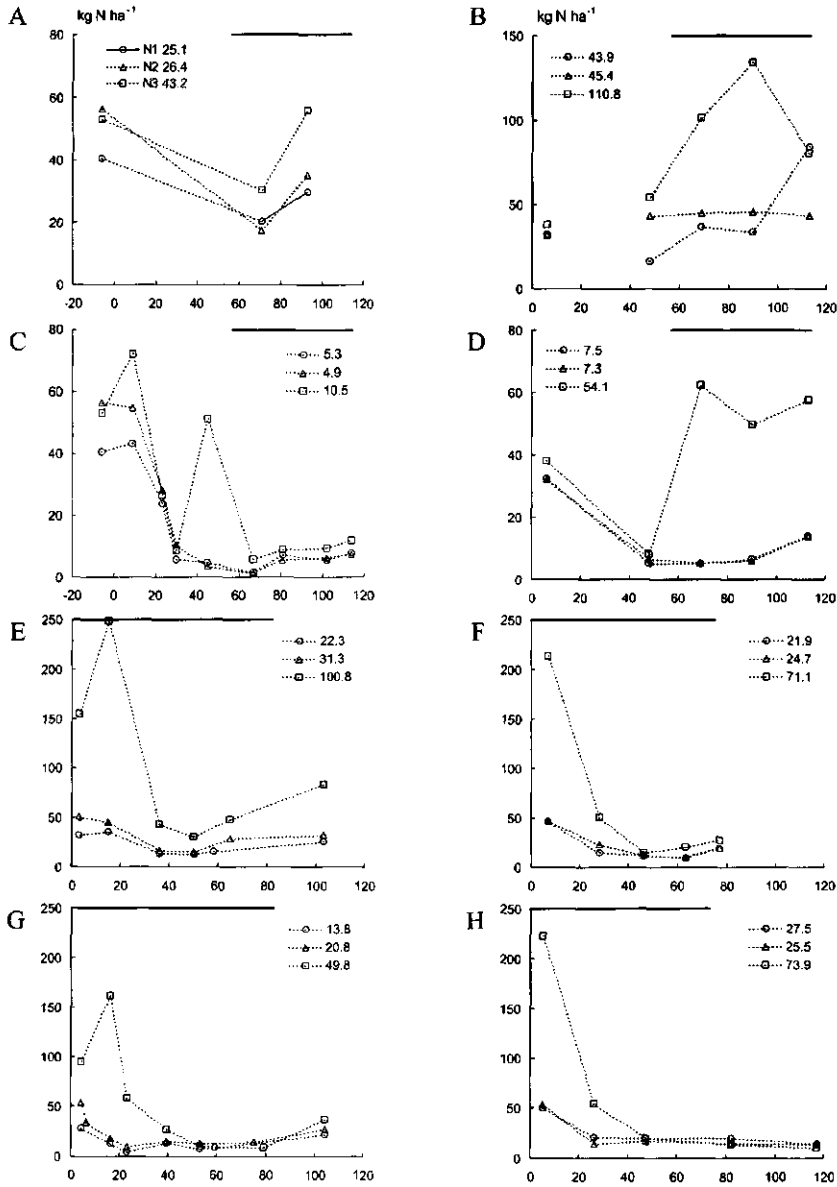


Figure 3. Symbols and broken lines are soil nitrogen content ( $N_{min}$ , ammonium-N and nitrate-N, 0–0.3 m) at three nitrogen levels, in monoculture of *S. media* in 1997 (A) and in 1999 (B), in wheat cultivars (pooled) in 1997 (C), and in 1999 (D), in potato cultivar Junior in 1997 (E) and in 1998 (F), and in potato cultivar Agria in 1997 (G) and in 1998 (H). Data near symbols are weighted average  $N_{min}$  from emergence of *S. media* until final sampling (dates in Table 1), with thick solid horizontal line representing that period.



smaller than in monoculture (Compare Figs. 2C–F with Fig. 2A,B). The *S. media* plants in wheat never exceeded 3 cm in height (not shown). In both years and wheat cultivars, biomass production of *S. media* in wheat was larger in N3 than in N1 and N2 (Figs. 2C–F), with final biomass as averaged over years and cultivars being about 3.2 times larger in N3 ( $95.1 \text{ mg cluster}^{-1}$ ) than in N1 and N2 ( $22.4 \text{ mg cluster}^{-1}$ ) (see Table 4B). Final biomass in wheat increased non-linearly with nitrogen uptake (Fig. 5B) but decreased with increased cumulative incoming PAR at the soil surface (Fig. 5C).

### ***Reproduction of S. media in wheat experiment***

In both years, the monoculture of *S. media* flowered at about 30 days after emergence. Final seed biomass and number per cluster, weight per seed and reproductive effort (mg seed per g total dry weight) of the monoculture of *S. media* were larger in 1997 than in 1999 (Table 4A), which was associated with the longer duration from start of flowering until the final harvest. Similarly to final total biomass, the final seed biomass per cluster of the monoculture of *S. media* increased with nitrogen, but the effect was only significant in 1997. As with seed biomass per cluster, the final seed number per cluster also tended to increase with nitrogen in 1997 ( $P=0.07$ ), but the effect was smaller because weight per seed tended to increase with nitrogen ( $P=0.06$ ).

In both years, *S. media* flowered about 7 days later in wheat than in the monoculture of *S. media*. Final seed biomass and number per cluster, weight per seed and reproductive effort of *S. media* in wheat were larger in 1997 than in 1999 (Table 4B) but did not differ between wheat cultivars. Final total biomass and final seed biomass per *S. media* cluster in wheat increased with nitrogen supply, the increase in N3 was smaller for seed biomass (206%) than for total biomass (325%). Final seed number per cluster showed the same nitrogen effect as final seed biomass per cluster, because seed weight was not affected by nitrogen. When seed production was regressed against vegetative biomass in 1999 a negative intercept was found ( $P<0.01$ , using all replicates), whereas in 1997, the intercept did not differ from zero. The intercept in 1999, resulted in an estimated vegetative biomass of 7.3 mg per cluster at zero seed production.

Table 4. Mean values, standard error of the means (within brackets), and effects of year (Y), nitrogen (N) and cultivar (C) on total biomass, seed biomass per cluster, seed number of cluster, seed weight and reproductive effort of *S. media* in monoculture (4A) or under a wheat canopy (4B), at maturity of wheat. A cluster (see Fig. 1, and Materials and methods) contains 4–6 plants. Reported values are original data, analysis of variance based on transformed data (see Materials and methods).

4A <i>S. media</i> monoculture						
Treatment		Biomass	Seed biomass	Seed number	Seed weight	Reproductive effort
		g cluster <sup>-1</sup>	g cluster <sup>-1</sup>	# cluster <sup>-1</sup>	µg seed <sup>-1</sup>	mg g <sup>-1</sup>
1997	N1	10.7 (1.2)	1.24 (0.02)	4.81 (0.38)*10 <sup>3</sup>	259 (18)	117.7 (11.9)
	N2	8.1 (1.2)	0.74 (0.15)	2.79 (0.54)*10 <sup>3</sup>	266 (5)	90.3 (5.8)
	N3	21.3 (6.8)	2.24 (1.04)	7.79 (3.98)*10 <sup>3</sup>	299 (20)	100.3 (18.8)
1999	N1	8.0 (0.9)	15.6 (6.9)*10 <sup>-3</sup>	149 (39)	95 (23)	5.7 (2.0)
	N2	12.2 (1.8)	59.0 (12.1)*10 <sup>-3</sup>	352 (44)	164 (15)	17.0 (2.1)
	N3	15.5 (2.4)	83.2 (26.5)*10 <sup>-3</sup>	507 (70)	155 (35)	15.7 (3.2)
Sig. Y <sup>a</sup>		n.s.	***	***	**	***
Sig. N		*	*	(P=0.06)	(P=0.06)	n.s.
Sig. YxN		n.s.	*	n.s.	n.s.	*
Transformation		log <sub>10</sub> (X)	log <sub>10</sub> (X)	log <sub>10</sub> (X)	no	(X) <sup>0.5</sup>

a \*: P<0.05, \*\*: P<0.01, \*\*\*: P<0.001, n.s.: P>0.05

4B <i>S. media</i> in wheat						
Treatment		Biomass	Seed biomass	Seed number	Seed weight	Reproductive effort
		mg cluster <sup>-1</sup>	mg cluster <sup>-1</sup>	# cluster <sup>-1</sup>	µg seed <sup>-1</sup>	mg g <sup>-1</sup>
1997		56.8 (10.6)	2.18 (0.33)	7.97 (1.04)	271 (11)	45.6 (4.8)
1999		39.0 (9.7)	0.21 (0.08)	1.44 (0.45)	95 (15)	3.6 (1.1)
Baldus	N1	21.7 (3.6)	0.63 (0.33)	2.26 (0.94)	215 (129)	23.8 (10.1)
	N2	26.2 (7.2)	1.32 (0.75)	4.92 (2.31)	184 (109)	37.0 (15.2)
	N3	112.1 (24.4)	1.58 (0.74)	6.41 (2.40)	179 (107)	14.0 (7.2)
Axona	N1	23.1 (4.7)	0.60 (0.27)	2.44 (1.00)	159 (112)	22.7 (11.3)
	N2	26.2 (6.3)	0.79 (0.39)	3.04 (1.41)	146 (129)	20.0 (9.0)
	N3	78.1 (4.5)	2.22 (0.69)	9.17 (1.90)	218 (65)	30.0 (10.8)
Sig. Y <sup>a</sup>		*	***	***	***	***
Sig. N		**	*	**	n.s.	n.s.
Sig. C		n.s.	n.s.	n.s.	n.s.	n.s.
Sig Interactions		n.s.	n.s.	NxC (P=0.05)	n.s.	N.C *
Transformation		log <sub>10</sub> (X)	log <sub>10</sub> (X+1)	log <sub>10</sub> (X+1)	no	(X) <sup>0.5</sup>

a \*: P<0.05, \*\*: P<0.01, \*\*\*: P<0.001, n.s.: P>0.05

### Potato production, nitrogen uptake and light interception

Both in 1997 and in 1998, final tuber fresh weight and nitrogen uptake increased with nitrogen supply and were smaller for cultivar Junior than for Agria (Table 3). The effect of nitrogen on tuber fresh weight depended on year and cultivar (Table 3). Averaged over years and cultivars, nitrogen supply increased tuber fresh weight ( $\text{Mg ha}^{-1}$ ) from 25.7 in N1, to 30.8 in N2 and 45.1 in N3, and tuber nitrogen uptake ( $\text{kg ha}^{-1}$ ) increased from 57.3 in N1, to 70.9 in N2 and 131 in N3. Averaged over years and nitrogen, tuber fresh weight was 20% more in cultivar Agria than cultivar Junior, whereas tuber nitrogen uptake was 31.2 % more.

In both years, PAR intercepted by the potato canopy peaked at about 40 DAE, thereafter declining to zero in cultivar Junior but declining only slightly in cultivar Agria (see Fig.4). In both years, average transmitted PAR (in %) decreased with increased nitrogen supply, from 57.5 in N1, 51.5 in N2 to 36.8 in N3 (not shown), as calculated from the last soil cultivation (close to emergence of potato, see Table 1) until the time of the weed counts (about 80 DAE of potato). In 1997, transmitted PAR was smaller for cultivar Agria (38.4%) than for Junior (54.0%), whereas transmitted PAR did not differ significantly between cultivars (51.0%) in 1998.

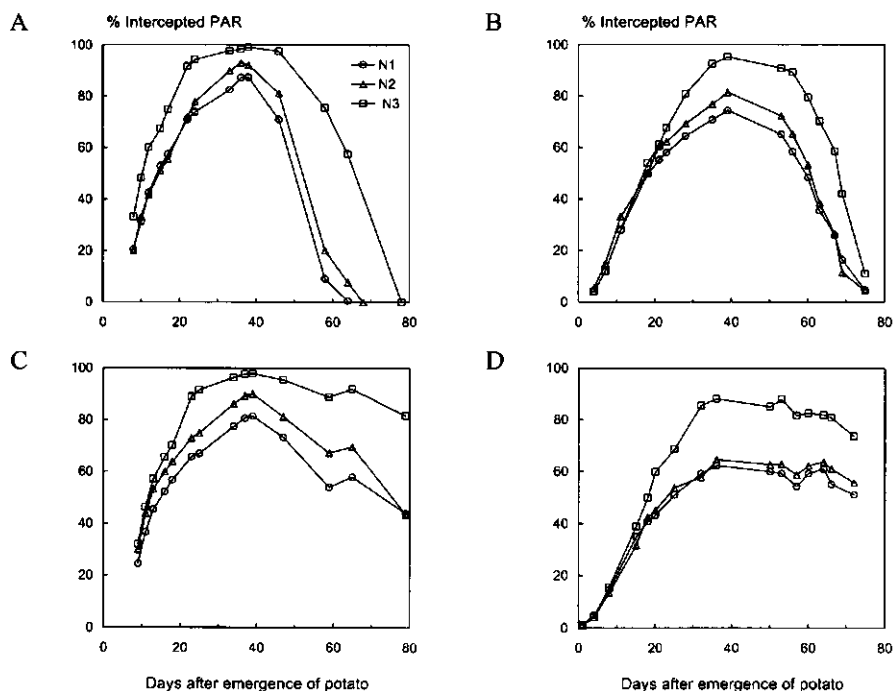


Figure 4. Percentage of intercepted PAR as a function of days after emergence of potato at three nitrogen treatments for (A) cultivar Junior, 1997; (B) Junior 1998; (C) Agria, 1997; (D) Agria, 1998.

In both years 1997 and 1998, the volumetric soil moisture content ( $\theta$ ,  $\text{m}^3 \text{m}^{-3}$ ; 0–30 cm depth) in potato fields varied by 2% between cultivars and at most by 8% with nitrogen treatments, as determined from last soil cultivation until the weeds were counted (not shown). Averaged over years and cultivars, the average  $\theta$  was 0.27 (range 0.20–0.30) in 1997 and 0.26 (range 0.23–0.28) in 1998.

### Reproductive weeds in potato

In both years and cultivars, soil nitrogen content fell rapidly after crop emergence and ranged between 15 to 20  $\text{kg N ha}^{-1}$  in N1 and N2 from about 30 days after potato emergence onwards (Figs. 2E–H). In both years, the weighted average  $N_{\min}$  (0–0.3m) (from the last soil cultivation until the weed counts) in N1 and N2 was larger in potato cultivars (average 22.8  $\text{kg N ha}^{-1}$ ) than in wheat cultivars (average 6.2  $\text{kg N ha}^{-1}$ , Fig. 2).  $N_{\min}$  in potato in N3 was larger than in N1 and N2, and larger in Junior than in Agria in 1997.

Combined over 1997 and 1998, 14 reproductive weed species were found, four of which accounted for 86% of total weed density: *S. media* (5.2 plants  $\text{m}^{-2}$ ), *Veronica hederifolia* L. (3.7 plants  $\text{m}^{-2}$ ), *Polygonum persicaria* (1.2 plants  $\text{m}^{-2}$ ) and *Sonchus arvensis* (1.1 plants  $\text{m}^{-2}$ ) (Table 5). The densities of the other ten species were 1 plant  $\text{m}^{-2}$  or less and were not affected by year, nitrogen or cultivar. The total density of reproductive weeds was smaller in 1998 (10 plants  $\text{m}^{-2}$ ) than in 1997 (16 plants  $\text{m}^{-2}$ ); this is attributable to the lower densities of *V. hederifolia* in 1998. At increased soil nitrogen supply, the total density of reproductive weeds was 13% less in N2 and 64% less in N3; this is attributable to the reduced densities of *S. media*, *V. hederifolia* and *S. arvensis*. Weed density was lower in cultivar Agria than in cultivar Junior, partly because of the lower densities of *S. media*. Densities of *V. hederifolia*, *P. persicaria* and *S. arvensis* also tended to be lower in cultivar Agria than in cultivar Junior, but the effect was not significant.

In contrast to wheat, the biomass of *S. media* in 1997 in potato decreased with nitrogen supply: by 19% in N2 and by 71% in N3 (Table 5). The number of seed capsules per plant also tended to decrease with nitrogen ( $P=0.08$ ). Total biomass and number of capsules per plant of cultivar Junior were about six times larger than those of cultivar Agria. In contrast to wheat, the biomass of *S. media* in 1997 in potato was positively associated with cumulative incoming PAR at the soil surface (Fig. 4D), with larger densities per unit cumulative incoming PAR for Junior than for Agria.

## Discussion

### *Growth of S. media in response to nitrogen supply*

The growth responses of *S. media* to an increased soil nitrogen supply as found in the present study, might be due to a direct effect of nitrogen availability on growth, or due to indirect effects because of a larger crop canopy. Even the direct effect of nitrogen supply is likely to be mediated through the crop, as nitrogen availability will be strongly affected by the nitrogen uptake of the crop. For this reason, the observed crop responses and the growth responses of *S. media* will be directly linked in the following sections of the discussion. A larger crop canopy transpires more water which might reduce the soil moisture content, and it intercepts more light, thus reducing light availability at soil level. It is unlikely that soil moisture content affected

Table 5. Mean values, standard error of the means (within brackets), and effects of year (Y), nitrogen (N) and cultivar (C) on density of weeds with flowers or seeds in potato and of dry weight (dm) and number of seed capsules (ca) per *S. media* plant (pt). Weed species are *Stellaria media* (STEME), *Veronica hederifolia* (VERHE), *Polygonum persicaria* (POLPE) and *Sonchus arvensis* (SONAR).

	Weed density (# m <sup>-2</sup> )					STEME	
	Total	STEME	VERHE	POLPE	SONAR	g dm pt <sup>-1</sup>	# ca pt <sup>-1</sup>
1997	16.2 (2.3)	4.69 (0.84)	7.11 (1.27)	1.23 (0.59)	1.04 (0.41)	2.56 (0.67)	120(33)
1998	10.1 (1.0)	5.70 (0.53)	0.30 (0.11)	1.22 (0.39)	1.19 (0.39)		
Sign. Y <sup>a</sup>	*	n.s.	**	n.s.	n.s.		
N1	17.6 (1.9)	5.67 (0.82)	5.72 (1.56)	1.61 (0.68)	1.78 (0.54)	3.65 (1.10)	177(60)
N2	15.4 (2.0)	6.69 (0.66)	3.54 (1.35)	1.11 (0.67)	1.56 (0.54)	2.95 (1.53)	153(69)
N3	6.4 (1.8)	3.24 (0.83)	1.85 (1.42)	0.96 (0.49)	0.00 (0.00)	1.08 (0.56)	31(14)
Sign. N	**	(*, P=0.05)	*	n.s.	*	*	n.s.
Junior	15.1 (1.9)	5.70 (0.77)	4.30 (1.33)	1.53 (0.57)	1.28 (0.41)	4.36(1.01)	207(51)
Agria	11.2 (1.8)	4.69 (0.63)	3.11 (1.08)	0.93 (0.40)	0.94 (0.39)	0.76 (0.28)	33(10)
Sig. C	*	*	n.s.	n.s.	n.s.	***	***
Sig. Int.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Transf.	(X+0.5) <sup>0.5</sup>	(X+0.5) <sup>0.5</sup>	(X+0.5) <sup>0.5</sup>	(X+0.5) <sup>0.5</sup>	(X+0.5) <sup>0.5</sup>	log <sub>10</sub> (X)	log <sub>10</sub> (X)

a \*: P<0.05; \*\*: P<0.01; \*\*\*: P<0.001; n.s.: P>0.05

*S. media* growth in the present study, as soil moisture content did not change with nitrogen supply, except for two dates in 1999 on which a decreased soil moisture content was associated with an increased biomass of *S. media*.

The direct effects of nitrogen on *S. media* growth and the indirect effects through light availability were confounded, which is inherent to such studies (Jørnsgård et al., 1996; Paolini et al., 1999). The regression analysis we used to ascertain whether light or nitrogen availability limited *S. media* growth under field conditions showed that in wheat (Figs. 5B and 5C) the increase of *S. media* biomass with soil nitrogen supply was associated with a greater nitrogen uptake despite smaller levels of incoming PAR at the soil surface. In potato the biomass of *S. media* decreased with increased soil nitrogen supply, which was associated with lower levels of incoming PAR at the soil surface (Fig. 5D). The nitrogen uptake *S. media* in potato (not measured) probably also decreased with increased soil nitrogen supply, given the smaller biomass, but was increasingly available with increased soil nitrogen supply (Fig. 3E–H). From this we conclude that at low soil nitrogen supply, *S. media* growth in wheat was limited by direct effects of soil nitrogen availability, whereas in potato, growth was limited by light availability which was an indirect effect of soil nitrogen supply.

The differences in the response of *S. media* to increased soil nitrogen supply in the two experiments may be explained by the larger mineral soil nitrogen content in potato than in wheat, as found in all nitrogen treatments (Fig. 3). The soil nitrogen content in N1 and N2, that was found to limit the growth *S. media* in wheat but not in potato, was larger in wheat mainly because of a larger nitrogen uptake (average over cultivars in 1997 127 kg N ha<sup>-1</sup> in N1, Table 3) than in potato (average over cultivars in 1997 52 kg N ha<sup>-1</sup> in N1, tubers, Table 3). Total available soil nitrogen (Table 3) in 1997 did not differ much for potato and wheat in N1 and N2. Nitrogen uptake in tubers at final harvest represents about 90% of uptake in potato (Vos, 1997). Another difference between the experiments was that the amount of measured light at the soil surface under a wheat canopy with rows 0.3 m apart, was never as small as in the potato crop.

Also in contrast to the wheat treatments, *S. media* biomass differed between cultivars of potato, when compared at the same cumulative levels of PAR at the soil surface (Fig. 4D). That difference is attributable to more soil nitrogen being available in cultivar Junior than in Agria for a given value of cumulative PAR at the soil surface (compare N2 Agria with N3 Junior, Fig. 5D). Cultivar Junior needed more soil nitrogen supply than Agria to obtain the same average cumulative PAR at the soil surface at the time of weed counts, because its leaf area index started to decline sooner than that of Agria (see Fig. 4).

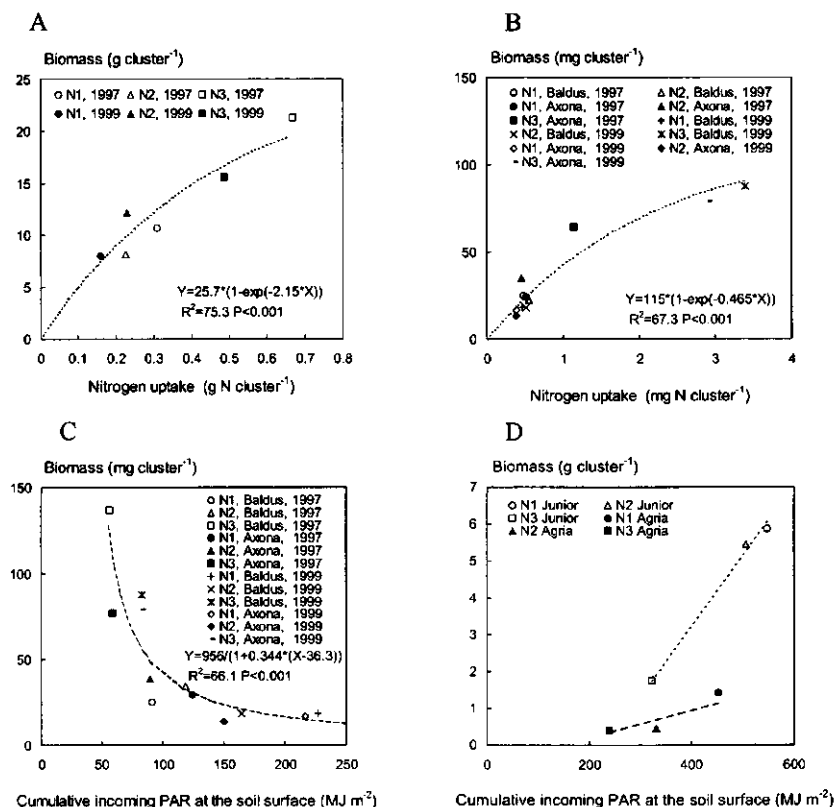


Figure 5. Dry weight of *S. media* per cluster at final harvest in three nitrogen treatments, in monoculture as a function of nitrogen uptake in 1997 and 1999 (A), in wheat as a function of nitrogen uptake in 1997 and 1999 (B), in wheat as a function of cumulative incoming PAR at soil surface in 1997 and 1999 (C), and in potato as a function of cumulative incoming PAR at soil surface in 1997 (D). A cluster (see Fig. 1, and Materials and Methods) contains 4–6 plants.

Like in the present study, Jørnsgård et al. (1996) found that the growth of *S. media* in winter wheat increased with soil nitrogen supply, despite an increase in winter wheat biomass. In their study that response was found only up to 54 kg N ha<sup>-1</sup>; unfortunately, the time of emergence of *S. media* was not recorded. Above this soil nitrogen content, winter wheat biomass still slightly increased, whereas growth of *S. media* was reduced. Although Jørnsgård et al. (1996) did not measure light interception it seems probable that the increased crop biomass reduced the light availability for the weeds. Thus, up to 54 kg N ha<sup>-1</sup>, it was nitrogen, not light, that probably limited the growth of *S. media* in winter wheat. Our results combined with these findings, indicate that the hypothesis that increased soil nitrogen supply

suppresses the growth of late-emerging weeds in a crop via a reduction of light availability, is only valid when soil nitrogen supply does not limit weed growth. However, to what extent a weed species responds to increased soil nitrogen supply is probably species-specific, as discussed in the Section ‘Densities of *S. media* and other weed species.’

### **Reproduction of *S. media* in response to nitrogen supply**

The finding that seed biomass, and number of *S. media* in wheat, in potato and in the monoculture of *S. media* generally showed the same response to soil nitrogen supply as total biomass allows us to conclude that the reproductive effort (g seed per g total biomass) and weight per seed were hardly affected by soil nitrogen supply. Schnieders et al. (1999) also found that the reproductive effort of the weeds *Senecio vulgaris* L., *Solanum nigrum* L. and *Chenopodium album* L. was robust over a range of competitive conditions, including differences in plant densities and soil nitrogen contents. Furthermore, Baumann et al. (2001b) found that the number of *S. vulgaris* seeds per plant increased linearly with above-ground dry weight; they brought about plant dry weight differences by established by using leek plants in pots to shade the weed plants at constant fractions of incident PAR. However, in our experiment the response of seed biomass and number of *S. media* in wheat to nitrogen in 1999 was not significant. This was probably due to the a short time (13 days) between flowering and determination of seed biomass. Under those conditions many small, unripe seeds were harvested (not shown).

The finding that *S. media* started flowering about seven days later in wheat than in the monoculture of *S. media*, echoes the observation by Bastiaans and Drenth (1999) that *Chenopodium album* and *Echinochloa crus-galli* L. flowered later following a late introduction in a maize crop than in a monoculture of the weeds. Part of that difference in flowering time might be attributable to a lower daily average temperature for *S. media* in a crop canopy than in monoculture, due to shading in the canopy. Jacobs et al. (1992) found temperatures at soil surface within a maize canopy (leaf area index=3.6) well supplied with water to be 1–2°C cooler during day time and 1–2°C warmer during night time than temperatures above that canopy. From their findings we estimate that the daily average temperature at soil level for *S. media* within a crop canopy during summer (14–16 h day length) was about 1°C cooler than the temperature in the monoculture of *S. media*. Using a base temperature for flowering of 0.5°C (Miura and Kusanagi, 2001), the thermal time until flowering as found in monoculture (about 500°Cd on average for the two years) was reached two days later for *S. media* in the crop canopy. Another part of the difference in flowering time may be that the *S. media* plants in the wheat canopy were much smaller than in the monoculture of *S. media*. Plants may need to achieve a minimum size before they are able to reproduce (Weiner, 1988). At the time of flowering of *S. media* in the wheat



canopy, the mean weight of *S. media* per cluster was 7–10 mg, which corresponds to the intercept of 7 mg per cluster at which seed weight was found to be zero.

The late-emerging *S. media* in spring wheat resulted in a low seed production of at most 13 seeds per cluster. Unlike in wheat, *S. media* in potato emerged at about the same time as the crop and produced up to 180 seed capsules per plant. In normal practice, weeds in potato are also controlled by earthing up the ridge near canopy closure, but in our study we did not do this because when the ridges were earthed up at that stage the equipment available severed the potato roots. Given an average of about 6 to 9 seeds per capsule (Sobey, 1981) a fecundity of about 1100–1600 seeds per plant is found in the present study. The latter figure corresponds with Mitze (1992), who studied the fecundity of *S. media* in winter wheat and found the seed production to range from about 450–5500 seeds per plant. The difference in fecundity of *S. media* in potato and wheat may be partly due to the higher soil nitrogen contents in potato. The lower fecundity in wheat could also arise from later emergence of the weed, as experimental and simulation studies have shown that a later emergence reduces the competitive ability of weeds (Kropff et al., 1992; Kropff and Van Laar, 1993). When late-emerging *S. media* is controlled immediately after the spring wheat has been harvested, only a few seeds are added to the seed bank. Under such management conditions, it is probably most important to focus weed management on the control of the early emerging weeds.

### **Densities of *S. media* and other weeds**

The second objective of the present study was to compare the response of *S. media* to soil nitrogen supply with that of other weed species, using weed density data. Our finding that the densities of *S. media*, and that of three other weeds: *V. hederifolia*, *P. persicaria* and *S. arvensis*, decreased with increased soil nitrogen supply, leads to the conclusion that the weed density response of *S. media* in potato to nitrogen supply was not specific for a weed species. Jørnsgård et al. (1996), also found that weed densities in canopies of barley and winter wheat were greater at low nitrogen supply than at high soil nitrogen supply.

The inverse relationship between weed density and soil nitrogen supply may be due to differences in germination rate and in death rate. Nitrogen supply is unlikely to have had major effects on weed germination rates, as in other studies no stimulation of weed emergence was found for *S. media* in winter wheat, when up to 162 kg N ha<sup>-1</sup> was added (Jørnsgård et al., 1996) and neither were various other weed species stimulated to emerge under field conditions after adding up 180 kg N ha<sup>-1</sup> as nitrate (Espeby, 1989) and up to 336 kg N ha<sup>-1</sup> as ammonium nitrate (Fawcett and Slife, 1978). Fawcett and Slife (1978) concluded that factors such as temperature, moisture levels and atmospheric composition near the seed may be more important. We therefore suspect that the inverse relationship between weed densities and nitrogen

supply is attributable to increased death rates, as a results of reduced light intensities (Fig. 4). At full crop canopy closure, the transmitted PAR at the soil surface was as low as 2 per cent of incoming PAR. Given about  $8 \text{ MJ PAR m}^{-2} \text{ d}^{-1}$  and 16 h of light during a midsummer day, that results in a light intensity of  $2.8 \text{ J m}^{-2} \text{ s}^{-1}$  at the soil surface, which is below the light compensation point of about  $4.5 \text{ J m}^{-2} \text{ s}^{-1}$  for  $C_3$  crops (Goudriaan and Van Laar, 1994).

Whereas the density response to soil nitrogen supply was not found to be species-specific in the present study, the growth response of late-emerging weeds to soil nitrogen supply might well depend on the crop–weed combination. In a study with early emerging weeds, Paolini et al. (1999) found early fertilisation reduced crop biomass more in the presence of *Sinapis arvensis* and less in the presence of *Chenopodium album*, compared to a later fertilisation. Jørnsgård et al. (1996) found average weed biomass per plant in a barley canopy and in a winter wheat canopy to be reduced, unaffected or increased with soil nitrogen supply, depending on crop and weed.

Previous studies indicate that the actual response of a weed species in a crop canopy to increased soil nitrogen supply depends on the influence of nitrogen and light availability on physiological characteristics, such as photosynthesis and on morphological characteristics, such as stem elongation and mass, and leaf area (Kropff and Van Laar, 1993; Ballaré and Casal, 2000; Baumann et al., 2001b). An example of species differences in such responses has been reported by Bastiaans and Drenth (1999). They found that the relative growth rate (RGR) of both *S. media* and *C. album* increased with soil nitrogen supply. For *C. album* this effect resulted from an increased net assimilation rate, and was more pronounced at high light intensities. For *S. media*, the increased RGR was caused by an increased leaf area ratio, which in turn resulted from an increased leaf weight ratio, an effect which did not depend on light intensity. To understand and quantify differences in response of weed species to soil nitrogen supply, the morphological and physiological responses of those species to nitrogen and light availability need to be studied. Such responses can be studied in experiments in which light and nitrogen availability are varied independently as Bastiaans and Drenth (1999) have done. In addition, simulation models (Graf and Hill, 1992; Kropff et al., 1992) could show the relative impact of physiological and morphological changes to crop–weed competition. Such knowledge could then be used to support improvements in organic nitrogen management.

### **Interaction between weed and nitrogen management**

The present study indicates that soil nitrogen content influences weed growth in different ways. Differences in the amount of soil nitrogen available to the weeds were the result of differences in time of weed emergence, the crop type and cultivar, and nitrogen supply. In the present study, the direct effect of nitrogen on weed growth was

confounded by the indirect effect of reduced light availability to the weed, because of enhanced leaf area development in the crop. Time of weed emergence affects the soil nitrogen available for the weeds. Late-emerging weeds in crops are shaded stronger by the crop canopy upon weed emergence than early-emerging weeds (Kropff et al., 1992; Baumann et al., 2001b) and experience lower soil nitrogen contents because the crop has taken up nitrogen. In the present study, soil nitrogen content fell rapidly after crop emergence (Fig. 3). The overall soil nitrogen content may be smaller in farming systems that use artificial fertilisers, because in such systems the crop nitrogen supply can be adjusted to crop requirements. The crop or cultivar grown also influences the soil nitrogen content throughout the growing season. As already discussed, in the treatment without additional nitrogen, the total nitrogen uptake was larger in wheat than in potato. This partly explained the lower soil nitrogen contents in wheat later in the season that limited the growth of *S. media*. Cultivars with a fast leaf area development may also suppress weeds; not only by reducing the light availability to the weed (Fig. 4), but also by reducing soil nitrogen availability (Fig. 3), as nitrogen uptake often increases linearly with leaf area increase (Grindlay, 1997).

Based on the results of the wheat and potato experiment, we expect that a low nitrogen application rate will reduce weed growth only in cropping systems that lead to a low soil nitrogen content during weed growth. Like in our experiments, we also expect that the relative response of the crop yield is smaller than the growth response of *S. media*. A low nitrogen application rate will also shorten the growth cycle of potato due to accelerated leaf senescence (Fig. 4). A low nitrogen application thus offers the opportunity of an earlier weed control after crop harvest.

The effect of nitrogen supply on weed growth per unit area in naturally emerging weeds depends both on the growth response of weed plants and on the weed density response. In our potato experiment, low nitrogen application rates were found to increase weed densities, because they reduced crop canopy development. That density response was found under conditions of high overall nitrogen availability. It remains to be investigated whether that finding is also only valid for cropping systems with a lower overall nitrogen availability.

The observations we have reported could be combined with weed density studies and studies with using different weed species, in order to design novel management options to that favour the crop versus rather than the weed. An example could be the timing and placing of nitrogen applications in the soil.

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# 7

## General discussion

## Problem analysis

Nitrogen (N) management and weed management are mentioned in a recent policy paper of the Dutch government (Anonymous, 2000b), and in past studies (Vereijken et al., 1994; Vereijken, 1998) as two key issues for improvement of organic farming systems. Organic N management is complex, because it requires not only matching of crop N supply with demand, but it also requires consideration of indirect effects on the occurrence of pests (including diseases) and weeds. Furthermore, the limited amounts of N often available on farms need to be distributed among the various crops of the rotation. Yields in organic farming are known to be 0–50% smaller than in conventional farming, but it is unclear to what extent these smaller yields are due to direct effects of N on crop growth, or due to indirect effects on pests and weeds. Weed management on organic farms requires long-term approaches that account for weed population dynamics over a rotation, and for the reproduction of uncontrolled weeds. In a survey on organic farms, many reproducing weeds were found in potato and wheat crops, with *Stellaria media* (L.) Vill. in the highest densities (Vereijken, 1998). Because weeds are controlled mechanically in potato and wheat crops during the first part of the growing season, the reproducing weeds are expected to be mainly late-emerging weeds (Chapter 6). The topics of organic N management and of weed reproduction were addressed in the present thesis, with a focus on two major objectives:

1. What is the direct effect of organic N management on growth and yield of potato and wheat?
2. What is the effect of organic N management on reproduction of late-emerging weeds?

The direct effect of N management on yield in organic farming cannot be fully quantified from survey studies (e.g. Stanhill, 1990) and from on-farm research (Vereijken, 1998) that were done so far. Firstly, because those yields were also (partly) affected by pests, and secondly because the decomposition and accumulation of N are often not in equilibrium on organic farms at present (Chapter 5). The amount of manure currently applied on arable organic farms in order to meet the crops N demand is associated with an over-use of phosphorus (P), which results in soil P accumulation (Water, 1999). To avoid future P leaching, smaller amounts of manure need to be applied on those farms, which will be associated with a smaller soil N supply (see Chapter 5).

To quantify the integrated effects of N on crop growth (Objective 1), two studies on crop growth processes were done. The first study aimed to determine relative effect of N on leaf area expansion, on the light use efficiency, and on the harvest index of potato and wheat. Conflicting reports existed on the relative effects of N on leaf area expansion and on the light use efficiency, especially so for wheat (Green, 1987). The relative effects of N on both processes determine the crop growth rate, and an understanding of both effects is, therefore, crucial for an accurate

simulation of N-limited crop growth. Various approaches have been used in published models to simulate N-limited crop growth. In some models, N is assumed to affect the light use efficiency (photosynthesis), while the leaf area expansion is only indirectly affected by N through a reduced leaf dry matter increase (e.g. Wolf, 2000). In other models, N does not affect the light use efficiency, but only directly affects the leaf area expansion (e.g. Jamieson et al., 2000). Most models, are between those two extremes (e.g. Meinke et al., 1998a).

The second study on crop growth processes aimed to determine the effect of temperature and radiation on early leaf area expansion of the canopy. Understanding early leaf area expansion is especially important for organic farming. Nitrogen-limited crops generally have smaller leaf area indices (Grindlay, 1997), and crop growth rates depend on the leaf area index (LAI) especially at small LAI values (see Chapter 1). Furthermore, differences in early leaf area expansion rates between crops and weeds are often decisive for the establishment and growth of crop and weed (Kropff et al., 1992). More knowledge about early leaf area expansion was needed, because summary models that predicted leaf area expansion of crops from temperature and/or radiation were found to be poor in predicting the LAI in new environments (see Chapter 4). In Chapter 4, the hypothesis was tested that leaf area expansion up to the maximum LAI of potato and wheat is better predicted when leaf area expansion switches from temperature to radiation-driven expansion, than when based on either of the two.

## Methodology

Field experiments (Chapters 2, 3) were used to investigate the two objectives about the crop growth processes. Field experiments were needed to study the responses of potato, wheat, and of *S. media* to organic N supply, as little quantitative data were available to date. New experiments on early foliar expansion of potato and spring wheat were needed, as available (published) experiments did not contain frequent measurements of both canopy leaf area and leaf dry weight up to maximum LAI. Understanding and quantification of crop growth processes, was used as a basis to understanding of complex effects of different organic N management strategies on crop growth and yield (Chapter 5). The steps used in the present thesis are shown in Fig. 1 of Chapter 1. The same processes, but now not only in relation to N, but also in relation to light availability of *S. media* were studied in field experiments in Chapter 6.

The field experiments with organic N supply treatments (Chapters 2, 6) were part of an arable *organic* farming rotation, but specific interventions were made in these fields:

- Pests and diseases were chemically controlled in order to avoid yield reductions and thus to assure that only direct effects of N were studied.

- Mineral fertiliser was applied on one of the N treatments to assure a broad range of N supply rates.

Two cultivars of potato and of wheat were used that differed in leaf area dynamics:

- Early maturing cultivar (small leaf area duration) and mid-late maturing (larger leaf area duration) potato cultivar.
- Wheat cultivar with a relatively smaller and one with a larger maximum leaf area index.

Two cultivars per crop species were used to investigate whether responses to N, temperature and radiation were affected by the leaf area dynamics of the cultivar.

By periodic sampling, LAI, organ dry weight, and their N contents were assessed for the two crops and for *S. media* throughout the season. Those results were used to establish relationships between crop N concentration, as a measure for N deficiency (Belanger et al., 1992) and leaf area expansion and crop light use efficiency. The number of (organic) N treatments was limited but aimed to cover a broad range of N supply rates. The derived relationships were then used as a basis for further explorations with more N supply rates, but still within the range of rates used in the experiments. Light use efficiency of the crops was calculated from intercepted PAR, as measured by a portable line sensor. Ground cover was also measured in potato, as it is a commonly used method to assess the proportion of intercepted radiation (Haverkort et al., 1991).

A model was developed which integrated the quantitative understanding of the effects of N limitation on crop growth processes, using the following steps:

1. Different summary approaches for simulation of the LAI expansion from temperature and radiation were tested across a set of environments (Chapter 4) and the best performing approach was further used.
2. Effects of N on LAI expansion, and on light use efficiency were integrated into the model, as derived from literature data and from the findings in Chapter 2.
3. Their integrated effects were then validated against the field experiments (Chapter 5).

Subsequently, the model was run for a set of scenarios, which investigated the response of crop yield, of crop N uptake, and of residual soil mineral N content at harvest to a number of instruments that can be used to match crop N supply with demand, and past N fertilisation (see Chapter 5). Each scenario was run at a range of N supply rates and for 30 years of historical weather data. Using that methodology, the study broadened the results of Chapter 2, which investigated crop growth and yield for a specific organic N management, with only three N rates and in two specific years only (Chapter 2). The results were used for recommendations on organic N management, see Section Implications for crop management.

## Scientific advancements

### *Crop level: effect of N on crop growth processes*

The first study on crop growth processes examined the response of potato and wheat to a limited (organic) N supply, with respect to leaf area expansion and intercepted photosynthetic active radiation, light use efficiency (LUE), and harvest index (Chapter 2). Crop N deficiency was well quantified by the previously proposed N nutrition index (NNI). When cattle slurry was applied in spring in potato and wheat crops, the NNI decreased rapidly during the first month after emergence. The harvest index of both crops at maturity was hardly affected by N. Both potato and wheat cultivars responded to increased N deficiency by a reduction in leaf area expansion rate and in light interception. The light use efficiency of wheat hardly responded to NNI, and that of potato decreased only with NNI at moderate of N deficiencies (NNI below 0.65). The sensitive response of the leaf area development of wheat to N limitation was not anticipated by Radin (1983), who found the leaf area development of monocots to be less sensitive to N limitation than that of dicots. According to Goudriaan (1995), crops maximise their daily gross photosynthesis when they maintain an optimal profile of leaf N content per unit leaf area, by adjusting their leaf area dynamics in response to N limitation. Grindlay (1997) hypothesised that selection of cultivated  $C_3$  species for crop productivity reduced the natural variability in the response of crop LUE and leaf area dynamics to N limitation. Natural variability could thus explain why in some experiments (e.g. Radin, 1983) the leaf area development of young wheat plants is not found to be very responsive to N.

The rate of leaf area expansion was found to be very responsive to the early N shortage as the time until 50% soil cover increased with smaller soil N supplies. Model explorations also showed early N limitations in potato (Chapter 5). Poutala et al. (1993) found that the N concentration at late tillering in a spring wheat crop that was grown in an organic farming system and without additional N supply in the form of animal manure to be much lower than in a crop supplied with sufficient N. In the present study, a low soil N supply at the onset of crop growth led to limitation of the leaf area expansion rate from emergence onwards. Understanding the mechanism of early leaf area expansion of potato and wheat thus is a crucial knowledge base for the quantification of their yield response to organic N management. An early nitrogen limitation is not so common in regular farming practices with mineral fertilisers, because there a sufficiently large amounts of N are supplied prior to sowing or planting of the crop (Van Dijk, 1999).

The methodology of measuring light interception in potato requires special attention. The light interception of potato as measured by a PAR line sensor appeared to be non-linearly related to ground cover as found previously by Van der Zaag (1984). This non-linear relationship was found already during the period of rapid leaf



area expansion, before the occurrence of yellow leaves. This non-linearity of the relationship can be explained by clustering of leaves. When assuming a 1:1 relationship between light interception and ground cover (c.f. Haverkort et al., 1991), light use efficiency values based on ground cover measurements are overestimated, the deviation being larger at smaller rates of N supply (not shown). Values of light use efficiency between crops can only be compared when using the same method. Measuring of soil cover is a useful method in potato, especially to distinguish green and yellow leaves (Haverkort et al., 1991), but should be correlated to direct measurements of intercepted PAR if the LUE is compared to other crops.

### ***Crop level: effect of temperature on early foliar expansion***

The second study on crop growth processes examined whether early foliar expansion of potato and wheat could be explained by temperature. Although temperature is the main factor determining early foliar expansion of field crops (Dale, 1988), the effect of air temperature on the early leaf area expansion rate (till LAI=1) in potato and wheat was not stable over environments and cultivars (Chapter 3). The specific leaf area of potato increased strongly from emergence till 155 °Cd (LAI=0.3), which suggested that sugars were in ample supply for the leaves shortly after emergence (see Chapter 3). The specific leaf area of wheat cultivars hardly changed over time, and was partly correlated with the relative leaf area expansion rate. Combining this information, early leaf area expansion (up to LAI=1) was expected to be driven mainly by temperature for potato, and may have been influenced by radiation as well in the case of wheat.

A summary model for early foliar expansion best predicted LAI when leaf area expansion was driven by temperature from emergence onwards after it was driven by temperature from emergence onwards until a LAI of 1 for potato and 1.5 for wheat. Thereafter, leaf area expansion was driven by radiation through photosynthesis and a pre-set specific leaf area. This summary approach that uses a switch between a temperature- and a radiation-driven expansion was previously introduced by Kropff (1988), but had never been tested formally. The present results showed that LAI was better predicted when based in a switch from temperature- and a radiation-driven expansion than when solely on one factor or the other. That summary approach was based on earlier assumptions by Loomis et al. (1976) that leaf area expansion gradually becomes more limited by assimilates during the growing season. The switching points that were found in the present study corresponded with the moment of decreased dry matter partitioning to leaves and increased partitioning to other organs (potato tuber, wheat stem).

### ***Simulation of N limitations***

The present study used a model for potato growth, crop and soil N dynamics developed by Wolf (2000). Two major adaptations were made to the crop growth section of that original simulation model (Chapter 5): simulation of leaf area expansion, and the effect of N on LUE. Leaf area expansion under conditions of sufficient N was described by assuming a switching point between temperature- and radiation-driven expansion (based on Chapters 3, 4). Under conditions of N limitation, the rate set by temperature and radiation decreased linearly with NNI (based on Chapter 2). This approach provided an accurate simulation of LAI expansion. A recently published model for wheat by Jamieson et al. (2000) in which leaf area expansion is directly affected by N, also provided a good representation of LAI expansion. The advantage of the new description of leaf area expansion is that it provides an improved representation of underlying processes, and that it accounts for effects of N on temperature-driven early foliar expansion and thus acts independently of effects of N on (leaf) dry matter production.

Nitrogen affected the light use efficiency, through its effect on the maximum rate of photosynthesis of upper leaves. As a result, LUE was non-linearly related to leaf N concentration, was found previously in experiments (e.g. Dreccer et al., 2000a). The approach resulted in an accurate simulation of crop dry matter production.

The model was assumed to be suitable for exploring crop yields under organic N management, because predictions of crop and tuber N uptake, and of crop and tuber dry weight explained 86–94% of the data variability. Moreover, the range of applied N rates in the validation set covered the range used in the scenarios.

### ***Scenarios***

The first major objective of the present study (see Problem analysis) was to quantify and understand the integrated, direct, effect of organic N management on growth and yield. The effects of organic N management on crop N uptake, yield and residual mineral soil N content at harvest of potato were studied in the evaluation of eight scenarios (Chapter 5). In those scenarios, several interventions (timing, cultivar maturity and N/P<sub>2</sub>O<sub>5</sub> ratio of manure) were tested to match N supply with demand (Chapter 5). Simulated potato yields were found to vary considerably in the scenarios and N supply rates. This suggests that there is scope for improvement of crop yields through judicious organic N management, provided that pests, diseases and weeds do not reduce yields. Crop N uptake and yields in general were with a spring-applied than autumn-applied slurry, but the results varied considerably with weather conditions. Nitrogen limited crop yields when soil mineral N content at the start of the growth was found at greater depths. This was the case when slurry was applied in autumn followed by winter precipitation or when precipitation in early spring was

considerable. Cereals are expected to be less sensitive to early N limitations than potato, because the roots of cereals penetrate the soil faster than do potatoes (A.L. Smit and J. Groenwold, Plant Research International, unpublished), they have larger root length densities and grow deeper than potatoes (Vos and Groenwold, 1986).

Matching of soil N release with crop N uptake was found to be better for a mid-late cultivar (Agria) than for an early cultivar (Junior) when the crops were harvested on September 1, as a large quantity of N was taken up by cultivar Agria in August (Chapter 5). The higher N uptake of the mid-late cultivar resulted in higher tuber dry matter yields. Advancement of the harvest date to August 1 or before, resulted in a lower tuber dry matter yield of the mid-late cultivar than of the early cultivar.

The amount of slurry-P that can be used on average over a whole rotation on average was set equal to the P-removal by crop products, to avoid future P leaching (see Section Problem analysis, and Chapter 5). A decrease in the N/P ratio of the slurry then leads to a smaller amount of slurry N that can be applied over a whole rotation on average. Tuber dry matter yield when using a rate of slurry N equal to the average rate used over the whole rotation, was only 5% smaller with an  $N/P_2O_5$  ratio of 1.7 than with an  $N/P_2O_5$  ratio of 2.7. Yields however would, quickly become smaller when even smaller ratios would be used (Chapter 5).

The variation in crop N uptake, tuber yield, and residual soil mineral N at harvest with historic N fertiliser use, as found in the present study was not greater than the year-to-year variability. This suggests that in experiments, an adequate number of years are needed to quantify effect of long-term applications of manure.

### ***Reproduction of weeds***

The second major objective of the thesis was (see Problem analysis): what is the effect of N management on reproduction of late-emerging weeds? The hypothesis that increased soil N supply suppresses the growth and reproduction of late-emerging weeds on a crop via a reduction in light availability due to an enhanced light interception by the crop, was found to be valid only when soil N supply does not limit weed growth (Chapter 6). In potato, it was found indeed that a higher rate of slurry N led to a smaller biomass and seeds production of *S. media*, due to increased shading of the weeds by the larger crop canopy. In wheat, however, with smaller mineral soil N contents than in potato, a higher rate of slurry N led to a larger biomass and seed production of *S. media* because soil N supply rather than light, was limiting *S. media* growth. Rasmussen et al. (2000) also found weed biomass in wheat to increase with manure application. *S. media* density in potato, decreased with soil N supply. Such a response was also found with other weeds (Chapter 6).

## Recommendations for further research

### *Better understanding of crop growth processes*

The adaptations of the original model for N-limited crop growth by Wolf (2000) (Chapter 5) on the simulation of leaf area expansion, and the effect of N on LUE, resulted in acceptable predictions, but also raised suggestions for further research.

Firstly, prediction accuracy of leaf area expansion from summary models, under conditions of sufficient soil N supply can still be improved (Chapter 4). To further improve that prediction accuracy, more knowledge is needed on the influence of number of factors on source- and sink limitations of leaf area expansion during early growth (Chapter 3): 1) humidity (Dale, 1988), 2) soil impedance (Masle, 1992), 3) physiological age of potato tuber (Van der Zaag and Van Loon, 1987), and 4) within-day switches between source- and sink-limitations of expansion (Loomis et al., 1976). It is also necessary to know whether those factors, as well as temperature and radiation, have similar effects on each of the processes underlying expansion of LAI: leaf emergence rate, rate and duration of expansion of individual leaves and longevity of leaves. More comprehensive models could be used that include each of those processes (such as in Porter, 1984), and the quantitative effect of the above-mentioned factors on each of those processes could be included. The outcome of those models should then be used to design improved summary models.

Secondly, more insight is needed in the interaction between processes underlying leaf (and stem) senescence. Many factors have been reported to affect leaf senescence: light intensity and quality, crop N shortage, limited life-span of individual leaves, and canopy transpiration (see Vos and Van der Putten, 2001), but how they quantitatively affect leaf senescence under various environmental conditions is not yet fully understood. An accurate prediction of leaf senescence is important for determination of light availability to (reproducing) weeds late in the season, in order to calculate their growth rates.

Thirdly, the quantification of the parameters underlying the LUE formula by Rodriquez et al. (1999) deserves further attention. The value of  $\gamma$ , that is the efficiency of conversion of gross assimilated  $\text{CO}_2$  into net dry matter, was estimated as outcome of the NPOTATO model (Wolf, 2000) and was found to be larger than for wheat, but it is unclear whether that is correct (see Chapter 5). Experiments could be used to verify its value, as LUE depends linearly on  $\gamma$ . Furthermore, the N profile with depth of the potato canopy deserves quantification, as values found in Chapter 5 for  $P_{\max}$  and  $N_b$ , suggested that leaf [N] declines less steep with depth of the potato canopy than light does. If measurements confirm this suggestion, calculation of the LUE should be adjusted to account for an extinction coefficient for N being different from that of PAR, as in Yin et al. (2000).

### ***Model refinements***

Through simulation, the results from field experiments of Chapter 2 were broadened, by investigating different organic N management strategies under a range of weather conditions. Because the simulation study aimed to explore yields, complexity and robustness of the model were balanced. Because certain processes were simplified in the present model, the predicted early N sensitivity and the calculated weather variability deserves further study.

The early N deficiency needs further quantification. Crop N uptake of potato was simulated accurately after calibration of the rate of vertical root extension, but the value was smaller than found in experiments (see Chapter 5). Probably that value was smaller because the present model assumed that N in the whole horizontal soil area could be accessed by the roots, whereas in fact potato roots are confined to the ridges (Vos and Groenwold, 1986). A model that accounts for the observed spatial distribution of potato roots (e.g. De Vos and Heinen, 1999), combined with measured root length densities, should be used to verify whether early potato N deficiency is indeed as large as predicted by simulations on Chapter 5. With such a model, placement of N in the ridges should be investigated as an option to improve crop N uptake.

Furthermore, uptake of organic forms of N by the crops (amino acids) was not considered in the present study, because the research results up to date suggest that uptake of nitrate and ammonium is far more important in agricultural production (e.g. Owen and Jones, 2001). If future research shows that uptake of organic forms of N is important for crop growth then it should be included in simulation models.

The predicted weather variability was considerable, but the simplified descriptions of denitrification, mineralisation / immobilisation, and capillary rise lead to a limited prediction accuracy in years with intensive rain and in dry years. For very wet years, the current model underestimated N denitrification and soil moisture content, whereas for dry years capillary rise might, and consequently N mineralisation, might have been overestimated. Development of robust models that can simulate soil water and N dynamics under those conditions is still needed. Detailed descriptions of those soil processes are currently available, e.g. for water balance based on Darcy's law for water movement (De Vos et al., 2000), and those are useful to understand the underlying processes. Up to now, they are less suitable for predictions because parameterisation and validation of those models are difficult, which is due to the limited amounts of experimental data are currently available. Measurements of denitrification and leaching are difficult and time consuming, because of the heterogeneity in time and space of those processes (Oenema et al., 2000).

### ***Reproduction of late-emerging weeds in organic farming***

Reproduction of late-emerging annual weeds in potato and wheat depends on the interacting effects of the relative level of light in the crop canopy and on the mineral soil N content, both being affected by organic N management (Chapter 6). Further study on N placement and on effects of row spacing is needed to limit seed reproduction of late emerging weed.

### ***Interactions between crop growth, pests and weeds***

Organic N management affects crop growth, as well as incidence of pests, diseases and weed. Further study on their interactions is needed. If natural variability exists in the response of leaf area dynamics to N (as suggested by for wheat by results in Sivasankar et al., 1998), breeding may be used to develop crops that are better able to suppress weeds by shading, under poor soil N conditions. However, a disadvantage of increasing the leaf area per unit of N may be that the total crop production per unit ground area may be reduced, as predicted by Goudriaan (1995). Further study is required to quantify weed suppressive ability and yields of crops that have a larger leaf area per unit of crop N. Simulation models such as LINTUL-N-POTATO (Chapter 6), and the LUE version of INTERCOM (Baumann et al., 2001a) may be useful tools for that purpose. By simulations and experiments it could be examined whether row fertilisation favours the crop relative to the weed.

## **Implications for crop management**

The implications of organic N management regarding 1) direct effects on crop growth rate and yields, 2) the occurrence of pests and weeds, and 3) effects over a whole rotation are discussed below, together with recommendations following from the present study.

### ***Nutrient management at field level***

Results described in the Chapters 2 and 5 offer opportunities to fine-tune current N recommendations (Van Dijk, 1999). Based on the mineral N content in spring, a basic dressing may be recommended in organic farming as to ensure unrestricted early growth. Such a basic dressing may as an organic N source with a large proportion of mineral N, or as mineral fertiliser in conventional farming. Both experiments and simulation studies could be used to quantify how much N would be needed for such a

basic dressing. The simulation models may be used to investigate the effects of weather on the basic N dressing that would be needed for unrestricted early growth.

### ***Pests, disease and weed management***

Not only direct effects of organic N management on crop growth and yield matters, but also indirect effects on pests, diseases and weeds. This is particularly so in farming systems where biocides are not applied, or where their use is restricted to a minimum. Such indirect effects may be important to potato late blight, as increased soil N supply may increase the risk for a late blight infection due to the longer presence of dew in the canopy (W.J.M. Meijer and P.C. Scheepens, Plant Research International, unpublished). The effect of N on that risk is, however, not yet quantified. As long as there is no effective control method for potato late blight in organic farming, green cover crops rather than later cultivars, may be grown to take up the N released late in the season.

Organic N management also effects the reproduction of annual weeds. Farmers tend to apply relatively more organic N to potatoes than to wheat, because potato needs more N than wheat because it has a smaller N recovery. Such a N management strategy disfavours the reproduction of *S. media* in both crops (Chapter 6). Additionally, N may be placed in the vicinity of the crop roots to reduce the establishment of annual weeds. Rasmussen et al. (1996) showed that selective placement of mineral fertiliser beside and below the barley rows reduced the weed biomass compared to a broadcast application. Such selective placement may also apply to organic N source, as Rasmussen (1999) showed that injection of slurry N decreased weed biomass compared to broadcast application of slurry.

At the same experimental farm as in Chapter 6 (Lovinkhoeve), S.K. Mertens (Plant Research International, personal communication) showed that up to 60% of early-emerged annual weeds in a wheat canopy with 30-cm spaced rows survived mechanical control. Fecundity of *S. media* plants (0–800 seeds per plant, 150 on average) that survived mechanical weed control, as found by Mertens, was larger than the fecundity of plants that emerged after that control (1.5 seeds per plant, Chapter 6). Fecundity of *S. media* plants was in potato much larger than in wheat (Chapter 6), with *S. media* in potato emerging shortly after the crop. Those results suggest that it is more effective to improve the control of early-emerged plants than to adjust N management to manipulate seed setting of late-emerged plants.

Weed control of early-emerged plants may be improved by further developing mechanical control techniques. For wheat, another option to improve control of early-emerged weeds might be a higher sowing density and a more uniform planting pattern (Griepentrog et al., 2000; Mertens, 2000), which increases the shading of the weeds by the crop canopy. The trade-off of a denser planting pattern is that it precludes hoeing. First results on row spacing, however, indicate that average seed production

of annual weeds in 30-cm spaced rows with hoeing was comparable to or greater than in 10-cm spaced rows without hoeing (Mertens, 2000).

### ***Management at farm level***

The whole set of activities at farm level, some of which were considered in the present study, offers opportunities to improve nutrient use efficiency (Oenema et al., 1999; Schröder et al., 2000b) and to improve weed (Kropff et al., 2000) and pest management (Vereijken, 1998). Where nutrient management in the past focused at economic optimal yields at *field* level especially in farming systems with mineral fertilisers, the focus now shifted towards the *farm* levels (Oenema et al., 1999). At farm level, the total nutrient budget assigned to a farm has to be partitioned over the fields and crops, taking into account the demand by the crop and the supply by the soil. In organic farming it is especially important to take soil N supply into account, because not all applied organic N is released within the first year after its application.

At farms, many activities are carried out (Fig. 1). Nutrients are applied to the soil as animal manure produced on the farm or imported, and as green manure crops. Nutrients are taken up from the soil, are removed by crops and side-products of crops, such as straw, are also removed or added to the soil as a nutrient source. In specialised arable or livestock farms, some of these activities are not present. An extensive review on the various options for improvement of nutrient use at the farm level was given by Schröder et al. (2000b). The present study dealt with the N dynamics during 'application of manure to the soil' and 'removal of nutrients by the crop' (Fig. 1). Some options for nutrient management in those two cases, not already mentioned in previous sections, are shortly mentioned below.

N management needs to consider long-term effects of manure applications on soil P content (see Introduction in Chapter 5). Soil P contents in Dutch soils that are sufficient for optimal crop growth should be maintained at their current level to avoid leaching (see Chapter 1). More long-term studies are needed to determine how much P input is needed to enable consolidation of current P contents (Schouwmans et al., 2000).

Results of Chapter 5 showed that early crop N uptake increased with the rate of vertical root extension of potato. If there is genetic variability in root growth of crop and in the root/shoot ratio, breeding may be used to improve N uptake efficiency. A simulation study estimated that the N uptake efficiency of rye grass can be improved by 10%, which was based on the existing variability in root/shoot ratio and in the rate of re-growth after cutting (Vellinga and Van Loo, 1994). For breeding in organic farming it is important to have insight in trade-offs between crop characteristics, such as between 1) an improved N uptake efficiency and 2) weed suppressive ability. Increasing N uptake by increasing the root/shoot ratio may lead to a smaller weed suppressive ability due to the smaller proportion of shoot biomass.



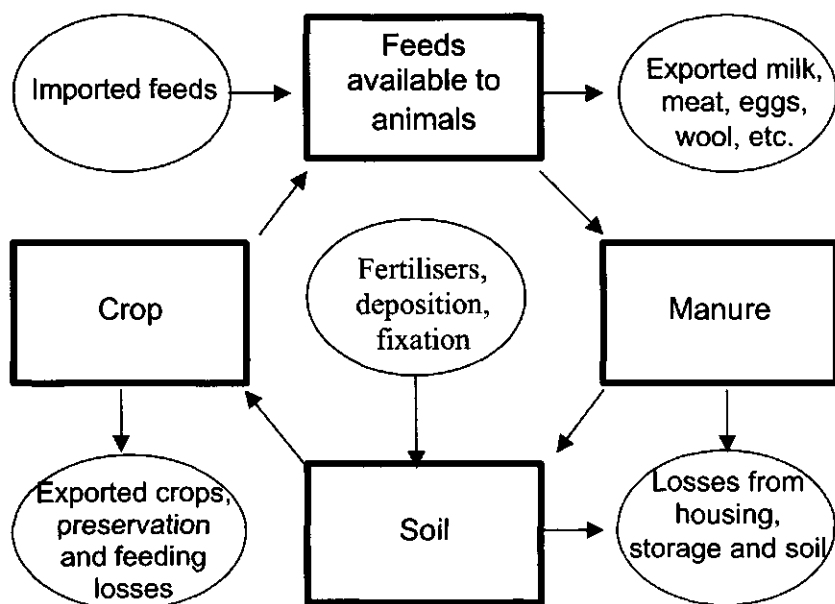


Figure 1. Simplified scheme of N flows in a mixed farming system (redrawn after Schröder et al., 2000a).

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## Summary

The increased use of pesticides and mineral fertilisers attributed to the raise in crop yields after 1945. However, over-use of pesticides and mineral fertilisers in intensive agriculture also raised a number of concerns about unintended consequences: such as environmental pollution and food safety issues. To minimise those negative side effects, the Dutch government restricted the use of pesticides and mineral fertilisers. The government also promotes the livestock farmers to export part of their manure to arable farmland, because the large production of manure from livestock farms is accompanied by a lack of farmland area to apply the manure (Chapter 1).

Different strategies exist to maintain crop yields while reducing nutrient and pesticide losses to the environment. This can be done by fine-tuning the application of mineral fertilisers and biocides, but also by decreasing the reliance on mineral fertilisers and pesticides. The latter requires a good insight of ecological processes underlying yield formation. Research in organic farming can be very useful to improve our understanding of those processes, as biocides and mineral fertilisers are not allowed.

Optimisation of N management with solely organic sources of N, in short organic N management is complex. It requires not only insight into the direct effects of N on crop growth but also into the indirect effects through pests, diseases and weeds. Crop yields in organic farming are known to be 0–50% lower than in conventional farming, but it is unclear to what extent the yields are N-limited, or reduced by pests, diseases and weeds. When properly fertilised, yields in Dutch arable organic farming are not often limited by K or P. Nitrogen, however, may be limiting for crop growth as it is more mobile than P and K, and the release of N from organic sources does not fully match crop N demand.

Optimisation of organic N management is an important issue in organic farming. Optimisation of organic N management concerns the division of manure of the crops in a rotation, the timing of application, the selection of a cultivar that efficiently takes up N, and so on. Optimisation of organic N management requires knowledge about the response of crop growth processes to N.

Weed management on organic farms requires strategies that account for long-term effects. That requires knowledge about the population dynamics of weeds over a rotation, and about the seed setting of weeds. Many reproducing weeds have been found in potato and wheat. These weeds do not cause crop damage, but they replenish the seed bank and may therefore influence the number of emerging weeds in subsequent crops in the rotation. N management may affect weed growth and reproduction.

The present thesis focused on two aspects of organic N management: 1) the effect on crop growth, and 2) the effect on weed growth and reproduction. That information can be used to improve organic N management. The issues were addressed by combining field experiments with modelling. Weights and yields mentioned in the present summary are all on a dry weight basis.

Potato (*Solanum tuberosum* L.) and wheat (*Triticum aestivum* L.) were chosen as target crops for the current study because 1) potato is an economically important crop in organic farming whereas wheat is important in a crop rotation because it reduces the intensity of soil-borne diseases and pests, and it improves the soil structure of heavily textured soils; 2) in both crops annual weeds replenish the seed bank of the soil; and 3) the crops were expected to respond differently to N limitation.

In Chapter 2, the response of potato and wheat to a limited N supply was examined, with respect to leaf area expansion and intercepted photosynthetic active radiation (PAR), light use efficiency (LUE), areal leaf N content ( $\text{g m}^{-2}$ ), and harvest index. Potato and wheat cultivars were grown in field experiments at three N levels: no N (N1), cattle slurry at a level corresponding to current organic N management (N2), and cattle slurry supplemented by mineral N fertilisers according to recommended levels used in conventional farming (N3).

N deficiencies were quantified by a N nutrition index (NNI), i.e. the actual N divided by the critical N concentration at which crop growth was just barely limited by N. For both crops, a smaller NNI (increased N deficiency) caused a linear decrease in crop dry weight, in cumulative intercepted PAR, in maximum leaf area index (LAI), and to a lesser extent in the leaf N concentration. The harvest index at maturity of both crops was not affected by N. The LUE, however, was unaffected by N in wheat (NNI 0.9–0.6), and was barely reduced in potato by N down to NNI 0.65, but decreased at still lower values of NNI.

The NNI for the N1 and N2 treatments decreased in the initial part of the growing season, up to 20 (potato) and 50 (wheat) days after emergence, with small changes thereafter. This early decrease in NNI reduced the early rate of foliar expansion (Chapter 2). Literature showed that the rate of foliar expansion can be found from the NNI and the actual rate of foliar expansion under conditions of sufficient N. The latter was further quantified in experiments (Chapter 3), and in a simulation study (Chapter 4).

In Chapter 3, the course of early leaf area expansion and specific leaf area (SLA) in potato and wheat cultivars was studied and it was tested whether air temperature explains differences in these courses within different environments. The LAI of potato and wheat increased exponentially with thermal time, at a relative rate ( $R_L$ ) that was nearly constant up to a LAI of 1, with mean values of  $17.9 \cdot 10^{-3} (\text{°Cd})^{-1}$  for potato,  $7.1 \cdot 10^{-3} (\text{°Cd})^{-1}$ , for winter wheat and  $10.9 \cdot 10^{-3} (\text{°Cd})^{-1}$  for spring wheat.  $SLA$  of potato increased nearly linearly with thermal time from 5 to  $15 \text{ m}^2 \text{ kg}^{-1}$  at 50% emergence to 20 to  $25 \text{ m}^2 \text{ kg}^{-1}$  at 155 °Cd and then decreased slightly. The  $SLA$  of both winter and spring wheat began at 16 to  $23 \text{ m}^2 \text{ kg}^{-1}$  and in most cases increased slightly with thermal time. For both crops, the course of early leaf area expansion and of  $SLA$  with air temperature were not stable over environments and genotypes, so it was concluded that those patterns were not *fully* explained by temperature.

Treatment effects on early foliar expansion of potato were not correlated with those on  $SLA$ , and were only partly correlated for wheat. A correlation between early

LAI expansion and SLA indicates that LAI expansion depends on leaf dry matter production. Literature suggests that the small SLA value of potato at emergence may be caused by storage of starch in the leaves. These results indicate that temperature is the main factor affecting early foliar expansion of potato ( $LAI < 1$ ), and that leaf assimilate availability might have influenced early foliar expansion of wheat.

In Chapter 4, the performance of a summary model for simulating increase in LAI was evaluated for potato and wheat cultivars across environments (sites and years). Rate of LAI expansion just after emergence was assumed to depend on temperature. After a predefined LAI,  $L_S$ , expansion was assumed to increase in proportion to leaf dry weight increase that depended on intercepted radiation, henceforward: radiation-limited expansion. The summary model was based on the idea that LAI expansion becomes gradually more limited by assimilates during the growing season, because of increased competition for assimilates by other organs. The  $L_S$  value at which the model performed best was considered to be the most realistic LAI at which expansion shifts from temperature to radiation-limitation. For potato and wheat, calibrated model parameters differed mostly across environments when either temperature or radiation drove LAI expansion. Parameters did not vary with potato or wheat cultivar. The model's predictions were best at  $L_S$  of 1.0 for potato and 1.5 for wheat. Using these  $L_S$  values, the coefficient of determination between observed and predicted values was 91% for potato and 88% for wheat. We concluded that LAI expansion is better predicted when it switches from temperature- to radiation-limited expansion, than when based on either of the two. However, the prediction accuracy could still be improved considerably, even for environments that were not yet very different. It is suggested that more knowledge of sink- and source-limitation of early foliar expansion is needed to further improve prediction accuracy in new environments.

A simulation study was used to investigate the effects of organic N management on attainable yields (Chapter 5). An existing simulation model for potato growth, crop and soil N dynamics was adapted to account for the release of N from crop residues and manure, and for effects of N on leaf area dynamics and on the LUE (cf. Chapters 2–4). The model accurately predicted potato yield, N uptake and soil mineral N residues at harvest, in response to mineral N applications ranging from 0–200 kg N ha<sup>-1</sup> yr<sup>-1</sup>, manure applications of up to 480 kg slurry N ha<sup>-1</sup> yr<sup>-1</sup> and green manure applications. Subsequently, the model was used to explore potato yield and residual soil mineral N at harvest under a range of weather conditions, as influenced by: 1) the time of application, 2) the lateness of the potato cultivar, 3) the N/P ratio of the manure, and 4) soil N content as a result of the fertilisation history.

Using 30 years of weather data (1959–1988), slurry increased simulated tuber yield from 8.0 Mg ha<sup>-1</sup> to 11.2 Mg ha<sup>-1</sup> when spring-applied and to 10.0 Mg ha<sup>-1</sup> when autumn-applied at a rate of 490 kg slurry N ha<sup>-1</sup>. Depending on the year, tuber yields associated with autumn-applied slurry were 77 to 100% of the yields associated with spring-applied slurry at a rate of 490 kg slurry N ha<sup>-1</sup>. Without slurry, tuber

yields varied with year from 57 to 83% of the yield at 490 kg spring-applied slurry N ha<sup>-1</sup>. Tuber dry matter yield and N uptake for a mid-late cultivar were higher than for an early cultivar when harvested on September 1, but tuber yield was generally lower when harvested on August 1. The response of tuber yield to slurry N varied little with N/P ratio's of the slurry. On recently converted farms, yields were at most 12% larger on farms with *large* historical N fertiliser inputs than on farms with *small* inputs. We conclude that spring-applied slurry is to be preferred over autumn-applied slurry to avoid losses of N during wintertime. Patterns of N uptake suggest that application of organic N with a large proportion of mineral N shortly after emergence could improve potato yields in organic farming.

The second topic of the study was to quantify effects of N supply on weed growth and reproduction in a crop. In Chapter 6, the hypothesis was tested that increased soil N supply reduces the growth of late-emerging weeds in wheat and potato by enhancing canopy leaf area development and thereby reducing the availability of light for weed growth. The hypothesis was tested by conducting two series of field experiments: one in wheat in which *Stellaria media* (L.) Vill. was sown at stem extension, and one in potato with naturally emerged weeds, including *S. media*. Results showed that the hypothesis is not always valid. In both crops, increased N supply indeed increased the leaf area development of the crop and thus decreased the light availability at soil surface for growth of the late-emerging weeds. In potato the total dry weight and number of seed capsules per plant of *S. media* decreased with increased soil N supply as expected, as growth was limited by light. In wheat, however, the total dry weight and seed dry weight, and seed number per cluster (4–6 plants per cluster) of *S. media* increased with soil N supply. Regression analysis showed that in wheat, growth of *S. media* was limited by mineral soil N availability, whereas light in wheat was not limiting because the 30-cm spaced wheat crop did not fully cover the soil. It was concluded that the differences between wheat and potato experiments in the influence of soil N supply on growth and reproduction of *S. media* are attributable to higher soil N levels in the potato crop. Biomass production of *S. media* differed among potato cultivars, which could be explained from differences in soil N contents at the same average light interception by the cultivars. Reproduction of *S. media* in the potato crop (estimated as up to 1400 seeds per plant) was much higher than in wheat (up to 1.5 seeds per plant). This difference in reproduction was not only due to a larger soil mineral N content in potato, but also due to the earlier emergence of *S. media* in potato. Because the density response of other weed species was the same as those of *S. media*, it was concluded that the weed density responses were not weed-specific.

In Chapter 7, the methodology, scientific advances, implications for organic N management, and recommendations for further research are given. From the experimental and simulation studies it was concluded that early N availability is crucial for crop growth and yielding ability under organic N management. A basic dressing of N near crop emergence is recommended to ensure unrestricted crop

growth. It was further concluded that it is important to take account of indirect effects of organic N management on pests, diseases and weeds. Two examples of such indirect effects were given. Firstly, it is important to understand and quantify whether improved early potato growth with N supply increases the risk of a premature crop harvest due to infection by *Phytophthora infestans*. Secondly, it is necessary to investigate whether such a basic N dressing can be given without simultaneously promoting the weed growth, i.e. by placing the manure in the vicinity of crop roots. N use in the agricultural sector cannot only be improved by minimising soil N losses en improving crop N use efficiency, but also by other farm activities such as the growth of leguminous crops and efficiency of the use of N from fodder crops by livestock.

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## **Samenvatting**

Sinds 1945 zijn de opbrengsten van akkerbouwgewassen sterk toegenomen, mede dankzij het intensieve gebruik van gewasbeschermingsmiddelen en kunstmest. Dit intensieve gebruik leidde echter tot toenemende ongerustheid over onbedoelde neveneffecten, zoals vervuiling van het milieu en problemen met voedselveiligheid. In een poging de onbedoelde neveneffecten van de intensieve landbouw te beperken, heeft de Nederlandse overheid het ongebreidelde gebruik van gewasbeschermingsmiddelen en kunstmest aan banden gelegd. Tevens stimuleert zij veehouderijbedrijven tot het afzetten van een gedeelte van de mest op akkerbouwbedrijven, omdat in de veehouderij aanzienlijk meer mest geproduceerd wordt dan aangewend kan worden op het eigen (gras)land (Hoofdstuk 1).

Er zijn verschillende mogelijkheden om gewasopbrengsten op peil te houden terwijl de milieuvervuiling beperkt blijft. Dit kan door fijnregeling van het toepassen van inputs, maar ook door het verminderen van de afhankelijkheid van kunstmest en pesticiden. Dit laatste vereist een goede kennis van de ecologische processen die ten grondslag liggen aan opbrengstvorming. Onderzoek binnen de ecologische landbouw is zeer bruikbaar om die processen beter te begrijpen, aangezien er in het geheel geen kunstmest en pesticiden mogen worden gebruikt.

Optimaliseren van stikstof (N)-beheer bij gebruik van uitsluitend organische bronnen voor N, kortweg ecologisch N-beheer, is lastig. Het vereist namelijk niet alleen inzicht in directe effecten van N op de groei van het gewas, maar ook van indirecte effecten van N op die groei door het beïnvloeden van ziekten, plagen en onkruiden. Opbrengsten van aardappel en tarwe in de ecologische teelt kunnen tot wel 50% lager zijn dan in de gangbare teelt. Onduidelijk is in welke mate deze lagere opbrengsten zijn toe te schrijven aan N-tekort, en aan ziekten, plagen en onkruiden. Bij een goede bemesting van de gewassen worden in Nederland geen gewastekorten van fosfaat (P) en kalium (K) verwacht. Stikstof is echter een mobiel element, en het vrijkomen van N uit organische bronnen is niet optimaal afgestemd op het aanbod, waardoor tekorten kunnen ontstaan.

Een belangrijke vraag binnen de ecologische landbouw is hoe N zo goed mogelijk kan worden beheerd, dus hoe de mest het best verdeeld kan worden over de verschillende gewassen binnen een rotatie, wanneer de mest het beste kan worden aangewend, welk ras het efficiëntste N opneemt, etc. Voor het verbeteren van het N-beheer is kennis nodig van de reactie van gewasgroeiprocessen op N-tekort.

In zijn algemeenheid zijn voor een effectieve onkruidbeheersing op ecologische bedrijven strategieën nodig die rekening houden met de meerjarige gevolgen van maatregelen. Daarom is kennis nodig van de dynamiek van onkruidpopulaties binnen een gewasrotatie en van de zaadzetting van onkruiden. Met name in aardappel en tarwe zijn veel onkruiden die zaadzetten. Deze onkruiden veroorzaken weliswaar geen directe schade aan de gewasgroei, maar zij vullen de zaadbank aan, waardoor er meer onkruiden zullen kiemen in volgteelten. Deze onkruidgroei en zaadzetting worden beïnvloed door de hoeveelheid beschikbare N.



Dit proefschrift richt zich op twee deelaspecten van ecologisch N-beheer:

1) wat is het effect op gewasgroei, en 2) wat is het effect op groei en zaadzetting van onkruiden. Met behulp van inzicht in deze deelaspecten kunnen aanbevelingen worden gedaan voor het verbeteren van ecologisch N-beheer. Ter verwezenlijking van deze doelen werden veldproeven en modelstudies uitgevoerd. Alle genoemde gewichten en opbrengsten in deze samenvatting zijn in termen van drogestof.

Het onderzoek is uitgevoerd met de gewassen aardappel (*Solanum tuberosum* L.) en tarwe (*Triticum aestivum* L.). Deze gewassen zijn gekozen omdat 1) aardappel een economisch belangrijk gewas is voor de ecologische teelt, en tarwe is een belangrijk gewas binnen de rotatie omdat het bodemgebonden ziekten en plagen beperkt en de structuur van zwaardere gronden verbeterd, 2) in beide gewassen veel onkruiden voorkomen die kans zien om zaad te zetten, en 3) verwacht werd dat beide gewassen verschillend op een N-tekort zouden reageren.

In het tweede hoofdstuk van dit proefschrift is beschreven hoe aardappel en tarwe reageren op een tekort aan N. In veldproeven is een aantal gewas-karakteristieken gemeten, namelijk (de groei van het) bladoppervlak (LAI), de onderschepping van fotosynthetisch actieve straling (PAR), de lichtbenuttingsefficiëntie (LUE), het blad N-gehalte ( $\text{g m}^{-2}$ ), en de oogstindex. Twee aardappelrassen en twee tarwerassen werden verbouwd onder drie verschillende bemestingscondities: geen N gift (N1), een runderdrijfmestgift die overeenkomt met een hoeveelheid die in de huidige ecologische landbouw wordt gebruikt (N2), en een runderdrijfmestgift aangevuld met kunstmest tot een niveau dat aangeraden wordt in de gangbare landbouw (N3). De mate waarin N-tekort een rol speelde bij de opbrengstderving is berekend met behulp van de N benuttingsindex (NNI, een maat voor de relatieve N concentratie). De NNI is de aanwezige N-concentratie in het gewas gedeeld door het N-gehalte dat nodig zou zijn om het gewas ongelimiteerd te kunnen laten groeien. Een lagere NNI (groter N-tekort) leidde in beide gewassen tot een lineaire afname van de biomassa, van de geaccumuleerde hoeveelheid onderschepte PAR, van de maximale LAI, en in mindere mate van de blad N-concentratie. Stikstoftekort had geen invloed op de oogstindex bij gewasrijpheid. De LUE van tarwe werd niet beïnvloed door N (NNI 0.9–0.6). De LUE van aardappel nam in geringe mate af met een groter N-tekort tot een NNI 0.65, en nam bij lagere NNI waarden sterk af.

De NNI van beide gewassen in de N1 en N2 behandelingen daalde gedurende de eerste 20 (aardappel) en 50 (tarwe) dagen na opkomst, en bleef daarna stabiel. Dit vroege N-tekort vertraagde de vroege bladexpansie van beide gewassen (Hoofdstuk 2). Uit literatuur kon worden afgeleid dat de snelheid van bladexpansie bij N-tekort kan worden berekend uit de NNI en de snelheid van bladexpansie bij voldoende N. De snelheid van bladexpansie bij voldoende N werd vervolgens gekwantificeerd in veldexperimenten (Hoofdstuk 3) en in een simulatiestudie (Hoofdstuk 4).

In Hoofdstuk 3 is het vroege verloop van de LAI toename en van het specifiek bladoppervlak (SLA) van aardappel- en tarwerassen bestudeerd. Het effect van temperatuur op dit verloop is bepaald door het te relateren aan de gemeten

luchttemperatuur van de omgevingscondities (locaties, jaren en teeltmaatregelen) van de proeven. De LAI van aardappel en tarwe nam exponentieel toe met de temperatuursom. De relatieve snelheid van LAI toename was vrijwel constant tot een LAI van 1, en had gemiddelde waarden (in graaddagen) van  $17.9 \cdot 10^{-3}$  voor aardappel,  $7.1 \cdot 10^{-3}$  voor wintertarwe en  $10.9 \cdot 10^{-3}$  voor zomertarwe. De SLA van aardappel nam lineair toe met de temperatuursom, van  $5-15 \text{ m}^2 \text{ kg}^{-1}$  bij 50% opkomst tot  $20-25 \text{ m}^2 \text{ kg}^{-1}$  bij 155 graaddagen en nam daarna licht af. De SLA van winter- en zomertarwe varieerde van  $16-23 \text{ m}^2 \text{ kg}^{-1}$  bij opkomst en nam licht toe met de temperatuursom. De resultaten geven aan dat het verloop van de vroege LAI toename en van de SLA niet *volledig* bepaald wordt door temperatuur, omdat dit verloop als functie van temperatuur varieerde met verschillende omgevingen en cultivars. Behandelings-effecten op de vroege LAI toename en op de SLA waren onafhankelijk bij aardappel, en waren slechts gedeeltelijk gecorreleerd bij tarwe. Een samenhang tussen beide wijst erop dat de bladgroei afhankelijk is van de bladdrogestofproductie. Dat aardappelbladeren bij opkomst erg dik zijn wijst erop dat zetmeel wordt opgeslagen in de bladeren, en dat de bladdrogestofproductie niet beperkend is voor vroege groei. Deze resultaten wijzen erop dat de vroege bladexpansie van aardappel ( $\text{LAI} < 1$ ), met name bepaald wordt door temperatuur. Voor tarwe wijzen de resultaten erop dat naast temperatuur, ook de dagelijkse hoeveelheid beschikbare bladdrogestof invloed had op de vroege bladexpansie.

In Hoofdstuk 4 is de mate waarin een eenvoudig model in staat is om de LAI-toename van aardappel en tarwe gewassen juist te voorspellen in verschillende milieus (locaties, jaren, teeltmaatregelen) geëvalueerd. Dit eenvoudige model is gebaseerd op de gedachte dat de hoeveelheid dagelijks geproduceerde assimilaten steeds sterker beperkend zijn voor de snelheid van LAI-expansie, omdat naast de bladeren andere organen een toenemend leggen op die assimilaten. De  $L_5$  waarde waarmee het model de beste voorspellingen van de LAI geeft, is beschouwd als de meest realistische waarde voor wisseling van temperatuurs- naar een stralingsgestuurde bladexpansie. De gekalibreerde waarden voor de parameters van het model varieerden het meest wanneer de bladgroei beschreven werd op grond van uitsluitend temperatuur of straling. De gekalibreerde parameterwaarden varieerden niet met ras bij aardappel of tarwe. Het verloop van de LAI werd het beste beschreven met  $L_5 = 1$  voor aardappel en  $L_5 = 1.5$  voor tarwe. Bij deze waarden werd 91% van de waargenomen variatie in de LAI van aardappel verklaard en 88% van de variatie in de LAI van tarwe. Op grond van deze resultaten wordt geconcludeerd dat de LAI-toename beter wordt beschreven met een wisseling van temperatuur- naar stralingsgestuurde expansie, dan uitsluitend op basis van één van deze twee. Bij vergelijking van de nauwkeurigheid van de meetgegevens met die van de voorspellingen, bleek dat de nauwkeurigheid van de voorspellingen nog aanmerkelijk kon worden verbeterd. Hiervoor moeten 'sink-' en 'source'-beperkingen van bladgroei beter worden begrepen.

De som van de effecten van ecologische N-beheer op opbrengstvorming werd bestudeerd met een bestaand model voor de simulatie van aardappelgroei en van de

dynamiek van N in gewas en bodem (Hoofdstuk 5). De aanpassingen betroffen het toevoegen van een beschrijving voor het vrijkomen van N uit gewasresten en mest, en het opnemen van de invloed van N op LUE en op de LAI-dynamiek, zoals gevonden in de Hoofdstukken 2-4. Het model leverde nauwkeurige voorspellingen op voor de opbrengst, de N-opname en de residuele minerale bodem-N bij de oogst. Dit alles bij minerale N-giften variërend van 0-200 kg N ha<sup>-1</sup> jr<sup>-1</sup>, bij mestgiften tot 480 kg drijfmest N ha<sup>-1</sup> jr<sup>-1</sup> en bij het gebruik van groenbemesters. Het model werd vervolgens gebruikt voor het verkennen van opbrengst, N-opname en minerale bodem-N bij de oogst voor een reeks van weersomstandigheden. De verkenningen bestudeerden het effect van: 1) toedieningstijdstip van mest, 2) de vroegheid van het aardappelras, 3) de N/P verhouding in de mest, en 4) het bodem-N-gehalte zoals bepaald door N-giften gegeven in het verleden. Gemiddeld over 30 historische jaren (1959-1988), nam bij een gift van 490 kg drijfmest-N ha<sup>-1</sup> de knol opbrengst toe van 8.0 ton ha<sup>-1</sup> tot 11.2 ton ha<sup>-1</sup> bij voorjaarsaanwending en tot 10.0 ton ha<sup>-1</sup> bij najaarsaanwending. Afhankelijk van het jaar was de verkregen opbrengst bij een najaarsgift van 490 kg drijfmest N ha<sup>-1</sup>, 77-100% van de opbrengst bij diezelfde mestgift in het voorjaar. Wanneer geen mest werd gegeven waren jaaropbrengsten 58 tot 83% van de opbrengst bij een voorjaarsgift van 490 kg drijfmest N ha<sup>-1</sup>. Wanneer de aardappels op 1 september werden geoogst, was de opbrengst van een middellaat ras hoger dan van een vroeg ras, maar bij vervroegde oogst op 1 augustus, was deze kleiner. Een mestsoort met een lagere N/P verhouding leidde slechts tot een geringe afname in de opbrengst. De N-voorziening op recent omgeschakelde bedrijven hangt sterk af van de hoeveelheid N die in het recente verleden is gegeven. Op bedrijven waar veel N werd gegeven in het verleden, lag de opbrengst 12% hoger dan op bedrijven waar weinig N werd gegeven. Op grond van de resultaten werd geconcludeerd dat drijfmest bijvoorkeur in het voorjaar moet worden aangewend, omdat daarmee het verlies van N in de winterperiode wordt beperkt. De resultaten geven tevens aan dat de opbrengst bij ecologische teelt kan worden verhoogd door in het vroege voorjaar al mest aan te wenden, met een hoog aandeel minerale N.

Het tweede deelaspect van dit proefschrift was het kwantificeren van effecten van ecologisch N-beheer op onkruidgroei en zaadzetting. In Hoofdstuk 6 werd de hypothese getoetst dat een N-gift leidt tot een vermindering van de groei van laatopkomende onkruiden doordat N de bladontwikkeling van aardappel en tarwe bevordert, en daarmee leidt tot een geringere lichthoeveelheid voor de onkruiden bij opkomst. Deze hypothese werd getoetst in veldexperimenten met aardappel en tarwe. Bij de proeven met tarwe, werd het onkruid vogelmuur (*Stellaria media* (L.) Vill.) gezaaid toen het tarwegewas ongeveer 50 cm hoog was. In de proeven met aardappel werden waarnemingen gedaan aan natuurlijk opkomende onkruiden. De resultaten toonden aan dat de hypothese niet onder alle omstandigheden opgaat. Een N-gift leidde in beide gewassen tot een versnelde bladontwikkeling, hetgeen de lichtbeschikbaarheid voor de onkruiden verminderde. In het aardappel nam het totaal gewicht per vogelmuurplant en het aantal zaaddozen per plant af met de N-gift omdat,

conform de hypothese, de onkruidgroei beperkt werd door lichtbeschikbaarheid. In tarwe nam het totaalgewicht en het aantal zaaddozen per vogelmuur cluster (4-6 planten per cluster) echter toe met de N-gift. Regressieanalyse toonde aan dat de groei van vogelmuur in tarwe beperkt werd door de minerale bodem-N. In tarwe was de lichthoeveelheid echter niet beperkend voor de onkruidgroei, omdat de tarwe door de grote rijafstand van 30 cm de bodem niet volledig bedekte. Uit de resultaten werd geconcludeerd dat het verschil in de respons in aardappel en tarweproeven van de vogelmuurgroei op N te verklaren is uit de hogere minerale bodem-N in het aardappelgewas. De drogestofproductie van vogelmuur varieerde met het aardappelras. Verschillen in lichtonderschepping bij gelijke bodem-N verklaarde deze variatie tussen de rassen. De zaadproductie van vogelmuur was veel hoger in het aardappelgewas (tot 1400 zaden/plant) dan in het tarwegewas (tot 1.5 zaden/plant), hetgeen niet alleen kwam door de hogere minerale bodem-N in aardappel, maar ook door de vroegere opkomst van vogelmuur. Uit vergelijking van metingen van aan dichtheden van vogelmuur en die van andere onkruiden volgde dat het effect van N op onkruidichtheden niet soortafhankelijk is. In Hoofdstuk 7 worden de methodologie, de wetenschappelijke vorderingen, de aanbevelingen voor toekomstig onderzoek en de betekenis van het onderzoek voor ecologisch N-beheer besproken. De resultaten van de experimenten en de simulaties leidden tot de conclusie dat een vroege N-beschikbaarheid belangrijk is voor een ongestoorde gewasgroei en -opbrengst bij ecologisch N-beheer. Om te zorgen dat het gewas over voldoende N beschikt in het voorjaar, wordt aanbevolen om een basisgift te geven met een organische meststof die veel minerale N bevat. Verder werd geconcludeerd dat het voor een goed ecologisch N-beheer belangrijk is om niet alleen rekening te houden met directe effecten en N-opbrengst, maar ook met indirecte effecten op ziekten, plagen en onkruiden. Er worden twee voorbeelden van zulke indirecte effecten gegeven. Ten eerste is het belangrijk om te kwantificeren of het bevorderen van aardappelgroei door een N-gift niet resulteert in een kortere groeiduur van het gewas, door een verhoogde kans op besmetting met *Phytophthora infestans*. Ten tweede moet bij het geven van een voorjaars N-gift worden voorkomen dat de onkruidgroei wordt gestimuleerd. Rijenbemesting kan dat misschien voorkomen. Tenslotte is het belangrijk dat ecologisch N-beheer niet alleen verbeterd kan worden door verminderen van N verliezen en verhogen van N-opname, maar dat allerlei activiteiten in de bedrijfsvoering, zoals N-benutting uit veevoer en het aandeel vlinderbloemigen in een rotatie, aanknopingspunten bieden voor het verbeteren van het N-beheer van de landbouwsector als geheel.

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## Curriculum vitae

Arnout van Delden werd geboren op 31 augustus 1969 te Hardenberg. Na het behalen van zijn VWO diploma aan de Christelijke Scholengemeenschap te Hardenberg studeerde hij vanaf 1987 aan de Landbouwuniversiteit Wageningen. In 1993 behaalde hij daar het diploma in de studierichting Planteziektenkunde, oriëntatie Ecologie en Epidemiologie, met als doctoraal vakken Entomologie, Fytopathologie en Theoretische Productie-ecologie. Na zijn studie deed hij diverse korte onderzoeksopdrachten bij de toenmalige Landbouwuniversiteit Wageningen (thans Wageningen Universiteit), voor de vakgroep Fytopathologie. Van 1994 tot 1995 was hij in dienst bij Long Ashton Research Station en bij de universiteit van Lancaster, beide in Engeland, voor een onderzoek naar twee bladvlekkenziekten (*Septoria spp.*) van tarwe. In 1996 trad hij in dienst bij de toenmalige vakgroep Theoretische Productie-ecologie (nu leerstoelgroep Gewas- en Onkruidecologie) van waaruit hij gedetacheerd werd bij het toenmalige DLO-instituut voor Agrobiologisch en Bodemvruchtbaarheidsonderzoek (AB-DLO), thans deel van Plant Research International. Tot juli 2001 werkte hij hier aan het onderzoek dat in dit proefschrift beschreven is. Vanaf augustus 2001 is hij in dienst bij het Bureau voor de Statistiek, Voorburg.

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