Understanding the reduction of nitrogen leaching by catch crops

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Understanding the reduction of nitrogen leaching by catch crops

Anne Marie van Dam

Proefschrift

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Abstract

A simulation model for catch crop growth and soil water and nitrogen dynamics was developed and used to evaluate the effect of crop characteristics and weather conditions on catch crop nitrogen (N) uptake and N leaching. The model was developed for winter rye and fodder radish. For model development, several experiments were conducted to quantify catch crop growth and N uptake, based on the rates of underlying processes like CO_2 assimilation, leaf and root expansion, and N uptake at the root level. Moreover, for the development and testing of the soil model, data were collected in detailed experiments on N mineralization rates of catch crop material, soil water dynamics and N leaching.

Variation in N uptake of catch crops found in experiments and the effect on N leaching is explained by a number of factors. First, sowing date determines the potential N uptake capacity of the catch crop. Under Dutch weather conditions, the simulated uptake capacity of a catch crop exceeds 200 kg N ha^{-1} when the crop is sown in the first half of August. For rye, the uptake capacity decreases on average by 3.3 kg N ha^{-1} per day postponement of sowing. Variation in catch crop N uptake and reduction of leaching is mainly explained by the variation in the N availability (determined by soil properties, soil processes, previous crop, precipitation and rooting depth) when this is smaller than the N uptake capacity. It is mainly explained by radiation available to the crop (determined by sowing date and weather conditions) when N availability is larger than the N uptake capacity.

The crop characteristic most determining for the effectiveness of the catch crop is deep rooting. When N availability is not limiting N uptake, also other characteristics are affecting the effectivity: factors influencing the fast development of an efficiently radiation intercepting canopy, a high radiation use efficiency and a high N concentration in the biomass. Sowing early is the most important cultivation strategy improving the reduction of N leaching by catch crops. If early sowing is not possible and N availability is expected to exceed the uptake capacity, increasing the seed rate may increase catch crop N uptake and reduction of leaching. Also, taking care that root growth is unhampered may improve the effectiveness of the catch crop. For a maximum N availability to the succeeding crop, a rye catch crop on a sandy soil is best incorporated in soil three months before the planting the next crop. Deviations up to a month from the optimal date had only a small effect on N available to the next crop (2 kg N ha^{-1}).

Keywords: nitrogen catch crop, nitrogen leaching, winter rye, *Secale cereale* L., fodder radish, *Raphanus sativus* L., SUCROS, crop model, CO_2 assimilation, leaf appearance, rooting depth, nitrogen mineralization

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Contents

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Chapter 1

General introduction

Nitrogen losses from agricultural systems

Nitrogen (N) is essential for plant growth and hence for crop production. Nitrogen fertilization is one of the factors that has greatly increased food production worldwide. In industrialized countries nitrogen fertilizers are a cheap input factor with a tremendous yield increasing effect. This has lead to ample use of N fertilizers in industrialized agricultural systems: a small investment effectively reduces the risk of yield losses by N shortage (Jenkinson, 2001). In the Netherlands this effect is still enhanced by the availability of cheap or free animal manure.

However, nitrogen losses from agriculture to the environment have adverse effects on the living conditions of people, flora and fauna, by e.g. increased nitrate concentrations in drinking water, eutrophication of terrestrial and aquatic biotopes that were naturally oligotrophic, and increased emission of the greenhouse gas N_2O (Jenkinson, 2001). Also, the energy requirement of N fertilizer production is high: 38.6 MJ per kg N (Evers *et al.*, 2000). Because of these undesirable environmental effects, reduction of agricultural N losses and increasing N use efficiency have become important aims for farmers and agricultural science, next to increasing production. Today, efficient use of nitrogen in European agricultural systems is required to maintain an optimal level of production within the restrictions set by European legislation, e.g. the Nitrate Directive (Council directive 91/676/EEC, 1991) which demands a nitrate concentration in groundwater lower than 50 mg l^{-1}.

Nitrogen losses from agricultural systems consist of gaseous emissions due to ammonification and denitrification from animal housing systems, from soil applied manure and from soil, and of nitrate leaching to groundwater and surface waters. In the Netherlands, denitrification from soil, other gaseous emissions (NH_3, N_2O, NO_x), and leaching, respectively, are estimated to account for losses of 37 ± 4 %, 14 ± 2 %, and 14 ± 2 % of total N input plus net mineralisation (data 1993, De Vries *et al.*, 2003). Another 7 ± 2 % of the leached N is denitrified.

Leaching from the root zone and denitrification from soil are thus responsible for a considerable part of the N losses. The leaching losses are especially problematic on sandy soils with a deep groundwater table, which have a naturally low denitrification rate. In these sandy soils, the nitrate concentration in the upper ground water in the Netherlands is, on average, 308 ± 174 mg l^{-1} under grassland and 126 ± 50 mg l^{-1} under arable land, compared to 27 ± 17 mg l^{-1} under non-agricultural land. Also, N losses to surface water are highest on sandy soils (1993, De Vries *et al.*, 2003).

Reduction of N leaching using catch crop cultivation

Nitrogen leaching occurs, in the temperate climate, mainly in autumn and winter, when rainfall exceeds evapotranspiration. On bare, flat arable land leaching is at its maximum, due to the absence of crop transpiration, crop N uptake and run-off. Leaching of nitrogen from arable land can be mitigated by several strategies.

Firstly, fertilizer use efficiency of crops can be maximized, thus minimizing the amount of residual (remaining) N in soil at harvest. This may work well in case of cereal crops, but for certain other crops, for instance potatoes and leafy vegetables, more N needs to be applied for optimal yield than the crop can take up during the growing season. These crops leave significant amounts of N in the soil and in crop residues at harvest (e.g. Jenkinson, 2001; MacDonald *et al.*, 1997; Vos & Van der Putten, 2000).

Secondly, leaching and denitrification of this residual N can be partially prevented. On arable land this can be done by immobilisation of N in organic materials with a low N concentration through their incorporation into the soil (e.g. De Neve *et al.*, 2004), or, more effectively, by cultivation of a catch crop after the harvest of the main crop, instead of leaving the soil fallow (Justes *et al.*, 1999; Landman, 1990; Vos & van der Putten, 1997). The catch crop may absorb residual N up to 200 kg N ha^{-1} and thus reduces N available for leaching and denitrification. The N uptake by the catch crop may depend on plant species, sowing date (determined by the harvest time of the previous crop), amount of available soil N and weather conditions. At the end of the catch crop growing season, just before or after winter, the crop can be harvested for fodder or be ploughed into the soil. After incorporation of the crop in the soil, N mineralization starts, so that, with a good timing, part of the mineralized N may become available for a next main season crop allowing the N application for this crop to be reduced (e.g. Vos & Van der Putten, 2001; Thorup-Kristensen, 1994; Thorup-Kristensen & Nielsen, 1998). Determining the optimal timing for incorporation is, however, not easy. Incorporating too early may lead to leaching of N later in the winter, incorporating too late may cause the catch crop to take up water and N that may otherwise be directly available for the succeeding crop, and mineralization of catch crop N may start too late.

Explaining variation in catch crop effects on N leaching

The N accumulation of catch crops and their effect on N leaching and N supply to a succeeding summer crop have been studied by many authors in various field experiments. Results show a considerable variation in effectiveness of catch crops in taking up nitrogen and reducing N leaching between sites, years, sowing dates and species (e.g. Elers & Hartmann, 1987; Landman, 1990; Schröder *et al.*, 1996). These variations have been attributed to differences in radiation intercepted by the catch crop (Vos & Van der Putten, 1997), temperature sum experienced from sowing onwards (Kersebaum, 1989; Schröder *et al.*, 1996) and root development (Thorup-Kristensen, 2001). Thorup-Kristensen *et al.*, (2003) state that catch crop growth is often N-limited, because the N-uptake capacity of the crop, determined by biomass production, tends to be larger than the catch crop N-uptake found in field experiments, unless the crop is established late or residual N is very high. There is, however, to my knowledge, no quantitative, systematic analysis of the possibilities to reduce N leaching by catch crop cultivation taking into account all weather variables and crop characteristics. With such an analysis, the importance of e.g. radiation and temperature for catch crop effects on N leaching may be compared. Also, selection of catch crops may then be well focussed using the results of this analysis, because in facilitates identification of desirable crop characteristics for various conditions. The aim of this study is to perform such an analysis and (1) explain variation in catch crop N uptake and reduction of leaching by catch crops with variation in weather conditions, N-availability and crop characteristics, and (2) identify desirable catch crop characteristics for selection and breeding and catch crop cultivation strategies for minimization of N losses from the crop-soil system.

Outline of this study

In this study, the effects of crop characteristics and weather conditions on catch crop N uptake and N leaching were evaluated using a simulation model integrating quantitative knowledge on all relevant processes within crop growth and crop and soil N dynamics. The model was used to identify desirable catch crop characteristics for selection and breeding, and catch crop cultivation strategies for minimization of N losses from the crop-soil system.

The model was developed for winter rye and fodder radish grown as catch crops. For model development, several experiments were conducted to quantify catch crop growth and N uptake, based on the rates of underlying processes like CO_2 assimilation, leaf and root expansion, and N uptake at the root level. Moreover, for the development and testing of the soil model, data were collected in detailed experiments on N mineralization rates of catch crop materials, soil water dynamics and N leaching. Other necessary data and process descriptions for model development and testing were taken from the literature.

In Chapter 2 of this thesis a pot experiment is described in which catch crop CO_2 assimilation rates were determined at the leaf scale and the appearance and turnover of leaves were recorded for winter rye and fodder radish. The temperature response of the N uptake capacity of the roots of these crop species was determined in a pot experiment with nutrient solution (Chapter 3).

Data for scaling up leaf CO_2 assimilation rates to the canopy level were collected in a Rhizolab experiment, measuring the CO_2 dynamics of crop canopies of about 1 m^2 (Chapter 4). The same experiments were used for acquiring detailed data on root development, on soil water dynamics and on nitrogen dynamics, especially on N leaching (Chapter 5). Nitrogen release from catch crop biomass, shoot and root, was measured in an incubation experiment with temperatures ranging from 1 to 15 °C (Chapter 6). The mineralization model developed and tested with these data is also described there. Chapter 7 and 8 give an account of the crop model that was developed and tested for winter rye and fodder radish. Chapter 7 gives the model description, calibration and validation. A sensitivity analysis and an exploration of the model by developing some scenario studies are presented in Chapter 8. Based on these, conclusions about the effect of weather conditions, catch crop management, soil N content and crop characteristics on N catching effectiveness are formulated. The results and methodology of the study and the possibilities for practical applications are discussed in Chapter 9.

Chapter 2

Leaf CO_2 assimilation and leaf dynamics in catch crops during autumn and winter at two levels of nitrogen supply

with E. A. Lantinga

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Abstract

This study relates the leaf CO_2 assimilation and leaf dynamics of nitrogen catch crops to environmental conditions. Winter rye (*Secale cereale* L.) and fodder radish (*Raphanus sativus* L.) were grown as catch crops in an outdoor pot experiment at two rates of nitrogen supply (N2 higher than N1) in Wageningen, the Netherlands, from August 1993 until April 1994.

Biomass increased with N increasing supply. There was no net growth after mid-November. The number of tillers in rye and of appeared leaves in radish were higher in N2 than in N1. Leaf appearance rate increased with temperature in fodder radish and rye. Tillering in rye ceased in mid-October. Leaf lifespan was related to the temperature sum between leaf emergence and leaf death. Leaf lifespan was 478 ± 68 °C day in fodder radish. In rye, the leaf lifespan gradually decreased from 592 ± 66 to 389 ± 25 °C day and from 545 (1 observation) to 401 ± 64 °C day in N1 and N2, respectively. In young leaves, A_{max} (light-saturated CO_2 assimilation rate) was approximately 1.2 mg CO_2 m^{-2} leaf s^{-1} in September and 0.5 mg CO_2 m^{-2} leaf s^{-1} later on, independent of species and N supply. N supply affected the organic N concentrations only in the older leaves. A_{max} was not dependent on temperature at measurement (range: 12-19 °C in September, 5-15 °C from November until March), but, in contrast, strongly related to temperature and irradiance during the preceding growth period. Leaf nitrate concentrations increased with N supply. Water-soluble carbohydrate concentrations were higher in N1 than in N2 and higher in rye than in fodder radish. They fluctuated during the season. It is concluded that overall growth rates were limited by process rates other than that of leaf CO_2 assimilation per unit leaf area in both N1 and N2.

Keywords: autumn, CO_2 assimilation, catch crop, fodder radish, irradiance, leaf appearance, leaf lifespan, site filling, temperature, winter rye, winter

Introduction

Many growth processes in plants have been well quantified under controlled temperature and irradiance conditions. In the field, crops often react differently to environmental factors from plants under controlled conditions, and growth processes are less well-understood in the field (Grace, 1988; Pollock & Eagles, 1988). Large variations in crop growth rates in the field in autumn and winter, at low irradiance and low temperatures (Vos, 1992; Lainé *et al.*, 1993), and the biomass production of overwintering crops, like nitrogen catch crops, cover crops, green manures, winter cereals, or grassland are only partly understood.

The effects of temperature, irradiance level and nitrogen supply on CO_2 assimilation rates have been studied under controlled conditions (e.g., Huner *et al.*, 1986; Dijkstra, 1989), but few data could be found for fluctuating autumn and winter field conditions. In some winter annuals, the optimum temperature for CO_2 assimilation shifts from 25-30 °C in summer to 15 °C in winter, while the maximum CO_2 assimilation rates per unit leaf area in winter are hardly lower than those in summer (Regehr & Bazzaz, 1976). In winter wheat grown under winter conditions (5 - 7 °C), however, the maximum CO_2 assimilation rate is about half that of plants grown at higher temperatures (25 °C) in a growth chamber (Sawada & Miyachi, 1974). In plants that were acclimated to winter conditions, light-saturated assimilation rates at air temperatures of 0 °C are about half those at the optimum temperature. The seasonal change in assimilation rates varies with species (Sawada & Miyachi, 1974).

At the molecular level, the tertiary and quaternary structure of ribulose bisphosphate carboxylase-oxygenase (RuBPCase) is influenced by growth temperature, resulting in a higher maximum carboxylation rate at low temperature and a lower temperature optimum in cold-hardened plants than in to non-hardened plants. Furthermore, thylakoids are altered by growth at low temperature, resulting in a greater capacity for electron transport (Huner, 1985). The combination of these features results in a higher maximum leaf CO_2 assimilation rate at low temperature in cold-hardened plants compared to non-hardened plants (Farquhar *et al.*, 1980). Irradiance conditions affect several factors determining the maximum leaf CO_2 assimilation: both the concentration of RuBPCase, and the capacity for electron transport are reduced at low irradiance levels, and mesophyll resistance is increased (Jones, 1992). But the effect of these changes on maximum leaf CO_2 assimilation in summer and winter in the field has not been well quantified.

Leaf appearance and turnover are important for determining the leaf area and thus for the estimation of gross and net growth in analysis of field experiments. Leaf appearance has often been related to temperature over winter (e.g. Hunt & Chapleau, 1986; Triboi-Blondel, 1988), but the variation is large. Leaf longevity data are scarce. In a perennial ryegrass (*Lolium perenne* L.) sward, the appearance and death rates of leaves are balanced, so that a constant number of leaves is present in the canopy (Harper, 1989). Therefore, leaf lifespan might also be related to temperature.

The aim of this study was to analyse growth and to determine rates of leaf CO_2 assimilation and leaf dynamics of catch crops during autumn and winter under Dutch conditions, and to relate process rates to the prevailing temperature and irradiance conditions. As catch crops are generally unfertilized and meant to minimize N losses from the soil, the processes were studied at two levels of N availability. Two contrasting species, chosen because they perform well as nitrogen catch crops, were compared. One was winter rye (*Secale cereale* L.), a monocot, which is frost resistant and performs relatively well when sown late. The other was fodder radish (*Raphanus sativus* L.), a dicot of the Brassicaceae, which accumulates large amounts of nitrogen under Dutch autumn conditions but is not winter-hardy.

Materials and methods

Plant cultivation

Winter rye (cv. Halo) and fodder radish (cv. Pegletta) were sown in drained 7.6 l pots filled with coarse sand, and thinned to 9 plants per pot after emergence. Rye was sown on 17 August 1993, fodder radish on 25 August 1993. A crop canopy with 100 plants m^{-2} was approximated with the pots, both for rye and radish. To reduce border effects, the pots were surrounded by an extra row of pots with plants of rye and radish, respectively. For exposure to ‘field’ weather conditions, the plants were grown outdoors in Wageningen (51° 58’ N), the Netherlands, until early April 1994. To reduce the risk of frost damage or early death, fodder radish was placed in an unheated greenhouse during frost periods from 19 to 20 October and from 16 November until 6 December. Despite this, the older leaves of fodder radish were affected by frost damage during the latter frost period.

There were two levels of nitrogen supply (Figure 1). One was aimed to be sufficiently high as not to limit crop growth (N2). N1 contained 30% of the N and 60% of the other nutrients of N2, so that growth was only limited by N shortage. Nutrients were added regularly using Steiner nutrient solution (Steiner, 1984). The N supply was matched to expected crop growth and nitrogen demand, following the patterns of

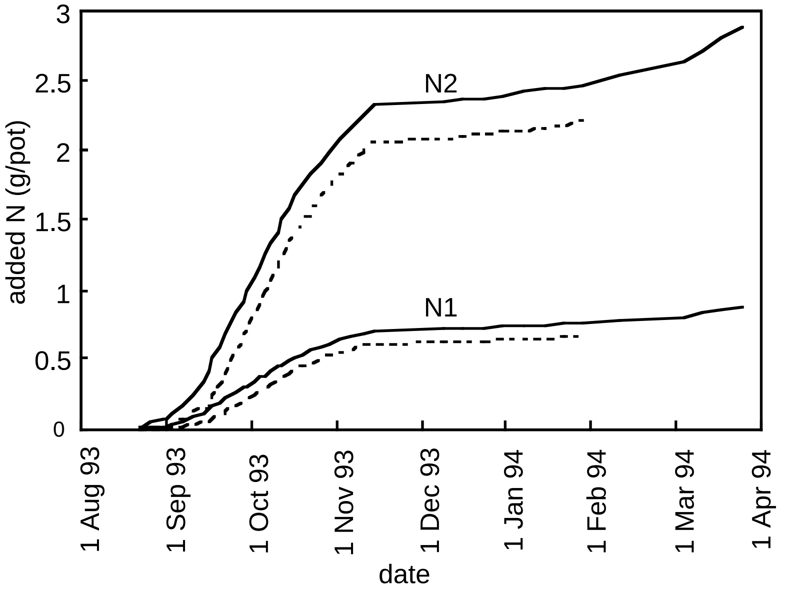

Figure 1. Cumulative amounts of N applied per pot during the experiment for fodder radish and winter rye at two N fertilisation levels. Solid line: rye; dashed line: radish.

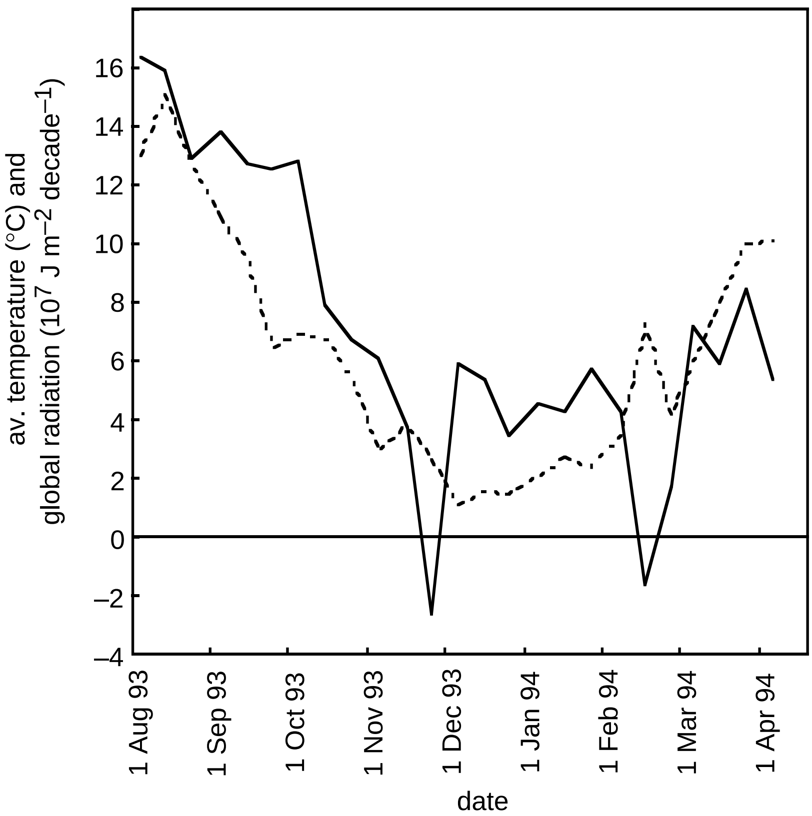

Figure 2. Average temperature and global irradiance per decade from August 1993 until March 1994. Solid line: temperature; dashed line: global irradiance.

irradiance and temperature (Figure 2). The soluble N content of the coarse sand was 57 ± 15 mg per pot (0.63 ± 0.17 g m^{-2}) before fertilization.

Leaf dynamics

The appearance and death of leaves on the main stem in both species and the number of tillers in rye were recorded at intervals varying from two days to one month, dependent on the season (Table 1), so that generally not more than one leaf had appeared and not more than one or two leaves had died between successive leaf countings. A leaf was recorded as appeared when more than about 0.25 cm^2 of the new leaf was visible. A leaf was recorded as dead when more than 50 % of its area was yellow, brown or frozen.

Leaf lifespan was calculated for those leaves of which both appearance and death were timely recorded.

CO_2 assimilation and leaf analysis

At several moments during the experiment (Table 1) leaves from successive leaf positions on one stem or tiller were selected. Only leaves without any sign of frost damage wereused. Young, full-grown leaves (age 1) were chosen because they were

Table 1. Dates of measurement of numbers of tillers, and appeared and dead leaves, biomass, A_{max} and leaf composition. Days are marked with ‘wr’ or ‘fr’, if measurements were done only on winter rye or fodder radish, respectively. *On this date only young leaves of age 1 were measured, not of age 2 and 3.

month	leaf number	biomass number of tillers	A_{max} leaf composition
August	30 wr		
September	1 wr, 3 wr, 6 wr, 8 wr, 10, 13, 15, 18, 21, 23, 27	27	24*
October	4, 11, 18, 25		
November	8	22	18-19
December	9		
January	10	26 fr	24 fr
February	7	10 wr	10 wr
March	4 wr	29 wr	29 wr

expected to have the highest assimilation rates. After September, also the second youngest and, when present, third youngest leaves on the same stem or tiller (age 2 and age 3) were selected. Light saturated net CO_2 uptake rates (A_{max}) and leaf chamber temperatures were measured with a portable leaf CO_2 assimilation meter (ADC Ltd., Hoddesdon, Herts. UK) on four leaves per age class per pot. A saturating light intensity was imposed with a Philips 12 V 75 W halogen lamp. The leaf temperature in the leaf chamber fluctuated during the days of measurement, due to warming by the lamp. To relate rates of CO_2 assimilation and overall growth to leaf characteristics, the leaves were harvested per age class per pot for further analysis after the A_{max} measurements.

Intact leaves were sampled for rye at all measurements, but for fodder radish only in September. After September, the thick veins in the fodder radish leaves were excluded, to make the samples representative for the leaf blades on which A_{max} was measured. Leaf areas and dry weights and total N concentrations (Novozamsky *et al.*, 1974, 1983) were determined. Concentrations of nitrate (Walinga *et al.*, 1989) and water soluble carbohydrates (total reducing sugars; Bran & Luebbe method NL 208-89FT) were measured after extraction in water (Walinga *et al.*, 1989, but with heating of the samples in the extraction fluid to 100 °C for 15 minutes before filtering). Organic N concentrations were calculated as the difference between total N and nitrate concentrations.

Biomass

Dry weights were measured on samples of above-ground biomass of 3 or 4 plants from the pots used for the CO_2 assimilation measurements on the dates indicated in Table 1.

Use of weather data

Weather data were recorded at 2 km distance from the experimental site at the same elevation. Daily average temperature was calculated as the average of maximum and minimum temperature. Photoperiod was calculated according to Goudriaan & Van Laar (1994) for relating CO_2 assimilation rate to radiation conditions. To establish a relation between leaf lifespan and weather conditions, the leaf lifespan was related to temperature sum, with an assumed base temperature of 0 °C. For other species temperature sum proved a good measure for predicting leaf lifespan (Leong & Ong, 1983; Ingram, 1980). It is useful for modelling leaf turnover (e.g. Van Keulen & Seligman, 1987; Spitters *et al.*, 1989).

To find the relation between temperature and leaf appearance rate, the average leaf appearance rate on the main stem between measurements was plotted against the average above-zero temperature in the same interval. Temperatures below zero were counted as zero, because leaf appearance rate was assumed to be zero at below zero temperatures (e.g. Hunt & Chapleau, 1986). Including below zero temperatures otherwise in the averages would yield an irrealistic view on the relationship above the base temperature. To reduce scatter due to measurement errors, intervals were chosen in which at least one leaf had appeared.

Statistical analysis

CO_2 assimilation measurements and leaf analysis were performed on 4 leaves per age class in each of 3 replicate pots in each combination of species, nitrogen supply and measurement date. Leaf dynamics and number of tillers (rye only) were recorded on 2 plants in 3 replicate pots in each combination of species and nitrogen supply. The pots were randomized per combination of species and N supply.

The experiment was set up as a split-plot design with species at the block stratum, N supply level at a sub-block stratum, month of measurement at a pot stratum and leaf age at the unit stratum. For biomass, A_{max}, and the concentrations of leaf organic nitrogen, nitrate and water-soluble carbohydrates, variance components were estimated by the method of residual maximum likelyhood (REML, Anonymous, 1993) and treatment effects were tested with the c-squared test. No distinction could be made between the effects of block and of species. The block effect was assumed to be absent, which is plausible because soil and weather conditions were the same.

For testing a possible relation of A_{max} to leaf chamber temperature, a regression model was used with linear terms for the treatments and two-way interactions between the treatments and leaf chamber temperature.

The temperature sums during the lifespan of the leaves of each species were linearly fitted to leaf number. The effect of N supply level on the fitted lines was tested with the F-test. Time courses of the numbers of appeared and dead leaves were fitted per species with expolinear curves and those of the numbers of tillers in rye with second-order rational functions. With the help of these curves, the effect of N supply on the time course of tiller numbers and numbers of appeared and dead leaves was tested by the F-test. Moreover, the relation of leaf appearance rate to temperature, often found in literature (e.g., Hunt & Chapleau, 1986; Hay & Abbas Al-Ani, 1983), was tested by fitting it to temperature and temperature squared. Significance of the terms was tested with the F-test. All analyses were conducted in Genstat (Anonymous, 1993).

Results

Biomass and development

Aboveground biomass (Figure 3) was higher in N2 than in N1 ($P < 0.001$) and did not increase after the second measurement on 22 November. Net growth is also absent in field experiments, after mid-November (Vos & Van Der Putten, 1997). Apparently, under Dutch conditions most of the growth of catch crops takes place before mid-

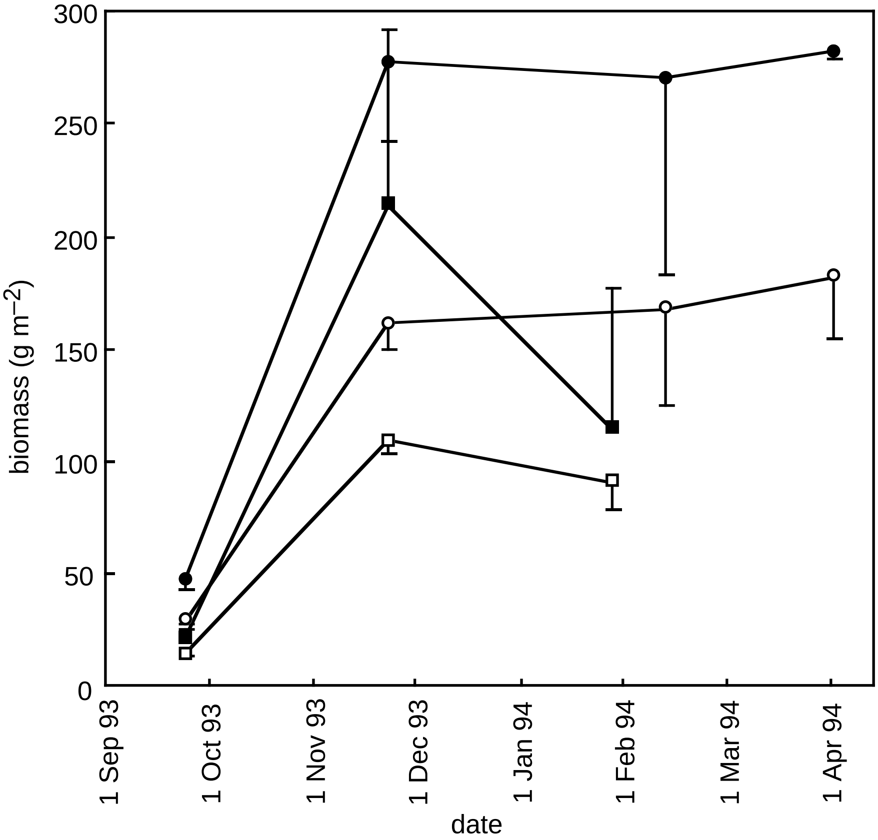

Figure 3. Aboveground biomass in fodder radish and winter rye at N1 and N2 from August 1993 until March 1994. Standard deviations are given by bars in one direction, when larger than the symbol. Symbols: —○— = rye N1, —●— = rye N2, —□— = radish N1, —■— = radish N2.

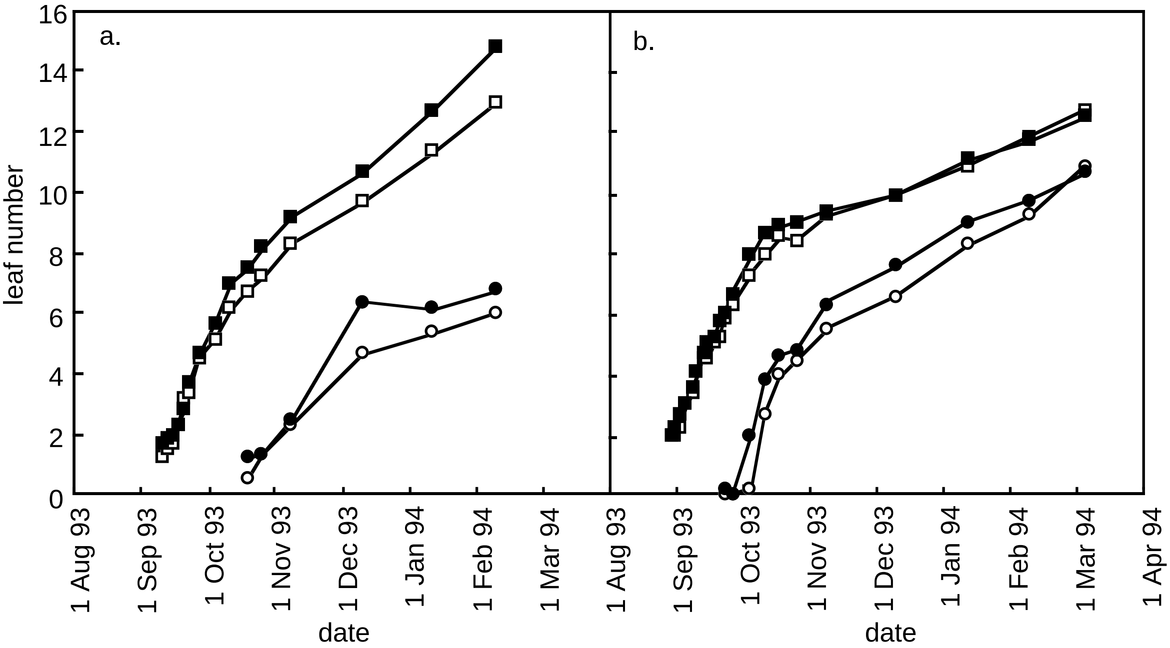

Figure 4. The number of appeared and dead leaves on the main stem in fodder radish and winter rye at N1 and N2 from August 1993 until March 1994. a. Fodder radish; b. Winter rye. Symbols: —□— (N1), —■— (N2) = appeared leaves; —○— (N1), —●— (N2) = dead leaves.

November. This is also to be expected because of the low levels of irradiance and temperature after early November (Figure 2). Biomass was higher in rye than in fodder radish, that was sown eight days later. The decrease in fodder radish biomass after November is attributed to normal turnover (cf. Vos & Van Der Putten, 1997) and to frost damage, which occurred despite transfer of the plants to the (unheated) greenhouse. Fodder radish froze to death in the second half of February, so that no later measurements could be made.

Stem elongation in fodder radish started around mid-October. Branches were initiated in leaf axils, but did not expand. Flower buds appeared from January onwards, but no flowering occurred. During the whole experiment, rye stems did not elongate.

Leaf and tiller dynamics

The numbers of appeared and dead leaves on the main stem are presented in Figure 4. Leaf appearance rate was high in September, and slowed down at about mid-October. The number of appeared leaves was higher in N2 than in N1 ($P < 0.001$ in fodder radish, $P = 0.007$ in rye), but in rye the difference was small and occurred for a short period only. The number of dead leaves was higher in N2 than in N1 ($P = 0.01$ in radish, 0.02 in rye). In N2 many older fodder radish leaves died during the frost period at the end of November. The number of living leaves on the main stem is represented by the vertical distance between the appearance and death curves, or, before the first leaves died, the appearance curve and the time axis. In rye, the number of living leaves on the main stem

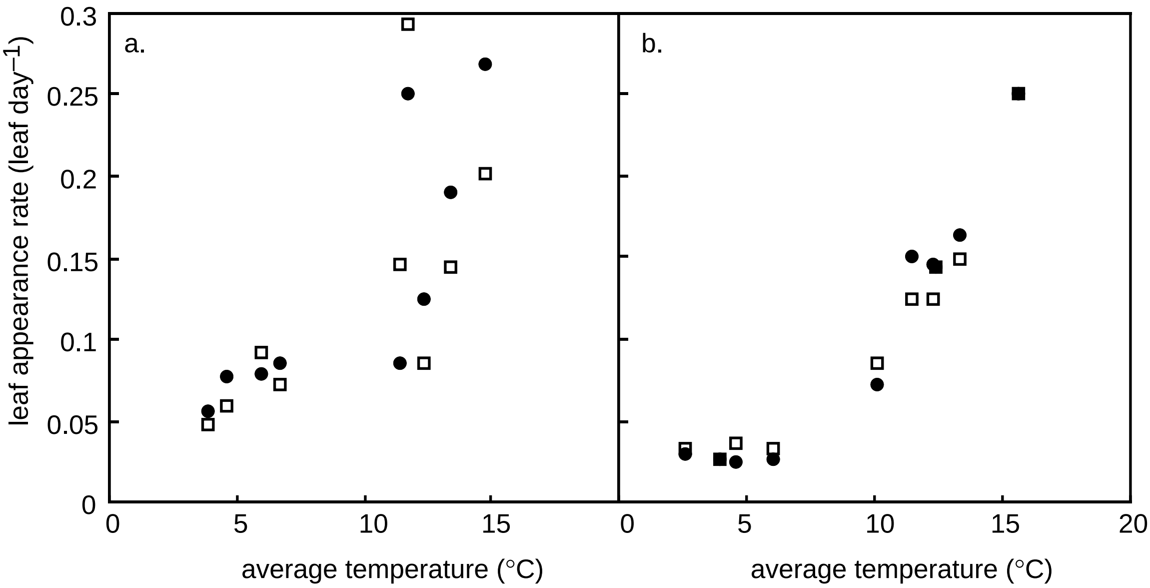

Figure 5. The leaf appearance rate as a function of average temperature during intervals of the growing season. a. Fodder radish; b. Winter rye. Symbols: □ = N1; ● = N2.

increased until the first leaves died, then decreased gradually. The same pattern was found for leaves on other tillers (data not shown). In fodder radish, the number of living leaves increased until the death of the first leaf, and was almost constant afterwards, except for a temporary decrease after the frost period in November.

The leaf appearance rate on the main stem increased with temperature in both species ($P < 0.001$, Figure 5). In rye it was significantly nonlinear ($P < 0.001$). Between 2 and 5 °C, rye leaf appearance rate was constant, and it increased only above this temperature. This may have been caused by the way of calculating average temperature: by taking daily average temperatures, and then averaging over the period between measurements counting negative temperatures as 0 °C. Just above the base temperature for leaf appearance this may lead to overestimation of the leaf appearance rate, because a low daily average temperature may be the average of temperatures fluctuating around the base temperature (e.g., 3 °C may be the daily average of 8 and -2 °C or of 5 and 1 °C, which can have different effects on leaf appearance rate when the base temperature for leaf appearance rate is 0 °C). It may also be, however, that leaf appearance rate does indeed increase nonlinearly with temperature near the base temperature, or that air temperature is not exactly the same as the temperature at the sit of leaf initiation.

The lifespan of the leaves expressed in degree days was 478 ± 68 °C day for fodder radish. In rye it decreased from leaf 1 (living from August until October) to leaf 9 (November-February) from 592 ± 66 to 389 ± 25 °C day at N1 and from 545 (one observation) to 401 ± 64 °C day at N2. Deaths of the first 5 and 9 leaves were recorded in all plants in fodder radish and rye, respectively. It is not clear whether the decrease that was found in rye also occurred in fodder radish, because less of its leaves were monitored. For rye, the lifespan of N2 leaves was, on average slightly shorter than that of N1 ($P = 0.01$). The N2 rye plants had rather soft leaves that were pushed down by

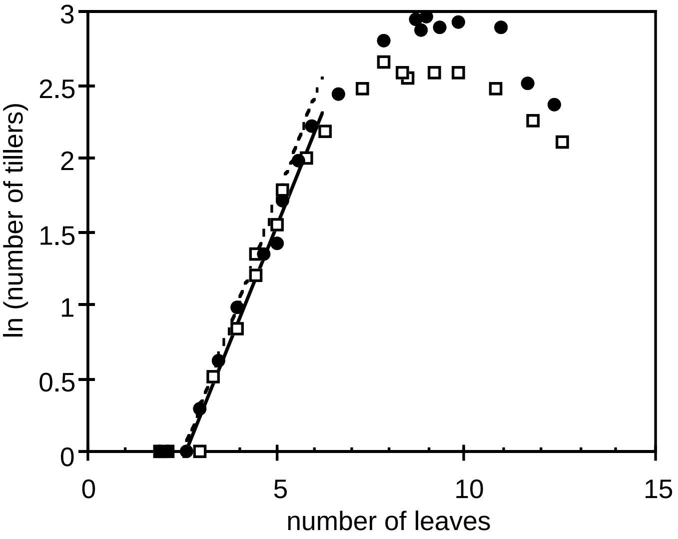

Figure 6. The natural logaritm of the number of tillers per plant in winter rye at N1 and N2, as a function of appeared leaf number. Symbols as in Figure 5. Solid line: mean site filling; dashed line: potential site filling.

wind. As a result the lower leaves were strongly shaded or completely covered by the young parts of the canopy.

The natural logaritm of the number of tillers in rye was plotted against the number of appeared leaves on the main stem (Figure 6). The number of tillers increased until the appearance of the eighth leaf (mid-October), at both N supply levels. Then it remained constant until January, and then gradually decreased until the end of the experiment. The slope of the curve expresses the mean site filling, i.e. the relative increase in tiller number per leaf appearance interval. Until the appearance of the sixth leaf it was 0.629 for both N supplies, rather close to the theoretical maximum of 0.693 (Neuteboom & Lantinga, 1989). After that it decreased to zero, more rapidly in N1 than in N2, resulting in a maximum of 14 and 19 tillers per plant in N1 and N2, respectively (a significant difference, $P < 0.001$).

CO_2 assimilation and leaf analysis

A_{max} was about 1.2 mg CO_2 m^{-2} leaf s^{-1} in September and significantly lower, about 0.5 mg CO_2 m^{-2} leaf s^{-1} during the winter months for both species (Figure 7; $P < 0.001$). A_{max} decreased with increasing leaf age ($P < 0.001$), as previously found for potato (*Solanum tuberosum* L.) (Vos & Oyarzún, 1987) and wheat (*Triticum aestivum* L.) (Keys *et al.*, 1983). This decrease was generally small, compared to the effect of month of measurement. A_{max} was independent of N supply. There was no relation between A_{max} and leaf chamber temperature, in the range from 12 to 19 °C in September and from 5 to 15 °C in the other months (data not shown).

Leaf organic nitrogen concentrations increased slightly with N supply ($P < 0.001$) (Figure 8), especially in the older leaves. They decreased with leaf age ($P < 0.001$), from

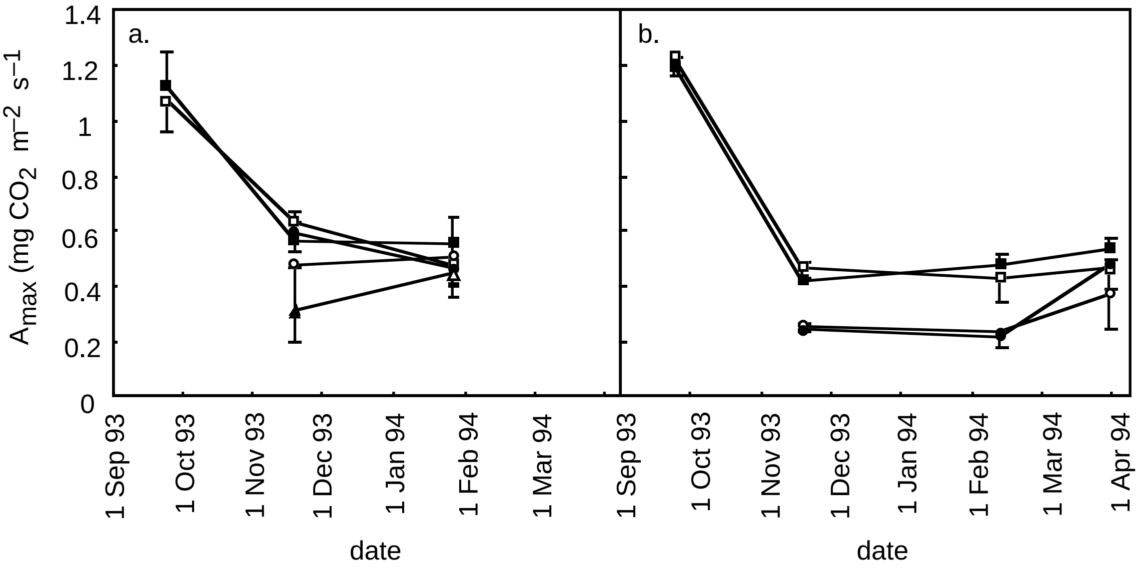

Figure 7. The light saturated CO_2 assimilation rate (A_{max}) in fodder radish and winter rye at N1 and N2 from September 1993 until March 1994. a. Fodder radish; b. Winter rye. Standard deviations are given by bars in one direction, when larger than the symbol. Symbols: —□— (N1), —■— (N2) = age 1; —○— (N1), —●— (N2) = age 2; —△— (N1), —▲— (N2) age 3.

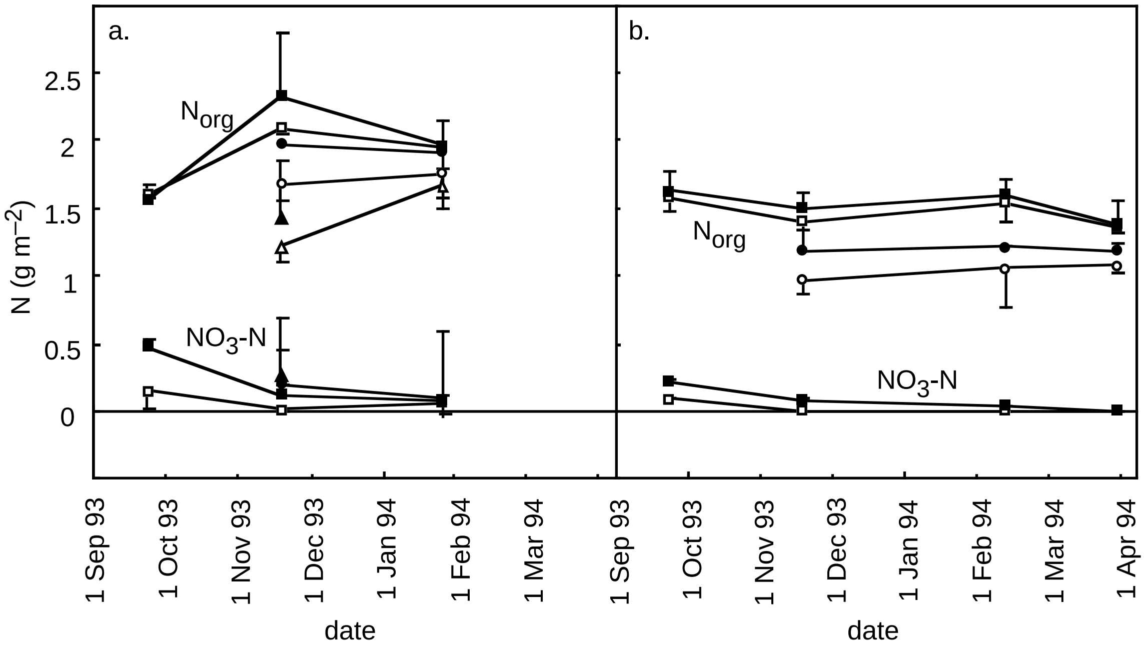

Figure 8. The leaf contents of organic (N_{org}) and nitrate (NO_3^--N) nitrogen in fodder radish and winter rye at N1 and N2 from September 1993 until March 1994. a. Fodder radish; b. Winter rye. Standard deviations are given by bars in one direction, when larger than the symbol. Nitrate levels were zero in leaf ages 2 and 3 at N1 in Fodder radish, and leaf age 2 in rye at both N-levels. These are not included in the figure. Symbols as in Figure 7.

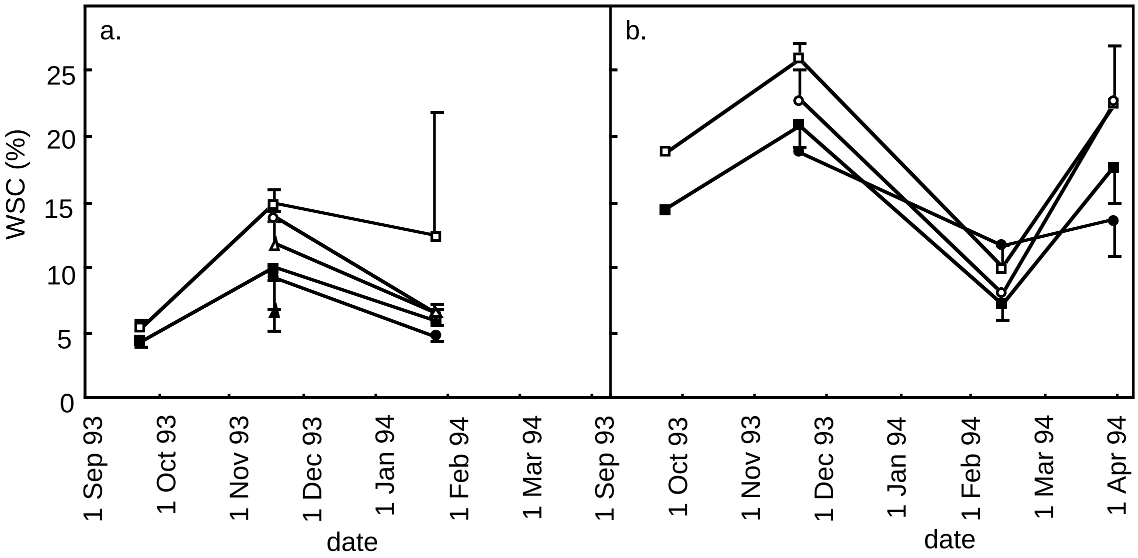

Figure 9. The leaf contents of water soluble carbohydrates (WSC) in fodder radish and winter rye at N1 and N2 from September 1993 until March 1994. a. Fodder radish; b. Winter rye. Standard deviations are given by bars in one direction, when larger than the symbol. Symbols as in Figure 7

1.5 ± 0.14 g m^{-2} at age 1 to 1.1 ± 0.16 g m^{-2} at age 2 in rye and from 1.9 ± 0.30 g m^{-2} at age 1 to 1.5 ± 0.30 g m^{-2} at age 3 in fodder radish, averaged over time and N supply levels. Nitrate concentration increased with N supply ($P < 0.001$, Figure 8) and decreased during the experiment from a high level in September to low values for both species at the end of January and to zero for rye on 4 March ($P < 0.001$). The highest value (0.47 ± 0.05 g m^{-2}) was found in radish at N2 in September.

Water-soluble carbohydrate concentrations in the leaves (Figure 9) were higher in rye than in fodder radish ($P < 0.001$) and higher in N1 than in N2. They fluctuated during the season ($P < 0.001$), with a peak in November for both species (up to 25.8 ± 1.2 % and 14.8 ± 1.1 % in rye and radish, respectively, at N1; percentage on a mass base) and lower values in September, January (fodder radish) and February (rye). They increased again in rye in March.

Model development

Relating light-saturated CO_2 assimilation rates to weather variables

The decrease in A_{max} from September onwards, similar in rye and radish (Figure 7), might be related to the decrease in temperature and irradiance level during autumn. Both factors affect the maximum CO_2 assimilation rate (Huner, 1985; Jones, 1992), and may be used to estimate A_{max} in varying conditions (e.g., Sheehy *et al.*, 1980). Below, models are formulated to relate A_{max} to temperature and irradiance during leaf development. With the models A_{max} could be estimated for situations other than those of the experiment. The estimated A_{max} may then be used to calculate crop growth rates in process-based simulation models.

For estimating A_{max} from the growth conditions of the leaves, the period of leaf growth must be determined. This period varies during the season; it is longest in winter (Harper, 1989). Van Loo (1993) estimated the duration of leaf expansion at 1.3 times the phyllochron in perennial ryegrass. The phyllochron in rye varies from 56 to 157 °C days (Van Dobben, 1962; Hay & Abbas-Al Ani, 1983) and for radish a phyllochron of 69 and 79 °C days can be calculated for N2 and N1, respectively, from the above data. These phyllochrons take 3.6 to 10 days at 16 °C and 14 to 39 days at 4 °C, which are the extremes in average temperature per decade in this experiment (Figure 2) when frost periods are excluded. If the duration of leaf expansion is estimated according to Van Loo (1993), it will last 4.6 to 51 days. A value of 20 days is taken as an estimate; this is closer to the period of leaf growth expected at the higher than at the lower temperatures, because more leaves appear at higher temperatures. Two models are proposed that relate A_{max} in young fully expanded leaves to (1) the average temperature and (2) the average irradiance intensity during 20 days before the measurement:

Model 1: $A_{max} = a \times T$
Model 2: $A_{max} = b \times I$

in which T is the average temperature (°C) and I the average global irradiance intensity during the photoperiod (J m^{-2} s^{-1}) during 20 preceding days. a and b were fitted using the A_{max} data of the young full-grown leaves grown at N2. The resulting values were: a = $8.875 * 10^{-2}$ mg CO_2 m^{-2} s^{-1} $°C^{-1}$ and b = $4.685 * 10^{-3}$ mg CO_2 J^{-1}. Both models had a high correlation coefficient, Model 1 even higher than Model 2. The difference in correlation is, however, determined by one point, that of the measurement on rye in March (Figure 10).

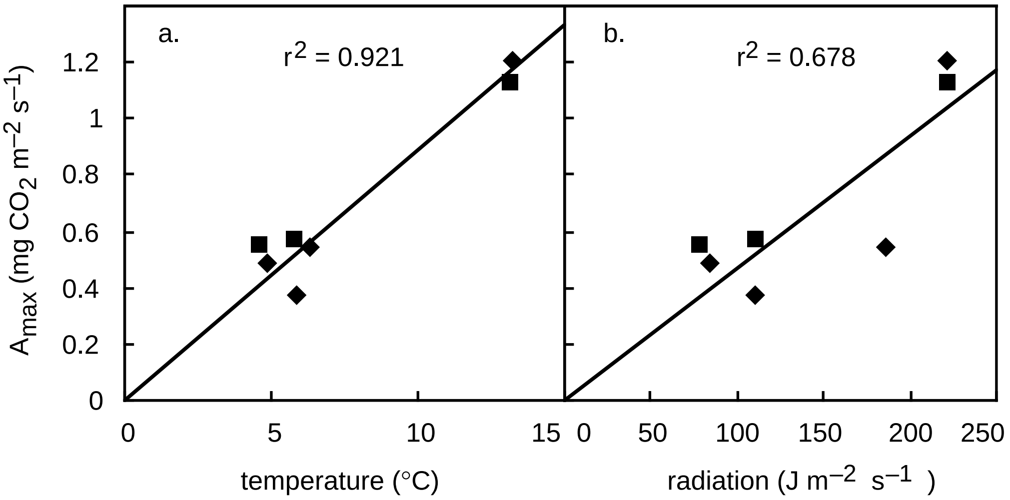

Figure 10. Fits of two models relating the light saturated CO_2 assimilation rate to temperature and radiation conditions during growth of the leaves. Curves are fitted models, symbols are observations. a. Model 1. b. Model 2. Symbols: ■ = radish; ◆ = rye.

Discussion

Leaf and tiller dynamics

N2 resulted in a higher leaf appearance rate in radish (Figure 4a) and a higher number of tillers in rye (Figure 6), compared to N1. Therefore the total number of produced leaves was higher in N2 than in N1 in both species. Differences in biomass with N supply (Figure 3) are larger than differences in numbers of tillers and leaves; sizes, thicknesses and mass densities of leaf blades and sheaths and radish stems may also have been important. Sizes of the harvested leaves indicate that leaf areas were generally larger at N2 than at N1, but there was little difference in specific leaf areas (data not shown). There was an effect of N on site filling only after appearance of the sixth leaf. This is in accordance with another study in which there was no effect of N supply on site filling of young plants (*Lolium perenne* L.), unless the supply was reduced to a very low level (Neuteboom *et al.*, 1988).

The leaf lifespan in degree days was shortened at N2 in rye, which may have been due to increased shading in the denser canopy and to a higher sensitivity to frost. Vine (1983) found this higher frost sensitivity in perennial ryegrass under autumn and winter conditions.

If leaf appearance rate in rye does indeed increase nonlinearly with temperature (Figure 5b), a linear temperature sum with a certain base temperature, as often used in leaf appearance studies (e.g. Hunt & Chapleau, 1986), cannot be used unequivocally for rye. In field experiments conducted over winter, low temperatures coincide with low irradiance (Figure 2), denser canopies (more biomass, Figure 3) and shorter daylengths (data not shown), which may reduce leaf appearance rates (J.C.J. Groot, pers. comm.; Baker & Gallagher, 1983). A nonlinear relation may therefore have been a ‘pure’ response to temperature, or it has been confounded by interactions with other growth conditions. The differences found in the relation of leaf appearance rate and temperature, from one year or sowing date to another (Hunt & Chapleau, 1986; Hay & Abbas Al-Ani, 1983) suggest the importance of other factors.

Both leaf appearance and leaf lifespan are related to temperature. They appear to be balanced, resulting in a rather constant number of living leaves in the canopy, as was found in perennial ryegrass (Harper, 1989). The temperature sum since the appearance of a leaf appears to be an almost constant parameter for prediction of its lifespan. The decrease in temperature sum during leaf lifespan observed in rye may have been due to unfavourable winter conditions, with low irradiance levels and frost. Therefore other factors, such as shading, low irradiance levels and below-zero temperatures, should also be taken into account.

CO_2 assimilation and leaf analysis

The temperature at measurement did not influence A_{max} above 5 °C, contrary to observations on rye and oilseed rape under controlled conditions (Huner *et al.*, 1986; Paul *et al.*, 1990), and temperature responses of gross CO_2 assimilation used in growth models for spring wheat, winter wheat and spring barley (*Hordeum vulgare* L.) (Spitters *et al.*, 1989; Hansen *et al.*, 1990).

Leaf development conditions affected A_{max} much more than current temperatures during the measurements. The high correlation coefficients of the models predicting A_{max} based on temperature and irradiance during leaf growth suggest that these may be useful parameters for estimating CO_2 assimilation rates of autumn and winter grown crops (Figure 10). Model 1 explained, in statistical terms, a little more variation in the data than Model 2. Low temperature and low irradiance usually occur simultaneously, however (Figure 2). The difference in correlation between Models 1 and 2 depends mainly on one point (Figure 10), so that no conclusion on the best predictive factor can be drawn from these data only. The models have to be tested in other situations to evaluate their applicability for prediction of CO_2 assimilation rates.

The difference in aboveground biomass between N1 and N2 (Figure 3) is unlikely to have been caused by differences in A_{max} (Figure 7); A_{max} differed between N1 and N2 only in the oldest leaves. The lower A_{max} in these leaves can have affected canopy CO_2 assimilation only slightly (Baker *et al.*, 1988). Since quantum yield is not either influenced by nitrogen availability (Farquhar *et al.*, 1980; Connor *et al.*, 1993; Tei *et al.*, 1993), processes other than leaf CO_2 assimilation must have limited the overall biomass production in N1 as compared to N2.

The concentration of soluble carbohydrates (Figure 9), the primary products of CO_2 assimilation, was higher in N1 than in N2, indicating that a shortage of N in N1 limited the conversion of soluble carbohydrates into structural biomass. This view is supported by the lower nitrate-N concentrations in N1 in September (Figure 8), and values near zero in N1 by November. This indicates that the conversion of soluble carbohydrates to structural biomass rather than CO_2 assimilation, limited the overall growth rate in N1. Apart from this, in N1 a greater part of the assimilates may have been allocated to the roots than in N2 (Brouwer, 1962). As a result of a lower rate of conversion to structural biomass and a possibly higher allocation to roots, the canopy may have closed later in N1, so that total light interception and canopy CO_2 assimilation were lower than those in N2.

The peak in water-soluble carbohydrate concentrations in November for both N supply levels suggests that the plants either stored carbohydrates for other use than in structural biomass, or that the rate of conversion to structural biomass was more limited than that of production of assimilates at both N supply levels. In case of the latter, this sink-limitation may have been due to nitrogen shortage in N1, but this is unlikely for N2, since nitrate was still present in the leaves in November (Figure 8). Low temperature can therefore be considered as the decisive factor, for both a limited conversion rate and for storage of water-soluble carbohydrates (e.g. for prevention of frost damage). By January, water-soluble carbohydrate concentrations had fallen in all treatments, after a period of short days with low irradiance, resulting in low CO_2 assimilation rates relative to conversion rates. In March, the water-soluble carbohydrate concentrations in the rye leaves had increased again, possibly due to the higher irradiance level.

We conclude that all measured growth-related parameters indicate that under Dutch conditions, vigorous catch crop growth takes place only before mid-November. Net growth ceases afterwards under the conditions of the experiment. Leaf appearance slowes down in October and tiller production in rye stops. Light-saturated net CO_2 assimilation rates are halved between September and November. Assimilates accumulate in the leaves during November.

Both leaf appearance rate and leaf lifespan are related to temperature. The resulting temperature sum during leaf lifespan may be used for estimation of turnover of leaves in winter grown crops. Light-saturated CO_2 assimilation rates can be estimated from leaf development conditions, which may improve estimation of biomass production of autumn and winter grown crops.

Chapter 3

Nitrate uptake by winter rye and fodder radish at low nutrient solution temperatures

with Lester Hüner

Abstract

Nitrate uptake rates in the catch crops winter rye (*Secale cereale* L. cv. Halo) and fodder radish (*Raphanus sativus* L. cv. Adagio) were measured at low root temperatures. Plants were pre-cultivated on a complete nutrient solution in two greenhouse experiments (air temperatures fluctuating from 6 to 35 °C in the first experiment and stabilized at 20 °C in the second experiment), then starved for N on nutrient solution without N at temperatures of 3, 10 and 17 °C, respectively, and finally exposed to a complete nutrient solution again with 1.2 mM nitrate. The depletion of nitrate from the solution was measured until no further decrease in concentration could be measured. The maximum nitrate uptake rates per unit of root length were estimated from the time course of nitrate depletion in the solution. The dry weights of roots and shoots and the specific root length were determined.

The maximum nitrate uptake rate strongly increased with temperature between 3 and 10 °C, and slightly between 10 and 17 °C. It varied from 0.068 ± 0.010 to 0.244 ± 0.050 μmol m^{-1} h^{-1} in rye and from 0.068 ± 0.025 to 0.275 ± 0.142 μmol m^{-1} h^{-1} in fodder radish. In Experiment 1, specific root length increased with temperature from 181 to 225 ± 27 m g^{-1} in rye and from 295 ± 29 to 409 ± 34 m g^{-1} in fodder radish between 3 and 17 °C root temperature, but there was no such clear trend in Experiment 2. Shoot root dry weight ratios decreased with increasing root temperature. The observations suggest a limitation in root extension rate at low temperatures. It was concluded that low temperature decreased both root growth and nitrate uptake.

Introduction

The success of catch crops in reducing nitrogen leaching and increasing nitrogen fertilizer efficiency depends on their ability to accumulate nitrogen under the growth conditions of autumn and winter, and their influence on the availability of nitrogen to the succeeding crop (Elers & Hartmann, 1987; Thorup-Kristensen, 1993b). Low temperatures and radiation levels limit crop growth and nitrogen accumulation in autumn and winter by limiting rates of growth processes like photosynthesis, extension of leaves and roots, and nutrient uptake. The overall effect on crop nitrogen accumulation can be estimated from the effects of environmental conditions on the rates of these processes.

One of the vital processes in catch crop growth is the uptake of nitrogen, which, in arable soils, is available to crops mostly in the form of nitrate (Young & Aldag, 1982).

The rate of nitrate uptake per unit of root mass varies with crop species and depends on the crop demand for nitrogen, the supply of nitrate to the roots and the capacity of the roots to absorb nitrate. When nitrate is both demanded by the plant and supplied to the roots, the uptake capacity, or maximum uptake rate, is mainly influenced by previous nitrate supply levels (Lainé *et al.*, 1993; Lee & Rudge, 1986), carbohydrate supply to the roots (Rufty *et al.*, 1992) and root temperature (Glass *et al.*, 1990; Lainé *et al.*, 1993).

Several studies have been undertaken to quantify the effect of temperature on the maximum nitrate uptake rate in roots, in the temperature range of 3 to 35 °C (Clarkson *et al.*, 1986; Cumbus & Nye, 1982). For catch crops experiments at temperatures under 7 °C (Lainé *et al.*, 1994) are not available. During catch crop growth under West European field conditions, soil temperatures can vary from below zero to over 20 °C. Therefore, information on the temperature effect on maximum nitrate uptake rate in this full range is needed to assess how maximum nitrate uptake rate may affect overall crop growth and nitrogen accumulation in this region.

The objective of this study is to assess the effect of root temperature on the maximum nitrate uptake rate by catch crops roots when no transport limitations of nitrate to the roots are present and the crop demands nitrogen. Additionally, the root temperature effect on plant weights, shoot root ratios and specific root length were determined. The results will be used in a simulation model (Chapter 7) to assess the effect of variation in the maximum nitrate uptake rate of the roots on the overall crop growth and nitrogen accumulation.

Materials and methods

General

In two experiments, catch crop plants were grown under different greenhouse conditions, to assess the influence of root temperature on the maximum nitrate uptake rate. The experiments consisted of three phases: 1. The plants were cultivated on Steiner nutrient solution (Steiner, 1984), in which nitrogen was supplied as 12 mM nitrate. 2. They were acclimated to different root temperatures of 3, 10 and 17 °C on an adapted Steiner solution without nitrogen, during six days. The plants were starved for nitrogen to increase maximum nitrate uptake rates upon resumption of nitrate supply (Lee & Rudge, 1986), and to ensure the presence of a nitrogen demand. 3. Nitrate depletion was measured in ten times diluted, complete Steiner solution, with a nitrate concentration of 1.2 mM, at different root temperatures. The solution was diluted to 1.2 mM to improve the accuracy of measurements of nitrate concentrations, by a nitrate electrode. This concentration is still high enough to prevent limitation of uptake by nitrate availability (Lainé *et al.*, 1993).

Two contrasting catch crop species were used. One was winter rye (*Secale cereale*

L., cv. Halo), a monocot, which is winter-hardy under West European conditions and performs relatively well when sown late. The other was fodder radish (*Raphanus sativus* L., cv. Adagio), a dicot of the Brassicaceae, which performs well under West European conditions but freezes to death in most winters.

Experiment 1

Experiment 1 was conducted in a greenhouse without temperature control in Wageningen, The Netherlands, from 7 June to 21 July, 1994. It started in rather cool weather, with minimum and maximum temperatures of 6 to 13 °C and 15 to 22 °C respectively, which changed to unusually warm weather from 24 June onwards, with minimum and maximum temperatures from 9 to 20 °C and from 19 to 32 °C, respectively (weather data from the station at Haarweg, Wageningen, at 2 km from the greenhouse, at the same elevation). The air temperatures in the greenhouse tended to be 0 to 5 °C higher.

Seeds of winter rye and fodder radish were sown on 7 June, 1994. The seedlings were transferred to aerated Steiner nutrient solution (4 plants on 1 l solution). The pH was maintained between 6 and 7 and rye was supplied with ample $FeSO_4$ in acid medium 3 times per week, because the Steiner solution contained Fe coupled to EDTA, which cannot be taken up by rye. Presence of nitrate was monitored daily with a test strip (Merck, Darmstadt, Germany). The nutrient solution was replaced when nitrate was almost or completely depleted.

After 29 and 36 days for radish and rye respectively, the nutrient solution was replaced by an adapted Steiner solution without nitrogen, which was cooled to 3, 10 and 17 °C.

Six days later the solution without nitrogen was replaced by temperature controlled 10 % complete Steiner nutrient solution, with nitrate at a concentration of 1.2 mM. The depletion of nitrate in the solution was monitored by taking 25 ml samples, which were replaced by water. Four to seven equidistant samples were taken between transfer of the plants to the nitrate containing solution and the moment of complete depletion (time intervals were 1 to 5 h). Transpiration was compensated for by adding water, so that roots did not dry out. The pots with solution but without the plants were weighed before and after the nitrate depletion for determining the solution volume.

Nitrate concentrations were measured with a nitrate sensitive electrode (Type: PW 9413, Philips, Eindhoven, The Netherlands) connected to a millivolt meter. Conversion of the millivolt data to concentrations was done with calibration lines obtained before and after a series of measurements, with 0.1, 1, 10 and 100 % Steiner nutrient solution. In this way, the calibration was done in about the same medium as the measurements. Because other solutes than nitrate can influence the concentration measured by the electrode, a selection of the solution samples was also chemically analysed by the method of Walinga *et al.* (1989) as a reference.

Shoots and roots were harvested per pot after the nitrate depletion. Radish roots were divided into fine roots and tap roots with attached roots of 1 mm or more thickness. Fresh and dry weights were determined. Lengths of rye roots and radish fine roots were measured with a root length scanner (Comair, Melbourne, Australia).

Experiment 2

Experiment 1 was repeated because of the unusually high temperatures during part of the pre-cultivation and during the measurements. This time it was done in a whitewashed, heated greenhouse with a temperature of 20 °C day and night, in Wageningen, The Netherlands. Sowing was on 1 September, 1994. Additional light was supplied by mercury lamps (Type: HPI-T, 400 W, Philips, Eindhoven, The Netherlands) for 13 hours per day. This daylength was chosen to prevent flowering in radish (Schuster & Brettschneider-Hermann, 1967). The light intensity of additional light at the top of the plants was 29 J m^{-2} s^{-1} on average until transfer to cooled, nitrogen free nutrient solution at 42 and 51 days after sowing for radish and rye, respectively. Thereafter, the intensity of additional light was 76 J m^{-2} s^{-1} on average. Nitrate depletion was measured in continuous light, to prevent a limitation of nitrate uptake by limited carbohydrate supply to the roots (Scaife & Schloemer, 1994). Time intervals of measurement were 2 to 12 h, which is longer than in Experiment 1, because depletion was slower in Experiment 2 due to a lower amount of roots per pot.

Calculations

The volume of the solution was calculated for every pot for every sampling time (t_t). This was derived from the weight of the solution per pot at the start of the measurements and the weight at the end of the measurements, assuming a density of 1000 g l^{-1}, and the volume of water added (A) to compensate for transpiration. A constant transpiration rate was assumed.

$$V_t = V_0 - \frac{t_t - t_0}{t_e - t_0} \times T + A_t \qquad (1)$$

in which T is the solution volume transpired during the deplention period:

$$T = V_0 - V_e + A_e \qquad (2)$$

in which:

V_t = Volume of the solution at sampling time t (10^{-3} m^3)
V_0 = Idem at the start of the depletion period (10^{-3} m^3)
V_e = Idem at the end of the depletion period (10^{-3} m^3)
t_t = sampling time t (h)
t_e = time at the end of the depletion period (h)

t_0 = time at the start of the depletion period (h)
T = Volume of solution transpired during the depletion period (10^{-3} m^3)
A_t = Cumulative volume of water added at sampling time t (10^{-3} m^3)
A_e = Idem at the end of the depletion period (10^{-3} m^3).

The concentrations in the selected samples measured by chemical analysis were lower than those measured by the electrode. There may have been a difference in composition between the nutrient solution used for calibration of the electrode, and the nutrient solution depleted by the roots. The measurements with the electrode may have been disturbed by this difference. Therefore, the electrode-measured concentrations were corrected by multiplication by a regression line:

$$C_t = -0.005 + 0.704 \times C_{e,t} \ (R^2 = 95.0\ \%,\ n = 48) \tag{3}$$

in which:
C_t= corrected concentration of nitrate in solution at sampling time t (μM)
$C_{e,t}$= concentration of nitrate in solution at sampling time t measured by electrode(μM).

Then the amount of nitrate in solution was calculated:

$$N_{sol,t} = V_t \times C_t \tag{4}$$

in which:
$N_{sol,t}$ = amount of nitrate in the solution at sampling time t (μmol).

The cumulative amount of nitrate taken up per pot was calculated as follows:

$$N_{upt,t} = N_{upt,t-1} + N_{sol,t-1} - N_{sol,t} - N_{sample,t-1} \tag{5}$$

in which:
$N_{upt,t}$ = amount of nitrate taken up at sampling time t (μmol)
$N_{upt,t-1}$ = idem at the previous sampling time t–1 (μmol)
$N_{sol,t}$ = amount of nitrate in the solution at sampling time t (μmol)
$N_{sol,t-1}$ = idem at the previous sampling time t–1 (μmol)
$N_{sample,t-1}$ = amount of nitrate removed with the sample at sampling time t–1 (μmol).

The maximum nitrate uptake rate was calculated for each pot as the slope of the steepest increase between two sampling points in the cumulative amount of nitrate taken up.

Dry weight shoot root ratios and specific root lengths (SRL) were calculated with exclusion of fodder radish tap roots, because these are storage organs that contribute to root weight but only very little to root length or uptake activity.

Statistical analysis

The experimental units were 6 cooling tanks, 2 for each temperature, arranged in 2 replicate blocks. Four 1 liter pots, each with 4 plants, were suspended in the cooling solution of each tank. Analysis of variance was performed on the data of both experiments together (Genstat 5 Committee, 1993). Effects were examined with the F-test. Interactions existed between the factor experiment and the other factors, species and temperature. Therefore, the experiments were further analysed separately.

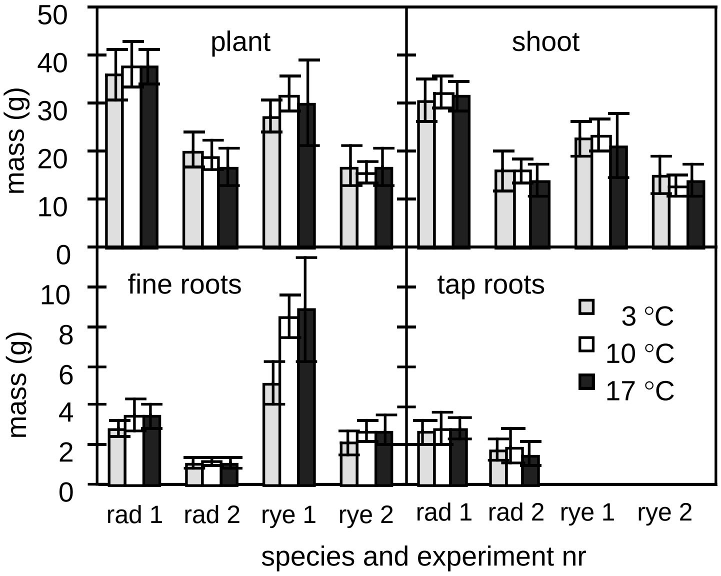

Figure 1. Final plant, shoot, fine root and tap root dry weights per pot in fodder radish (rad) and rye at different temperatures in Experiments 1 and 2.

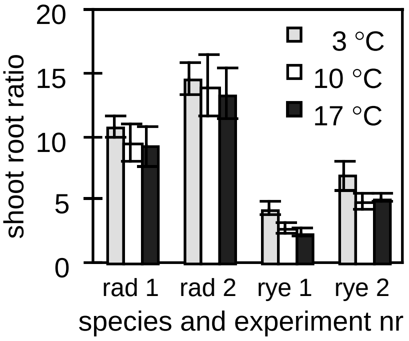

Figure 2. Shoot root ratio (excluding tap roots) per pot in fodder radish (rad) and rye at different temperatures in Experiments 1 and 2.

Results

Plant weights, specific root lengths

Root temperature affected plant dry weight per pot only in Experiment 2, and dry matter per pot did not consistently increase or decrease with root temperature (Figure 1). This was expected, because most of the plant biomass was formed before the low root temperatures were imposed, and the growth during the short period of six days of cooling must have been limited by lack of nitrogen. Plant dry weight per pot was higher in fodder radish than in rye (Figure 1), in spite of the one week longer growth period of rye. Plant dry weight per pot, and also shoot, fine root and tap root dry weight were higher in Experiment 1 than in Experiment 2. This can be explained by the much higher amounts of radiation received by the plants in Experiment 1 (estimated from weather data and light transmission of the greenhouse: 6 * 10^2 MJ m^{-2} in Exp. 1 vs. 3 * 10^2 MJ m^{-2} in Exp. 2). On the other hand, the air temperatures in the second half of Experiment 1 may have been too high for maximum crop growth rates, but this apparently did not compensate the stimulating effect of increased radiation.

Fine root biomass showed a tendency to increase with root temperature, except in fodder radish in Experiment 2, where it was not affected (Figure 1). Shoot biomass was not affected by root temperature. Shoot root ratios (fodder radish tap roots excluded, Figure 2) were higher in Experiment 2 than in Experiment 1, which can be related to the difference in radiation level (Bastow Wilson, 1988). Shoot root ratios decreased with root temperature in both experiments.

Specific root length (SRL, Figure 3) increased from 181 to 225 ± 27 m g^{-1} in rye and from 295 ± 29 to 409 ± 34 m g^{-1} in fodder radish between 3 and 17 °C root temperature in Experiment 1, but there was no such clear trend in Experiment 2. In Experiment 1 the 3 °C point in rye is less reliable because it is based on data of one pot only, due to

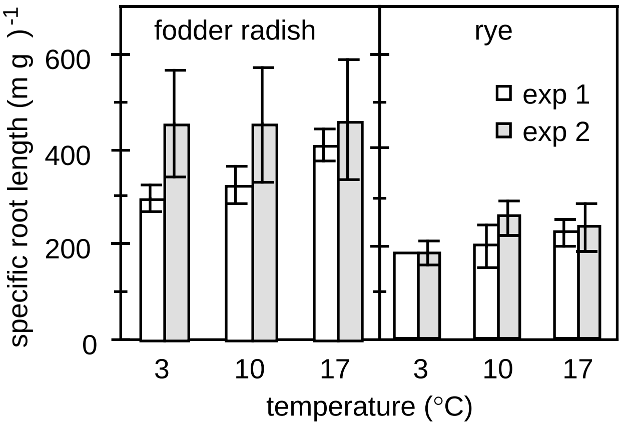

Figure 3. Specific root lengths in fodder radish and rye in Experiments 1 and 2.

failure of root length measurements in the rest of the pots in this treatment. SRL was higher in Experiment 2 than in Experiment 1 and higher in fodder radish than in rye. The experiment effect might be caused by a limitation of root extension at the high temperatures during the pre-treatment cultivation in Experiment 1.

Nitrate uptake

Uptake rate, i.e. the slope of the cumulative uptake curve in Figure 4, typically first increased to a maximum and decreased again towards the end of the depletion. The maximum rates, expressed per length of root, are presented in Figure 5.

The strongest increase in maximum uptake rates occurs between 3 and 10 °C in both species and both experiments. The increase from 10 to 17 °C is slight, or, in fodder radish in experiment 2, absent. Although radiation and shoot temperature conditions were very different between the experiments, both the levels of the maximum nitrate uptake rates and their reaction to root temperature were rather similar in both experiments.

Table 1. Maximum nitrate uptake (in μmol g^{-1} h^{-1}) at different root temperatures in winter rye and fodder radish in Experiments 1 and 2.

species	experiment	temperature 3 °C	10 °C	17 °C
fodder radish	1	2.9 ± 0.6	5.8 ± 1.3	6.4 ± 3.3
	2	1.1 ± 0.4	4.0 ± 0.8	4.8 ± 1.3
rye	1	1.3 ± 0.2	2.7 ± 0.3	3.4 ± 1.2
	2	1.2 ± 0.3	3.2 ± 0.5	3.5 ± 0.9

Discussion

Plant weights, specific root lengths

The lower SRL values at low temperatures (Figure 3) indicate that root extension must have been hampered, so that root growth was sink-limited. This is supported by the increase in root weight with temperature (Figure 1) and the decreasing trend in shoot root ratio with increasing temperature (Figure 2). In other experiments, both root and shoot growth decreased at suboptimal root temperatures, so that the shoot root ratio was not affected (Brouwer, 1962b). Shoot root ratios can, however, also increase with root temperature up to the optimum temperature of the species (Brouwer & Van Vliet, 1960; Davidson, 1969). This was suggested to result from a compensation in root mass for a decrease in root activity at low temperature. Apparently, details in the

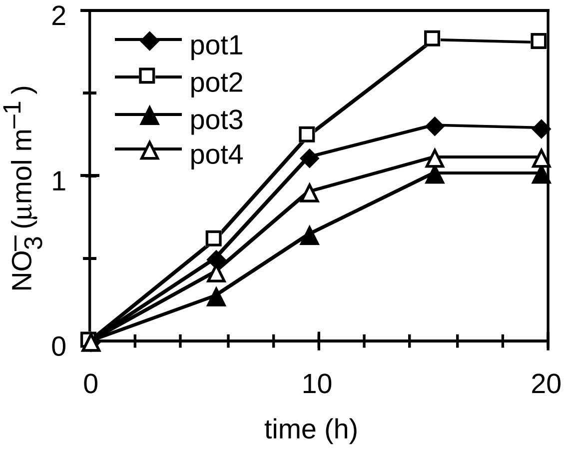

Figure 4. Example of the time courses of the cumulative nitrate uptake per pot. 4 pots are represented from which fodder radish took up nitrate at 3 °C on 1 cooling tank (experimental unit) in Experiment 1.

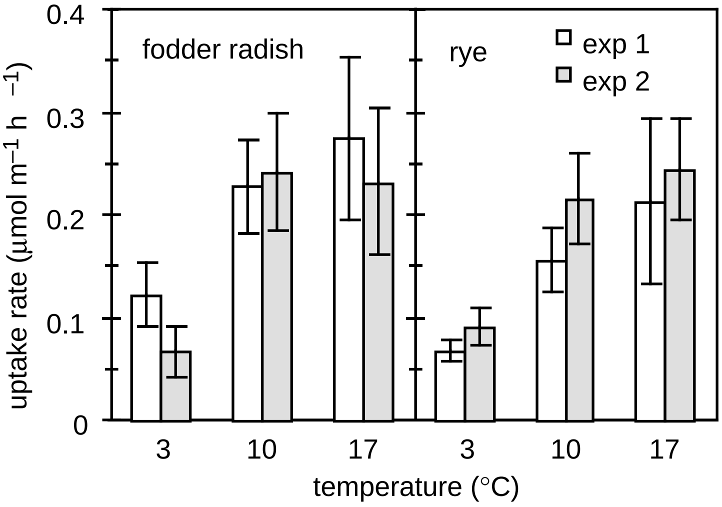

Figure 5. Maximum nitrate uptake rates in fodder radish and rye at different temperatures in Experiments 1 and 2.

circumstances may cause opposite effects in the ratio. Shoot root ratios were higher in fodder radish than in rye, as also found by Lainé *et al.* (1993).

Nitrate uptake

The uptake rate appears to be sensitive to root temperature over the whole measured range in both species, but most strongly so below 10 °C (Figure 5). The reaction to root temperature was stronger below than above 10 °C in barley (*Hordeum vulgare* L.) (Glass *et al.*, 1990), as was the case here. No temperature effect on the nitrate uptake rate in rape (*Brassica napus* L.) was found in the range of 10 to 30 °C (Cumbus &

Nye, 1982), comparable to the results found here in fodder radish in Experiment 2.

When the uptake rates are expressed per gram fresh weight of the roots, instead of root length (Table 1), they can be compared with those in other studies. Lainé *et al.* (1993) found uptake rates of 12.9 and 28.7 µmol g^{-1} h^{-1} in rye and fodder radish, respectively, at 25 °C without previous starvation. These rates are higher than those found here: maximally 6.4 µmol g^{-1} h^{-1} and 3.5 µmol g^{-1} h^{-1} were measured in fodder radish and rye, respectively, at 17 °C in Experiment 2. Uptake rates in barley at 20 °C increased from 3.4 µmol g^{-1} h^{-1} without previous starvation to 7.9 µmol g^{-1} h^{-1} after 3 days of starvation and then decreased to 7.0 µmol g^{-1} h^{-1} after 5 days of starvation (Lee & Rudge, 1986). These rates are in the same range as those measured in Experiments 1 and 2. Glass *et al.* (1990) found uptake rates in barley of 3.4 µmol g^{-1} h^{-1} at 5 °C and 5.3 to 6.4 µmol g^{-1} h^{-1} at 10 °C, slightly higher than the values found here at 3 and 10 °C. In conclusion, the maximum nitrate uptake rates found here are generally in the low part of the range found in comparable species and similar experimental conditions.

The initial increase in uptake rate (Figure 4) indicates induction of nitrate uptake enzymes after the six days of starvation. In the literature, the duration of induction to constant uptake rates generally varies with species and solution nitrate concentration. Full induction is reached after 12 to 24 h in barley at concentrations of 1.0 and 1.5 mM (Siddiqi *et al.*, 1989), similar to the 1.2 mM used here. After that, the uptake rate declines again to about half the value reached at full induction. This final level is also measured at 6 h after the start of induction. The rise in uptake rates starts at 1 to 1.5 h after the start of nitrate supply in *Sinapis alba* L. and *Brassica rapa* L., both Brassicaceae related to fodder radish (Lainé *et al.*, 1993). Here, the depletion took 4 h (at 17 °C in Exp. 1) to over 46 h (at 3 °C in Exp. 2.). The duration of induction was not measured. Generally, a Michaelis-Menten relation describes the reaction of the uptake rate to low nitrate concentration (0–1 mM) (Engels & Marschner, 1995). According to this relation, 95 % of the maximum uptake rate is achieved at nitrate concentrations of 0.494 mM for fodder radish and 0.190 mM for rye (Lainé *et al.*, 1993). This was independent of root temperature at measurement, because temperature did not affect the Michaelis-Menten constant (Km). A lower saturating concentration is suggested by Glass *et al.* (1990), who found that an increase in nitrate concentration from 0.1 to 0.3 mM did not affect uptake rates in barley. Due to the large amount of roots per pot in Experiments 1 and 2, the nitrate concentration in some of the pots could have been decreased below these values before the uptake of nitrate was fully induced, so that the measured maximum uptake rates might have been limited by low nitrate concentration or incomplete induction. The real maximum rates therefore might be somewhat higher.

Extrapolation to field conditions

Despite largely different radiation levels and shoot temperatures, root temperature affected root mass, specific root length and maximum nitrate uptake rates in the same way in both experiments. Moreover, the levels of the maximum nitrate uptake rates were rather similar, indicating that this parameter behaves in a consistent way in widely varying conditions.

Comparison of uptake rates in solution and soil cultivation is necessary to use the data for understanding field situations. In another study, with roots of corn, onion and spinach, the maximum rates of nitrate uptake from nutrient solution were similar to the average nitrate uptake rate from a loamy sand soil in pots, when the soil was well supplied with nitrate (Heins & Schenk, 1986). Although possibly different effects might occur under other conditions due to drought, root hairs, mucigel excretion and mycorrhizae (Nye & Tinker, 1977), this indicates that the maximum uptake rates measured in solution culture can be used as estimate for those occurring in soil.

The temperature range that occurs in West European field soils is wider than the range used in the experiments, namely from below 0 °C to temperatures optimal for temperate plant species (about 25 °C). At the lower extreme of this range, it is unknown how nitrate uptake reacts to temperature, so that extrapolation to temperatures below 3 °C can only be based on assumptions. In fodder radish, the nitrate uptake rate seems to have reached its maximum at 10 °C, with no further increase with raise in temperature. Therefore, the value found at 10 and 17 °C could be used for the higher temperatures. Maximum nitrate uptake rates in rye increased up to 17 °C, so that no maximum can be deducted from these data. Extrapolation to higher temperatures could be based on data from literature (e.g. Lainé *et al.*, 1993; White *et al.*, 1991).

The maximum nitrate uptake rates may limit crop nitrogen uptake rates, when the crop demands nitrogen and nitrate is supplied to the roots. Whether the maximum uptake rate affects the overall nitrogen accumulation of a catch crop, will depend on environmental conditions. This can be evaluated with the help of an explanatory crop growth simulation model, with which the nitrogen accumulation can be estimated for various situations, with and without limitation by a maximum to the nitrate uptake rate.

Conclusions

The maximum nitrate uptake rate strongly increases with temperature below 10 °C, and slightly above 10 °C in both fodder radish and winter rye. The values found can be used as estimates for maximum uptake rates in the field. A rise in temperature caused increases in specific root length and root weight, and a decrease in shoot root ratio, indicating that root extension was reduced at low temperatures, and root growth sink limited.

Chapter 4

Canopy CO_2 assimilation in catch crops during autumn and winter

with E.A. Lantinga

Abstract

CO_2 exchange rates of canopies of winter rye and fodder radish, grown as catch crops, were observed at several temperatures during regular intervals from October until March (1993 - 1995). Maximum canopy CO_2 assimilation rates were about 1.1 and 0.9 mg CO_2 m^{-2} soil s^{-1} in October for radish and rye, respectively, at about 200 W m^{-2} absorbed PAR. They decreased to about 0.6 mg CO_2 m^{-2} soil s^{-1} during autumn and winter for both species at about 100 W m^{-2} absorbed PAR and increased again to 0.7 mg CO_2 m^{-2} soil s^{-1} towards spring (March) in rye, at 220 W m^{-2} absorbed PAR. CO_2 assimilation rates at high light intensities were not affected by temperature (range 4–16 °C).

The effective light saturated assimilation rate of the leaves in the canopy ($A_{max,eff}$) was estimated from the measurements for each interval, by inverse modelling with the assimilation subroutines of the crop growth model SUCROS. $A_{max,eff}$ was compared with estimates of the light saturated CO_2 assimilation rates of individual young full-grown leaves ($A_{max,0}$), using two models. The model estimating $A_{max,0}$ as a linear function of the average radiation intensity during 20 preceding days had the highest correlation with $A_{max,eff}$. The modelled $A_{max,0}$ predicted canopy CO_2 assimilation rates for fodder radish satisfactorily, but overestimations occurred for winter rye. This difference may be related to canopy structure. In fodder radish, the youngest leaves with the highest assimilatory capacity are positioned in the upper layers of the canopy, whereas in rye both young and old leaves are present at all depths in the canopy. This might also have been the reason for the observed differences between the two species in canopy CO_2 assimilation rate at high light intensities in October.

Keywords: winter rye, fodder radish, temperature, radiation, CO_2 assimilation, catch crop, Rhizolab

Introduction

Cultivation of catch crops may reduce leaching of nitrogen (N) in autumn and winter. Catch crops can accumulate up to 200 kg N ha^{-1} under West-European conditions (Landman, 1990; Vos & Van der Putten, 1997), but the amount of N that is taken up and the reduction in leaching vary widely with sowing date, N supply, species and weather conditions (Landman, 1990; Schröder *et al.*, 1992). This variation in N uptake complicates the estimation of the effectiveness of catch crops to decrease N losses from agricultural soils.

Insight in the effects of environmental conditions on the processes that determine growth and N uptake rates of catch crops may be used to estimate catch crop N accumulation for specific conditions, and thereby improve the assessment of catch crop effectiveness and optimization of catch crop cultivation methods. CO_2 assimilation is the primary process in crop production. Knowledge of the response of catch crop CO_2 assimilation to changing environmental conditions can therefore be used to estimate growth and N uptake of catch crops. The relation between CO_2 assimilation and radiation at leaf level can be characterised by the assimilation rate at high, saturating light intensity (A_{max}) and the initial slope at low intensities (Goudriaan, 1982). In several plant species, the assimilation rate at saturating light intensity is decreased or unaffected in winter, compared to summer conditions, whereas initial light use efficiency is not affected by the season (Sawada & Miyachi, 1974; Regehr & Bazzaz, 1976). There is, however, ample evidence that temperature and light conditions during leaf growth affect A_{max} under controlled conditions (e.g. Huner *et al.*, 1986; Dijkstra ,1989).

In the current study we analyse results of an earlier experiment where the light saturated CO_2 assimilation rates of individual leaves were measured in winter rye and fodder radish (Chapter 2). Amax in the youngest full-grown leaves was about 1.2 mg CO_2 m^{-2} leaf s^{-1} in September, and about half as high from November until March. It did not vary with temperature during the measurements, in the range from 5 to 19 °C. To analyse the effect of environmental conditions, the measured Amax of the youngest full-grown leaves was related to temperature and radiation conditions during their growth by regression. Thus, weather conditions were assumed not to have an immediate, but only a long term effect on A_{max}. The correlation of A_{max} was high both with temperature during leaf growth and with radiation during leaf growth (Chapter 2). With the regression models, A_{max} can be estimated for conditions in which it was not measured.

Based on these data, we hypothesize that (1) the change in A_{max} in the youngest full-grown leaves of catch crops during autumn and winter is reflected in the CO_2 assimilation rate of a catch crop canopy in the same season and (2) canopy CO_2 assimilation rate of the two crops at high light intensities is not influenced by temperature above 5 °C. Moreover, we want to test whether (3) the light saturated CO_2 assimilation rate of the youngest full-grown leaves of catch crops, predicted as a function of temperature or radiation conditions during leaf growth (Chapter 2), can be used to estimate an effective A_{max} for the leaves in a whole crop canopy. Such an effective A_{max} could be used for estimating canopy CO_2 assimilation by means of simulation. Measured canopy CO_2 assimilation data have been used to test these hypotheses.

Materials and methods

General

Daily courses of canopy CO_2 assimilation rates were measured on enclosed crop canopies of the catch crops winter rye (*Secale cereale L.*, cv. Halo) and fodder radish (*Raphanus sativus L.*, cv. Adagio) during four (rye) and three (radish) periods between October and March (1993–1994 for radish and 1994–1995 for rye).

To this aim, fodder radish and winter rye were grown under ambient temperature and radiation conditions in the Wageningen Rhizolab (Van de Geijn *et al.*, 1994) in two consecutive experiments. Data concerning CO_2 assimilation and leaf N concentrations are reported here. A separate paper presents data on water and nitrogen dynamics and root growth from the same experiments (Chapter 5).

Experiment 1. Fodder radish

Growth of a fodder radish catch crop and its effect on N leaching was investigated at two irrigation rates (supplied twice a week), of which one was comparable to an extremely wet season (equivalent to 3 mm day^{-1}), and the other to a very dry season, for Dutch conditions (equivalent to 1 mm day^{-1} until 2 November, and 2 mm day^{-1} thereafter).

Two rhizolab compartments (1.25 × 1.25 m^2) were filled with a sandy soil from 0 to 100 cm depth and with white sand from 100 to 170 cm depth. Soil treatment and properties are described in Chapter 5. Rhizolab equipment was installed as described by Van de Geijn *et al.* (1994), apart from the changes mentioned below.

Fodder radish was sown on 1 September 1993 at 12.5 cm row distance in the compartments. After emergence plants were thinned in the rows to 1 per 4 cm. This is comparable to the normal seeding density of 2.5 g m^{-2}. Fodder radish was also sown around the compartments to minimize border effects, e.g. the incidence of light directly on the edges of the canopy. The crop was protected from frost by covering it with transparent plastic, below which the air was heated to 4 ± 2 °C and ventilated. This

Table 1. $A_{max,0}$ (kg CO_2 ha^{-1} h^{-1}) values calculated with models 1 and 2 and the range in $A_{max,eff}$ estimated with the optimisation with SUCROS; the ranges in Leaf Area Index (LAI, in m^2 leaf m^{-2} soil) and the diffusion coefficient for diffuse radiation (K_{dif}), both inputs in SUCROS. The subscripts of the (measured) LAI in March refer to the treatments: 0 = N0, 14 = N14**.**

	$A_{max,0}$ Model 1	$A_{max,0}$ Model 2	$A_{max,eff}$ SUCROS		LAI	K_{dif}
Fodder radish			Ilow	Ihigh		
18-22 Oct 1993	0.98	0.84	0.89-1.17	0.73-0.93	2-3	0.7 - 0.8
22-26 Nov 1993	0.40	0.48	0.82-1.21	0.69-0.98	3-4	0.7 - 0.8
17-21 Jan 1994	0.44	0.36	0.31-0.39	0.30-0.38	3-4	0.7 - 0.8
Winter rye			N0	N14		
4-7 Oct 1994	1.16	0.88	0.36-0.50	0.45-0.62	3-4	0.5 - 0.7
28 Nov-2 Dec ‘94	0.83	0.34	0.25-0.32	0.27-0.33	4-5	$0.7\text{-}0.9_0/0.9\text{-}1.1_{14}$
1 - 3 Feb 1995	0.52	0.41	0.34-0.42	0.24-0.29	4-5	0.5 - 0.7
6-10 Mar 1995	0.49	0.73	0.39-0.46	0.50-0.59	$5.1_0/4.1_{14}$	0.5 - 0.7

happened during frost from 19 November until 6 December 1993 and from 11 until 25 February 1994. The border plants around the compartment had frozen to death after the first frost period. Therefore, on 10 December 1993 the crop was surrounded by vertically installed shade gauze (transmitting about 50 % of the light) with the same height as the crop. The crop was harvested on 15 March 1994, the normal time of incorporation in the soil in practice.

Experiment 2. Winter rye

The effects of different placement and levels of N fertilization were investigated on growth and N accumulation of a winter rye catch crop and on N leaching. CO_2 assimilation rates were determined at two N supply levels.

The two rhizolab compartments were filled with soil in the same way as in Experiment 1. Before sowing fertilizers were mixed with the soil. Both compartments received 3.07 g m^{-2} P and 10.0 g m^{-2} K, respectively, in the top 10 cm. N was supplied at rates of 0 and 14 g m^{-2}, coded N0 and N14, respectively. In N14, 7 g m^{-2} N was mixed with the top 10 cm of the soil profile before sowing, and the other 7 g m^{-2} was supplied with the irrigation water, equally divided over three applications at 26, 36 and 47 days after sowing. In this way, any possible shortage of N was avoided in N14. Winter rye was sown on 24 August 1994 at 12.5 cm row distance in the compartments. Only seeds of 2.5 to 3 mm in diameter were used, to obtain a homogeneous crop. Winter rye was also sown around the compartments. The distance between seeds in the rows was 1.5 cm, corresponding to the normal seeding density of 18 g m^{-2}. On 30 August all rows contained 70 plants or more. Irrigation was supplied twice a week and was equivalent to 3 mm day^{-1}. The crop was harvested on 13 March 1995.

Measurements

Dates of measurements are given in Table 1. Daily courses of canopy CO_2 assimilation and respiration were measured on enclosed crop canopies in the rhizolab compartments according to Louwerse & Eikhoudt (1975). Net CO_2 assimilation, CO_2 concentration of the air, temperature, vapour pressure, and the flux of incoming global and absorbed photosynthetically active radiation (PAR) were determined every 5 minutes during the days of measurement. This was done at several constant temperatures (Table 1), in such a way that a temperature effect relevant for the season could be determined. All measurements were carried out with closed canopies, intercepting most incoming light. During a four day measurement period data could be collected at one, two or three different temperatures, depending on the duration of radiation conditions suitable for measurement (i.e. at least a partly clear sky).

The shoots of both crops were harvested in March. Total N concentration in leaf material was determined after destruction (Novozamsky *et al.*, 1974 and 1983). Areas of green leaf blades and sheaths of rye and fodder radish leaves were measured with a leaf area meter for determination of Leaf Area Index (LAI, m^2 leaf m^{-2} soil).

Data analysis

The experiments were set up as a split plot design with a block stratum containing the treatments (irrigation in Exp. 1 and N supply in Exp. 2), a subblock stratum at which time of measurement was analysed and a unit stratum at which the temperatures were compared. Data analysis was conducted with Genstat statistical package (Genstat 5 Committee, 1993).

CO_2 release of the canopy in darkness was plotted against temperature and a line was fitted through the data to estimate dark respiration rate as a function of temperature during daytime. Dark respiration rates were added to the measured net assimilation rates to obtain gross CO_2 assimilation rates.

Net canopy CO_2 assimilation rate was plotted versus absorbed PAR. For comparison and statistical analysis of the data, a non-rectangular hyperbola appropriate for description of CO_2 assimilation - light response data (Thornley & Johnson, 1990) was fitted to each series of data on a unit:

$$P_t = -P_0 + \frac{1}{2\theta}\{\varepsilon I_t + P_{max} - [(\varepsilon I_t + P_{max})^2 - 4\theta\varepsilon I_t P_{max}]^{1/2}\} \qquad (1)$$

where

P_t = the net CO_2 assimilation rate of the canopy at time t (mg CO_2 m^{-2} soil s^{-1}),
I_t = the absorbed PAR at time t (J s^{-1} m^{-2} soil),
P_0 = the dark respiration rate of the canopy (mg CO_2 m^{-2} soil s^{-1}),
ε = the initial light use efficiency (mg CO_2 J^{-1}),
P_{max} = the light saturated gross canopy CO_2 assimilation rate (mg CO_2 m^{-2} soil s^{-1}),
θ = a dimensionless parameter determining the convexity of the curve.

P_{max} and θ were fitted to the measured data of P_t and I_t. Analysis of variance was performed on the fitted parameter P_{max}, and effects were tested with the F-test. For this purpose the imposed temperatures were categorized in three temperature levels for radish and two levels for rye (Table 1).

Model comparison

The third hypothesis to be tested is that the effective light saturated CO_2 assimilation rate of the leaves in a canopy can be predicted with one of two models that relate measurements of $A_{max,0}$ (in mg CO_2 m^{-2} leaf s^{-1}) on individual young, full-grown leaves to temperature and radiation during leaf growth, for which a duration of 20 days was assumed (Chapter 2). $A_{max,0}$ of young full-grown leaves predicted by the models was compared to $A_{max,eff}$ calculated for the whole canopy with SUCROS (further referrred to as $A_{max,eff}$) (Goudriaan & Van Laar, 1994). $A_{max,eff}$ is taken as a measure for the effective A_{max} in the canopy, assuming no differences between leaves. Earlier studies have proven that canopy assimilation can be well simulated with SUCROS using one effective A_{max} for all leaves in a canopy (Goudriaan, 1982). Below the model comparison is described in more detail.

The two models relate $A_{max,0}$ to the temperature and light conditions during 20 preceeding days. Weather data were used from the weather station at Wageningen.

Model 1: $A_{max,0} = a \times T$ (2)
Model 2: $A_{max,0} = b \times I$ (3)

where
T = average temperature (°C) during 20 preceding days
I = average global radiation intensity (J m^{-2} soil s^{-1}) during 20 preceding days
a = $8.875 * 10^{-2}$ mg CO_2 m^{-2} leaf s^{-1} $°C^{-1}$
b = $4.685 * 10^{-3}$ CO_2 J^{-1} (Chapter 2).

$A_{max,0}$ was estimated with both models for all of the four-day periods in which canopy CO_2 assimilation was measured.

$A_{max,eff}$ was determined by optimization as follows. The CO_2 assimilation rates of the fodder radish and winter rye canopies were calculated with the CO_2 assimilation routines of the crop growth model SUCROS. Inputs were global radiation, measured in 5 minute intervals, the time of the day, Julian day number, LAI, the extinction coefficient for diffuse radiation (K_{dif}), initial light use efficiency, canopy dark respiration rate and $A_{max,eff}$. LAI was determined in March, and estimated from photographs for the earlier measurements. K_{dif} was estimated from photographs for all dates. Initial light use efficiency was 0.0145 mg CO_2 J^{-1} at 5 °C, linearly decreasing to 0.0135 mg CO_2 J^{-1} at 15 °C (Jones, 1992). Differences between the calculated and measured CO_2 assimilation rates were minimised with the Simplex method (Press *et al.*, 1986) by varying $A_{max,eff}$. In this way $A_{max,eff}$ was optimized for a range around the estimates of LAI and K_{dif} values (Table 1).

To test which model estimated the $A_{max,eff}$ best, $A_{max,eff}$ was fitted to $A_{max,0}$ derived with models 1 and 2, respectively, and correlation coefficients were evaluated. To test the suitability of the best fitting model, its $A_{max,0}$ estimates were used for simulation of CO_2 assimilation rates and the results were visually compared with the measurements.

Results and discussion

Leaf area and N concentration

N concentrations in the living leaves of fodder radish and winter rye were between 45 and 50 mg g^{-1} dry matter at harvest in March (Figure 1). The rye leaf sheaths had a lower N concentration of about 35 mg g^{-1}. These rather high levels indicate that the crops were well supplied with N in both N treatments (see Vos & Van der Putten, 1997), although a difference in N supply between the treatments was intended. LAI at harvest was 3.3 and 3.8 m^2 leaf m^{-2} soil in radish Ilow and Ihigh, respectively, and 5.1 and 4.1 m^2 leaf m^{-2} in rye N0 and N14, respectively. The lowest N supply level resulted therefore in the highest LAI in rye. N0 had a higher Specific Leaf Area than N14; both treatments had the same leaf biomass, and N14 had more mass in sheaths than N0 (Chapter 5).

Canopy dark respiration

Rates of dark respiration increased with temperature. A linear relationship was fitted to the data, to estimate respiration during daytime at intermediate temperatures:

$$P_0 = d + f \times T \tag{4}$$

where T is temperature in °C and d and f are coefficients. Overall, most of the data were approximately on the same line, despite possible differences in biomass. Only the data of radish in November and January diverged from the line. $d = 13.7*10^{-3}$ mg CO2 m^{-2} soil s^{-1} and $f = 4.0*10^{-3}$ mg CO_2 m^{-2} soil s^{-1} °C^{-1} for radish in November and January, and $d = 1.4*10^{-3}$ mg CO_2 m^{-2} soil s^{-1} and $f = 8.9*10^{-3}$ mg CO_2 m^{-2} soil s^{-1} °C^{-1} for the other measurements.

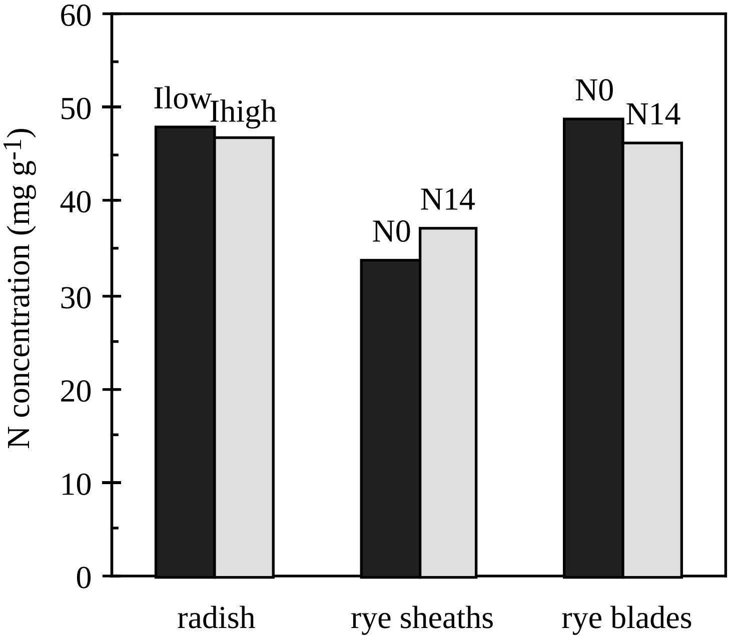

Figure 1. Nitrogen concentrations (mg g^{-1}) in the leaves of fodder radish and winter rye.

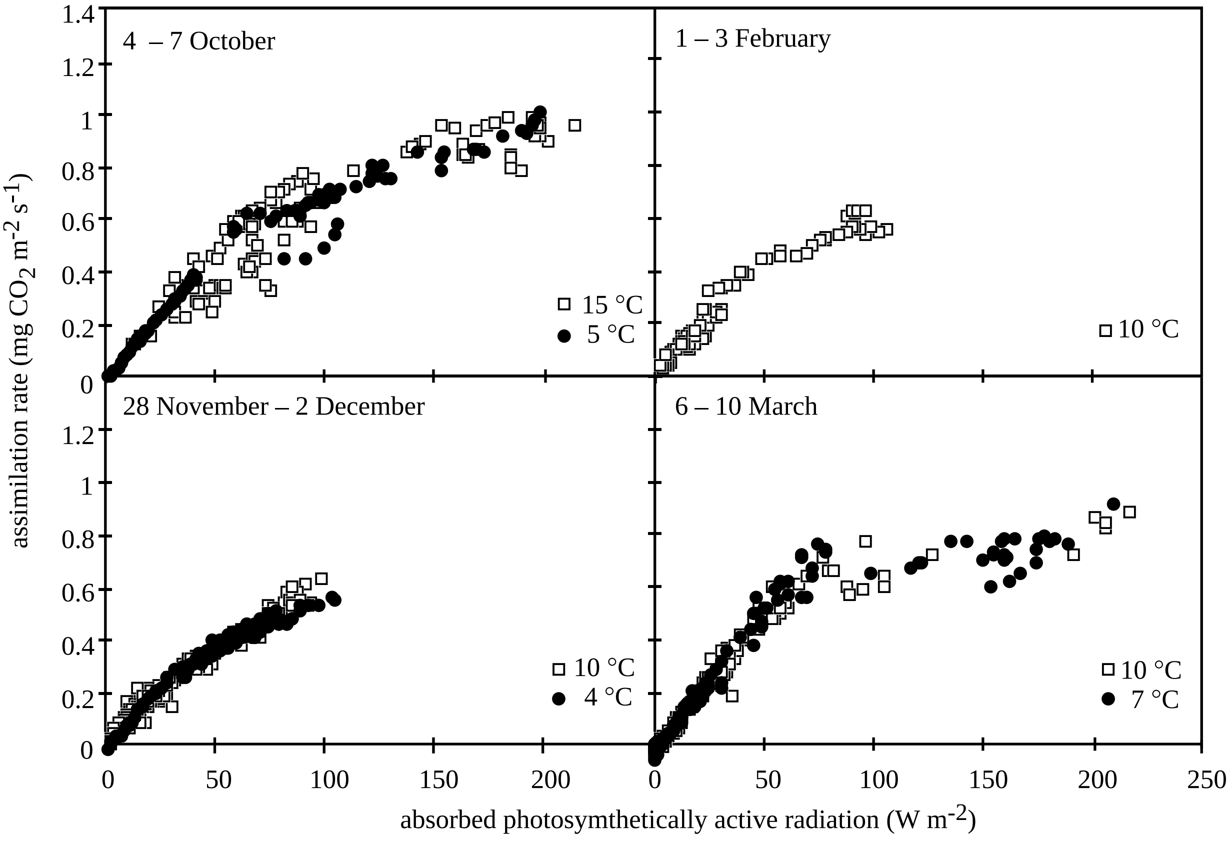

Figure 2. Canopy assimilation rate as a function of absorbed photosynthetically active radiation in winter rye at N0 at different temperatures in four measurement periods.

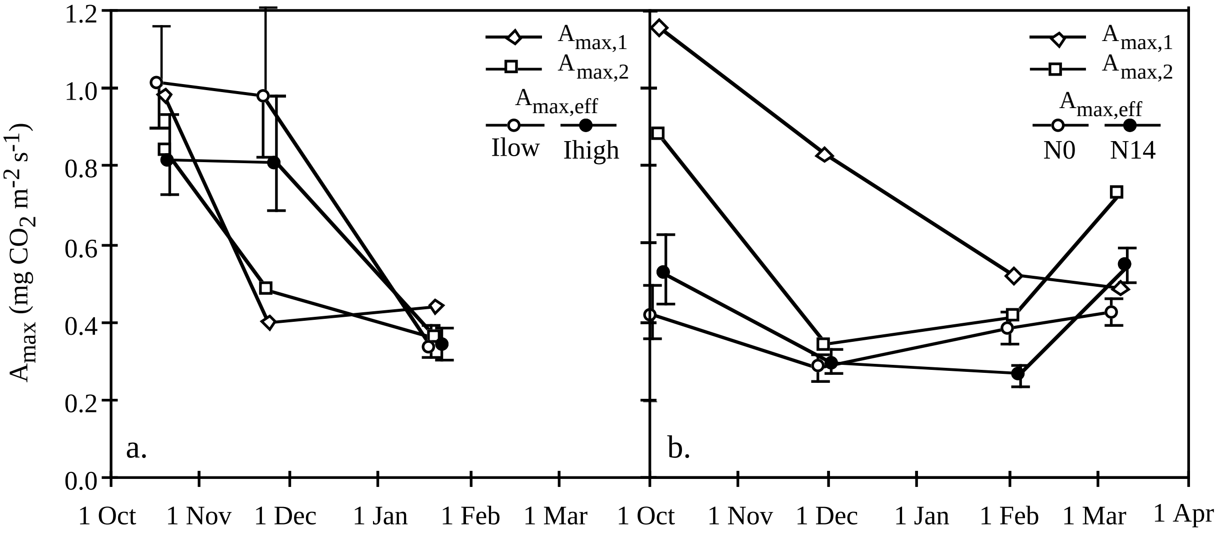

Figure 3. $A_{max,1}$, $A_{max,2}$ and $A_{max,eff}$ during the growing season. a. fodder radish. b. winter rye. Bars give the range in $A_{max,eff}$ for the ranges in K_{dif} and LAI.

Canopy CO_2 Assimilation

The data of net canopy CO_2 assimilation rates are given as a function of absorbed PAR for winter rye at N0 in Figure 2. The trends shown were also present for the fertilized rye treatment (N14) and fodder radish at both irrigation levels. Maximum radiation intensities, and hence absorbed PAR, were higher in October and March than in November and February, due to the annual course of solar radiation intensity. The canopy CO_2 assimilation rates at 200 W m^{-2} absorbed PAR were about 1.1 and 0.9 mg CO_2 m^{-2} s^{-1} in October in radish and rye, respectively. They decreased to about 0.6 mg CO_2 m^{-2} s^{-1} at 100 W m^{-2} absorbed PAR during autumn and winter for both species and increased again to 0.7 mg CO_2 m^{-2} s^{-1} towards spring (March) in rye at 220 W m^{-2} absorbed PAR. Temperature did not affect P_{max}. At high light intensities canopy CO_2 assimilation rate was not affected by temperature in the measured ranges (minimally 4–10 °C, maximally 6–16 °C), as hypothesised. Therefore, the data from different temperatures were lumped in further analysis. The scatter in the graphs was sometimes different for the different temperatures. This was due to inavoidable variation in the radiation conditions during the successive measurements, and not to the imposed temperatures. CO_2 assimilation rate at the same value of absorbed PAR was higher for conditions with a higher fraction of diffuse radiation (Lantinga, 1985). The canopy CO_2 assimilation rate at high absorbed PAR was lower in November and January than in October, which was reflected in a significant effect of the time of measurement on P_{max}. This largely followed the fluctuation found in the light saturated CO_2 assimilation rate of young full-grown leaves that was found earlier (Chapter 2).

Comparison of leaf models and SUCROS

$A_{max,0}$, derived with models 1 and 2, and $A_{max,eff}$ are presented in Figure 3. Models 1 and 2 each yield one value for each month per species, independent of treatment; $A_{max,eff}$ was optimized separately for the different treatments. In fodder radish, low irrigation (Ilow) yielded a higher $A_{max,eff}$ than high irrigation (Ihigh) in October and November. This may have been due to a higher N supply in Ilow, where less N had been leached (Chapter 5). There was no effect of N supply on $A_{max,eff}$ in rye, consistent with the absence of effects on leaf N concentration. The N supply was already very high in N0 (Chapter 5), so that there was no N limitation in N0. Therefore, no nitrogen effect could be tested.

The leaf models estimated $A_{max,eff}$ in fodder radish well in October and January, but underestimated it in November (Figure 3). The exact value of $A_{max,eff}$ in November was however very sensitive to the estimates of dark respiration, LAI and K_{dif}, which can be seen from the large ranges for $A_{max,eff}$ obtained for the different input values (Figure 3). In linear regression, Model 2 gave the highest correlation with $A_{max,eff}$ for fodder radish ($R^2 = 0.87$). In winter rye, the leaf models generally overestimated $A_{max,eff}$. Model 1 estimated $A_{max,eff}$ best only in March, whereas Model 2 gave good estimates in November and February. The overestimation in October was smallest for Model 2. The

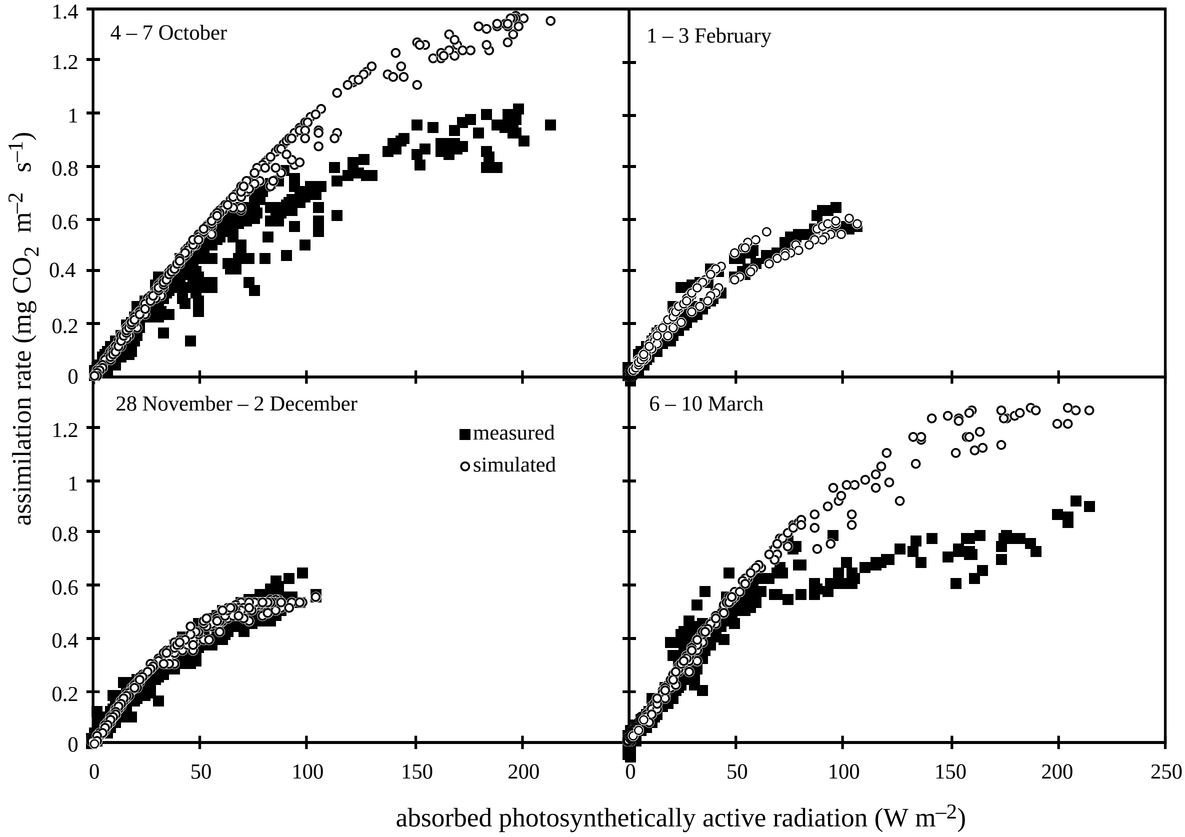

Figure 4. Simulated and measured values of canopy CO_2 assimilation in winter rye at N0 rate as a function of absorbed photosynthetically active radiation.

highest correlation with $A_{max,eff}$ for rye was found for $A_{max,0}$ derived with Model 2 ($R^2 = 0.70$). Therefore, it is concluded that Model 2, estimating $A_{max,eff}$ as a function of radiation during leaf growth, gave the best estimates of $A_{max,eff}$ for both species.

$A_{max,0}$ derived with Model 2 was used to simulate canopy CO_2 assimilation rates for the dates of the measurements. In Figures 4 and 5 the results are plotted together with the measured data. For rye (Figure 4) only N0 is shown, as N14 showed the same trend. The shape of the measured and simulated curves is similar, supporting Goudriaan's conclusion that canopy CO_2 assimilation can be well simulated with one effective A_{max} for the whole canopy (Goudriaan, 1982). In radish (Figure 5) the assimilation rate is very well estimated for Ihigh in October and January and Ilow in January, and only slightly underestimated it for both treatments in November and Ilow in October. The difference between irrigation rates might have been due to a higher availability of nutrients in Ilow. In an earlier pot experiment (Chapter 2), N supply did not affect Amax,0, but it did influence biomass, and therefore probably LAI and thus $A_{max,eff}$, as the error bars in Figure 3 indicate.

In rye, the canopy CO_2 assimilation rate was well simulated in November and February (Figure 4), in accordance with Figure 3. However, in October and March the assimilation rates were overestimated at high light intensities.

The difference in suitability of Model 2 for radish and rye may be due to differences in canopy structure. In fodder radish, which had a main stem with only apical leaf development, the youngest leaves are positioned at the top of the canopy, and the older

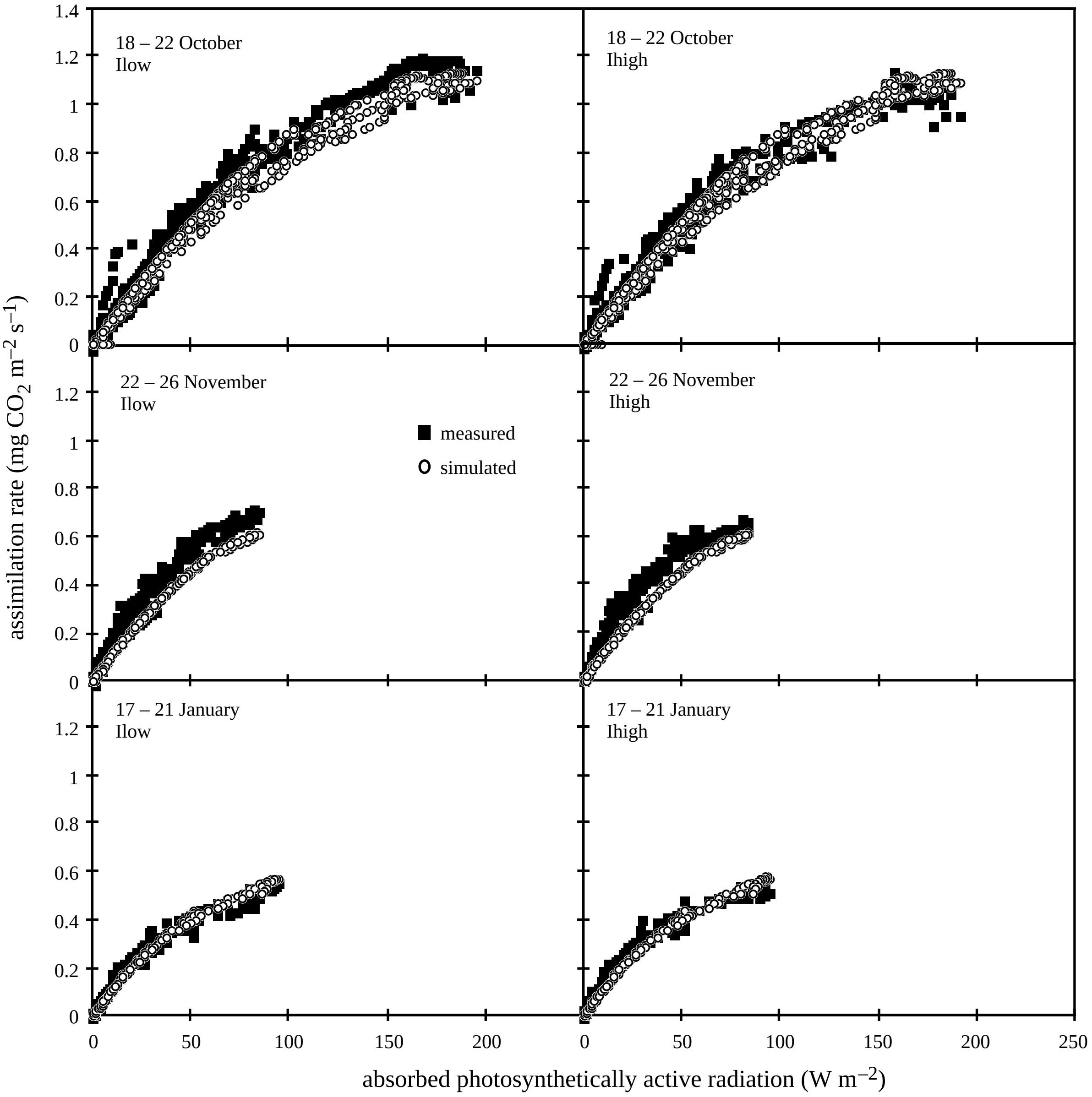

Figure 5. Simulated and measured values of canopy CO_2 assimilation rate in fodder radish as a function of absorbed photosynthetically active radiation.

leaves are below them. In this way the youngest leaves, with the highest A_{max}, receive most of the light. The lower leaves, with lower A_{max} (Chapter 2), are seldomly saturated with light, so that their assimilation rates are determined by initial light use efficiency rather than by A_{max} (Baker *et al.*, 1988). In vegetative rye, however, stems and leaf sheaths are relatively short and leaves long, which implies that both old and young leaves are present at all depths in the canopy. In this way leaves of all ages can receive high light intensities, so that the A_{max} of older leaves, lower than that in the young leaves, is more important for the CO_2 assimilation rates of the canopy than in radish. The same effect occurs in grass, with a similar canopy structure (Davidson *et al.*, 1981). Therefore, the effective $A_{max,eff}$ of the canopy, as estimated from optimization with SUCROS, will be lower than $A_{max,0}$ of the young, full grown leaves, on which Model 2 was parameterised. The $A_{max,eff}$ values found in October (0.42 and 0.52 mg CO_2 m^{-2} leaf s^{-1}) are comparable to those measured for perennial ryegrass (0.55 mg CO_2 m^{-2} leaf s^{-1} at a LAI of 2), with a similar canopy structure, in the same month (Lantinga, 1985). This difference in canopy structure will, when $A_{max,0}$ in the young leaves is the same, cause a difference in radiation use efficiency. In radish, the youngest leaves, with the highest A_{max}, intercept most radiation, whereas in rye the young leaves may be shaded by older leaves. For maximum growth and N uptake, a catch crop with a high radiation use efficiency is desirable. Fodder radish has a better canopy structure for this than winter rye. However, in the field no consistent differences in radiation use efficiency occur between rye and radish (Vos & Van der Putten, 1997). The benefits of a high A_{max} are likely to be limited at the relatively low radiation intensities and low temperatures during the catch crop growing season.

Conclusions

As hypothesised, for both crops, the canopy CO_2 assimilation rates at high light intensities were high in October, decreased during autumn and winter and increased again towards spring (March) for rye. Canopy CO_2 assimilation rates at high light intensities were not affected by temperature, in accordance with our second hypothesis. Model 2, calculating $A_{max,0}$ as a linear function of the average radiation intensity during leaf growth, estimated A_{max} well for the fodder radish canopy obtained from optimization ($A_{max,eff}$). For winter rye, both regression models overestimated $A_{max,eff}$ of the canopy. This is attributed to differences in canopy structure between fodder radish and winter rye.

Chapter 5

Root, soil water and nitrogen dynamics in a catch crop - soil system in the Wageningen Rhizolab

with P.A. Leffelaar

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Abstract

Catch crops (winter rye and fodder radish) were grown on lysimeters with rhizotron facilities from August or September till March in two consecutive years, to study root growth and water and nitrogen dynamics under different regimes of irrigation and N supply. Catch crops took up 20 to 30 g N m^{-2}, of which a considerable part (37 - 48 %) was present in dead leaves in March. Rooting depth increased by 2.6 cm day^{-1} for both species at the start of the growing season.

Catch cropping reduced the NO_3^--N concentration in the soil considerably during the whole duration of the experiments, first in the top layers, than further down the soil profile. The reduction in total leached N was similar to the total crop N uptake. Nitrate-N concentrations in leached water were reduced by 49 - 85 mg l^{-1} (by 62 to 99 %), dependent on N availability and irrigation. Due to catch cropping the NO_3^--N concentration in the percolate decreased with increasing irrigation (or precipitation), whereas the amount of N leached increased with irrigation. Evapotranspiration from a catch cropped soil is close to the potential evapotranspiration under optimal growth conditions.

Keywords: winter rye, fodder radish, catch crops, evapotranspiration, nitrogen leaching, mineralization, nitrogen uptake, rhizotron, rooting depth

Introduction

Catch crops are cultivated after the harvest of a summer crop to reduce losses of N by leaching during autumn and winter. They often effectively reduce the nitrate concentration in leaching soil water by absorbing up to 19 g m^{-2} N (Vos & Van der Putten, 1997). The N uptake by catch crops and the resulting reduction in N leaching from the soil widely vary with specific conditions in field experiments (Landman, 1990; Schröder *et al.*, 1992). Analysis of the processes determining catch crop growth and N leaching may make it possible to relate observed variations to environmental conditions so that the effectiveness of catch crops in reduction of N leaching may be improved. The nitrogen uptake depends on the uptake capacity of the crop and the availability of N in the rooted soil. Rooting depth and root density are important characteristics and determine how much nitrogen can be taken up (Van Noordwijk, 1982). Catch crop species differ in root density and in the rate at which rooting depth increases (Thorup-Kristensen, 1993a), and consequently, the rate at which N in various soil layers can be taken up by the crop.

The rate of N leaching depends on the percolation rate of soil water and its N concentration. Both will vary from one year and location to another. Both percolation rate and N concentration in the soil solution are reduced by catch crops. Little is known about transpiration by catch crops and the subsequent reduction in percolation rate. Simulated transpiration by a catch crop under Swedish conditions is 30 to 50 mm water from mid August until the start of April (Lewan, 1993).

The aim of this paper is to quantify the effects of precipitation, catch cropping and N fertilizer rates on soil water and N dynamics and catch crop biomass, N uptake and root growth.

Materials and methods

The Wageningen Rhizolab (Van De Geijn *et al.*, 1994) is a facility to monitor both soil N transport and root length in a soil profile throughout the growing season of crops; it combines the features of a lysimeter with those of a rhizotron. Time courses of root development, soil solution nitrogen concentration, water content and temperature in the soil profile can be followed. Soil N transport and relevant catch crop growth processes, such as root growth and N uptake were studied in the Rhizolab, and the results were used to interpret results of field studies better, and to estimate how much N will leach with and without cultivation of a specific catch crop, in various conditions. Two experiments were done in the Rhizolab. Experiment 1 in 1993-1994 with fodder radish and Experiment 2 in 1994-1995 with winter rye.

Experiment 1

In Experiment 1, from 1 September 1993 until 14 March 1994, fodder radish was grown on two 1.25 × 1.25 m Rhizolab compartments at two irrigation regimes. Two other compartments were kept fallow and received the same irrigation. The low irrigation rate (Ilow) was equivalent to 1 mm day^{-1} until 2 November, and to 2 mm day^{-1} thereafter, comparable to a rather dry autumn and normal Dutch winter. The high rate (Ihigh) was equivalent to 3 mm day^{-1}, comparable to an extremely wet winter. Irrigation was supplied twice a week. Below, treatments are indicated with CIlow, CIhigh, FIlow and FIhigh, where C stands for ‘cropped’ and F for ‘fallow’.

The Rhizolab compartments filled from 0 to 100 cm below ground level with a sandy soil with an organic matter content of 41 mg g^{-1} dry matter and a pH-H_2O of 6, and packed to a dry bulk density of 1.35 g cm^{-3}. From 100 to 170 cm below ground level, a river sand without organic matter was used with pH-H_2O of 4.5, packed to a bulk density of 1.54 g cm^{-3}. The soil profiles were unfertilized, and drained at 170 cm below ground level. After Experiment 1 the sandy soil was taken out of the Rhizolab compartments and stored until August 1994 when it was used in Experiment 2.

Fodder radish was sown on 1 September 1993 at 12.5 cm row distance. After emergence the plants were thinned in the rows to 1 per 4 cm. This is a bit higher than to the normal seeding density of 1.2 to 2.0 g m^{-2}. Fodder radish was also sown around the compartments to minimize border effects, e.g., incidence of light directly on the side of the canopy.

Crop management was aimed at optimal growth conditions: sowing depth and distances between the seeds were standardized. Spots with low plant densities were filled with plants transplanted from outside, assuring a good and homogeneous crop establishment. Water shortage, sometimes delaying emergence in field experiments, was absent. The radish crop was protected against frost by covering it with transparant plastic, below which the air was heated to 4 ± 2 °C and ventilated. This happened during frost periods from 19 November to 6 December 1993 and from 11 to 25 February 1994. The border plants had frozen to death in the first frost period. Therefore, on 10 December 1993 the crop was surrounded by a vertically installed shade gauze transmitting about 50 % of the light, with the same height as the crop. The crop was harvested on 15 March 1994, about the normal incorporation time in practice.

Because of the limited number of Rhizolab compartments available it was impossible to replicate the treatments. Everything possible was done to avoid differences from one compartment to another, except for the imposed treatments: the compartments were filled with the same soil in the same way and were placed next to each other, so that environmental conditions were similar. Because of these precautions it is plausible that clear differences between compartments are due to the treatments and not to compartment effects.

To determine the nitrogen mineralization rate, sandy soil was stored in plastic bags with the open end rolled up (about 200 g soil per bag with a gravimetric water content of 20 %). The samples were buried at 15 cm below ground level next to the Rhizolab compartments, so that they were subject to the same temperatures as the soil in the compartments. At two to four week intervals during the experiment, five bags were removed for determination of mineral N fractions. The mineral N present in the bags after incubation, minus that present at the start of the experiment, was assumed to be mineralized from organic matter. It increased in time, and in Experiment 2, then decreased, presumably due to denitrification. The maximum value of mineralised N in the course of time was taken as the total N mineralized during the experiment.

Experiment 2

Winter rye was grown in four Rhizolab compartments from 24 August 1994 until 17 March 1995. The compartments were filled with the same soil in the same way as in Experiment 1. All compartments received 3.07 g m^{-2} P and 10.0 g m^{-2} K, respectively, in the top 10 cm. There were four N fertilization rates: (1) zero N (N0), (2) 7 g m^{-2} at sowing in the upper 10 cm of the soil profile (N7s), (3) the same plus an extra application of 7 g m^{-2} N, supplied with the irrigation water, equally divided over three applications at 26, 36 and 47 days after sowing (N14), and (4) 7 g m^{-2} N placed at 40-50 cm depth in the soil (N7d). The deep placement was meant to test the effect of N that has ‘leached’ already to a certain depth before the catch crop starts to grow. N14 is meant to be amply supplied with N during the whole experiment. The irrigation rate was equivalent to 3 mm day^{-1}, to study the performance of the crop at a high percolation rate. Soil properties and drainage conditions were the same as in Experiment 1.

Winter rye was sown on 24 August 1994 at 12.5 cm row distance in the compartments. Only seeds of 2.5 to 3 mm in diameter were used, to obtain a homogeneous crop. Rye was also sown around the compartments. The distance between seeds in the row was 1.5 cm, corresponding to the normal seeding density of 18 g m^{-2}. On 30 August all rows contained 70 plants or more. There were no replications. The same precautions to avoid compartment effects were taken as in Experiment 1. Net N mineralization was determined from the increase in mineral N in soil buried in plastic bags near the Rhizolab compartments, similar to Experiment 1.

Measurements

Rhizolab measuring equipment was installed in the soil profiles according to Van de Geijn *et al.* (1994) unless changes are mentioned below.

Root number was determined regularly as described by Smit *et al.* (1994), by recording the roots on video tape in horizontally installed glass tubes (minirhizotrons) and counting the number of roots at regular positions in the profile. Root length was measured in auger samples taken at 10 cm depth intervals at 3 occasions during the growing season (October, November, March).

Soil moisture content was determined hourly by capacitive moisture sensors, and daily averages were calculated for selected days (matching N measurements) and used in further calculations. In soil solution and in drainage water, NO_3^--N and NH_4^+-N concentrations were determined according to Walinga *et al.* (1989). The soil solution was sampled with under-pressurized ceramic cups and porous tubes. The amount of drainage water was recorded and it was sampled weekly for determination of NO_3^--N and NH_4^+-N concentrations. For Experiment 1, the measurements of NO_3^--N concentrations in the drainage water failed. To estimate leached N, the concentrations measured once every 14 days at 150 cm depth were used. The concentrations in the weeks between these measurements were obtained by linear interpolation.

For determination of mineral N balances, NO_3^--N and NH_4^+-N were determined in auger samples of the soil collected at two occasions during the growing season (at sowing and at harvest).

Capacitive sensors, thermocouples, ceramic cups and porous tubes were installed in duplicate at 5, 10, 15, 20, 30, 40, 60, 85, 115 and 150 cm below ground level in Experiment 1. In Experiment 2, the depths were adapted to have a better monitoring of the fate of fertilizer N applied from 40 to 50 cm below ground level. They were installed in duplicate at 5, 15, 30, 45, 55, 70, 90, 115 and 150 cm below ground level.

Soil from the bags incubated to determine mineralization was dried at 40 °C and extracted with 0.01 M $CaCl_2$ and subsequently concentrations of NO_3^--N, NH_4^+-N and total soluble N were determined (Walinga *et al.*, 1989). Mineralization data were converted to g m^{-2} in the Rhizolab compartments assuming a uniform bulk density and a uniform mineralization rate in the layer 0-100 cm below ground level.

At the end of the experiment, the crops were harvested. For fodder radish (Experiment 1) living and dead leaves, stems and pen roots were distinguished. Winter rye (Experiment 2) was separated in living leaf blades and sheaths, dead leaves and stubbles. Root weights were determined in auger samples. Total N concentrations were determined in all plant parts (Novozamsky *et al.*, 1974, 1983) except for radish fine roots, in which the same N concentration as in pen roots was assumed.

Calculations

Radiation use efficiency was calculated by assuming half of radiation between emergence and canopy closure to be intercepted, and all radiation after canopy closure. For estimating amounts of nitrogen and water in the profile the point measurements were assumed representative for a layer around the point of measurement (e.g. the measurement at 5 cm for 0-10 cm depth, at 90 cm for 80 -100 cm depth). Evapotranspiration during a period was calculated according to Equation 1 with all terms in mm:

$$\text{evapotranspiration} = \text{irrigation} - \text{change in soil water content} - \text{leaching} \qquad (1)$$

For comparison, the potential evapotranspiration (Penman, 1948) was calculated. Data were used from the weather station at Wageningen, at 2 km from the experimental site.

Results

Soil water balance

The soil water balance was evidently affected by the treatments in Experiment 1 (Figure 1a-d), but not in Experiment 2 (Figure 1e-h): the differences in N supply did not affect transpiration by the rye crop (Figure 1h). The water storage in the profile (0-170 cm depth) increased to an equilibrium level that increased with irrigation rate (Figure 1b). In CIlow the soil water was temporarily depleted, but the equilibrium level was the same as in FIlow after the irrigation rate had been increased from 1 to 2 mm day^{-1}. At the end of the experiments (cumulative) evapotranspiration was on average 40 ± 11 mm (average and standard deviation over the specified group of compartments) for the fallow compartments, 204 ± 15 mm in radish (Figure 1d) and 168 ± 9 mm in rye (Figure 1h). Rye had a high evapotranspiration rate until the end of November and did not transpire much until february, when it increased again. Radish continued to transpire throughout

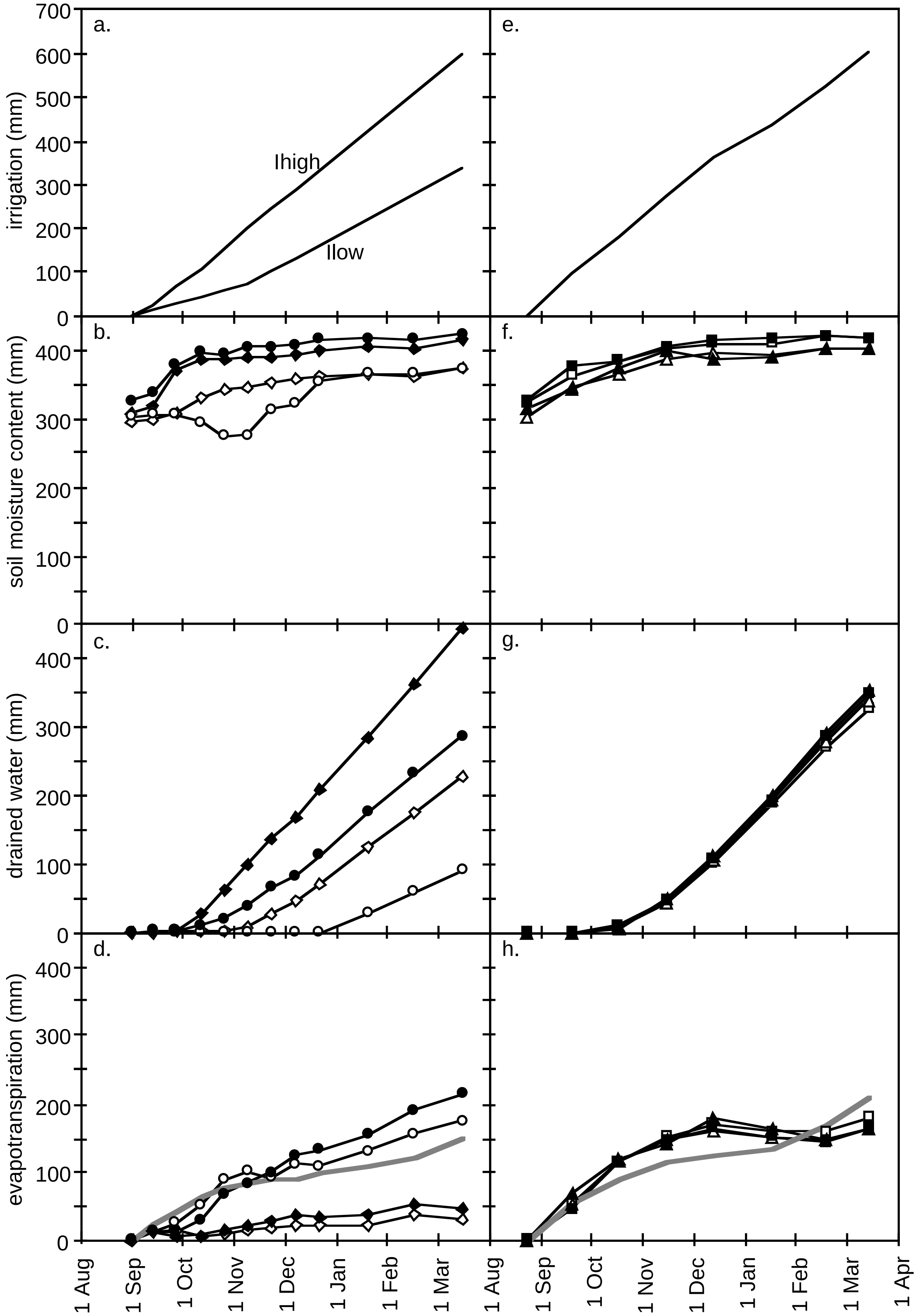

Figure 1. Soil water dynamics in Experiments 1 (fallow/fodder radish; a-d) and 2 (winter rye; e-h). a and e: Cumulative irrigation. b and f: Total soil water in the profile. c and g: Cumulative drained water. d and h: Cumulative evapotranspiration and potential evapotranspiration. Symbols: b-d: —◇— = FIlow, —◆— = FIhigh,—○— = CIlow, —●— = CIhigh. f-h: —□— = N0, —△— = N7s, —▲— = N7d, —■— = N14. The thick line in d and h is the potential evapotranspiration.

the winter. Radish reduced total leaching by 155 ± 2 mm, compared to fallow (Figure 1c). The difference in leaching between Ihigh and Ilow was 215 ± 2 mm, not as large as the difference in irrigation, 259 mm (Figure 1a). This is also reflected by a higher water storage at the high irrigation rate (Figure 1b). The evapotranspiration in the cropped treatments was sometimes higher than the potential evapotranspiration that was calculated from the weather data.

Soil N balance

The N balances of Experiments 1 and 2 (Table 1) differ considerably in both their input and output terms. Firstly, the mineral N content at the start of the experiment is higher in Experiment 2, in N0, than in any treatment of Experiment 1. This is probably because a crop had grown on the soil just before Experiment 1, whereas it had been stored for 5 months before the start of Experiment 2. During that time, Nmin had increased by mineralization, from the low final Nmin concentrations of Experiment 1. The rigorous mixing of the soil before filling the Rhizolab compartments will also have increased Nmin by stimulating mineralization. The balances of the profiles are mostly not zero, and differ from one treatment to another. Positive balances, (2-18 % of N present at the start, applied or mineralized) mean that not all N is recovered at the end of the growth period in the profile, the leachate and the crop. This may be due to inaccuracies in measurements, or to unquantified processes: denitrification was not measured, but may

Table 1. Mineral N balances (g m^{-2}) of soil profiles in Experiments 1 and 2. See text for explanation of treatments.

Experiment 1	FIlow	FIhigh	CIlow	CIhigh
a. Profile start (8 September 1993)	12	12	12	12
b. Mineralisation	21	21	21	21
c. Leaching	18	22	0	1
d. Crop uptake radish	0	0	20	20
e. Profile end (16 March 1994)	11	11	9	6
Balance (a+b-c-d-e)	5	0	5	6

Experiment 2	N0	N7s	N7d	N14
a. Profile start (24 Aug 1994)	19	20	18	18
b. Mineralisation	23	23	23	23
c. Fertilisation	0	7	7	14
d. Leaching	9	12	17	18
e. Crop uptake rye	27	25	27	28
f. Profile end (13 Mar 1995)	2	3	3	3
Balance (a+b+c-d-e-f)	4	9	1	6

amount up to 20 % of the available nitrate under winter field conditions (Richter & Richter, 1991). Moreover, some N may be present in unrecovered decomposing crop material. In Experiment 2, the unrecovered Nmin was higher in N7s and N14, that were fertilized at the top of the profile, than in the other treatments. Denitrification may have been higher in N7s and N14, due to the extra N available from fertilization, compared to N0. In N7d, N leaching was earlier and more intensive, so less N could be denitrified than in N7s and N14. Apparently this was not counteracted by a possibly lower oxygen concentration in the subsoil than at the top of the profile.

Crop N uptake was not affected by the treatments (Table 1). Fodder radish depleted the profile in March, compared to fallow. It reduced leaching effectively. At the very high N availability in Experiment 2, rye could not prevent N leaching completely, despite its high N uptake.

Crop biomass and N accumulation

Both biomass and N in the crop were higher in rye (Experiment 2) than in radish (Experiment 1) (Figure 2). Experiment 2 also had the highest N supply in the soil, both in fertilized and unfertilized treatments (Table 1). Also, sowing was 8 days earlier in Experiment 2, allowing the rye crop to grow longer at relatively high light intensities in September and October (Table 2). Radiation use efficiency was on average 0.70 g MJ^{-1}

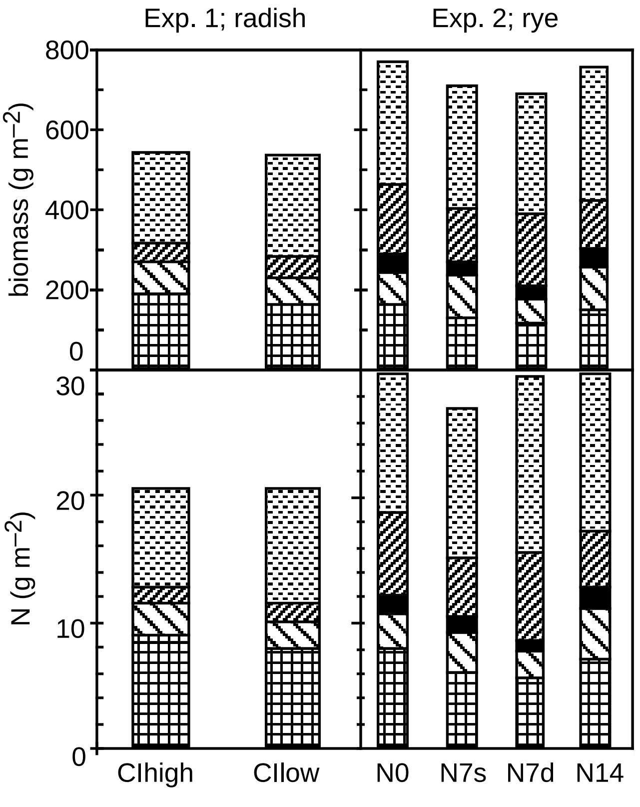

Figure 2. Crop biomass and N contents at the end of the experiments. ⊞ = green leaves, ⧅ = stems (incl. rye sheaths), ■ = stubble, ▨ = roots, ⬚ = dead leaves.

Table 2. Monthly average weather data during Experiments 1 and 2, compared to long term averages for the Netherlands (Bor et al., 1994). Temperature in ˚C; Global radiation in 10^7 J m^2 $month^{-1}$.

	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
Temperature								
Experiment 1	14.7	12.8	9.1	2.4	4.6	4.8	1.2	7.0
Experiment 2	17.4	13.8	9.3	9.7	4.9	3.3	6.4	5.2
Long term av.	16.7	14.2	10.7	6.1	3.3	2.2	2.5	4.9
Radiation								
Experiment 1	40.7	26.9	19.1	9.3	4.0	7.1	14.7	23.7
Experiment 2	48.9	23.9	21.1	8.6	6.3	8.1	11.3	30.9
Long term av.	47.4	31.8	19.2	9.0	5.5	7.1	13.8	26.0

global radiation in radish and 1.0 g MJ^{-1} in rye. Moreover, November was warmer in 1994 (rye) than in 1993 (radish) (Table 2). Total biomass was not affected by the treatments; in rye N7s and N7d had a somewhat lower biomass than N0 and N14, but for N only N7s is lower. There was no consistent effect of increase in N supply on total biomass. This can be explained by the high N availability in the soil without fertilization (Table 1). However, root biomass decreased with N supply in rye (N0 - N7d - N7s - N14). The shoot root ratio (dead leaves excluded) was higher in radish than in rye, confirming results from other experiments (Van Dam & Hüner, unpublished results; Vos & Van der Putten, 1997). 40 to 50 % of biomass and 37 to 48 % of N was present in dead leaves, indicating a considerable biomass turnover.

N concentrations were 47 mg g^{-1} in green leaves, 35 mg g^{-1} in dead leaves, 32 mg g^{-1} in stems and 27 mg g^{-1} in pen roots of radish. In rye these concentrations were 47 mg g^{-1} in green leaves, 39 mg g^{-1} in dead leaves, 35 mg g^{-1} in sheaths and stems and 24 mg g^{-1} in roots.

Root length

The rooting depth reached 100 cm on 6 and 13 October in radish at low and high irrigation respectively, and on 29 September in rye in all treatments (Figure 3a, d). On average the rooting depth increased 2.6 cm day^{-1} in radish and rye.

The numbers of roots counted on the glass tubes are presented in Figure 3b and e for a selection of measurement dates. After 12 October in rye and 13 October in radish, the changes in root numbers were small (data not shown). Therefore, for later dates the root length densities (RLD) in the auger samples are presented (Figure 3c, f). Both on the glass tubes and in the auger samples rye had more roots than radish. The shape of the root profile was similar for both species; Root density was high in the top 10 cm and much lower and slightly decreasing with depth in the rest of the profile. After mid

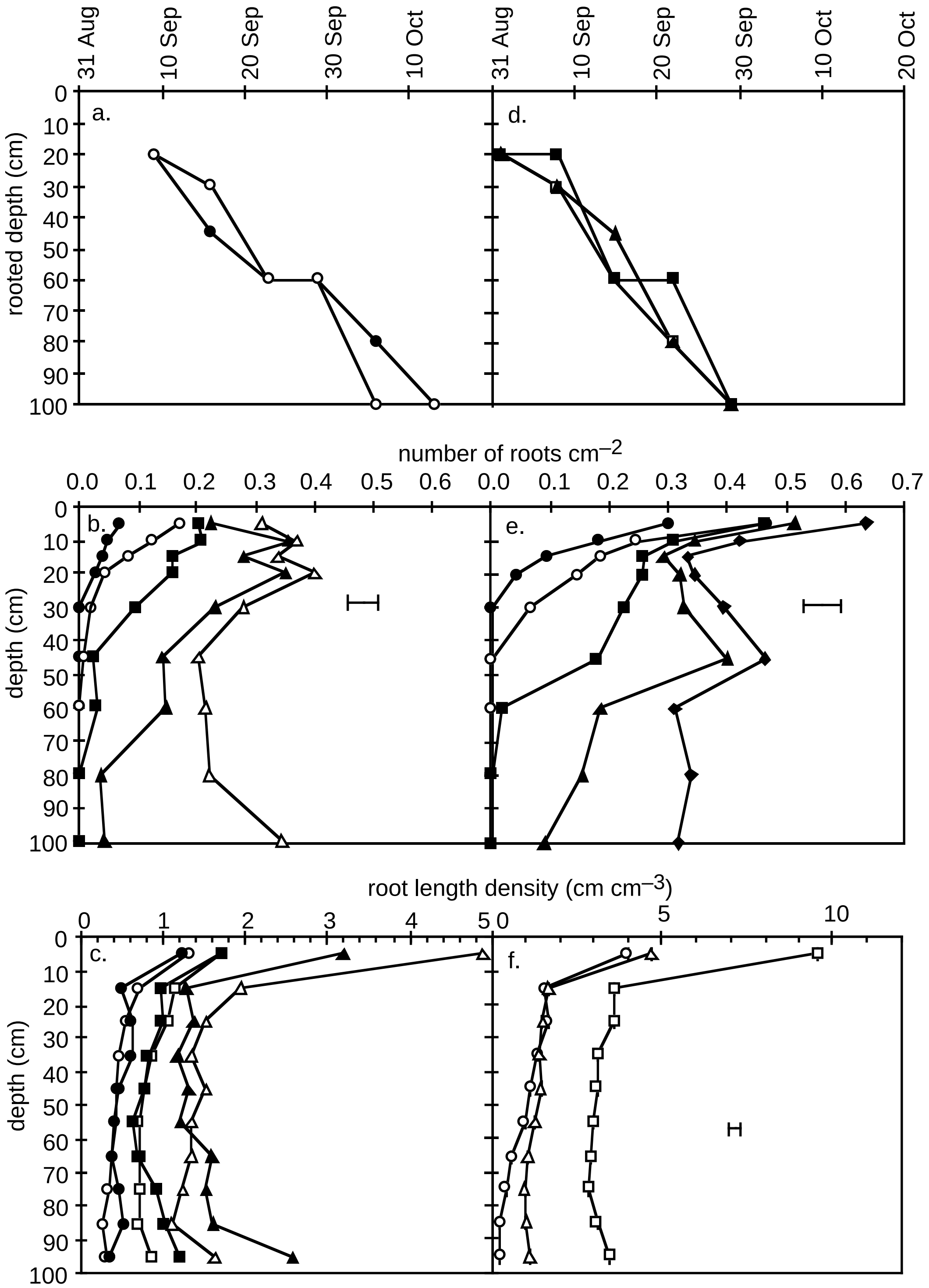

Figure 3. Root profiles during Experiments 1 (a-c) and 2 (d-f). In b, e and f, root parameters are averaged over the treatments (bars are average standard deviations). a and d: Rooted depth. b and e: Numbers of roots in the profile at several moments from sowing to mid October. c and f: Root length density at three moments during the growing season. (Note: X-axes in c and f have different scales). Symbols: a: —●— = Ihigh, —○— = Ilow; b: —●— = 9 September, —○— = 16 September, —■— = 23 September, —▲— = 6 October, —△— = 13 October; c: Ilow: —○— = 15 October 93, —□— = 17 November 93, —△— = 15 March 94, Ihigh: —●— = 15 October 93, —■— = 17 November 93, —▲— = 15 March 94 ; d: —□— = N0, —△— = N7s, —▲— = N7d, —■— = N14; e: —●— = 1 September, —○— = 8 September, —■— = 15 September, —▲— = 29 September, —◆— = 12 October; f: —○— = 12 October 94, —△— = 10 November 93, —□— = 14 March 94.

October, roots accumulated at 100 cm depth, on the interface of the topsoil and the subsoil, into which the roots did not grow. This effect was more pronounced in radish than in rye. In radish, RLD was lower in the top 50 cm in Ihigh than in Ilow, but below 60 cm depth the root length density was higher in Ihigh than in Ilow; the roots in Ihigh showed a greater tendency to explore deeper layers as compared to Ilow.

Nitrogen in soil and drainage water.

Leaching started later in Ilow than in Ihigh in Experiment 1, and later in the cropped than in the fallow compartments (Figure 4). The amount of N leached increased with irrigation (Experiment 1) and with N supply (Experiment 2: N0 - N7s - N7d - N14) (Table 1). In N7d the increase in N leaching compared to N0 (8 g m^{-2}) was slightly larger than the nitrogen application. In N7s and N14 only a part of the applied N leached. Nitrate concentrations in drainage water were higher in FIlow (78 mg l^{-1} on average) than in FIhigh (50 mg l^{-1} on average). The radish catch crop reduced the average NO_3^--N concentration in drainage water to 1 and 5 mg l^{-1} in CIlow and CIhigh, respectively. The difference in N leaching between FIlow and FIhigh is relatively small: the amount of N leached in FIlow was 82 % of that in FIhigh (Table 1) although the amount of leached water in FIlow was only 51 % of that in FIhigh. In CIlow, leaching started only after the irrigation had been increased from 1 to 2 mm day^{-1}. In rye the NO_3^--N concentration in the leachate increased with N supply, from 26 mg l^{-1} in N0 to 51 mg l^{-1} in N14. The effect of growing a catch crop on the amount of NO_3^--N in soil and drainage water was evident: the maximum difference in the NO_3^--N content of profiles between fallow and radish-cropped treatments is 22 g N m^{-2}, quite similar to the N present in the radish crop at harvest (20 g m^{-2}, Table 1). On 14 March the nitrate content of the profile in the fallow treatment was still higher than in the cropped treatment on 14 March (Figure 4), suggesting that fodder radish continued to take up N until the end of the experiment. The Nmin content of the radish-cropped profiles in March, based on N concentrations in the auger samples (Table 1), were however higher than those of NO_3^--N based on the soil solution measurements (Figure 4). NH_4^+-N concentrations were negligible. Therefore, it seems that in some cases not all mineral N can be measured from soil solution samples extracted with suction cups and porous tubes. This method may lead to underestimation of Nmin.

In Experiment 2 (Figure 5) the time course of the nitrate content of the profile had the same pattern in all treatments: N present at the start was depleted, first in the upper soil layers, than also in the deeper ones. On 17 October no nitrate was left in the soil down to 50 cm depth in N7s and to 60 cm depth in N0 and N7d. Thereafter a net increase in NO_3^- occurred in that layer until 16 February, after which the nitrate content of the soil profile decreased, suggesting an increase in rye uptake activity towards spring; leaching rate was constant during that period. In N7s and N14 the NO_3^- content of the soil increased at the start of the experiment. In N14 this will have been due to the split application of N, but the difference in behaviour between N7s on one hand and N0

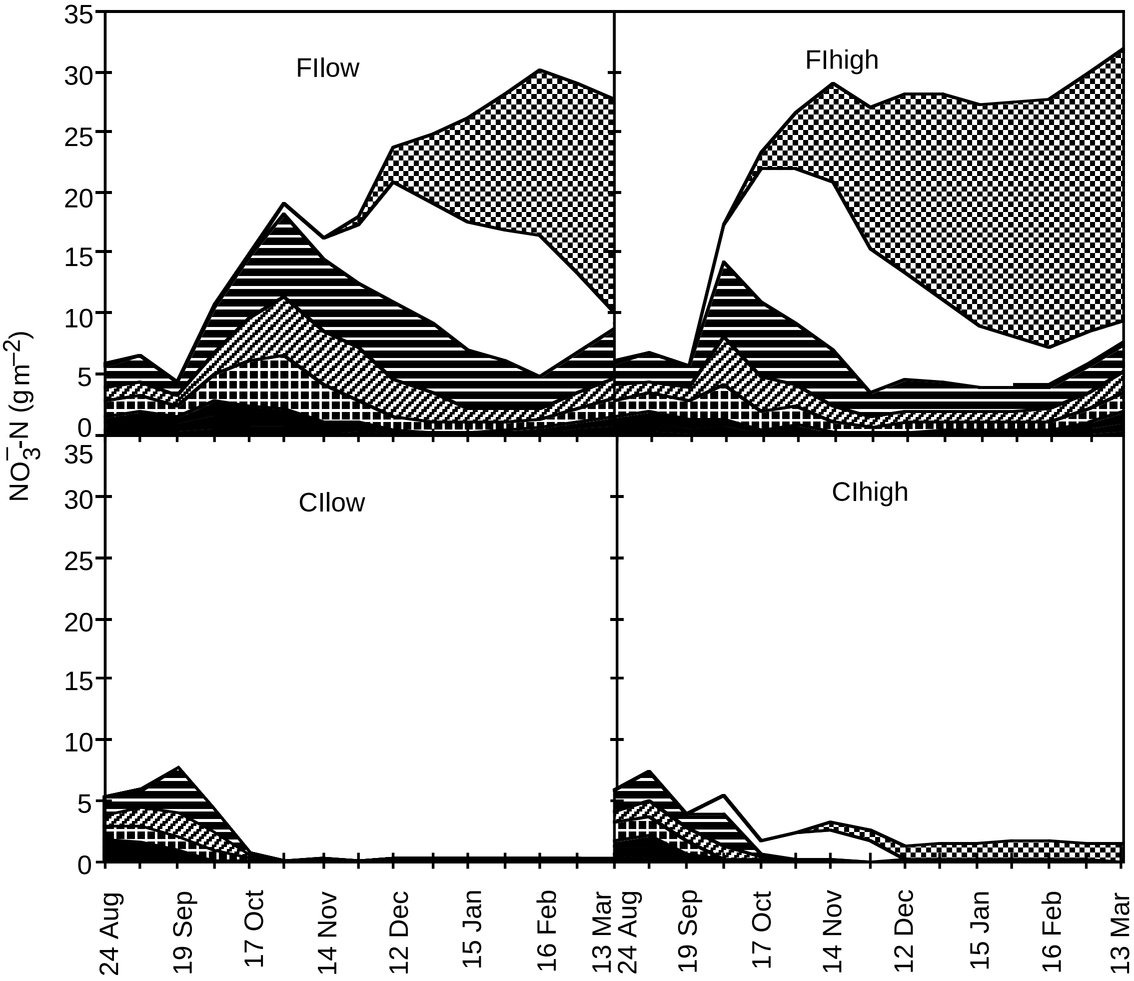

Figure 4. NO$_3^-$-N contents in layers of soil profiles and in drainage water during Experiment 1. Areas represent contents (g m^{-2}) measured in soil solution in different layers (in cm depth) and leached water. Symbols: ■ = 0 - 30 cm depth,▦ = 30 - 50 cm, ▨ = 50 - 70 cm, ☰ = 70 - 100, ☐ = 100 - 170 cm, ▩ = leached.

and N7d on the other cannot be explained by this. NH$_4^+$-N concentrations in soil were low during the whole of the experiments (data not shown).

Discussion

N accumulation

Crop management was directed at optimal growth conditions and resulted in a high N uptake in both experiments. Treatments had no effect on total biomass production or N accumulation, although the partitioning to root increased when supply of water or N decreased. The small magnitude of the treatment effects indicate that growth conditions were already close to optimal at the lowest levels of N and water supply. Despite the precautions to minimize edge effects of the compartments, growth may have been

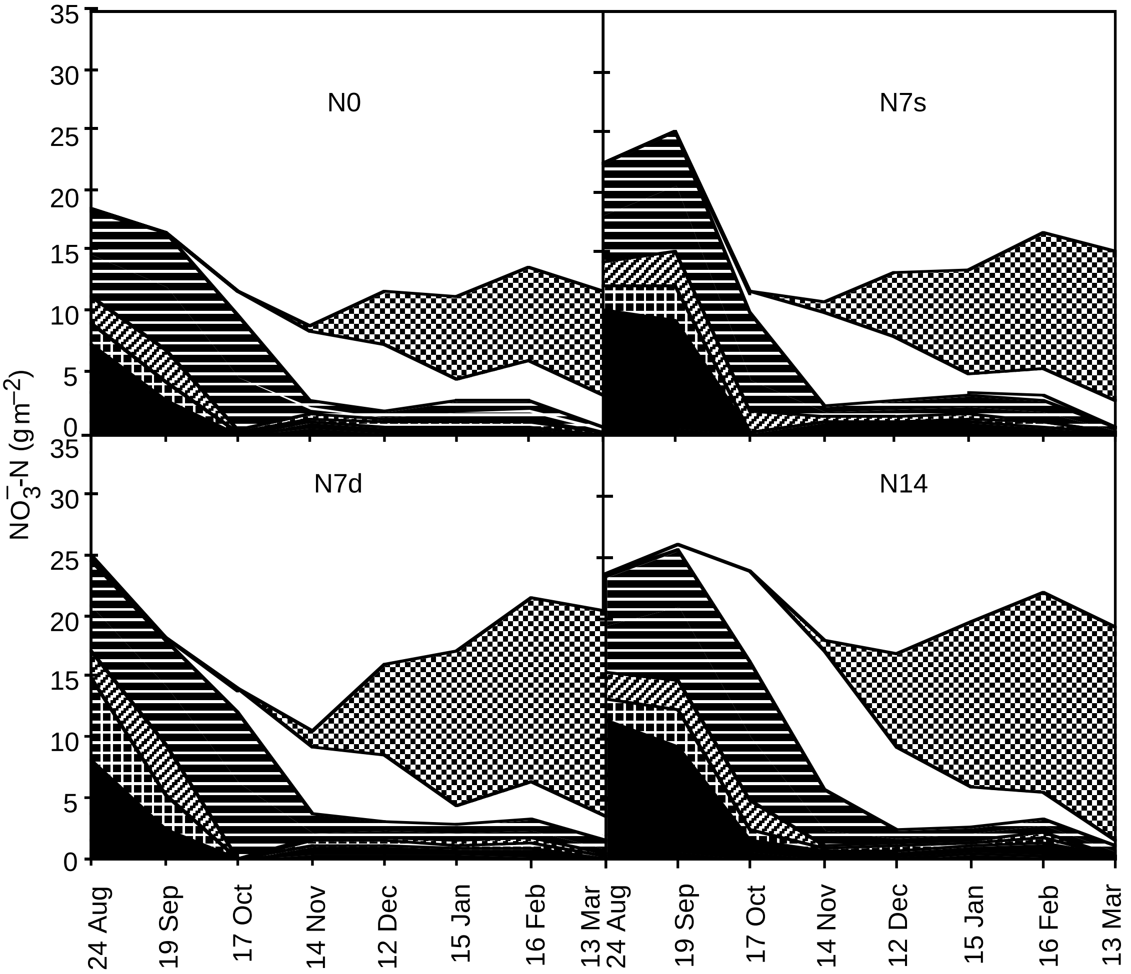

Figure 5. NO$_3^-$-N contents in layers of soil profiles and in drainage water during Experiment 2. Areas represent contents (g m^{-2}) measured in soil solution in different layers (in cm depth) and leached water. Symbols: ■ = 0 - 40 cm depth, ⊞ = 40 - 50 cm, ▨ = 50 - 60 cm, ▤ = 60 - 100, □ = 100 - 170 cm, ▩ = leached.

slightly enhanced by light falling on the side of the canopy. The high transpiration, sometimes higher than the potential evapotranspiration, is an indication of this.

Nevertheless the radiation use efficiency was rather low when compared to other studies (e.g. 1.25 g MJ^{-1} global radiation for cereals, Gallagher & Biscoe, 1978; 1.19 g MJ^{-1} for catch crops, Vos & Van Der Putten, 1997). Weather conditions were not exceptional for the Netherlands (Table 2).

The shoot to root ratio was higher in radish than in rye, as is also found in other experiments (Vos & Van der Putten, 1997; Lainé *et al.*, 1993). This implies that radish invested relatively less biomass in roots without any evidence that the amount of roots limited nutrient uptake. This may be so because radish compensated for the smaller investment in root biomass by its higher specific root length (667 ± 82 cm g^{-1} in radish and 254 ± 53 cm g^{-1} in rye). Yet, when evaluated by root length instead of biomass, rye still had a more extensive root system than radish (Figure 3c and f). At the start of the growing season, before the canopy is closed, this may enhance growth: more biomass can be invested in shoots, and thus more light can be intercepted. Rye has, however, a higher specific leaf area (Vos & Van der Putten, 1997), so that it would need less leaf mass for the same light interception.

The nitrogen content of the crop were high compared to summer crops of the same biomass (Greenwood *et al.*, 1990) but in the same range as those reported for amply fertilized catch crops by Vos & Van Der Putten (1997). This may be due to the different growth conditions as compared to summer crops, and the resulting difference in development stage: both rye and radish consisted mainly of vegetative material at harvest. Therefore in modelling the growth of a rye catch crop, the crop N concentration is related to temperature sum rather than biomass (Van Dam *et al.*, 1996). In most catch crop studies, less biomass was formed, and less nitrogen accumulated (e.g. Landman, 1990; Sörensen, 1992). Vos & Van der Putten (1997), however, found biomass and nitrogen accumulation in catch crops in the same range as reported here. Nitrogen concentrations in dead leaves were also high compared to other studies, e.g. in grassland (Whitehead, 1995). Redistribution of N from senescing tissue is less important in a catch crop in winter than in a summer crop: in winter the growth rate of the crop may be so low that not all N from the dying tissue is needed for new biomass.

The amount of dead leaves is mostly lower in field experiments than found here (Figure 2; Vos & Van der Putten, 1997). This may be due to the lush growth of the crops here, which promoted senescence by shading. Also, in the field decomposition of dead leaves may occur, where the N content of a catch crop may show a net decrease of as much as 6 g m^{-2} N from November to March (Vos & Van der Putten, 1997). In Experiments 1 and 2, the dead leaves accumulated on top of the gravel layer, above the irrigation system, so that they were rather dry and less susceptible to decomposition than dead leaves on a moist soil surface in the field. The decomposition in the field experiments may lead to underestimation of total growth and N accumulation of catch crops.

Deep rooting assured the possibility to take up all N in the 0-100 cm layer, so that N transported downward could yet be absorbed. In October in both experiments the rooting density was much higher than required for unrestricted N uptake (Van Noordwijk, 1982). The average rate of increase in rooting depth of 2.6 cm day^{-1} is comparable to the average rate in fodder radish in a field soil, 2.3 cm day^{-1}, calculated from data of Thorup-Kristensen (1993a). In the field, increase in rooting depth in rye is much slower than in radish (Thorup-Kristensen, 1993a), a difference that did not occur in the Rhizolab. Here, the soil profile was homogeneous from 0 to 100 cm depth and initially Nmin was high in this whole layer. This may have caused rye roots to grow deeper and faster in the Rhizolab than in a field soil, in which nutrients and organic matter are mostly concentrated in the top 40 cm of the profile. Later in the season, radish had a stronger tendency than rye to accumulate roots at the bottom of the topsoil (at 100 cm below ground level, Figure 3e and f). This may be caused by a relatively greater tendency in radish than in rye to grow deep into the soil. However, it may also be influenced by smaller amounts of N available to radish than to rye: in Experiment 1 there was no nitrate left to radish in the top 100 cm at the beginning of November. This is supported by a stronger accumulation of roots at 100 cm below ground level in CIhigh, in which N leached faster, than in CIlow (Figure 3 c). For rye, N was available in the top 100 cm during the whole experiment.

The results show that nitrogen accumulation by a catch crop is potentially very high. From field experiments lower values have been reported (Landman, 1990; Schröder *et al.*, 1992). Differences may be due to a slower or less complete crop establishment, freezing of non-winterhardy crops, shallower rooting and lower nitrogen availability trough autumn and winter. Exploring these factors may yield clues to improvement of catch crop efficacy.

Leaching

When reduction of nitrogen leaching is considered, two factors are important. Firstly, the concentration of nitrate in the leaching water should preferably be lower than the Maximum Allowable Concentration (MAC) of 11.3 mg N l^{-1}, according to the EC Nitrate Directive (Tunney, 1992). Secondly, the amount of N that is leached from the plant-soil system is important, because N losses cost much energy, if they are replaced by fertilizer (i.e. 38.6 MJ kg^{-1} N, Evers & Pothoven, 1995).

The average nitrate concentrations in the leachate were reduced to values below the MAC by radish in Experiment 1. Concentrations were reduced by 73 and 49 mg N l^{-1} in Ilow and Ihigh, respectively. No fallow treatments were included in Experiment 2, but if all N taken up by rye had leached, average concentrations in the leachate would have been 85 ± 4 mg N l^{-1} higher than they were now. Catch crops are effective in reducing the N concentration in leaching water, and the reduction is larger at low than at high irrigation (and hence percolation). For reducing the nitrate concentration in the leachate it is desirable that a catch crop transpires little water. Figure 1d and h suggest that evapotranspiration is not dependent on species, but on the potential evapotranspiration rate.

The amount of nitrogen that leached increased with irrigation (Experiment 1, Figure 4) and with N supply (Experiment 2, Figure 5). Thus, the effect of irrigation (or precipitation) on the amount of leached N is different from the effect on the concentration in the leachate, which decreased with increase in irrigation. Deep placement of fertilizer in N7d increased leaching, compared to N7s; in N7d fertilizer N was less available to other processes, like uptake and denitrification, because it leached earlier. However, N uptake was about the same in N7s and N7d. In N7s more N may have been denitrified than in N7d, resulting in more unrecovered nitrogen in the balance (Table 1). Compared to field experiments (e.g. Wyland *et al.*, 1996; Schröder *et al.*, 1996), leached N was high, because N supply was also high. The high N supply by mineralization presumably resulted from soil mixing at the start of the experiments.

N availability in the soil profile

Ideally, catch cropping will reduce N in soil during autumn and winter, so that less N leaches. Moreover, it will increase N availability in the succeeding spring and summer for the next crop, by mineralization of N from the catch crop. As proved in this study (Figures 4 and 5) and other ones (Elers & Hartmann, 1987; Breland, 1996), catch cropping indeed reduces N in the profile in autumn and winter. However, in March, N in soil is still lower in the cropped profiles compared to the fallow treatments. In Experiment 2, the soil N content is even decreased from February to March, presumably by increased uptake activity of rye at increasing temperatures in this period. At that moment, N availability is decreased by the catch crop, so that extra fertilizer might be required to reach the same N availability as in the fallow soil. In the field, decomposition of dead leaf material may increase soil N, especially when a catch crop is killed by frost. Therefore, the optimal moment for harvesting a catch crop or incorporating it in the soil would be after the main leaching period, but, in case of a winter-hardy catch crop species, before the start of renewed growth at the end of winter. When the catch crop is ploughed into the soil, the time needed for mineralization of catch crop N and the time course of the N demand of the succeeding crop should also be taken into account for optimizing N availability after a catch crop.

Conclusions

We conclude that under Rhizolab conditions a considerable percentage (up to 48 %) of catch crop N was present in dead material at the end of the catch crop growth period, which is more than in field experiments. Dead material may decompose faster in the field (due to wetter conditions) so that catch crop N accumulation in field experiments may be underestimated. A rye catch crop sown at the end of august can potentially take up 30 g m^{-2} N. Potentially, rooting depth increases by 2.6 cm day^{-1} for both species at the start of the growing season.

Catch cropping greatly reduced the NO_3^--N concentration in soil, first in the top layers, then further down the soil profile. The reduction in N leaching is similar to crop N uptake. Nitrate-N concentrations in leached water can be reduced by values up to 49 - 85 mg l^{-1}, depending on N availability and irrigation. The reduction in NO_3^--N concentration in the leachate by catch cropping decreases with irrigation (or precipitation), whereas the leached amount of N increases with irrigation. Evapotranspiration from a catch cropped soil is close to the potential (Penman) evapotranspiration.

Chapter 6

Mineralisation of nitrogen from an incorporated catch crop at low temperatures: experiment and simulation.

with L.Van Schöll (first author) & P.A. Leffelaar

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Abstract

The release of nitrogen from incorporated catch crop material in winter is strongly influenced by soil temperatures. A laboratory experiment was carried out to investigate this influence in the range of 1-15 °C. Samples of sandy soil or a mixture of sandy soil with rye shoots were incubated at 1-5-10-15 °C, and samples of sandy soil with rye roots were incubated at 5-10-15 °C. Concentrations of Nmin (NH_4^+-N and NO_3^--N) were measured after 0-1-2-4-7-10 weeks for the sandy soil and the sandy soil:rye shoot mixture, and after 0-2-7-10 weeks for the sandy soil:rye root mixture. At 1 °C, 20% of total organic N in the crop material had been mineralised after ten weeks, indicating that mineralisation at low temperatures is not negligible. Maximum mineralisation occurred at 15 °C; after ten weeks, it was 39% of total applied organic nitrogen from shoot and 35% from root material. The time course of mineralisation was calculated using an exponential decay function. It was found that the influence of temperature in the range 1-15 °C could be described by the Arrhenius equation, stating a linear increase of ln(k) with T^{-1}, k being the relative mineralisation rate in day^{-1} and T the temperature (°C). A simulation model was developed in which decomposition, mineralisation and nitrification were modelled as one step processes, following first order kinetics. The relative decomposition rate was influenced by soil temperature and soil moisture content, and the mineralisation of N was calculated from the decomposition of C, the C to N ratio of the catch crop material and the C to N ratio of the microbial biomass. The model was validated first with the results of the experiment. The model was further validated with the results of an independent field experiment, with temperatures fluctuating between 3 and 20 °C. The simulated time course of mineralisation differed significantly from the experimental values, due to an underestimation of the mineralisation during the first weeks of incubation.

Key words: catch crop, mineralisation, nitrogen, simulation model, temperature.

Introduction

In regions with a precipitation surplus during winter and a high level of fertiliser application, there is a risk of ground water contamination by excess mineral nitrogen after cultivation of a summer crop. Catch crops can be used in the cultivation scheme to improve the efficiency of nitrogen fertilisation; firstly, by taking up the mineral nitrogen that is left in the soil after harvesting the main crop, thus preventing leaching to and contamination of the groundwater, and secondly, by making this nitrogen available again for plant uptake, thereby reducing the fertiliser requirement of the succeeding crop.

The success of catch crops in reducing the mineral nitrogen leaching has been demonstrated in several experiments (Landman, 1990; Martinez & Guiraud, 1990; Muller *et al.*, 1989; Thorup-Kristensen, 1994a).

The results from experiments done on the nutrient effect of catch crops are not so unequivocal. Thomsen (1993) and Thorup-Kristensen (1994a) found that incorporated catch crop material reduced the fertiliser requirement of the succeeding crop, whereas Muller *et al.* (1989) found a negative effect of the catch crop on the biomass production of the following crop. The incorporation date and the persistency to winter temperatures of the species used are important factors. Incorporation before winter or the use of non-persistent crops can lead to early mineralisation of plant nitrogen and subsequent leaching from the soil profile (Landman, 1990). Late winter nitrogen uptake by the catch crop when incorporating in spring will lead to a temporary loss of easily available soil mineral nitrogen into an unavailable form, only some of which will become mineralised in time to be used by the succeeding crop (Thorup-Kristensen, 1994a).

A determining factor for the mineralisation rate is the soil temperature. Little research has been done to quantify the effect of temperature on the mineralisation rate in the low temperature range prevailing during winter and spring. In many simulation models the mineralisation is assumed to decline strongly at low temperatures to become nil at 0 °C (Hansen *et al.*, 1990; Johnsson *et al.*, 1987; Van Keulen & Seligman, 1987; Van Veen & Frissel, 1981). This is based on the assumption that microbial activity stops at the freezing point. The actual soil freezing point might however be expected to be below 0 °C due to the salt content of the soil moisture. This can lead to an underestimation of the amount of N present in mineral form. Especially in models developed to predict the amount of N susceptible to leaching during cold periods, this may seriously affect the outcome of the simulations. Incubation experiments by Van Dam & Fu (1996) and Stadelmann *et al.* (1983) show that mineralisation of N (i.e. ammonification) and nitrification proceed at 0 °C, and the results of Franko (1984) suggest that biological activity under freezing point is significant.

Experiments done at higher temperature ranges (10-35 °C) show that the relation between temperature and relative mineralisation rate can be well described by an Arrhenius equation, stating a linear increase of ln(k) with T^{-1}, with k the relative mineralisation rate (day^{-1}) and T the temperature (°C) (Addiscott, 1983; Ellert & Bettany, 1992; Kladivko & Keeney, 1987; Nordmeyer & Richter, 1985; Stanford *et al.*, 1973). For the lower temperature range, relevant in winter and spring, data are lacking to validate the relation. In the experiments done at 0 °C, the mineralisation rate might have been affected by freezing and thawing of the samples, depending on the constancy of the incubation temperature.

The aim of this study is firstly to establish the mineralisation rates at temperatures in the low range (1-15 °C); secondly to test the validity of the Arrhenius equation at low temperatures; and thirdly to develop, calibrate and validate a model to estimate the mineralisation of nitrogen from incorporated catch crop material.

Table 1. Physical and chemical properties of 0-30 cm soil layer used in experiments I and II.

Soil density (without gravel) (kg dm^{-3})	1.37
Gravel (kg dm^{-3})	0.08
Gravel perc.	5.6
pH-KCl	5.5-5.8
% Org. matter	3.0-3.2

Materials and methods

Experiment I

Samples containing a sandy soil or a mixture of sandy soil and rye shoot were incubated at constant temperatures of 1-5-10-15 °C, and samples containing a mixture of sandy soil and rye root were incubated at 5-10-15 °C. The NH_4^+-N and NO_3^--N were measured after 0-1-2-4-7-10 weeks for the samples containing soil or soil:shoot mixture, and after 0-2-7-10 weeks for the samples with the soil:root mixture. There were 3 replicate bags for each treatment at each measurement.

One day before the start of the experiment the soil, a glacial sand with properties listed in Table 1, was collected at Wageningen, The Netherlands, and passed through a 1 cm sieve to remove stones. The soil was not dried since this changes the proportions of the different micro-organisms developing after incubation compared to incubated samples of fresh soils (Sparling & Cheshire, 1979), and drying and rewetting is known to influence the mineral N (Scherer *et al.*, 1992).

Shoot and root from winter rye (*Secale cereale*, cv. Halo), grown from August 24 1994 till March 17 1995 at Wageningen, were used (Table 2). Winter rye is often used as a catch crop and is persistent to low temperatures.

The shoot and root material was cut into pieces of 1-3 cm and mixed thoroughly by hand with the soil. Water was added to bring the soil to a water content of 18.5% (dry weight basis), the water content of the fresh plant material included. The soil:rye shoot ratio was 100:1.11 (g dry soil g^{-1} dry matter) or 100: 3.39 (g dry soil g^{-1} fresh matter),

Table 2. Characteristics of winter rye used in experiments I and II, grown from August 24 1994 to March 17 1995 at Wageningen.

	Dry weight % of fresh weight	N content g N g^{-1} dry weight	C/N quotient[a]
Total above ground	24.6	0.0393	10.6
Root	12	0.0239	17.3

[a] a C content of 415 g kg^{-1} was assumed (Vigil & Kissel, 1991).

and the soil:rye root ratio was 100:2.10 (g dry soil g^{-1} dry matter) or 100:15 (g dry soil g^{-1} fresh matter). Approximately 200 g of soil or soil:shoot mixture, or 185 g of soil:root mixture were put into poly-ethylene bags. These bags had been perforated with a fine needle to ensure a good aeration during the experiment to prevent denitrification. Air humidity around the incubated samples was kept high to minimise loss of soil moisture. At each sampling, the bags were weighted to determine water loss during the incubation period.

The N measurements were done with continuous flow analyses as described by Houba *et al.* (1986) after an 0.01 M $CaCl_2$ extraction, also described by Houba *et al.*, but slightly modified as follows: extractions were done with 30 g of moist sample and 300 ml 0.01 M $CaCl_2$.

Experiment II

Samples were prepared as in experiment I, using the same materials, but incubated in the field at a depth of 15 cm. They were covered with soil which was kept bare during the experiment. Soil structure allowed for sufficient aeration. Temperature was monitored at the exact site with the use of a thermo-couple. The samples were collected and analysed as in experiment I

Derivation of rate constant and temperature relation

From the mineralisation data of the soil:shoot samples, incubated at 1-5-10-15 °C, the relative mineralisation rates were derived using an iterative Non Linear Least Square method. The mineralisation process was described by a single factor exponential decay function:

$$N_{min} = N_{min.ini} + N_{max}(1-e^{-kt}) \tag{1}$$

with N_{min} the total amount of N mineralised (g N kg^{-1} dry soil), $N_{min.ini}$ the initial amount of mineral N present (g N kg^{-1} dry soil), N_{max} the maximum amount of organic N that can be mineralised (g N kg^{-1} dry soil), k the relative mineralisation rate (day^{-1}) and t time. The N_{max} was calculated as total amount of organic nitrogen minus the fraction that will be assimilated within the microbial biomass:

$$N_{max} = Fm \times N_{cont,Fm} - Fm \times \{C_{cont,Fm} \times (N/C)_{biom} \times (dis/(dis+ass))\} \tag{2}$$

with Fm the amount of fresh matter (g dry weight kg^{-1} dry soil), $N_{cont,Fm}$ the N content of the fresh matter (g N g^{-1} dry weight), $C_{cont,Fm}$ the C content of fresh matter (g C g^{-1} dry weight), $(N/C)_{biom}$ the N to C ratio of the microbial biomass, taken as 1:10 (Groot, 1987) dis and ass the dissimilation and assimilation fraction respectively of the microbial biomass, with value of 2 and 1 (Groot, 1987). In this case it is thus assumed that all fresh shoot material will be decomposed, i.e. there is no build up of humus from this material. The decomposition of the microbial biomass itself is considered negligible during the period over which mineralisation is calculated.

The Arrhenius relation, $k = A \times \exp(-B/(T+273))$, with A and B constants and T the temperature (°C), was used to quantify the relation between temperature and decomposition. It applies to relative rates, not absolute rates. Rewriting the Arrhenius relation gives $\ln(k) = -B/(T+273) + \ln(A)$. Plotting ln(k) against $(T+273)^{-1}$ should yield a straight line with slope B, while a non-linear curve would indicate that the Arrhenius relation is not valid to describe this process (Precht *et al.*, 1973).

The simulation model

To simulate the influence of temperature on the mineralisation rate, a descriptive model was developed based on the 'organic matter dynamics' subroutine of the model NWHEAT by Groot (1987), also described in Groot & De Willigen (1991). In constructing the model, no use was made of the data of experiment I and II. Modifications and extensions were made using empirically derived relationships found in the literature.

In the model, all incubated plant material enters one fresh organic matter pool. Decomposition, ammonification and nitrification are assumed to follow first order kinetics (Van Veen, 1991). Nitrogen fluxes are proportional to carbon fluxes (Gilmour *et al.*, 1985) and are calculated using the C/N ratio of the plant material. The microbial biomass, existing on the decomposition of the fresh organic material, makes up a second organic matter pool, and is subject itself to decomposition, with a relative decomposition rate k_{MB}. The decomposition serves the single purpose of new cell synthesis; the decomposition used for maintenance respiration by soil micro-organisms is neglected.

The relative decomposition rate for the fresh organic material k_{FM} is influenced by soil temperature and soil moisture content through reduction factors.
The relation between temperature and relative mineralisation rate is assumed to be described by the Arrhenius equation, $k_{FM} = A \times \exp(-B/(T+273))$, with A and B constants and T the temperature (°C) in the range 0-30 °C. The relative mineralisation rate at temperature T is calculated as a fraction of the relative mineralisation rate at reference temperature T_{ref}, using the soil temperature reduction factor $f_{Tdec} = k_{FM}/k_{FM,T_{ref}} = \exp(-B/(T+273))/\exp(-B/(T_{ref}+273))$. Below 0 °C the reduction factor proceeds linearly to the value zero at actual soil freezing point (set below 0 °C because of the salt content of the soil moisture).

The influence of soil moisture content on the relative mineralisation rate is given by the reduction factor f_{sm}, which takes the value of 0 when the soil is dryer than at pF 4.2 (wilting point) and increases linearly to the value of 1 at pF 2.4 (field capacity). Soil moisture contents between pF 2.4 and pF 2 are considered optimal for decomposition so that the reduction factor is 1. (Myers *et al.*, 1982; Stanford & Epstein, 1974). A further increase in soil moisture content gives a linear decline of the value of the reduction factor to 0.8 at saturation point (following Van Keulen & Seligman, 1987; Stol *et al.*, 1993).

The ammonification rate is calculated from the decomposition rate and the N content of the fresh organic material. The nitrification rate is calculated from the amount of ammonium, the relative nitrification rate k_{nit}, the soil moisture reduction factor f_{sm} and a temperature reduction factor f_{Tnit}. The temperature reduction factor for nitrification ranges linearly from value 0 at soil freezing point to the value of the f_{Tdec} at 5 °C, and for temperatures above 5 °C is equal to f_{Tdec}.

If the nitrogen, released from the plant material, is not sufficient to satisfy the demand of the soil micro-organisms that make up the microbial biomass, (i.e. if the C:N ratio of the plant material is too high) mineral N from the soil solution will be immobilised, and nitrification is halted. Nitrate will be immobilised only after all ammonium in the soil solution is depleted. If the nitrogen demand of the soil micro-organisms cannot be fulfilled, decomposition is reduced.

Denitrification is assumed to occur only at soil moisture contents above 80% of saturation level (Rolston *et al.*, 1984). The denitrification rate is calculated from the amount of nitrate, the relative denitrification rate k_{deni} and the reduction functions for soil moisture content and temperature. The reduction factor for soil moisture content f_{smden} ranges linearly from 0 at 80% of saturation point to the value of 1 at saturation point. For temperature, the reduction function f_{Tnit} is taken. Carbon is not considered a limiting factor for denitrification.

The daily temperature pattern is described with a sinusoidal curve, using the daily soil minima and maxima to calculate the amplitude. To assess the model’s sensitivity to the diurnal temperature fluctuations, a comparison was made with simulations using a constant temperature over the whole day, taken equal to the average day temperature.

Except for the constant B in the soil temperature correction factor and the value of the rate constant at T_{ref} (=15 °C), the model was not calibrated. All input values were derived from literature. The data from the soil:root samples of experiment I and the data from experiment II were not used for calibration, but were used for validation.

Model performance was assessed using a method developed by Whitmore (1991), which compares the sum of squares from the differences between the model and the mean of the replicate measurements (‘lack of fit’) and the sum of squares calculated from the variance within each set of replicated measurements, (‘pure error’). If the lack of fit is significantly larger than the pure error, the model could almost certainly be improved.

Results

The N_{min} is given as NO_3^--N plus NH_4^+-N, with the NO_3^--N plus NH_4^+-N as measured in the blank soil samples already subtracted. It is assumed that the added plant material is not significantly influencing the mineralisation of nitrogen from the soil organic matter.

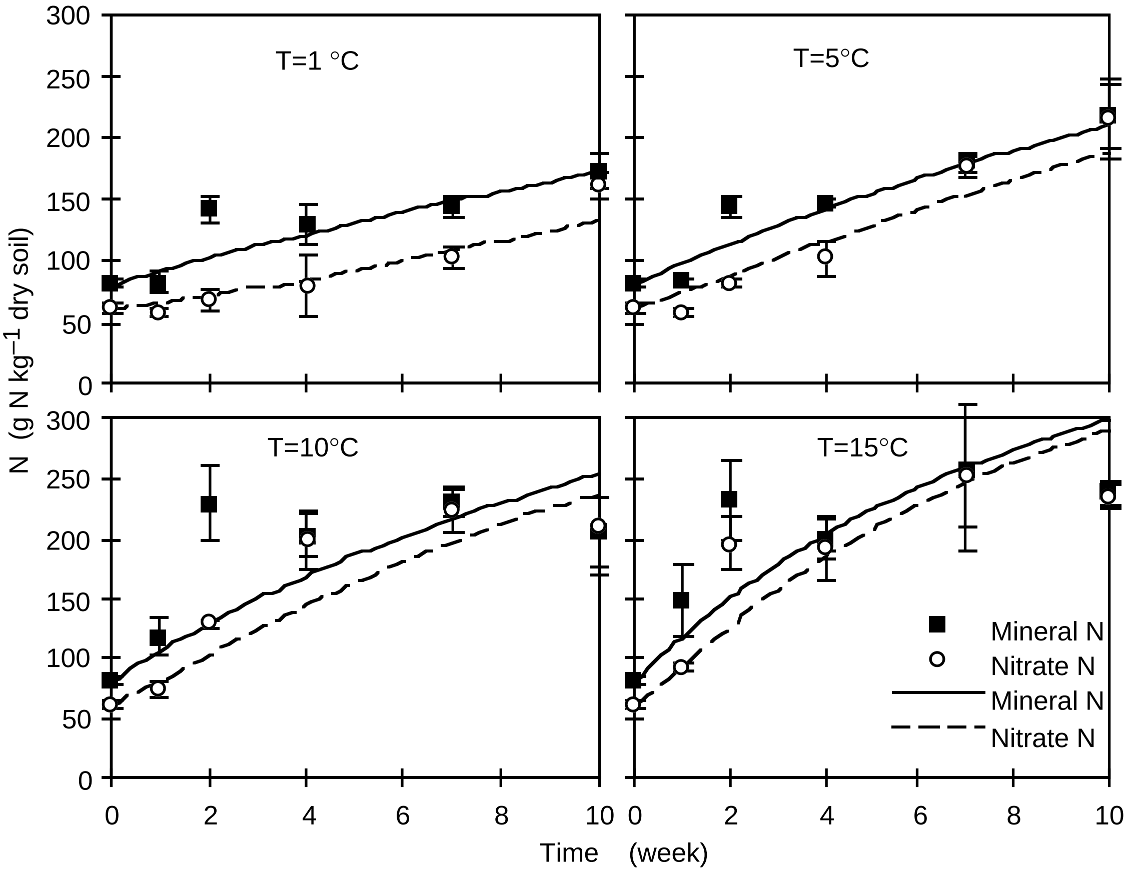


Figure 1. The time course of N_{min} and NO_3^--N in soil:rye shoot samples (dry weight ratio 100:1.11) incubated at 1-5-10-15 °C. Values measured (dots) and simulated (line).

Experiment I

The N_{min} and NO_3^--N measured for the soil:shoot and soil:root samples generally increased with temperature and time (Figures 1 and 2). During the first week the amount of Nmin and NO_3^--N from the soil:shoot samples at 1 °C and 5 °C did not increase. At 10 °C and 15 °C, the Nmin and NO_3^--N levelled off after a rapid increase at the start of the experiment. Mineralisation at 1 °C is still considerable, being 20% of total organic nitrogen (total N from fresh material minus NO_3^--N and NH_4^+-N at start of incubation) in shoot material at week 10. Maximum mineralisation occurred at 15 °C, where 39% of total organic nitrogen in shoot and 35% root material had been mineralised after 10 weeks. The standard deviation of up to 24% of the values measured is explained by the fact that all measurements were done on separate samples, so that each point is independent of other points.

The relative mineralisation rate k at 1-5-10-15 °C, derived from the soil:shoot mineralisation data, is given in Table 3. Plotting ln(k), derived from the soil:shoot mineralisation data, against $(T+273)^{-1}$ in the so-called Arrhenius plot (Figure 3) yields a straight line, with the value of the slope B=7161 (R^2=0.98, n=4).

Table 3. The relative mineralisation rate k, derived from incubation data of soil:winter rye shoot samples (dry weight ratio 100:1.11) at 1-5-10-15 °C during ten weeks.

T (°C)	k (day^{-1})	R^2 (n=6)
1	0.0057	0.74
5	0.0092	0.92
10	0.0152	0.58
15	0.0201	0.70

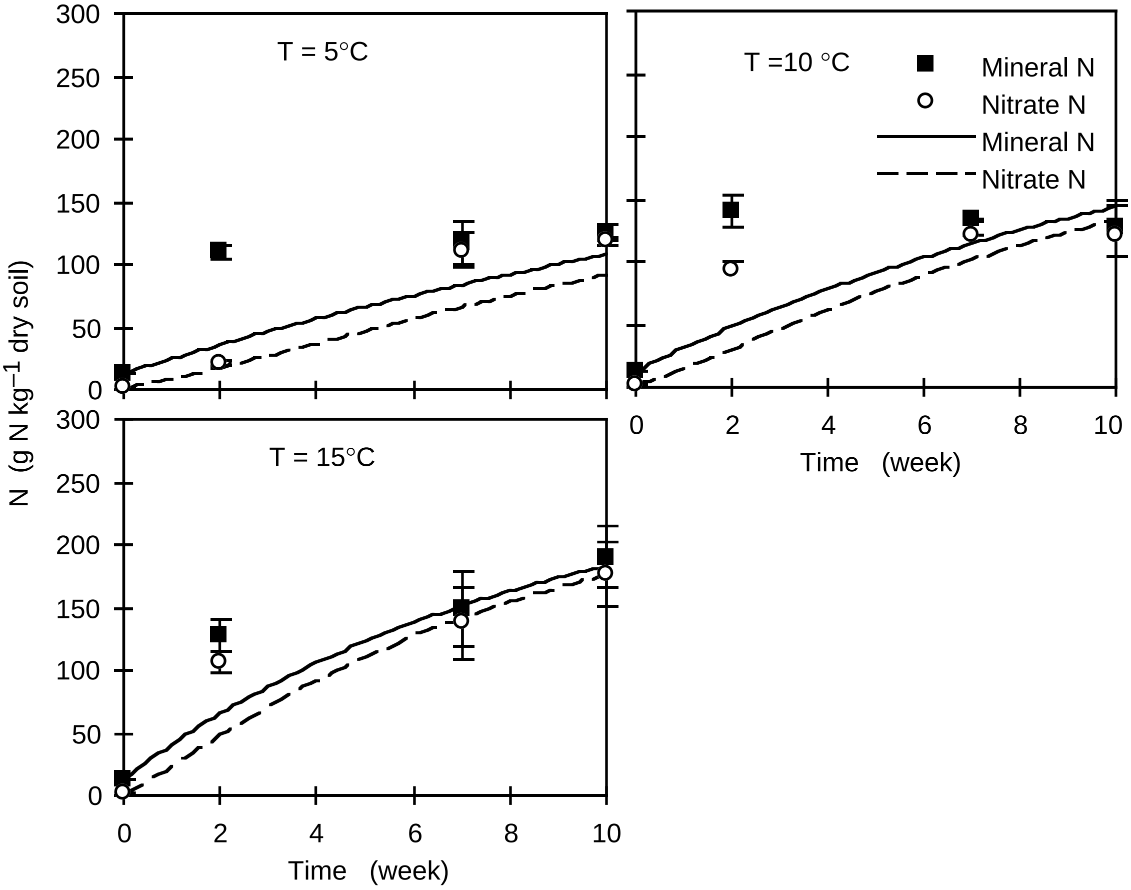


Figure 2. The time course of N_{min} and NO_3^--N in soil:rye root samples (dry weight ratio 100:2.1) incubated at 5-10-15 °C. Values measured (dots) and simulated (line).

The simulated time course of mineralisation is also plotted in Figures 1 and 2. In week 1 the values for the soil:shoot samples at 1 °C and 5 °C are overestimated by the model. The values of week two are underestimated for all temperatures, except for the NO_3^--N values at 1 °C and 5 °C. At week 10, the model overestimated the N_{min} and NO_3^--N of the soil:shoot samples at 10 and 15 °C. The difference between the simulated values and the measurements due to lack of fit over the whole time course is not significantly larger than the difference due to pure error for the soil:shoot samples at 5 °C, but at 1 °C, 10 °C and 15 °C and for the soil:root samples the difference is significant.

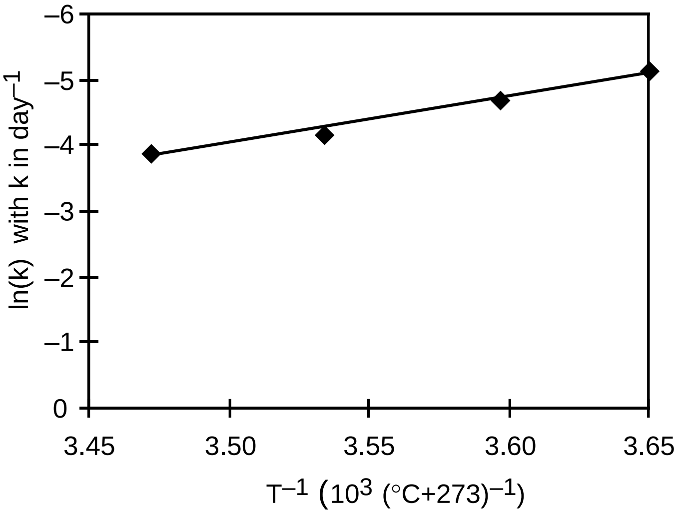


Figure 3. Arrhenius plot of ln(k) against T^{-1}, with k the relative mineralisation rate, derived from incubation of soil:winter rye shoot (dry weight ratio 100:1.11) at 1-5-10-15 °C during ten weeks.

Soil moisture contents of the samples incubated in the lab declined during the incubation period, with a stronger loss at the higher incubation temperatures. The initial moisture content of the soil:shoot samples was 18% on a weight base. This declined to 16.5-17-15.5-13.5% for the 1-5-10-15 °C treatments respectively after ten weeks of incubation. The initial soil moisture content of the soil:root samples was 21%, and declined to 18-17.5-14% for the 5-10-15 °C treatments after ten weeks. The soil moisture characteristics were not established experimentally. Assuming the soil to have the soil moisture characteristics of the topsoil B1, described by Wösten *et al.* (1994), a soil moisture content as low as 12.5% is still considered optimal for decomposition (Myers *et al.*, 1982).

Denitrification is considered not to have taken place, as anaerobic conditions are not likely to have occurred: the soil moisture content of the samples was field capacity or less and there was a very loose soil structure without any aggregates. As evidenced by the water loss of the samples, gas exchange with the environment was possible.

Experiment II

The N_{min} and NO_3^--N as measured in the samples incubated in the field is given in Figure 4. During the first week N_{min} and NO_3^--N decreased. After week 1 mineralisation and nitrification increased and after ten weeks N_{min} and NO_3^--N was as high as for the samples incubated at 15 °C. This was in agreement with the seasonal temperature pattern (Figure 5). After ten weeks 36% of the total applied organic N in the shoot and 29% in the root material had been mineralised.

The simulated values for the soil:shoot samples fall within the range of values measured, except for an overestimation in week 1 and 10. The N_{min} and NO_3^--N of the

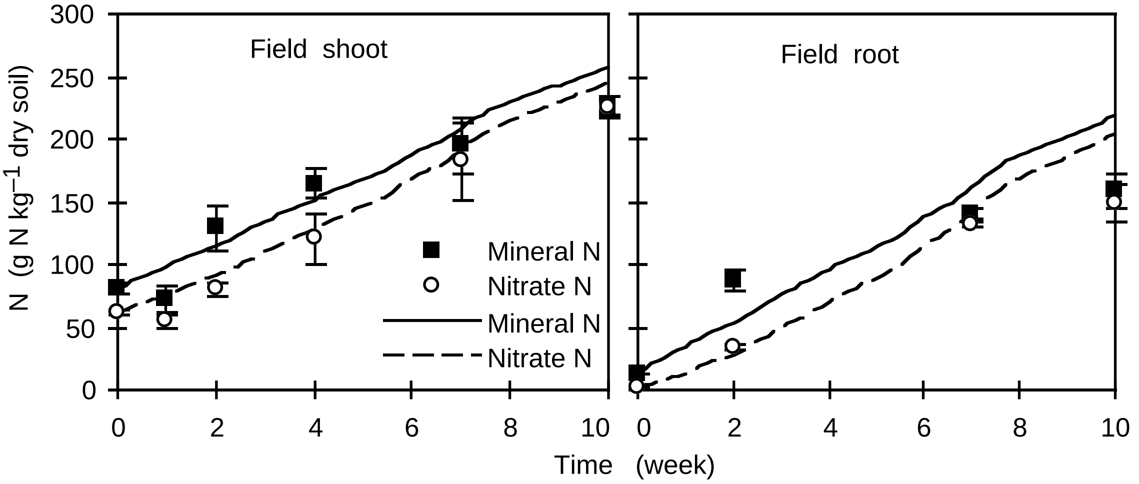


Figure 4. The time course of N_{min} and NO_3^--N for soil:rye shoot (dry weight ratio 100:1.11) and soil:rye root (dry weight ratio 100:2.1) samples incubated in the field. Values measured (dots) and simulated (line).

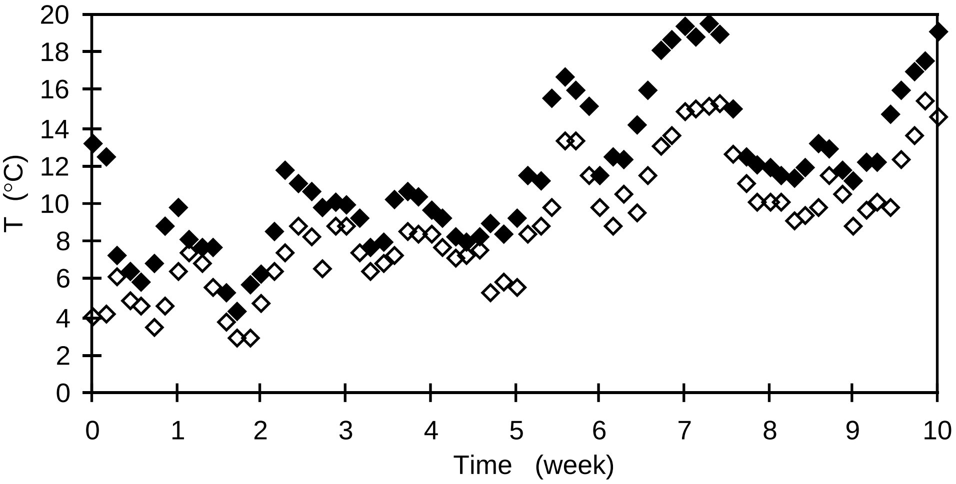


Figure 5. The daily maximum (closed dot) and minimum (open dot) soil temperatures at depth of 15 cm, measured from March 17 to May 30 1995 at Wageningen.

soil:root samples are underestimated at week two, while the values are overestimated at week 10. The difference between the simulated values and the measurements due to lack of fit is significantly larger than the difference due to pure error over the whole time period, for both soil:shoot and soil:root samples.

Simulation of temperature with a sinusoidal curve or with the daily average temperature, both calculated using the daily soil temperature extremes did not yield a different mineralisation rate. After a simulation run of the whole experiment, the final difference was 0.55 mg N kg^{-1} dry soil. This is negligible considering the model's accuracy.

The initial soil moisture content was 18.6% for soil:rye shoot samples and 20.9% for the soil:rye root samples, and declined to 18.5% and 20.2% respectively at week 10. Losses of N were considered to be negligible.

Discussion

At 1 °C considerable mineralisation occurred, confirming the results from Hanschmann (1983). Compared with the results of earlier experiments in which mineralisation proceeded at 0 °C (Van Dam & Fu, 1996; Stadelmann, 1983) this signifies that the temperature relation used in many models, in which the decomposition declines strongly at low temperatures to nil at 0 °C, should be replaced by a temperature relation that does allow the decomposition to proceed in the low temperature range. The straight line of the Arrhenius plot, obtained with the mineralisation data from the soil:shoot samples of experiment I, show that this relation can be described by an Arrhenius equation in the temperature range of 1-15 °C.

In general, the simulated values fell within the range of the values measured. In some points, the measured and simulated values diverged. For the soil:shoot samples at 1 °C and 5 °C and in the field no increase of N_{min} occurred at week 1, leading to an overestimation by the model. These low values measured are explained by the slow growth of the decomposing population, combined with a high amount of carbohydrates and easily available nitrogen, released upon the fine cutting of the plant material. The slow initial growth of decomposing population was also found by Stott (1986) upon incubation of wheat residues at 0 °C.

In week 2, the values measured were relatively high for all temperatures as well as in the field, resulting in an underestimation by the model. Similar results were found by Whitmore & Groot (1994) upon incubation of spinach and beet leaves, with treatments very similar to experiment I. This deviation from the first order decay relation presumably arises from the heterogeneity of the plant material, which is not accounted for by the model. Different decomposability of plant components can cause the resistant components to get more dominant in the course of time, resulting in a lower rate of decomposition and mineralisation. This would also account for the levelling off of the N_{min} at 10 and 15 °C at the end of the experiment. To simulate this heterogeneity, the fresh organic material entering the soil could be fractionated into different pools. Reliable methods to partition the fresh organic material among different pools, with the use of easily available parameters, in a biologically meaningful way are not available yet. Experiments, done to relate chemical composition of plant material to relative decomposition rate show diverging results. Vigil & Kissel (1991) found that 75% of the variability in the amount of N mineralised during eight experiments could be explained using the C/N ratio only. Consideration of both C/N and lignin did not increase this percentage to more than 80%. Thorup-Kristensen (1994b) found the amount of NO_3^--N, organic N and C from incubated catch crop material to be significantly related to the amount of N mineralised, but no correlation was found between mineralisation and content of lignin or total polyphenols. These findings suggest that fractionation of the plant material into different pools, based on chemical composition, is not likely to improve the predictive capability of the model. For the situation that this model is meant to be applied, information on the chemical composition, except for the nitrogen concentration, will generally not be known. An empirical solution to this problem does not seem feasible, due to the diversity of the plant material entering the fresh matter pool. Moreover, upon fractionation, each pool would require a specific relative decomposition rate and yield efficiency factor, for which parameterisation would be rather speculative.

The nitrification is calculated from the amount of ammonium mineralised, with reduction factors for soil temperature and soil moisture content. The over- and underestimation of the amounts of NO_3^--N can therefore mostly be explained by the over- and underestimation of the mineralisation process. At 1 °C and 5 °C and in the field, the amount of NO_3^--N in the soil:shoot samples is simulated correctly in week two, despite an underestimation of the mineralisation. This is due to the slow adaptation of the nitrifying population, which growth depends on the generation time of two genera, which can be expected to be slowed down by the low temperatures.

Further validation should be directed at the behaviour of the model at different soil moisture contents, as the experiments conducted in this study considered only the temperature relation. Also, the denitrification part remains to be validated.

Concluding remarks

Mineralisation and nitrification do proceed at temperatures as low as 1 °C. After ten weeks of incubation, 20% of the total added organic N was mineralised. Of this 20%, more than 90% was nitrified. In addition to its validity in the higher temperature regions, as established by other workers, the modified Arrhenius equation was found to be empirically valid to describe the effect of temperature on the rate constant of decomposition in the temperature range of 1 to 15 °C.

Fractionation of the added fresh organic material in the model can be expected to give a better fit of the simulation on the experimental data. However, as long as reliable estimates for the fractionation coefficient, the rate constant and yield efficiency factor for each fresh organic matter pool are lacking, no improvement in predictive capacity of the model is expected from fractionation.

Chapter 7

Growth and nitrogen uptake in catch crops and their effect on nitrate leaching – model and validation

with J. Vos, P.A. Leffelaar & R. Rabbinge

Abstract

Catch crops, cultivated after the harvest of summer crops, generally reduce N leaching by taking up N, but their effectiveness in reduction of leaching is variable. In this study, a simulation model was developed to simulate and evaluate the effectiveness of catch crops for different weather conditions, crop characteristics, crop management and N supply. The crop model is based on SUCROS and adapted to simulate crop growth of winter rye and fodder radish under conditions of relatively low radiation, low temperature and low N supply, which are common during catch crop growth. The light saturated CO_2 assimilation rate was modeled as a function of radiation during leaf growth and was not dependent on temperature above 5 °C. Structural growth of aboveground biomass was controlled by leaf expansion, which was a function of availability of N, carbohydrates, and temperature. Reserve carbohydrates might accumulate when they were not in demand for maintenance or growth. Turnover of leaves and stems was described using a fixed lifespan in degree days for these organs. Soil water dynamics were described with the ‘tipping bucket’ water balance model which was adapted by including a drainage coefficient determining which fraction of soil water can drain during one day. Nitrogen leaching was described by the complete mixing theory. Mineralization of N from soil organic matter was described with a zero order approach and that from fresh catch crop material by a first order approach. Simulation results were compared to data of experiments in lysimeters and in the field.

The model underestimated N leaching relative to percolation of water, for which underestimation no explanation could be found. Crop N content was rather well simulated when N was not limiting growth, but measured values were sometimes underestimated and sometimes overestimated at limiting N supply. This was partly caused by an imperfect simulation of soil N availability, but it was also due to an overestimation of N uptake at low N supply per se. Although exact levels of the crop N content could not always be simulated adequately, the measured time courses of crop N content and leached N were generally nicely simulated by the model. Therefore, the model is regarded suitable for explorative studies to assess the effect of crop characteristics, crop management, weather and N supply on the effectiveness of catch crop N uptake and reduction of N leaching.

Introduction

Cultivation of catch crops after the harvest of the main crop, in the otherwise fallow autumn and winter period, can reduce nitrogen leaching by catching up to about 200 kg nitrogen ha^{-1} (Landman, 1990; Vos & Van der Putten, 1997). After incorporation in the soil before or after winter, nitrogen is mineralized from the crop material. Then it is available again for leaching or for use by a succeeding summer crop, depending on the time of incorporation and mineralization (e.g. Sørensen & Thorup-Kristensen, 1993). Field experiments with catch crops show a large variation in crop nitrogen uptake for different years, sowing dates, crop species and locations (Elers & Hartmann, 1987; Landman, 1990, Vos & Van der Putten, 1997). Also catch crop effects on leaching and on the nitrogen nutrition of the succeeding crop is very variable (Thorup-Kristensen, 1994). Effects of growing catch crops on nitrogen leaching can be estimated from these data for the conditions of these experiments, but it is hardly possible to extrapolate such findings to other situations.

Detailed analysis of the different plant physiological and environmental conditions determining nitrogen accumulation by catch crops, combined with a quantitative study of the transformation of catch crop N in soil, can be used to develop a coherent explanatory model. Such a model would allow assessment of the efficacy of catch crop cultivation in reducing nitrogen leaching in various situations.

Crop growth models that include nitrogen uptake and nitrogen limitations were developed for several crops and purposes (e.g. Van Keulen & Seligman, 1987; Hansen *et al.*, 1990). For catch crops, however, only very simple models were developed, describing catch crop growth as a linear function of radiation (Vos, 1992) or temperature sum (Kersebaum, 1989). They give an estimate for catch crop nitrogen accumulation under optimal growing conditions but they do not include the effects of nitrogen supply and crop characteristics on growth. Therefore, an explanatory SUCROS winter wheat model (Groot & De Willigen, 1991) was adapted and used to simulate the growth of a winter rye catch crop. This model estimates final biomass yield well for optimal (i.e. nitrogen-rich) conditions (Van Erp & De Jager, 1992).

The objective of this study was to develop and validate an explanatory simulation model for the growth and nitrogen uptake by catch crops and soil nitrogen dynamics, based on detailed plant physiological, environmental and decomposition studies (Chapter 2 through 6). The model will be used to explore the effectiveness of catch crop cultivation in reducing nitrogen leaching as affected by crop characteristics, weather conditions, nitrogen supply and crop management (Chapter 8).

Model Description

General

To evaluate the effect of crop characteristics on the effectiveness of a crop species used as an N catch crop, the crop growth processes should be described correctly and in some detail. Furthermore, the dynamics of nitrogen in crop and soil must be modeled. These are dependent on soil water dynamics and soil temperature. To describe all relevant processes, the model has been divided into four main parts describing the dynamics of crop biomass and nitrogen, soil water, soil temperature and soil nitrogen. The crop model has been developed for winter rye and for fodder radish, which are often used as catch crops.

Crop dynamics

Crop processes are modeled as a function of crop characteristics, sowing date, weather conditions and nitrogen supply. Other factors (e.g. water availability, diseases, pests) are supposed not to affect crop growth. For nitrogen catch crops grown under Dutch conditions, nitrogen is often the most important factor limiting growth. Growth limitation by water shortage is much less likely to occur because catch crops are grown in a period with a precipitation surplus and nutrients other than nitrogen are normally present at non-limiting levels in Dutch agricultural soils.

Crop parameters are derived from pot experiments (Chapters 2 and 3), rhizolab experiments (Chapter 4) and literature, particularly Vos & Van der Putten (1997). From this publication one catch crop field experiment is used for parameterisation (experiment sown in 1992, further called Exp. 92; winter rye (*Secale cereale* L.) and forage rape (*Brassica napus* L.)). Two other experiments are used for validation (experiments sown in 1991 (further called Exp. 91; rye) and 1995 (further called Exp. 95; rye and fodder radish (*Raphanus sativus* L.))). Because fodder radish is lacking in the data of the experiments of 1992, the data of the related crop forage rape are used for parameter estimation for the radish model. These data were the best approximation for radish that could be found.

Phenology

A description of phenology is included in the model because it affects allocation of carbohydrates to various plant parts. Germination occurs at a fixed number of degree days after sowing (65 °C days for rye; 115 °C days for radish, derived from Vos & Van der Putten (1997)). Winter rye is assumed to be vegetative thereafter. It consists of belowground parts (further called roots), leaf sheaths (further called sheaths) and leaf blades (further called leaves). For radish, growth of leaf, stem and roots are described in the model. Flowering is not included, because no data can be found for its parameterization. However, radish may flower when sown before August. Therefore, the model can be used only for fodder radish sown from August onwards.

Crop nitrogen

The maximum nitrogen concentration in the leaves is an exponentially decreasing function of the temperature sum after emergence (Eq. 1) (Figure 1; data from Exp. 92 of Vos & Van der Putten (1997)).

$$C_{N,max,t} = C_{N,max,\infty} - (C_{N,max,\infty} - C_{N,max,0}) \times e^{-a \times Tsum} \qquad (1)$$

where:

$C_{N,max,t}$ = current maximum nitrogen concentration in the leaves (%)
$C_{N,max,\infty}$ = asymptote of maximum N concentration in the leaves, reached at an infinite Tsum (%)
$C_{N,max,0}$ = Maximum N concentration in the leaves at emergence (%)
Tsum = temperature sum above a threshold of 0 °C after crop emergence (°C days)
a = relative physiological decrease rate (°C day)$^{-1}$.

Equation (1) may be justified as follows: the N concentration in leaves decreases with leaf aging, which depends on temperature. The average age of the canopy increases with temperature sum, so that the average N concentration decreases. For rye the parameter values for equation 1 are: $C_{N,max,0}$ = 7.0 %; $C_{N,max,\infty}$ = 4.8 %; a = 0.00279 (°C day)$^{-1}$ with r^2=0.92. For radish the values are: $C_{N,max,0}$ = 7.1 %; $C_{N,max,\infty}$ = 4.3 %; a = 0.00183 (°C day)$^{-1}$ with r^2=0.71. The N concentrations in the roots, rye sheaths and forage rape stems are linearly related to the nitrogen concentration in the leaves (Figure 2). Data of forage rape are used for radish.

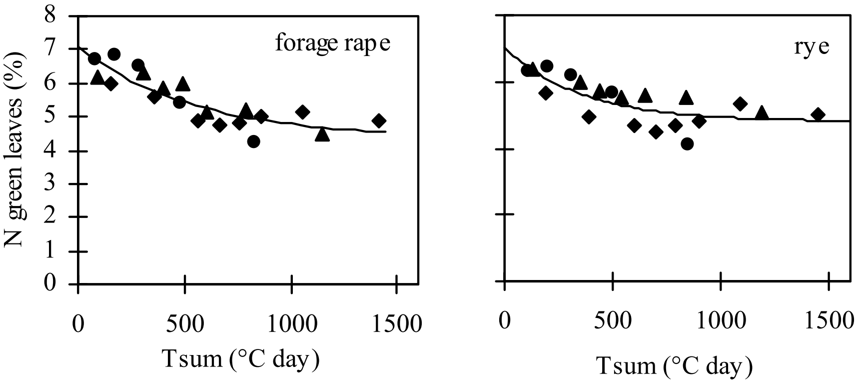


Figure 1. N concentration in green leaves as a function of temperature sum from crop emergence (Tsum). The symbols are the experimental field data at N2 of Vos and van der Putten (1997): diamonds: first sowing; triangles: second sowing; circles: third sowing. The line is the fit to equation 1. Parameter values are in the text. The forage rape curve is used in the fodder radish model.

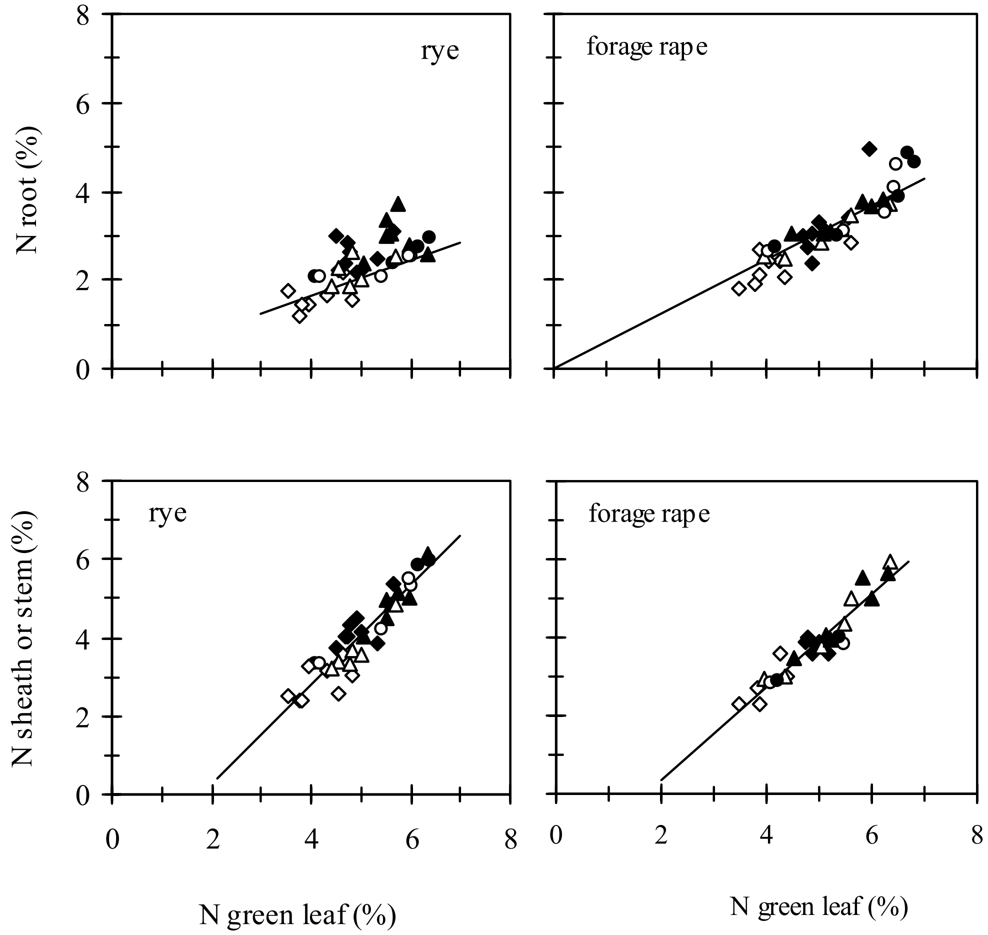


Figure 2. Sheath N content, stem N content and root N content as function of green leaf N content. The symbols represent field data from Vos & van der Putten (1997): diamonds: first sowing; triangles: second sowing; circles: third sowing; open symbols: N1; closed symbols: N2. Linear regressions are: for rye N root (%)=0.471 × N leaf (%) with n=37 and r^2 =0.47 and N sheath (%)=-2.22+1.26 × N leaf (%) with n=37 and r^2=0.87. For forage rape N root(%)=0.613 × N leaf(%) with r^2=0.77 and n=39 and N stem(%) = -2.04 + 1.20 × N leaf(%) with r^2=0.90 and n=28. The forage rape lines are used in the fodder radish model.

The nitrogen demand of the crop organs (leaves, stems, sheaths, roots) is calculated as the difference between their maximum and the current N contents. The N demand of the crop is the sum of the demands of the organs, minus the amount available by reallocation of N from dying plant tissue (see Turnover). Nitrogen effects on crop growth processes are modeled by effects of N concentrations in leaves, stems, sheaths and roots on process rates. This is described separately for the growth processes concerned.

CO_2 assimilation

CO_2 assimilation is described by the SUCROS algorithm (Goudriaan & Van Laar, 1994). The light saturated CO_2 assimilation rate of the canopy ($A_{max,eff}$, in mg CO_2 m^{-2} s^{-1}) depends on the average daily irradiance (I_{av}) during the previous 20 days (Chapter 2), the structure of the canopy (by f_{crop}), current temperature (by f_{temp}) and the nitrogen concentration of the leaves (by f_N). $A_{max,eff}$ is calculated as:

$$A_{max,eff} = f_{crop} \times f_{temp} \times f_N \times A_{max,0} \tag{2}$$

with

$$A_{max,0} = f_I \times I_{av} \tag{3}$$

f_I is the radiation factor (mg CO_2 J^{-1}) and I_{av} is the average radiation intensity during the photoperiods of the previous 20 days (in J m^{-2} s^{-1}). $A_{max,0}$, the light saturated assimilation rate of young leaves, is thus a linear function of I_{av} (Chapter 2).

f_{crop} (-) is a crop species specific factor converting the $A_{max,0}$ of young leaves to the effective $A_{max,eff}$ of a crop canopy. f_{crop} was based on measurements of $A_{max,0}$ at the leaf level (Chapter 2) and of the time course of the CO_2 assimilation rate at the canopy level (Chapter 4). For fodder radish, $A_{max,eff}$ was the same as $A_{max,0}$, in which case f_{crop} is 1. For rye, $A_{max,eff}$ was 0.6 times $A_{max,0}$ (calculated from Chapter 4), so f_{crop} ror rye is 0.6.

f_{temp} is the temperature multiplication factor for A_{max}. f_{temp} is assumed to increase linearly from 0 to 1 between 0 and 5 °C and remains 1 above 5 °C. In the measurements discussed in Chapters 2 and 5 no temperature effect on $A_{max,eff}$ was measured above 4 °C. Kavanagh (1989) found that the assimilation rate of winter rye at 1 °C was about 25% of that at 9 °C. In the current model this would be 20%, which is close to Kavanagh's observation.

$A_{max,eff}$ is also dependent on the N concentration in the leaves (C_N), which is expressed by the nitrogen limitation factor f_N in equation (2). Although this dependency was not significant in measurements on individual leaves (Chapter 2), it was found at both the leaf and the canopy level in another study with rape and wheat (Dreccer, 1999). The nitrogen limitation factor (f_N) increases linearly with the nitrogen concentration, from 0 at $C_{N,min,A,t}$ (see below) to 1 at $C_{N,max,t}$: $C_{N,min,A,t}$ is assumed to decrease during the growing season, proportionally to $C_{N,max,t}$:

$$C_{N,min,A,t} = C_{N,min,A,0} \times C_{N,max,t}/C_{N,max,0} \tag{4}$$

where $C_{N,min,A,t}$ and $C_{N,min,A,0}$ are the minimum N concentrations for CO_2 assimilation in the leaves at time t and at crop emergence (1 %).

Interactions are assumed between all factors influencing $A_{max,eff}$(Eq. 2 and 3): they are multiplied in Equation 4.

Carbohydrate and nitrogen partitioning

Assimilates are first used for maintenance respiration. When CO_2 assimilation is higher than maintenance respiration, the remainder of the assimilates is available for growth. Then for rye, 13 % of the assimilates is partitioned to the roots (f_{root}), 27 % to the sheaths (f_{sh}) and 60 % to the leaves (f_{leaf}). These parameter values are based on Exp. 92 by Vos and Van der Putten (1997), by plotting root and sheath weights against leaf weights for the period before the start of leaf turnover (maximally 443 °C day after crop emergence, see Turnover) (Figure 3). The plotted proportions leaf:sheath:root are

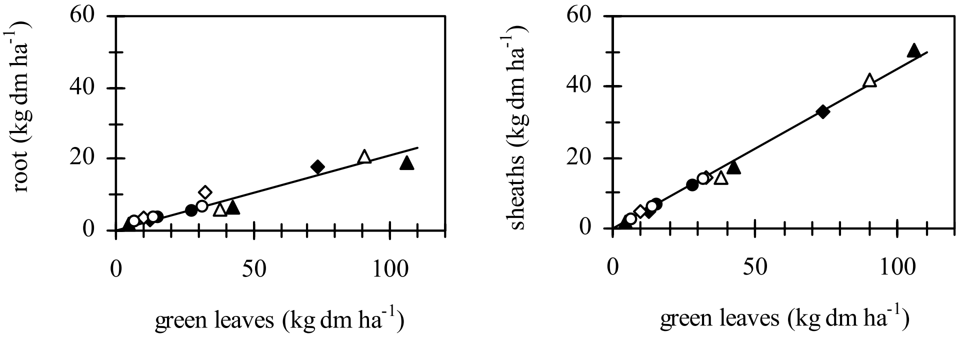


Figure 3. Partitioning of leaves, roots and sheats for rye. The symbols represent field data from Vos and van der Putten (1997), symbols as in Figure 2. Linear regressions are (n=15): sheaths (kg dm ha^{-1}) = 0.453 leaves (kg dm ha^{-1}) (r^2 =0.99) and roots(kg dm ha^{-1}) = 0.212 leaves (kg dm ha^{-1}) (r^2 = 0.91).

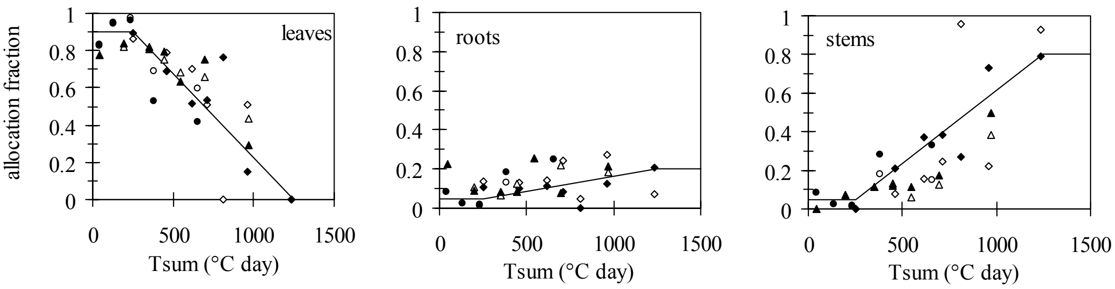


Figure 4. Partitioning fractions for leaves, roots and stems of forage rape as a function of the temperature sum from crop emergence (tsum). The symbols refer to experiments of Vos and van der Putten (1997), symbols as in Figure 2. The lines were drawn by hand. For tsum smaller than 250 °C day the model allocation fraction for the leaves is 0.90 and for the roots and shoots 0.05. For tsum larger than 1250 °C day the model allocation fraction for the leaves is 0, for the roots 0.2 and for the shoots 0.8). The lines are used in the fodder radish model.

1:0.45: 0.21 (= 60:27:13). For radish, at emergence 90% of the assimilates is partitioned to the leaves, 5 % to the stems and 5% to the roots. During development the percentage allocated to leaves decreases, and that allocated to stems increases (Figure 4). Data were used from forage rape (Exp. 92, Vos & Van der Putten, 1997). When structural growth is limited by low temperature or low N availability (see section 'leaf expansion'), carbohydrates accumulate as reserves. Reserves can be recycled later. Then they can be used with 88% efficiency. Nitrogen is partitioned to roots, sheaths and leaves proportional to their fraction in the total N demand.

Maintenance respiration

Maintenance respiration is modeled following Van Keulen and Seligman (1987), but with the maintenance respiration coefficient for roots (m_r) and sheaths (m_s) as high as that for leaves (m_l), namely 0.03 mg mg^{-1} s^{-1}, based on data of Bouma *et al.* (1996) and Van der Werf *et al.* (1988).

Aboveground growth

Above ground growth can be source-limited, determined by the availability of carbohydrates for growth (see section 'carbohydrate and nitrogen partitioning'), or sink-limited, determined by the maximum expansion rate of the leaf area. Here, this maximum leaf expansion is described.

The expansion of rye leaf area is calculated using leaf appearance rate, site filling (Chapter 2) and leaf expansion per tiller. A detailed explanation and motivation of the approach is presented in the Appendix to this chapter. The leaf expansion rate is proportional to the number of tillers, temperature, and to the leaf N concentration above a threshold N concentration:

$$dLAI/dt = \{(C_{N,t} - C_{N,min,L,t}) / (C_{N,max,t} - C_{N,min,L,t})\} \times c_{LE} \times temp \times T \tag{5}$$

$$\text{if } C_{N,t} < C_{N,min,L,t}\text{: } dLAI/dt = 0 \text{ m}^2 \text{ leaf m}^{-2} \text{ ground area d}^{-1} \tag{5a}$$

where LAI is the leaf area index (m^2 leaf m^{-2} ground area), $C_{N,t}$ is the actual N concentration in the leaves, $C_{N,min,L,t}$ is the minimum nitrogen concentration in the leaves for leaf expansion (%), c_{LE} is the LAI expansion coefficient (m^2 leaf m^{-2} ground area tiller^{-1} °C^{-1} d^{-1}), temp is the mean daily air temperature (°C), and T is the number of tillers. $C_{N,min,L,t}$ is a fixed fraction of $C_{N,max,t}$:

$$C_{N,min,L,t} = C_{N,min,L,0} \times C_{N,max,t} / C_{N,max,0} \tag{5b}$$

where $C_{N,min,L,0}$ is the minimum N concentration in the leaves for leaf growth at crop emergence (%).

The maximum LAI expansion rate of radish is modeled using a simpler approach. When LAI is below 1, maximum LAI expansion is determined by a temperature dependent relative growth rate:

$$\text{dLAI/dt} = \text{RGRL} \times \text{LAI} \tag{6}$$

$$\text{RGRL} = \text{c1} \times \text{temp} + \text{c2} \times \text{temp}^2 \tag{7}$$

When LAI is larger than 1, the maximum expansion rate is dependent on temperature only:

$$\text{dLAI/dt} = \text{c3} \times \text{temp} \tag{8}$$

in these equations: RGRL (m^2 leaf m^{-2} ground area d^{-1}) is the relative growth rate of LAI; c1 ($1.415 * 10^{-3}$ °C^{-1} d^{-1}), c2 ($8.127 * 10^{-4}$ °C^{-2} d^{-1}) and c3 ($1.23 * 10^{-2}$ m^2 leaf m^{-2} soil area °C^{-1} d^{-1}) are temperature coefficients. Radish leaf expansion depends on leaf N concentration in the same way as that of rye.

The LAI expansion rate is converted to the rate of leaf biomass growth by dividing by the specific leaf area (SLA, see below). The rate of rye sheath biomass growth is proportional to the rate of leaf growth by the same proportionality as used for carbohydrate partitioning. SLA is set at 26.2 m^2 kg^{-1} for rye (data from Chapter 2) and decreases from 22.6 to about 15.0 m^2 kg^{-1} during the growing season for radish (see Figure 5, derived from forage rape data of Vos and Van der Putten (1997)). For radish SLA is related to the temperature sum after emergence. The scatter in the relationship is rather large. A better description of radish SLA is, however, not available.

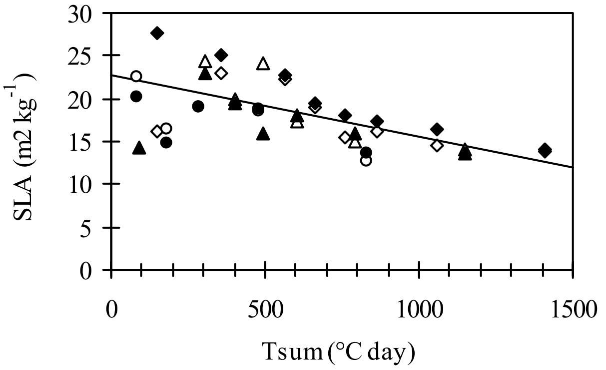


Figure 5. Specific leaf area (SLA) for forage rape as a function of temperature sum from crop emergence, tsum. The symbols represent field data from Vos & van der Putten (1997), symbols as in Figure 2. Linear regression yields: SLA (m^2/kg) = 22.6 − 0.00713 × tsum(°C day) with $r^2 = 0.46$ and n=36. The line is used in the fodder radish model.

Root growth

The maximum rooting depth (rd_{max}), as determined by soil properties, must be given as input in the model. The maximum rate of root zone extension is 0.02 m per day for both crops. The actual rate is dependent on temperature and soil water content (Groot & De Willigen, 1991). Root distribution is modeled following Groot and De Willigen (1991) with an exponential decrease of root density with soil depth. The root distribution factor, determining the curvature of the relation of root density to depth, is 2.5 m^{-1} for rye and 4.5 m^{-1} for radish, based on Rhizolab data (Chapter 5).

Turnover

Leaves live during a fixed lifespan (LS_{leaf}): 443 °C days in winter rye (Chapter 2); 700 °C days in radish (fitted to the Exp. 92 forage rape data of Vos & Van der Putten, 1997). Rye leaf sheaths live during 700 °C days (LS_{sh}), obtained by calibration with field data of living LAI (data of Vos & Van der Putten, 1997). Turnover of roots or radish stems is assumed not to occur, which is appropriate for the duration of the catch crop growing season. Leaf or sheath tissue that is about to die is assumed to have the same N concentration as the rest of the living canopy. When this tissue dies, maximally 34% (for rye) or 48 % (for radish) of its nitrogen is available for reallocation to other plant parts. This is based on the relation between N concentrations in living (green) and dying (yellow) leaves (Vos & Van der Putten, 1997) (see Figure 6). When there is no demand for N, N from dying tissue is not reallocated. Effects of frost or self shadowing on turnover or crop vitality are not modeled. This restricts the use of the model for radish to periods without severe frost (temperature lower than about -5 °C).

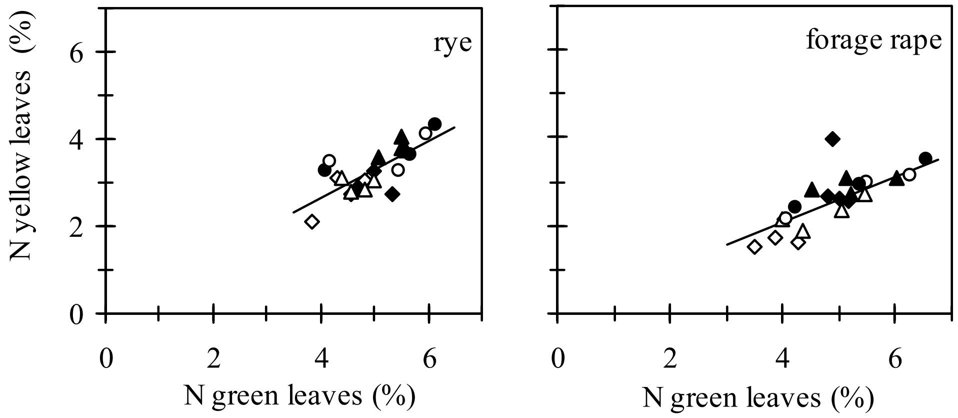


Figure 6. Relation between N concentration in living (green) and dying (yellow) leaves. The symbols represent field data from Vos & van der Putten (1997), symbols as in Figure 2. Linear regressions yield for rye N% yellow = 0.658 × N% green with r^2 =0.57 and n=22 and for forage rape: N% yellow = 0.519 × N% green with r^2 =0.77 and n=20.

Soil Water Dynamics

Soil water dynamics is based on the water balance or ‘tipping bucket’ model (Van Keulen, 1975). The tipping bucket concept is adapted by including a drainage coefficient (Ritchie, 1984; Emerman, 1995). An extensive description of the soil water model is given by Rijneveld (1996). It is shortly described below. The water balance model was preferred to other soil water models because it has a relatively low requirement of input data and can deal with the large timestep of one day. The tipping bucket model describes soil water dynamics well when compared with simulation results of a Richards-model (Rijneveld, 1996).

Soil profile

To simulate vertical water movement, the soil profile (0-100 cm depth) is divided into horizontal layers of 5 or 10 cm thickness (optional in input). The layer thickness (5 or 10 cm) has only a negligible effect on model output. The upper layer is always 2 cm, which is necessary to simulate the effect of a dry top layer on evaporation. No horizontal water movement is assumed, and the profile is draining freely to the subsoil. There is no groundwater table. Up to five different soil horizons can be parameterized in the input files. For each horizon the pF curve was defined using the Van Genuchten approach (Van Genuchten, 1980).

Drainage

Drainage occurs when the volumetric soil water content is higher than that at field capacity (pF = 2). A drainage coefficient determines which fraction of the water present between the water content at field capacity and that at saturation drains during the timestep of one day (Ritchie, 1984; Emerman, 1995). A drainage coefficient of 0.5 was found appropriate by testing the simulation results against those of the well validated, Darcy-type model HYSWASOR (Dirksen *et al.*, 1993; Rijneveld, 1996; Van Laar *et al.*, 1997). If more water is calculated as present in a layer than the soil can hold at saturation, the excess water drains to the next layer, so no run-off is assumed to take place, as is normal in flat areas. Drainage is calculated from the top of the soil profile downward.

Transpiration and evaporation

The maximum transpiration rate is calculated as (Van Laar *et al.*, 1997):

$$TR_{max} = ET_o \times (1 - e^{(-g \times LAI)}) \tag{9}$$

where TR_{max} is the maximum transpiration rate (m d^{-1}); ET_o is the potential transpiration of a closed crop canopy (m d^{-1}); g is the transpiration coefficient (0.56 m^2 ground area m^{-2} leaf for radish and 0.53 m^2 ground area m^{-2} leaf for rye); LAI is the green leaf area index of the crop (m^2 leaf m^{-2} ground area). ET_o is calculated by the Penman equation (Penman, 1948), using a reflection coefficient of the soil of 0.15 (Groot, 1987). The actual transpiration rate is lower than the maximum when water supply is limited. It is calculated following Van Keulen and Seligman (1987).

Capillary rise

Redistribution of water by capillary flow is modeled according to Verberne *et al.* (1995). The capillary flow between two adjoining soil layers is related to the pressure heads of those layers. The average pressure head of the layers is calculated, and from that the average volumetric water content, by use of the pF curve of the upper layer. The capillary flow between two layers is calculated as the difference between the actual water content of the upper layer and the average water content of the two layers, multiplied by a conductivity factor. This factor is a function of the relative water content for capillary rise (Figure 7). This relative water content increases from 0 at pF = 6 to 1 at field capacity. The lowest relative water content of the two layers is used for the calculation of the conductivity factor.

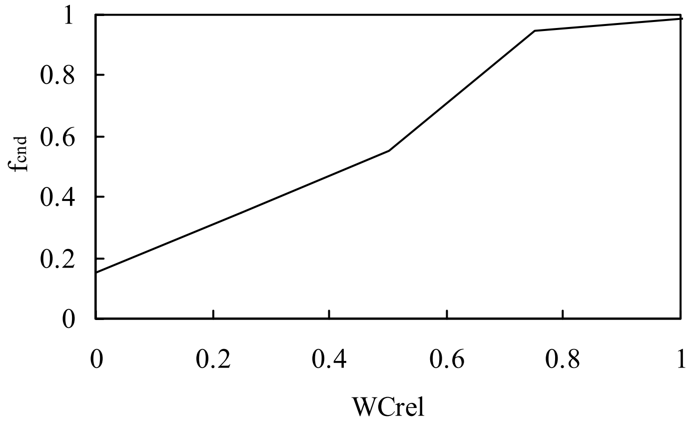
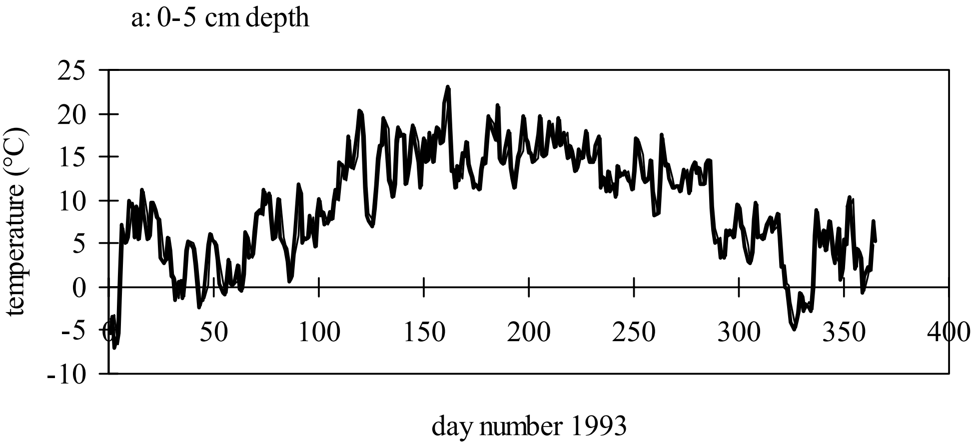
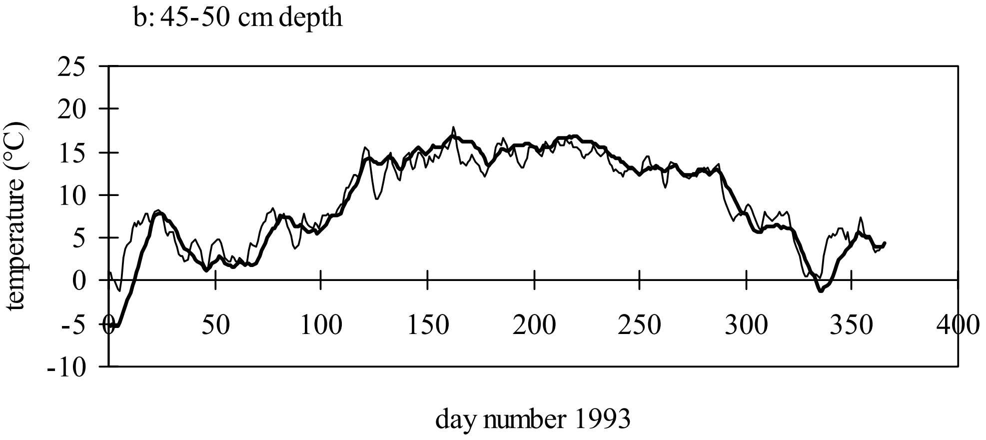


Figure 7. Conductivity factor, f_{cnd}, as a function of relative water content, WC_{rel}. The line is given by the coordinates (0,0.15), (0.5,0.55), (0.75,0.95) and (1,0.986).

Soil temperature

For the simulation of soil nitrogen dynamics and root growth, the soil temperature needs to be known. It is calculated on the basis of the heat conducting properties of the soil; soil temperature at a certain depth lags behind with respect to the air temperature and shows a smaller amplitude. Both this phase shift and the decrease in amplitude is





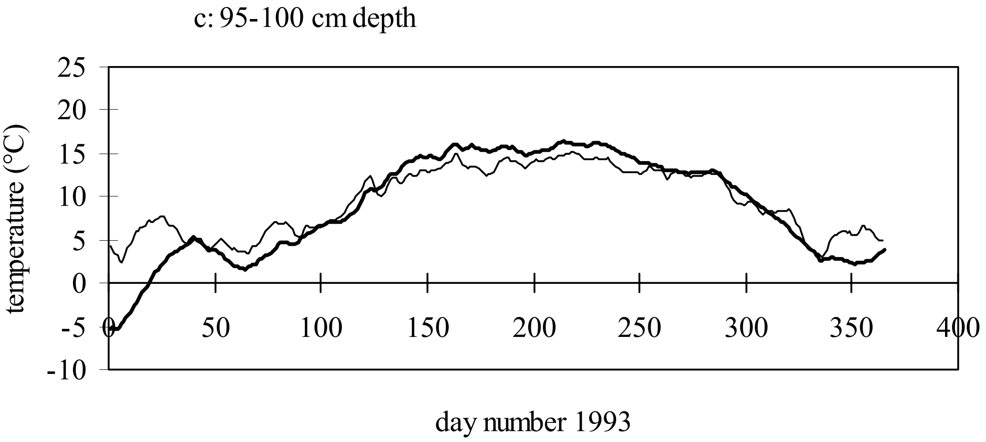


Figure 8. Comparison of simulation of soil temperature by the current model (thick lines) and by the heat diffusion equation as programmed by Leffelaar (1993) (thin lines). a: 0-5 cm depth (lines coincide); b: 45-50 cm depth; c: 95-100 cm depth.

calculated using physical soil characteristics, but an explicit physical description of heat diffusion is avoided because of the small time scale of this process (<< 1 day).

The phase shift in the yearly soil temperature cycle, compared to the cycle of air temperature, is calculated as a function of depth according to Koorevaar *et al.* (1983). The number of preceding days that is used in the calculation of the temperature of a certain soil layer is taken as twice the phase shift, so that the average delay between air temperature and soil temperature is the phase shift. For each layer the phase shift is calculated using its average depth. The heat capacity of the soil is estimated to be 1.9 MJ m^{-3} °C^{-1}, following Campbell (1985) and assuming that 0.5 m^3 m^{-3} of the soil volume is filled by quartz sand, 0.2 m^3 m^{-3} by water and 0.3 m^3 m^{-3} by air. The thermal conductivity is estimated to be 0.17 MJ m^{-1} °C^{-1} d^{-1} (Campbell, 1985; sandy soil at 0.2 m^3 m^{-3} water content).

The model was tested with weather data from 1993 against the results of a simulation with a numerical algorithm for the diffusion equation for heat (Leffelaar, 1993). It was assumed that the soil surface had the same temperature as the air and the same soil characteristics were used as before. Soil layers were 0.05 m thick. Soil depth was 6 m, almost twice the attenuation depth of the yearly temperature cycle (3.2 m, calculated following Koorevaar *et al.*, (1983) using the above mentioned parameter values). Results for both models coincided well except for differences at 1 m depth, of 1 to 2 °C in summer and of 3 °C for 20 days in December (see Figure 8) and a difference at the start of simulation, which was due to lack of temperature data of previous days at the start of the simulation in the current model. The number of previous days was 1, 17 and 35 for the depths of 0-5, 45-50 and 95-100 cm, respectively.

Soil nitrogen dynamics

Soil nitrogen pools modeled include soil organic matter, crop residues, ammonium and nitrate. Nitrogen dynamics comprise nitrogen application, transport, mineralization, nitrification, denitrification and uptake.

Only application of mineral fertilizer, not organic manures (except for crop residues) can be taken into account. Mineral fertilizer is assumed to be instantly dissolved and present in the top 2 cm soil layer. Nitrate transport between soil layers is described following Burns (1974): water and nitrate entering a soil layer are mixed with water and nitrate already present in the layer at every timestep. Water with the resulting nitrate concentration is subject to drainage. Nitrate is assumed not to be adsorbed to the solid phase, in contrast to ammonium, which is assumed not to move between soil layers.

Soil organic matter decomposition is modeled for each soil layer following Groot & De Willigen (1991):

$$dN/dt = OM \times k_{om} \times f_{t,m} \times C_{N,om} \qquad (10)$$

where dN/dt is the N mineralization rate in a soil layer (g N m^{-2} d^{-1}), OM is the amount of organic matter in that layer (g m^{-2}), k_{om} is the specific decomposition constant (d^{-1}), $f_{t,m}$ is a factor representing the combined effect of temperature and moisture (Chapter 6) and $C_{N,om}$ is the N concentration of the soil organic matter (g g^{-1}). k_{om} is derived from Kortleven (1963): 2 % of OM is decomposed per year, at an yearly average temperature of 9 °C. Changes in OM are neglected because they amount to 1 % or less of the total organic matter pool during one catch crop growing season. Decomposition of crop residues and consequent immobilization or mineralization of organic matter, and nitrification are modeled as described in Chapter 6. Denitrification occurs only when soil water content is higher than 80% of the content at saturation (Chapter 6).

Nitrogen uptake is calculated as the minimum of the crop demand, the availability of nitrogen in rooted layers and the uptake capacity of the roots. The demand is the difference between the maximum and current nitrogen content of the crop, determined by biomass and maximum and current N concentrations. The availability of N in the layers is modeled by estimating the N flow to the roots through convection and by diffusion following Van Keulen & Seligman (1987), but with the time constant for diffusion set to 10 d. This was estimated during calibration of the model. It means that every day one tenth of soil mineral N is available for uptake by diffusion. Uptake takes place in the rooted zone, where it is independent of root density. Uptake of both ammonium and nitrate is modeled. The uptake process is the same for both mineral N pools, but ammonium is taken up only if supply of nitrate-N cannot meet the N demand. All ammonium and nitrate is assumed to be available for uptake. The uptake capacity of the roots is a function of temperature ($F_{max,t}$), based on the experiments described in Chapter 3.

Technical model aspects

The model consists of four submodels: crop growth (including N uptake), soil nitrogen dynamics, soil water dynamics and soil temperature. It is written in the Fortran Simulation Environment (FSE, Van Kraalingen, 1995).

Integration proceeds by the Euler method with a time step of one day, the interval at which weather data were supplied. This time step is appropriate for the time coefficients of the crop processes, which are normally not smaller than 7 to 10 days. For the soil water and nitrogen dynamics, this is not always the case: time constants are smaller. In the tipping bucket soil water model, a rather large time step (here 1 day) is needed to allow working with a fixed field capacity and drainage coefficient. This time step is, however, too large to allow correct parallel integration of all soil water flow rates, because it is not adapted to the time coefficients, which may be smaller than 1 day in case of high precipitation rates. Therefore, serial integration of drainage and evapotranspiration rates for each day is used. The soil water model was validated with a serial integration method (Rijneveld, 1996). The soil N model was successfully validated in this form by Van Keulen & Seligman (1987) for arid conditions (Israel) and, for temperate (Dutch) weather conditions, by Groot & De Willigen (1991). Therefore, we consider it valid to use it for our study on catch cropping under temperate weather conditions.

Method of model validation with field and rhizolab data

The aim of the model described here is to be an instrument to assess the effectiveness of catch crop cultivation for reducing nitrogen leaching in various situations. Therefore, it is necessary that the model predicts nitrogen leaching accurately, with and without cultivation of catch crops. To compare different strategies of catch crop cultivation, i.e. choice of species, sowing date and date of incorporation, the model should also simulate N uptake and N mineralization from catch crop material satisfactorily. The simulation of N mineralization was tested in Chapter 6. Here we deal with the model’s capacity to simulate N leaching and catch crop N accumulation.

N leaching

Model validation with regard to N leaching was performed by comparison with data from the Wageningen Rhizolab (Van de Geijn *et al.*, 1994). Catch crops were sown on the Rhizolab lysimeter compartments in 1993 (fodder radish) and 1994 (winter rye). Soil water and mineral nitrogen were measured at several depths. These experiments have been described in detail in Chapter 5. The following treatments were used for validation with independent data: FIlow and FIhigh (fallow with low and high irrigation, respectively) and CIlow and CIhigh (radish crop with low and high irrigation, respectively) in the experiment sown in 1993, and in the experiment sown in 1994 N7d (rye crop fertilized with 70 kg N ha^{-1} at 40-50 cm depth) and N14 (rye crop fertilized with 140 kg N ha^{-1} in the top 10 cm). Parameters were obtained as described below.

For the Rhizolab the general decomposition rate of Kortleven (1963) could not be used because of large priming effects due to intensive soil handling during filling of the Rhizolab compartments. The relative rate of soil nitrogen mineralization was therefore estimated from data obtained with the same soil as used in the Rhizolab, in buried bags as described in Chapter 5. We assumed a C/N ratio of 10 for soil organic matter. The time course of net nitrogen mineralization in 1994-95 (Chapter 5) could not be explained by the model, because there was a substantial decrease in available N in the second half of the experimental period, which could not be explained by the modeled denitrification. To estimate the relative mineralization rate, the amount of mineralized N at the end of the experiment was taken as reference. The fitted value of the mineralization rate was therefore lower than the real one, because it implicitly included a decrease in soil mineral N by denitrification.

For modelling soil water dynamics, the α and n values in the Van Genuchten pF-curve were estimated as 0.0394 and 1.389 for the top 100 cm (as derived from measurements in a comparable sandy soil (Rijneveld, 1996)) and 0.023 and 1.8, respectively, for the lower layer (100-170 cm) (data of Wösten *et al.* (1994) for a sandy subsoil).

The initial soil water contents were taken from the data of the treatments N0 (unfertilized rye crop) and N7s (rye crop fertilized with 70 kg N ha^{-1} in the top 10 cm) in 1994. The subsoil in the Rhizolab appeared not to be freely draining. Therefore, to obtain a good simulation of the water and nitrogen transport in the subsoil, the model should have been changed. But, as no nitrogen transformations were supposed to occur in the subsoil (which did not contain organic matter), we considered that only a correct description of 1. processes in the top soil, 2. the time course of the amount of water leached from the subsoil, and 3. the residence time of water and nitrogen in the subsoil, were important for having a correct comparison between measured and simulated leached N. Therefore the average water content of the subsoil was taken as a reference, and differences in water content with depth within the subsoil were ignored.

For the fallow Rhizolab compartments, evaporation was set to 0.2 mm per day, fitted to measured values. This was because in the experiment a layer of gravel was placed on top of the soil to minimize evaporation, which was not included in the model.

N accumulation

For validating the model with regard to crop growth and N accumulation, data were used from field experiments performed in Wageningen, the Netherlands (Vos & Van der Putten, 1997). For validation, independent data from the experiments sown in 1991 (Exp. 91, rye only) and 1995 (Exp. 95, rye and radish) were used. From the experiment sown in 1992 (exp. 92), data were used for parameterization (see Model Description), so the N accumulation data of this year cannot be used for independent validation of the model. Still, they can be used to check wether the model’s structure is right to simulate N accumulation with these parameters. Therefore, a ‘partial’ (that is: not independent) validation is performed with the data of the 1992 experiment. Some assumptions had to be made for the validation. Decomposing soil organic matter was assumed to be present only in the layer 0 - 25 cm below field level. Maximum rooting depth was set to 60 cm depth in the field experiments and at 100 cm depth in the Rhizolab. Weather data were used from the weather station at Wageningen, The Netherlands, which is about 2 km from the Rhizolab and about 3 to 4 km from the sites of the field experiments.

Results

Validation of soil processes with the Rhizolab data

First we studied the fallow Rhizolab treatments in the experiment started in 1993, FIlow and FIhigh. These, together with the fitted mineralization rate, offered the opportunity to test the soil water and N transport model separately. For FIlow and FIhigh, N leaching was underestimated by the model, whereas leaching of water and total

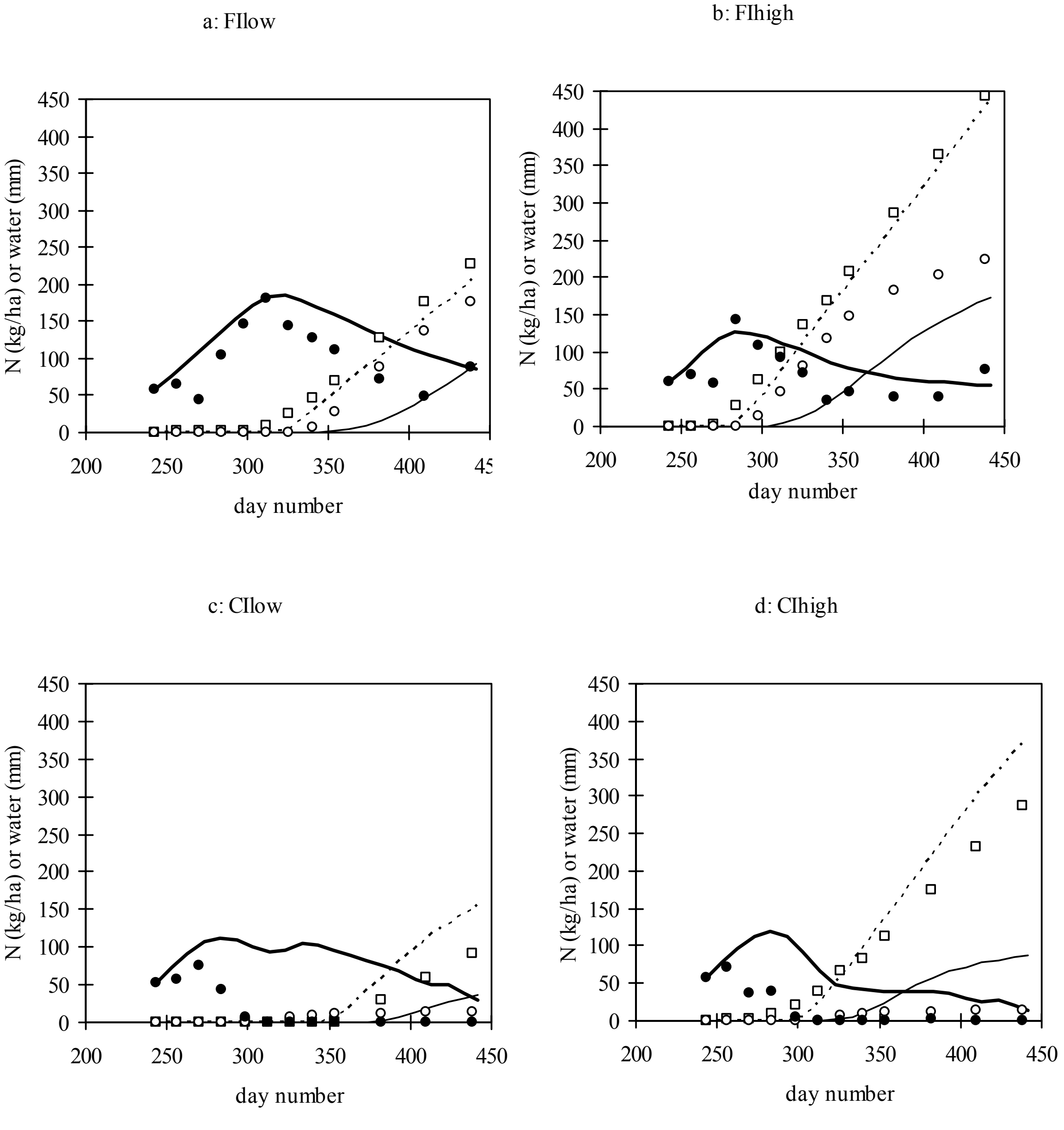


Figure 9. Simulated (lines) and measured (points) values of soil mineral nitrogen, leached water and leached nitrogen in the Rhizolab experiment started in 1993. a: FIlow; b: FIhigh (Fallow rhizolab compartments with low and high irrigation rate, respectively); c: CIlow; d: CIhigh (Cropped with low and high irrigation rate, respectively). For further explanation of the experiment see Chapter 5. Symbols: Closed dots and thick black lines is soil mineral N in kg ha^{-1}; Open squares and dotted lines is leached water in mm; Open dots and thin solid lines is leached N in kg ha^{-1}.

mineral N in the system (soil + leachate) were well predicted (see Figures 9a-b). The simulated leached N was still lower than the measured value when no adsorption of NH_4^+ was assumed and transport of NH_4^+-N between soil layers was included in the model (even when the soil was fertilized with ammonium), or when a larger dispersion coefficient, apart from the numerical dispersion in Burns'model (1974), was included in the model. Another possible cause of the underestimation would be an overestimation of soil water content and, consequently, an overestimation of the residence time of N in soil. However, for FIlow soil water content was well simulated and for FIhigh soil water content in the topsoil (0.0-1.0 m) was underestimated from mid October onwards, and the underestimation gradually increased to 42 mm (measured 283 mm vs. simulated 241 mm) in March. Apparently, and remarkably, the complete mixing theory (Burns, 1974), which was used for the soil N transport model, underestimated the N leaching rate. This was also clear from the N distribution in the topsoil (Figure 9a-b). The amount of N in the topsoil (0.0-1.0 m) was overestimated during the leaching period (from about day 300), consistent with the underestimation of leached N. Topsoil N was not overestimated at the time of the last measurements in Figure 9 a-b, taken mid March, when temperature and mineralization rate had increased. Unfortunately, as treatments in the Rhizolab could not be replicated, there remains uncertainty about the exact value of measured parameters, but because differences between measurements and simulation were consistent, we suspect that not only experimental uncertainty causes the discrepancies.

For the cropped Rhizolab compartments CIlow and CIhigh (cropped with low and high irrigation rate, see Chapter 5) in the experiments sown in 1993, crop growth and evapotranspiration were included in the model. Here, N leaching was overestimated. This was due to several factors. Firstly, percolation was overestimated, by 64 mm in CIlow and 97 mm in CIhigh, which could for the largest part be explained by an underestimation of evapotranspiration by 75 mm in CIlow and 108 mm in CIhigh over the whole experiment. Evapotranspiration in the Rhizolab may have been increased, compared to the model, by an additional evaporative demand from the side of the crop in the rather small plots (1.25×1.25 m^2) (which demand is not included in the model), although shade nets were used to minimize this effect. Secondly, total crop N uptake was underestimated by 30 kg ha^{-1} (170 instead of 200 kg ha^{-1} in March; Chapter 5). Like evapotranspiration, crop growth in the Rhizolab might have been increased by radiation on the sides of the crop. Moreover, the model parameters were partly derived from field experiments, where conditions (e.g. soil structure, spatial distribution of fertiliser N) may have been different from those in the Rhizolab. Lastly, the N content in soil and in the leached water was overestimated by 30 to 100 kg ha^{-1} (Figures 9 c-d). This was partly explained by the underestimation of N uptake. Also, in the experiment 50 to 60 kg ha^{-1} of N present at the start or mineralized was not recovered later.

For the rye experiment (sown in 1994) leached N was better simulated (Figure 10). This is because evapotranspiration was underestimated less in this case. N uptake was

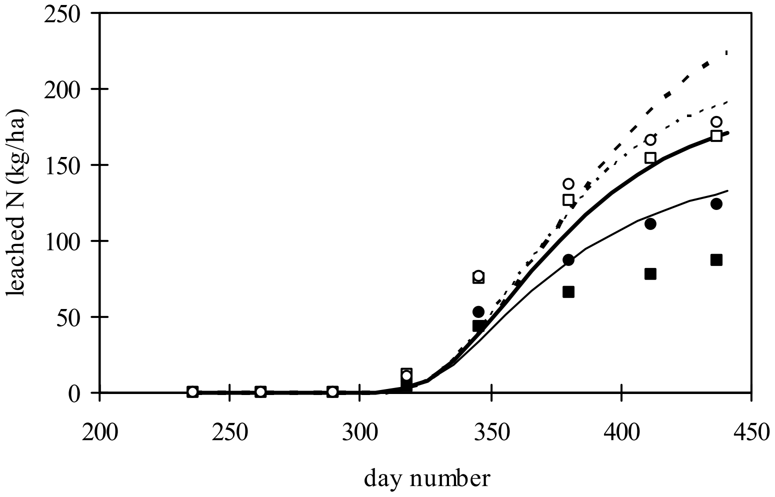


Figure 10. Simulated (lines) and measured (points) values of leached nitrogen in the Rhizolab experiment started in 1994. Symbols: thin solid line and closed squares: N0; thick solid line and closed dots: N7s; thin dotted line and open squares: N7d; thick dotted line and open dots N14. For further explanation of the treatments see Chapter 5.

underestimated (by 70 to 90 kg ha^{-1}; uptake data in Chapter 5), so that leached N was in most cases overestimated. Increasing N uptake by multiplying N demand by the ratio of measured and simulated uptake resulted in a correct simulation of N uptake and an underestimation of leached N, similar as in FIlow and FIhigh (data not shown).

Measured and simulated leached N values were plotted in Figure 11a-b. The fit was much better for the rye experiment (1994) than for the fallow and radish experiment (1993), due to a more accurate simulation of evapotranspiration (less border effects here because the rye crop was lower) and compensation of the underestimation of the N leaching rate by an underestimation of N uptake.

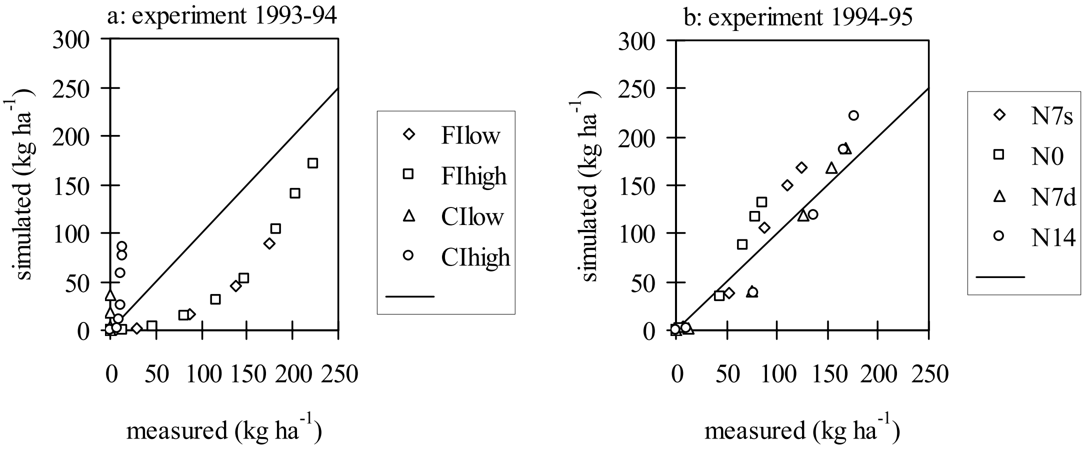
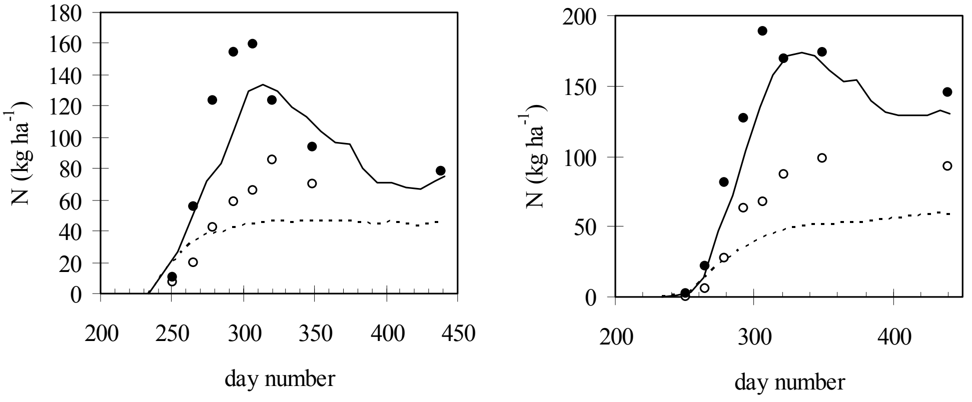
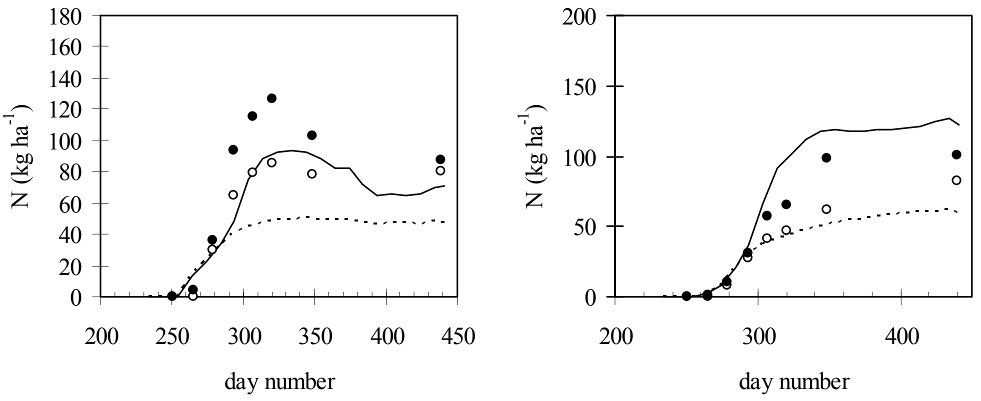


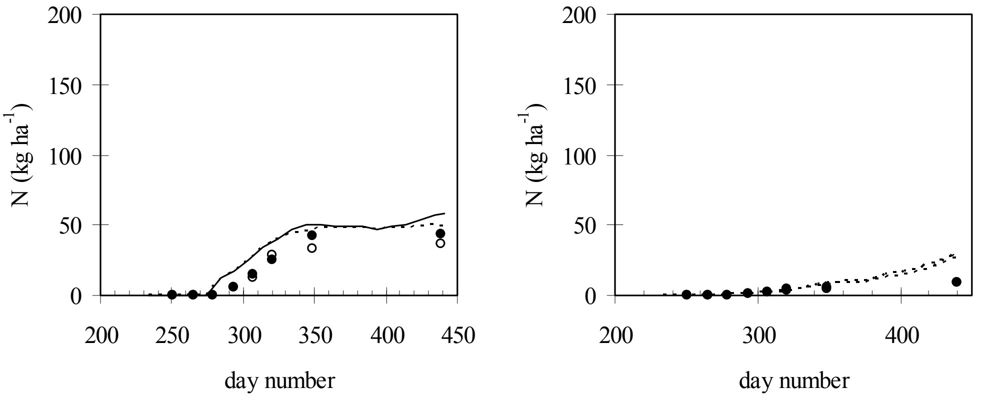
Figure 11. Measured and simulated values of leached N in the Rhizolab experiments, with 1:1 lines. a: experiment 1993-94, with fallow and radish; b. experiment 1994-95, with winter rye.


a: rye first sowing

d: forage rape first sowing


b: rye second sowing

e: forage rape second sowing


c: rye third sowing

f: forage rape third sowing

Figure 12. Simulated (lines) and measured (points) time courses of crop N content of winter rye an forage rape in the field experiment sown in 1992. a, b and c: rye at the first, second and third sowing, respectively; d, e and f: forage rape rye at the first, second and third sowing, respectively. In c and f the lines for n1 and n2 coincide. Open symbols and dotted lines: N1; closed symbols and solid lines: N2.

In summary, lack of fit of the model to the measurements was caused by the underestimation of N leaching rate relative to water leaching rate, underestimation of evapotranspiration and of crop N uptake by the model and by the unexplained N losses in the experiments.

Partial validation of N accumulation with the parameterization experiment

Total N accumulation simulated by the model was compared to the field data of the parameterization experiment sown in 1992. In the field it was difficult to measure total N accumulation by the crop, due to turnover and decomposition of crop material. Therefore, the data on N content of living crop biomass, which could be measured more accurately, was used for the comparison.

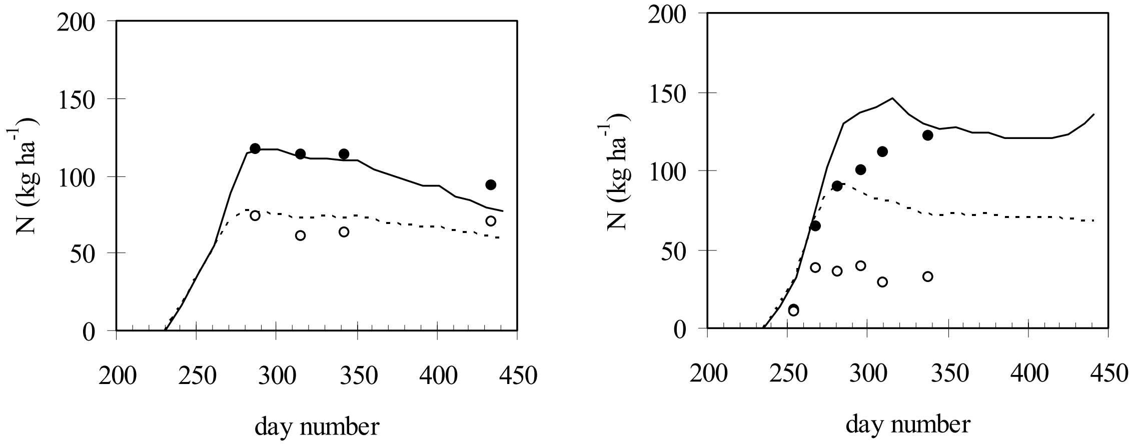
Simulated and measured N accumulation for rye and forage rape sown in Exp. 92 (Figure 12) were plotted against day numbers on the X-axis, starting with day 1 on 1 January in the year of sowing. Crop N content was well simulated for rye and forage rape at N2 (non-limiting N supply). The only underestimation, by about 40 kg N ha^{-1}, was for rye at the second sowing date (Figure 12b). At N1 (low N supply level), crop N uptake was underestimated in the first and the second sowing (Figures 12 a, b, d and e). In the third sowing, N supply was not limiting growth at N1: there was no difference in N uptake between the N supply levels (Figures 12 c and f). Total biomass was, however, well simulated for all treatments (data not shown). The underestimation of N content at N1 was related to an underestimated shoot-root ratio in the simulation. As N concentrations in roots are lower than those in shoots, this decreased the demand for N.

A good simulation of limited soil N availability is a prerequisite for a good simulation of N uptake at N1. In the experiment, soil mineral N in 0-0.6 m depth in a fallow, unfertilized plot increased, presumably mainly by mineralization, from 41 kg ha^{-1} at 21 August to 125 kg ha^{-1} at 28 September. This increase (84 kg N ha^{-1}) is much higher than the simulated mineralization in the same period: 14 kg N ha^{-1}. Simulated soil mineral N in 0-0.6 m in fallow soil this period decreased by 13 kg ha^{-1}. Obviously, mineralization in the experiment is much higher than in the simulation. This may explain the underestimation of N accumulation at N1: N shortage was higher in the model than in the experiment. This is also reflected by underestimation of soil mineral N in March, at the end of the experiment: in fallow soil measured mineral N was 58 kg ha^{-1}, averaged over N1 and N2. In the simulation this was 18 kg ha^{-1}.

Validation of N uptake with independent field data

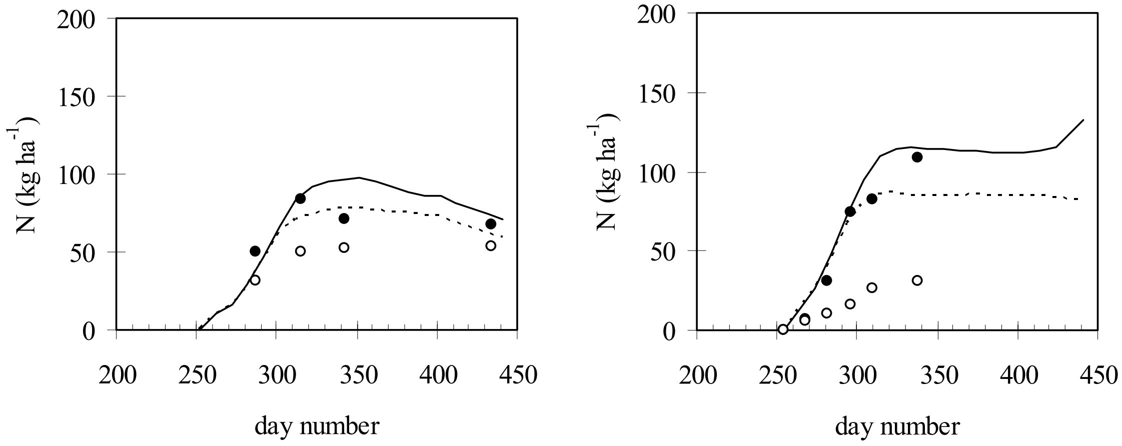
For rye two experiments could be used for model validation with independent data, Exp. 91 and Exp. 95. Data of fodder radish were available from Exp. 95 only. For rye, a: rye exp 91 first sowing

d: rye exp 95 first sowing



b: rye exp 91 second sowing

e: rye exp 95 second sowing



c: rye exp 91 third sowing

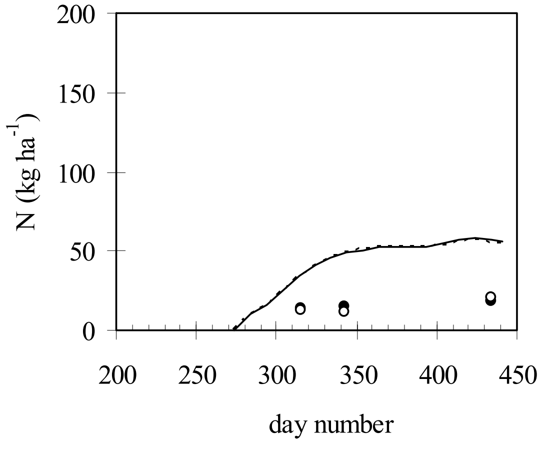


Figure 13. Simulated (lines) and measured (points) time courses of crop N content of winter rye in the field experiments sown in 1991 and 1995. a, b and c: first, second and third sowing, respectively in the experiment sown in 1991; d and e: first and second sowing, respectively in the experiment sown in 1995. Open symbols and dotted lines: N1; closed symbols and solid lines: N2.

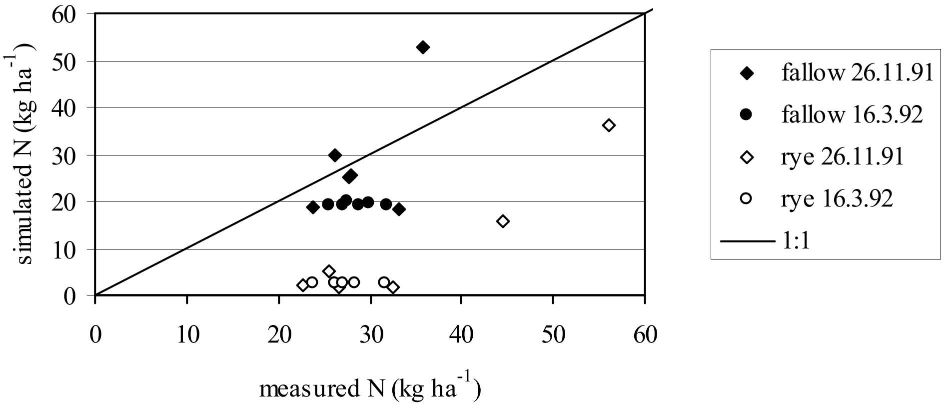


Figure 14. Simulated versus measured values of soil mineral N in the layer 0-0.6 m depth, measured in the fallow and rye-cropped treatment of Exp. 91. Squares: measurement date 26.11.91; Circles: date 16.3.92. Closed symbols: Fallow soil. Open symbols: Rye-cropped soil.

crop N was well simulated at N2 (Figure 13a-e). The only deviation was in the third sowing in 91 (Figure 13c), where uptake was overestimated by 40 kg ha^{-1}. Apparently, the large difference in rye growth and N uptake after late sowing from 1991 (Figure 13c) to 1992 (Figure 12c), could not be explained by differences in radiation and temperature conditions between the two years. At N1, crop N was generally overestimated, with the exception of the first sowing in Exp 91 (Figure 13a). The different result between Exp. 92 at one hand (underestimation of crop N at N1 by the model), and Exp 91 and Exp. 95 on the other (overestimation of crop N at N1) may be explained by differences in mineralization in the experiments. In Exp. 91, mineral N in 0-0.6 m increased by 25 kg ha^{-1} in fallow soil from 19 august to 1 October (reflecting a much lower mineralization in Exp. 92), whereas simulated mineral N increased by 16 kg ha^{-1}, mainly by mineralization. In this period, measured and simulated soil mineral N are in 1991 thus much closer than in 1992, when soil mineral N was strongly underestimated by the model. Moreover, soil mineral N in fallow soil in 1991 was much better simulated by the model in 1991 than in 1992 (Figure 14), in contrast to 1992. However, soil mineral N was underestimated by the model for the treatments with a rye crop (at both N1 and N2). This shows that the model tends to overestimate N uptake by the catch crop when limited availability of N in the soil is well simulated. The same can be found for the experiment in 1995, for both radish and rye (data not shown). In fodder radish (Figure 15), N accumulation was overestimated from day 300 onwards at N2 in the first sowing, which may be caused by incorrect simulation of growth and turnover of fodder radish in a period with night frost from day 302 until day 310: the effect of frost was not modeled. For N1, the overestimation of N uptake of fodder radish is rather similar as for rye in the same year. In summary, rye N content was simulated well at N2 but less good at N1 (Figure 13). Radish N content was simulated reasonably well.

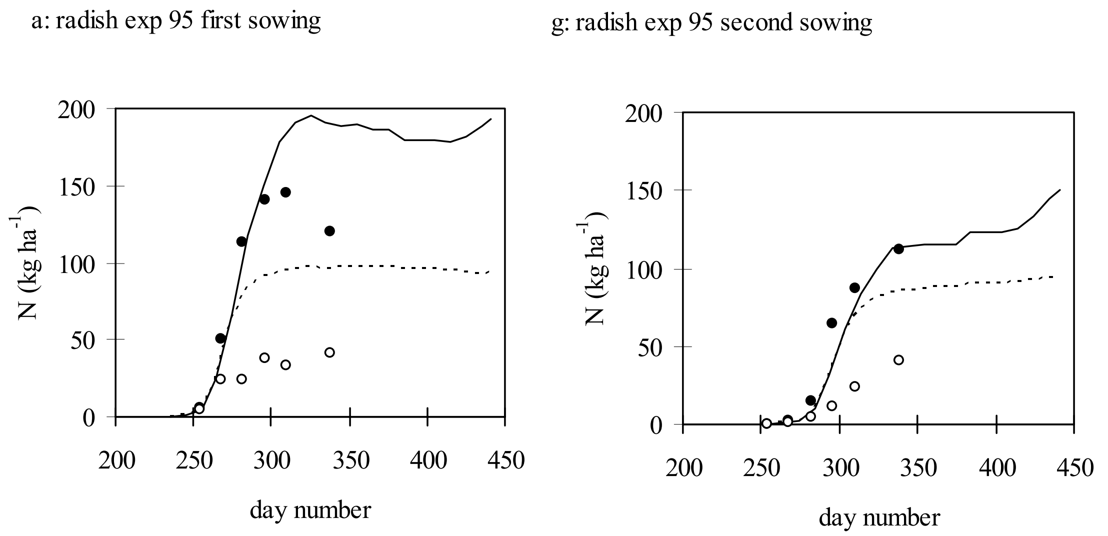


Figure 15. Simulated (lines) and measured (points) time courses of crop N content of fodder radish in the field experiment sown in 1995. a: first sowing; b: second sowing. Open symbols and dotted lines: N1; closed symbols and solid lines: N2.

Discussion

Evaluation of process descriptions

The model was developed using existing, validated descriptions of crop growth and soil water and nitrogen dynamics. The existing models were mainly developed for the simulation of growth and N dynamics in the main cropping season: spring and summer. To simulate the growth and N accumulation of catch crops new mathematical descriptions had to be developed, mainly to simulate crop and soil processes at low temperature and radiation, because measurements of CO_2 assimilation rates at the leaf and canopy level (Chapters 2 and 4, respectively), combined with literature data, showed that CO_2 assimilation proceeds at a much faster rate at low autumn and winter temperatures than is assumed in existing models. Moreover, assimilates accumulate as soluble carbohydrates in crop biomass (Chapter 2). This means that a correct description of crop growth in autumn and winter must include CO_2 assimilation, accumulation of carbohydrates and growth of structural biomass. To develop an improved description of CO_2 assimilation, a light dependency of Amax was introduced in the SUCROS-based algorithm for this process. Subsequently, structural aboveground growth was described as a function of assimilate availability and temperature. Furthermore, low N concentrations in biomass affect both assimilation and growth processes. In this way, more input data were required, but crop growth in winter could be simulated more realistically. Because the limitation of growth is placed on the aboveground plant parts, also the simulated shoot root ratio is influenced by low temperature and low N-supply. By this mechanism, overestimation of growth, if present, generally first results in overestimation of root mass (data not shown) when compared to field data, rather than an overestimation of aboveground biomass. Another new model aspect developed to better simulate growth in autumn and winter is the relation between leaf aging and temperature. This resulted in two new model elements: (1) the leaf lifespan, calculated in degree days, based on the experiment in Chapter 2, and (2) the relation between temperature sum after emergence and the maximum N concentration in leaves. With the leaf lifespan, leaf turnover could be accurately simulated. The relation between N concentration and temperatures sum after emergence was, for catch crops, better than the Greenwood curve (Greenwood *et al.*, 1990), relating N concentration to biomass. The new relation could better fit data of different sowing with one line. Finally, a simple but satisfactory description of soil temperature that could work with the timestep of one day was included in the model. This greatly simplified modeling of soil temperature, with a good result.

Other aspects that would improve catch crop growth include descriptions of the development towards flowering for fodder radish, which may flower before winter, and of the frost tolerance of radish, which is killed by frost in part of the winters. These aspects were not included due to scarcity of data. Moreover, the effect of drought on the germination rate and the successful establishment of a catch crop, was not modeled. These omissions limit the range of conditions in which the model can be applied. The model can beneficially be used, however, for the simulation of growth of rye and fodder radish sown from August onwards, until March the next year, or, for fodder radish, until air temperature drops below ± –5 °C.

The detailed description of growth processes in the model was chosen in order to evaluate which crop characteristics and which growth processes are important in determining the N accumulation by the crop (see Chapter 8: sensitivity analysis). This results in a model with a rather large data requirement, which appears problematic for fodder radish, for which not all necessary data could be collected from our own experiments and from the literature. For rye, a crop with a higher economic value and a longer history in agricultural research, most relevant data were available. This difference in data availability between the crops is reflected in the accuracy of the simulated crop N content, which is better for rye than for radish.

The underestimation of N leaching by use of Burns' (1974) complete mixing theory is unexpected: the theory results in a theoretical maximum leaching rate. If mixing of N in soil water were less than complete in reality (e.g. in case of preferential flow), one would have expected an overestimation of leaching by the model. If preferential flow occurred, water would have percolated at various rates. Fast percolating water would be likely to have a lower N concentration than slowly percolating water, because in case of fast percolation, mineralized N would be diluted in more water than with slow percolation. We searched for other reasons than an imperfect simulation of N transport, but we could not find any logical way in which interaction of soil N transformations with transport processes could cause the underestimation of leaching by the model.

Performance of the model

Although the exact level of crop N content could not always be simulated, its measured time course was well represented by the model. Differences in e.g. the decrease of rye crop N content between years or between rye and forage rape in the 1992 experiment can be reproduced by simulation. Also, the difference between crops in N accumulation at the start of growth was reproduced by simulation. This indicates that, in general, the model is sensitive to the differences in crop characteristics and to differences in weather conditions between years. Therefore, we are confident to use the model for exploring the importance of different crop characteristics for the success of a catch crop in storing N in autumn and winter.

Soil N transport is also rather well simulated, in spite of the underestimation of the N leaching rate (Figure 9a and b). Differences in amounts of soil N or irrigation rate in the Rhizolab are reflected in the simulation results. Therefore, the model may also be used for the exploration of different catch crop cultivation strategies to reduce N leaching. Because simulation of rye was better than that of fodder radish, these explorations may best be performed with the rye model. Because the exact levels of crop N content were not always reproduced, the model is perhaps less appropriate for exact prediction of N uptake by a catch crop, especially if it grows with limited N supply or if it is sown late in the season (second half of September or later).

To improve model performance, several aspects can be thought of. For most of these, however, more data need to become available. The accumulation of reserve carbohydrates can still be improved. At the moment reserve carbohydrates are rather too easily available for root growth, which leads in some cases to an overestimation of root growth, and to simulated soluble carbohydrate levels that are lower than those measured in the experiment in Chapter 2. Changing this would lead to a better estimate of N demand, as roots contain N, contrary to carbohydrate reserves. Currently, there is no restriction in the model on the root length or weight that can grow in one day. To improve this, root architecture should be included, or e.g. a relative root expansion rate must be defined. For a wider model application, simulating the effect of drought on germination should be included, so that crop emergence may be delayed ore reduced by dry soil conditions. This affects the initial growth of the crop, which is determining the interception of radiation in the period with the highest radiation levels. Moreover, the frost tolerance of the crops may be included in the model. This will not greatly influence the N-uptake, which mostly takes place before the first frost, it strongly affects the conservation of N in the crop over winter. Moreover, more parameter values could be collected for fodder radish, so that there is no need to use data of related crops, like forage rape. This may relate to parameters determining the rate of leaf area and rooting depth expansion. Lastly, the amount of N in soil should be better known or simulated to have a better simulation of N supply to the catch crop. This may partly explain the differences in simulation of N-limited growth from one experiment to another.

Conclusions

Generally, the model simulated the N accumulation by the catch crops reasonably well. Effects of N-limited growth on N accumulation were overestimated in one experiment, and underestimated in another. This is due to differences in the soil N availability between the experiments, which were not captured in the model. The overestimation of crop N in 1991 and 1995 is also due to overestimation of the capacity of catch crops to take up N at a given soil N availability. Leached N was underestimated, even though percolation of water was simulated accurately. Overall simulation of crop N accumulation was best for rye at high N availability, somewhat less for rye at low N availability and still less for fodder radish. As measured time courses of crop N content, soil N and leached N were generally well reproduced by simulation, the model is considered suitable to explore the relative importance of particular crop characteristics and catch crop management strategies for high N accumulation by the crop, and their effectiveness in reducing N leaching. As the model performed slightly better for rye than for fodder radish, the model will be used with rye for these explorative studies.

Appendix

Estimation of the limitation of leaf area growth of rye by suboptimal temperature.

Introduction

Temperature affects the leaf area of gramineae by effects on leaf appearance (e.g. Chapter 2; Bos & Neuteboom, 1998a) and the area of individual leaves (e.g. Van Dobben & Hoogland, 1953; Bos & Neuteboom, 1998b). Tillering is hardly affected by temperature (Bos & Neuteboom, 1998a). Hence, the temperature effect can be calculated per tiller, and the dynamics of the number of tillers determine the temperature effect on the canopy level. Below, a quantification of how temperature affects leaf area expansion of a winter rye catch crop is developed, based on numbers of leaves and tillers, and leaf expansion per tiller. The relations are calibrated with data from detailed studies on winter rye, and validated with data from field experiments.

Modelling the relative growth rate of the number of leaves and the leaf area

The increase in the number of leaves of a plant (L) is:

$$dL/dt = k1 \times T \tag{a1}$$

where t is time (in days) and k1 is the leaf appearance rate per tiller (in leaves tiller $^{-1}$ d^{-1}) and T is the number of tillers. The increase in T is described:

$$dT/dt = k2 \times T \tag{a2}$$

where k2 is the tiller appearance rate (tiller tiller^{-1} d^{-1}). The site filling (Fs in tiller leaf $^{-1}$; Davies, 1974) can now be described:

$$Fs = k2/k1 \tag{a3}$$

The relative rate of increase in L, denoted by RGRL (in d^{-1}), can be calculated:

$$RGRL = (dL/dt) / L \tag{a4}$$

Analogously, this equation can be used for leaf area of a plant (LA, in m^2):

$$\mathrm{RGRLA} = (\mathrm{dLA/dt}) / \mathrm{LA} \qquad \text{(a5)}$$

where RGRLA (in d^{-1}) is the relative rate of increase in leaf area.

LA is the product of L and the average area of the leaves on a plant (a; in m^2 leaf $^{-1}$).

$$\mathrm{LA} = \mathrm{L} \times \mathrm{a} \qquad \text{(a6)}$$

The area of individual leaves depends on temperature and the position on the plant (Van Dobben & Hoogland, 1953), and therefore it varies in time. In a short period, e.g. a day, a will, however, not change much, because it mainly depends on full-grown leaves developed before a specific day, and hence on plant history. For a short period, it is assumed that a is constant. Then follows that RGRLA is equal to RGRL:

$$\mathrm{RGRLA} = (\mathrm{d}(\mathrm{L} \times \mathrm{a})/\mathrm{dt}) / (\mathrm{L} \times \mathrm{a}) = (\mathrm{a} \times \mathrm{dL/dt}) / (\mathrm{L} \times \mathrm{a}) = (\mathrm{dL/dt}) / \mathrm{L} = \mathrm{RGRL} \qquad \text{(a7)}$$

Parameterization and validation of this model when Fs is constant

For deriving the relationship between RGRL and temperature data from a pot experiment were used in which the leaf appearance rate and the site filling of winter rye were determined (Chapter 2). The resulting relationship was tested with data on RGRLA from a field experiment (Vos & Van der Putten, 1997). RGRLA was not determined for individual plants, but for a whole crop canopy. Its value is the same as for individual plants, as long as mutual shading is not affecting growth rate. Both RGRL and RGRLA can be assumed independent of L and LA at low values of L and LA, respectively. At large leaf areas mutual shading of leaves will decrease RGRLA (Goudriaan & Van Laar, 1994).

From the pot experiment, conducted with optimal nutrient and water supply (Chapter 2) the following is used:

$$\mathrm{k1} = (e^{(-4.316+0.186 \times \mathrm{temp})}) \text{ leaf tiller}^{-1}\ \mathrm{d}^{-1} \qquad \text{(a8; Figure A1)}$$

$$\mathrm{Fs} = 0.629 \text{ tiller leaf}^{-1}\text{, during the first six weeks of growth} \qquad \text{(a9; Chapter 2)}$$

in which temp is expressed in °C.

The measured relation between k1 and temperature is described by an exponential curve, rather than a constant level below 6 °C and a line above that temperature. This is because there is no reason why a threshold or base temperature should be assumed at this temperature level in the physiology of leaf appearance. The data were collected

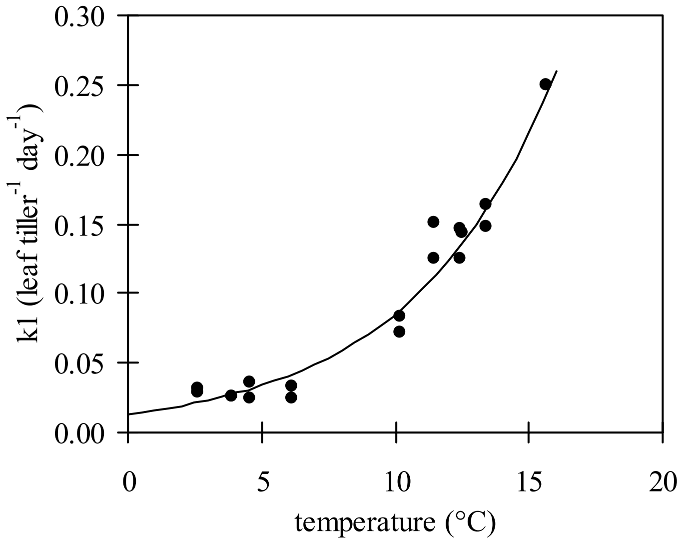


Figure A1. The relation between k1 and temperature based on the rye data of Chapter 2. Dots refer to the measured data, the line is the exponential function fitted to the data (a8).

during autumn and winter. Low temperatures coincided with low light intensities and short days and higher temperatures with higher light intensities and longer days. This may explain why the relation is not linear as found elsewhere (e.g. Hunt & Chapleau, 1986): k1 increases with light intensity (Bos & Neuteboom, 1998a) and photoperiod (Gan & McLeod, 1997). For the current study, the effects of light intensity and photoperiod are thus incorporated in the relation of k1 to temperature. This is thought acceptable because the coincidence of low temperature, low light intensities and short photoperiod will generally occur in the situations for which the model is to be used. Also, there is no possibility to separate the factors in the used datasets. With these data, RGRL can be calculated for different temperatures, using a timestep of one day, because of use of daily weather data. This was done with weather data from Wageningen in 1992, so that the results could be compared to the field data of Vos & Van der Putten (1997). To avoid accumulation of integration errors with the chosen timestep and the rectangular integration method, T was integrated analytically for each day. The derivative of this analytical integral was used for each timestep in the numerical integration, instead of the original differential equation:

$$\Delta T/\Delta dt = T \times (e^{(k2 \times \Delta t)} - 1)/ \Delta t \quad \text{instead of} \quad \Delta T/\Delta t = k2 \times T. \qquad \text{(a10)}$$

The RGRLA of the winter rye canopy at the beginning of the growing season was calculated for three sowing dates in the field experiment (Vos & Van der Putten, 1997). This was done for measurements in the first 3 to 6 weeks after crop emergence, when mutual shading by the plants was still negligible. Also, the average temperature in the 14 day period in which RGRLA was measured was calculated from daily average temperature data, so that RGRLA could be plotted against temperature.

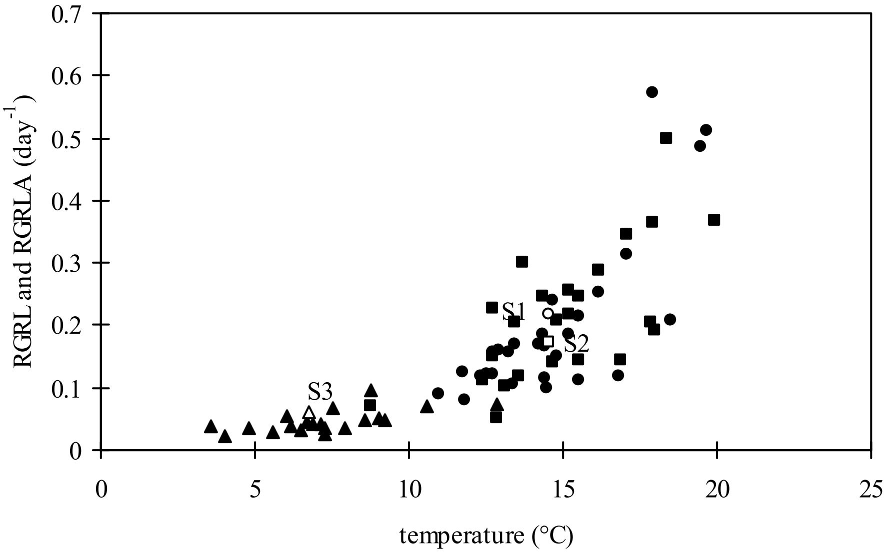


Figure A2. RGRL (modeled as described above, Equation a4; closed symbols) and RGRLA(measured; open symbols) in winter rye in the 1992 field experiment of Vos and Van der Putten (1997), plotted against temperature. Rye is sown on 21 Aug (S1; dots), 7 Sep (S2; squares) and 28 Sep (S3; triangles).

In Figure A2 both RGRL and RGRLA are plotted against temperature, based on data of the pot experiment and the field experiment, respectively, for the three sowings in 1992 at ample N supply (Vos & Van der Putten, 1997). Both the results based on the pot experiment and those from the field experiment yield a nonlinear relation between both RGRL and RGRLA and temperature, and their values are rather close. Because of the nonlinearity, the use of 14 day average temperatures related to RGRLA was not strictly correct. It is, however, the best we can get from field data. Furthermore, RGRL equaled to RGRLA in the model, based on the assumption that the average area of individual leaves does not change over the period that RGRL and RGRLA are determined. This assumption holds for RGRL, calculated with a timestep of one day, but RGRLA is determined for periods if 14 days, in which a may change. Apparently, this does not greatly influence the results. It is concluded that the data from the pot experiment, applied in the above model, can be used to describe RGRLA of winter rye canopies when mutual shading of leaves is negligible.

Modelling changes in site filling

Later on, Fs decreases from its original value to zero at the end of tillering (Chapter 2). Several factors can influence Fs: 1. The red/far red ratio in irradiation. This ratio decreases with increasing depth in the canopy (Casal *et al.*, 1990). Therefore, site filling decreases with increasing leaf area index (Van Loo, 1993); 2. Low carbohydrate availability (Bos & Neuteboom, 1998a); 3. Low nutrient supply (Van Loo, *et al.*, 1992); 4. Crop development (e.g. Schädlich & Schulzke, 1985). For the above data, nutrient supply was optimal, and during most of the season, high levels of carbohydrates were found in the rye leaves (Chapter 2). Crop development will not limit tillering of winter rye grown as a catch crop for most of its growing season. Therefore, only leaf area index remains to influence Fs in this model, but no data are available to describe the effect for rye. Therefore, the number of tillers is taken instead to describe the effect of increase of the size of the canopy. In literature the maximum number of tillers per square meter does not vary strongly. Generally, for small grains maximally 1600 tillers m^{-2} are formed (De Jong, 1986), which number decreases in winter and spring. In an other study, winter rye had maximally about 1600 - 2200 tillers m^{-2} in winter (Schädlich & Schulzke, 1985). In the experiment in Chapter 2 there were maximally about 2000 tillers m^{-2}. In this study Fs could be related to the number of tillers, as a measure for LAI. The increase in number of tillers was well described by assuming that Fs was at maximum when there were less then 500 tillers m^{-2}, and decreased linearly to zero between 500 and 2000 tillers m^{-2}. The resulting fit is shown in Figure A3. With this relation and the leaf appearance data the increase in number of tillers of a canopy can be modeled for the whole growing season. To simulate leaf area index the leaf expansion rate per tiller must be described.

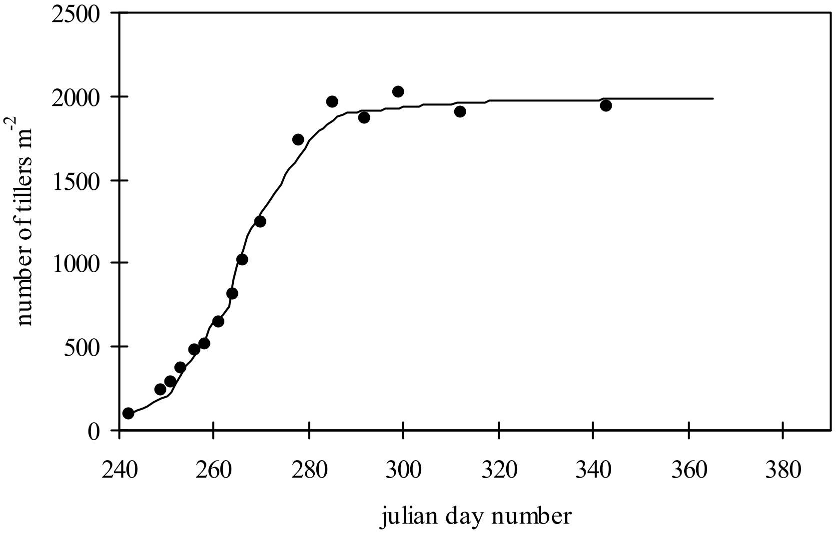


Figure A3. Simulated (line) and measured (dots) number of tillers (T) in winter rye with time in the pot experiment in Chapter 2.

Modeling the effect of temperature on leaf expansion rate

For several Gramineae the effect of temperature in the expansion rates of individual leaves have been derived, and for rye also some data are available under controlled conditions (Krol *et al.*, 1984). A rather linear relation was found in wheat (Kemp & Blacklow, 1980):

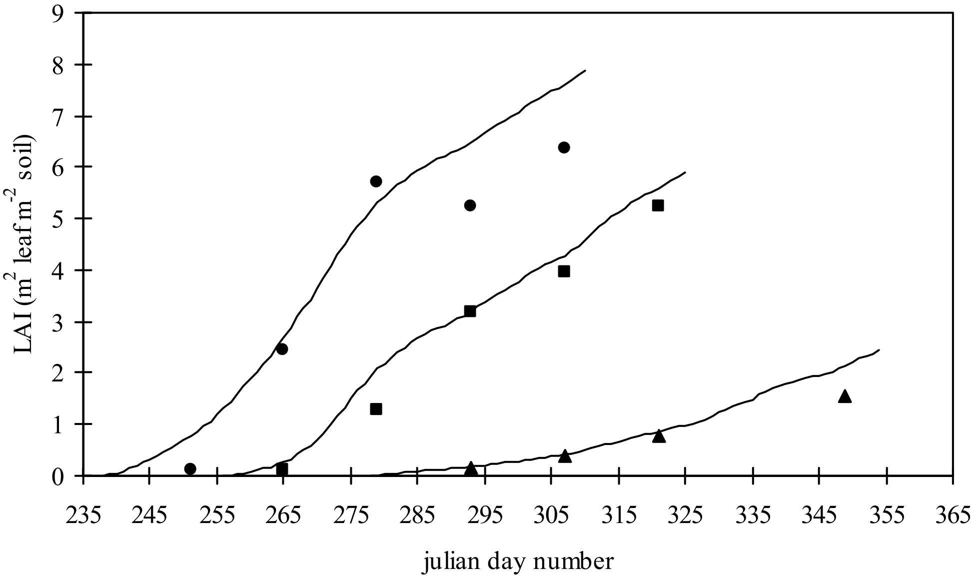


Figure A4. Calibrated (lines) and measured (dots) data of LAI with the experiment of 1992 (Vos & Van der Putten, 1997). Circles: sowing 21 Aug; squares: sowing 7 Sep; triangles: sowing 28 Sep.

$$\mathrm{LER} = \mathrm{k3} \times \mathrm{temp} \qquad \text{(a11)}$$

in which LER is the leaf expansion rate (in m^2 leaf^{-1} d^{-1}) and k3 is a leaf expansion temperature coefficient (m2 leaf^{-1} d^{-1} °C^{-1}).

The duration of the expansion of a leaf (LED, in d) is proportional to the leaf appearance interval (k1^{-1}) (Van Loo, 1993). Therefore, the number of expanding leaves per tiller (n, in leaves tiller^{-1}) can be calculated:

$$n = \mathrm{LED} \times \mathrm{k1} \qquad \text{(a12)}$$

The growth rate of the leaf area can be described:

$$\mathrm{dLAI/dt} = T \times n \times \mathrm{LER} = T \times n \times \mathrm{k3} \times \mathrm{temp} \qquad \text{(a13)}$$

Fitting this relation to the field data resulted in: n × k3 = 0.046, for all sowings in 1992 (Figure A4). The parameter was thus derived by calibration with field data, because detailed data from literature were not sufficient to derive a quantitative relationship for rye. In Figure A4, the measured LAI of green and yellow leaves is represented for the period that leaf death is still negligible.

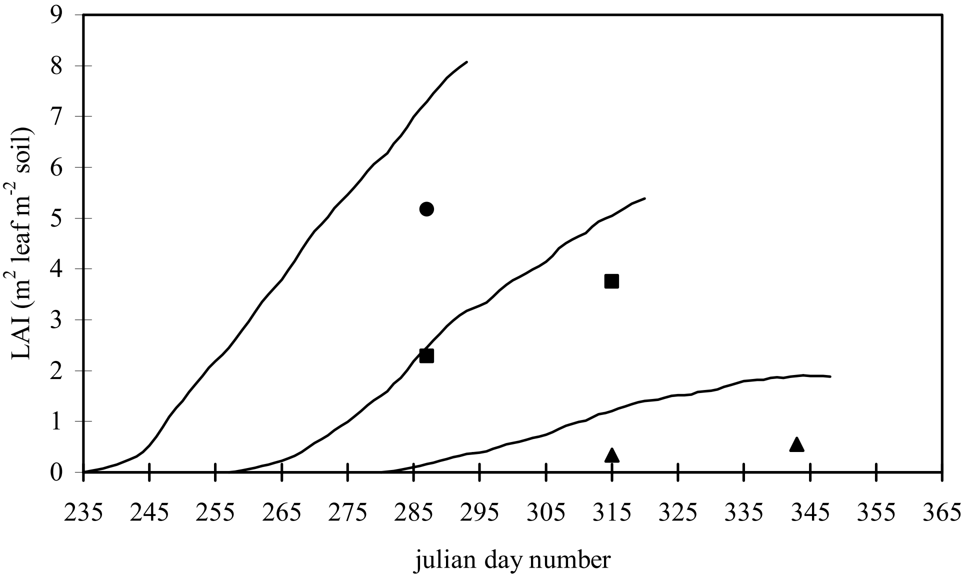


Figure A5. Simulated (lines) and measured (dots) data of LAI with the experiment of 1991 (Vos & Van der Putten, 1997). Circle: sowing 19 Aug; squares: sowing 9 Sep; triangles: sowing 1 Oct.

Validation of the model with an independent data set

The model was tested by simulating the leaf area index of winter rye sown at three dates in 1991 (Vos & Van der Putten, 1997). LAI was well estimated by the model for the first two sowing dates, but was overestimated for the third sowing date (Figure A5). The small overestimation of the first sowing may be due to nitrogen shortage (Vos & Van der Putten, 1997) or leaf death in the experiment. The overestimation of LAI of the third sowing can not be explained in this way. It is not clear whether this is due to failure of the model, or growth reduction in the experiment which was not described in the model. It is concluded that the performance of the model is adequate for the first two sowings, and is good enough to be used for sink limited leaf area expansion of a winter rye catch crop.

Chapter 8

Growth and nitrogen uptake in catch crops and their effect on nitrate leaching: sensitivity analysis and scenario study

Abstract

A sensitivity analysis and a scenario study were performed with the model, described in Chapter 7, for the simulation of N accumulation by rye catch crop and the effect on N leaching.

In the sensitivity analysis, parameters crucial to all growth processes were changed by +10% and –10%, in order to investigate how strongly parameter values affected the simulated crop N content, or the simulated amount of N leached. These changes in parameters were all within their normal range of variation. In general, crop N content and leached N were not very sensitive to changes in input parameters. Maximum deviations from the ‘standard’-output were 5.9 kg N ha^{-1} for leached N and –7.8 and –10.1 kg N ha^{-1} for crop N on 19 November and 14 March, respectively. In percentages, maximum deviations were 22% for leached N and 11% for crop N on both dates. Model results were most sensitive to: 1. the maximum rooting depth (especially when N availability limited growth); 2. parameters determining how much biomass can be produced per unit radiation (maintenance respiration coefficients, a crop specific factor determining the light saturated rate of CO_2 assimilation, the fraction of assimilates partitioned to leaves and the light extinction coefficient of the canopy); 3. the maximum N concentration in the biomass. Larger changes in these parameters were tested only when within a realistic range of variation. Changes in rooting depth had the largest effect on catch crop N.

In the scenario study, simulation with weather data of 30 years showed that weather conditions became stronger determinants of crop N content and leached N when sowing was later in the season and when the amount of N in soil was higher at sowing. Both radiation and precipitation in the first month after sowing were determinants for the reduction of the amount of leached N by the catch crop, when compared to leached N under fallow land. Postponement of sowing from mid August onwards decreased the simulated potential N uptake by the crop with 3.3 kg N ha^{-1} d^{-1} on average. Application of 30 kg N ha^{-1}, in addition to 50 kg N ha^{-1} present in soil at sowing, only lead to a considerable increase in simulated leached N if sowing was late (20 September) with high precipitation soon after sowing. Application of 60 kg N ha^{-1} increased leaching for sowing on 20 September, and, with weather conditions unfavorable for catch crop effectiveness, also for sowing on 11 August. Change in seed rate from 50 to 250 kg ha^{-1} only had considerable effect on crop N accumulation with later sowing, on 20 Sep. Seed rate had little effect with sowing on 11 Aug, when it was always high enough to ensure a high light interception and a fast enough growth and N uptake by the crop. The time of incorporation of catch crops into soil that maximized transfer of the catch crop N to the next crop, was mid January. However, incorporating the crop 30 days earlier or later had only a small effect.

In conclusion, the reduction of N leaching by a catch crop is determined by the N leaching rate (determined by the precipitation surplus) on one hand and the capacity of the crop to catch and accumulate N before it has leached on the other hand. When N availability is limiting catch crop growth, rooting depth and the amount of precipitation determine how much soil N can be intercepted before it is leached. When there is more N in the soil than can potentially be stored in crop biomass, the amount of radiation, and the crop characteristics influencing how much biomass can be produced per unit radiation, determine the reduction of N leaching by the catch crop. The incorporation date of the catch crop biomass is relatively unimportant for the conservation of N and the use of catch crop N by a succeeding crop.

Introduction

Catch crops, cultivated after the harvest of summer crops, generally reduce N leaching by taking up N, but their effectiveness in reduction of leaching is variable (Thorup-Kristensen, 1994). A simulation model was developed to simulate and evaluate the effectiveness of catch crops for different weather conditions, crop characteristics, crop management and N supply (Chapter 7).

The crop model is based on SUCROS (Goudriaan & Van Laar, 1994) and adapted to simulate crop growth of winter rye and fodder radish under conditions of relatively low radiation, low temperature and low N supply, which are common during catch crop growth. The light saturated CO_2 assimilation rate was modeled as a function of radiation during leaf growth and was not dependent on temperatures above 5 °C. Structural growth of aboveground biomass was controlled by leaf expansion, which was a function of availability of N and carbohydrates, and of temperature. Reserve carbohydrates accumulated when they were not needed for maintenance or growth. Turnover of leaves and stems was described using a fixed lifespan in degree days for these organs. Soil water dynamics were described with the ‘tipping bucket’ water balance model which was adapted by including a drainage coefficient determining which fraction of soil water may drain during one day. Nitrogen leaching was described by the complete mixing theory (Burns, 1974). Mineralization of N from soil organic matter was described with a zero order approach; that from fresh catch crop material by a first order approach. The model was validated with data on catch crop N accumulation from field experiments (Vos & Van der Putten, 1997) and soil N and leaching data from lysimeter experiments (Chapter 5). Although exact levels of the crop N content could not always be simulated accurately, the measured time courses of crop N content and leached N were generally adequately reproduced by the model. Therefore, the model can be used in explorative studies to determine which crop characteristics and what crop management and N supply are needed to maximize the effectiveness of catch crop N uptake and reduction of N leaching under varying weather conditions.

In this chapter we perform a sensitivity analysis and an explorative scenario study with the model. In the sensitivity analysis, we aim to evaluate the importance of various model parameters as determinants of the simulated N uptake by catch crops and the simulated leached N. The results will be used to gain insight in the strong and weak aspects of the model for simulating N dynamics in catch crops. In the scenario study, we evaluate the effect of different catch crop characteristics and management practices on the efficacy of these crops to reduce N leaching. With this scenario study, several strategic questions arising in use of catch crops for reduction of leaching can be answered. Firstly, the variation in catch crop effectiveness can be related to the variation in several factors: weather conditions, sowing date, soil residual N at sowing of the catch crop and N mineralization rate. Also crop management aspects like seed rate, fertilizer application at sowing and moment of incorporation of the catch crop are investigated and effects of catch crop characteristics on N uptake and reduction of leaching are tested. The results of this study are used to optimize catch crop breeding and cultivation.

Methods

Sensitivity analysis

The model comprised a number of crop growth processes. For each of these processes a crucial parameter was chosen (Table 1), variation of which could show how strong this process affected the simulated N accumulation by the crop, or the reduction of N leaching when compared to leaching under fallow land.

For the sensitivity analysis a standard variation of plus and minus 10 % was examined of the value in the model used for simulating winter rye. Ten percent deviation was chosen because this is a realistic variation that may occur for most parameters, and that may matter for the model results. To check the (non-)linearity of the response, the relative effects of negative deviations from the standard values were compared to those with positive deviations. When these differed by a factor 2 or more, more values of the parameter were tested. Normally, only one parameter was changed at a time. Exceptions to this are: 1. the maintenance respiration coefficients for leaves (m_l), sheaths (m_s) and roots (m_r) were changed only in combination, to test the overall effect of changes in the rate of maintenance respiration; 2. the maximum N percentage in the leaves at emergence ($C_{N,max,0}$) and at an infinite temperature sum after emergence ($C_{N,max,\infty}$) were changed only in combination, so that the effect of a change in the maximum N percentage over the whole growing period was tested; 3. the maximum uptake capacity of the roots ($F_{max,t}$) is a function of temperature and was changed by 10% for the whole temperature range.

Three model outputs were used to evaluate the sensitivity to a change in input parameter values. First, the crop N content at mid November (19 Nov, day nr 323) was chosen, because at about this time of year, crop N content typically reached a maximum

Table 1. Parameters varied in the sensitivity analysis, with related processes and references to the parts of Chapter 7 where the parameters are used. *: $F_{max,t}$ is a function of temperature. Between the mentioned temperature values a linear interpolation of the function values is performed.

symbol	**name**	**unit**	**related process**	**default value**	**related part of chapter 7**
K_{dif}	extinction coefficient for diffuse light	m^2 ground area m^{-2} leaf	light interception	0.7	CO_2 assimilation
f_{crop}	crop species specific factor converting the A_{max} of young leaves to the effective A_{max} of a canopy	-	CO_2 assimilation	0.6	eq. 2
m_l, m_s, m_r	maintenance respiration coefficients for leaves, sheaths and roots, resp.	kg kg^{-1} d^{-1}	Maintenance respiration	0.03	Maintenance respiration
c_{LE}	Leaf expansion coefficient	m^2 leaf m^{-2} ground area $tiller^{-1}$ $°C^{-1}$ d^{-1}	leaf expansion	$6.0*10^{-6}$	eq. 5
rd_{max}	maximum rooting depth	m	root growth	0.6	Root growth
f_{leaf}	fraction of assimilates partitioned to leaves	kg kg^{-1}	partitioning	0.6	Carbohydrate and nitrogen partitioning
LS_{leaf}	leaf lifespan	°C days	turnover	443	Turnover
$C_{N,max,0}$ $C_{N,max,\infty}$	Maximum N percentage in the leaves at emergence and at an infinite temperature sum after that event	% of dry crop biomass	N accumulation	7.0 and 4.8, resp.	eq. 1
$C_{N,min,L,0}$	minimum N percentage for leaf growth, at crop emergence	% of dry crop biomass	leaf expansion	1.0	eq. 5b
$C_{N,min,A,0}$	minimum N percentage for CO_2 assimilation in the leaves at crop emergence	% of dry crop biomass	CO_2 assimilation	1.0	eq. 4
$F_{max,t}^{*}$	maximum uptake capacity of the roots as a function of soil temperature	mg N cm^{-1} root day^{-1}	N uptake	0 °C: 0.0 3 °C: 0.267 17 °C: 0.676 35 °C: 0.767	Soil nitrogen dynamics

(see Chapter 7). In some cases, the crop N content decreased after November until mid February, after which net increase might start again. Therefore, crop N content at mid

February (18 Feb., day nr. 413 counted from 1 Jan in the year of sowing of the catch crop) was chosen as a second model output. This value may serve as a measure for N uptake and conservation in the crop in winter. Thirdly, the amount of N leached in the period from sowing till early spring (16 March, day nr. 441) gives an overall measure of the effectiveness of catch crops in reduction of leaching. The period of leaching was taken longer than that of catch crop growth (until mid March instead of mid February) because soil water percolation generally occurs till (at least) mid March. Nitrogen was supposed to be leached, and lost from the crop-soil system when it was leached below 1 m depth.

Model sensitivity to parameter changes was tested for a range of situations. Firstly, an early and a late sowing date (S1: 11 Aug (day 223) versus. S2: 20 Sep (day 263)) were chosen. These were combined with a high N supply (N2: 100 kg N ha^{-1} in four doses, the first at sowing and the others at 14 d intervals) and a low N supply (N1: no fertilizer). At sowing, 50 kg N ha^{-1} was present in 0-1.0 m depth (36 kg N ha^{-1} in 0 – 0.6 m and 14 kg N ha^{-1} in 0.6 – 1.0 m depth). Tests were performed for two seasons: 1978-79 and 1995-96. These seasons differed widely in the amounts of radiation and the average temperature in the months of August, September and October, in which most of catch crop N uptake takes place. For 1978 the average temperature in these three months was 12.7 °C, versus 15.4 °C in 1995. The global radiation sum was 0.83 GJ m^{-2} in 1978 and 1.08 GJ m^{-2} in 1995 and the accumulated precipitation was 114 mm in 1978 and 119 mm in 1995.

Scenario study

Scenarios were defined such that it was possible to explain the variation found for catch crop effectiveness and to test the effects of management aspects and crop characteristics on N uptake and N leaching. Table 2 gives an overview of the scenarios.

Weather conditions

The effect of weather conditions was tested by running the model for a rye crop sown at 11 Aug (S1) or 20 Sep (S2) in 1970-1999, with 50 or 150 kg N ha^{-1} present in the 1 m topsoil (N50 and N150, respectively). Simulated cumulative amounts of leached N (16 March, day nr 441) were compared with those obtained without a crop: the reduction in leaching is the best measure for the effectiveness of the catch crop. To find out how weather conditions affect catch crop effectiveness, we calculated the fraction of variation in reduction of leached N that is explained by sums of radiation, precipitation

Table 2. Input, output and conditions of the scenarios simulated with the model. N50 = 50 kg N ha^{-1} present in soil at sowing (36 kg N ha^{-1} in 0 – 0.6 m and 14 kg N ha^{-1} in 0.6 – 1.0 m depth); N150 = 150 kg N ha^{-1} present in soil at sowing (108 kg N ha^{-1} in 0 – 0.6 m and 42 kg N ha^{-1} in 0.6 – 1.0 m depth); rd_{max} = maximum rooting depth; f_{crop} = crop species specific factor converting the A_{max} of young leaves to the effective A_{max} of a canopy; f_{leaf} = fraction of assimilates partitioned to leaves.

	Input	**Output**	**Sowing year**	**Sowing date 11 Aug (S1)**		**Sowing date 20 Sep (S2)**	
				N50	**N150**	**N50**	**N150**
Weather conditions	weather data	Reduction of leached N	1970 - 1999	x	x	x	x
N availability	N fertilizer 0/30/60 kg ha^{-1} N mineralization default/+30/+60 kg ha^{-1}	Leached N; Crop N	1991, 1992	x	x		
			1984, 1989			x	x
Sowing date	Sowing dates 11 Aug – 15 Oct	Crop N	1991, 1992	N50 , N150 at all sowing dates			
			1970 - 1999	N150 + 4 × 25 kg N per ha			
Seed rate	50 - 250 kg ha^{-1}	Leached N	1991, 1992	x	x	x	x
Crop characteristics	rd_{max}: 0.2 - 1.0 m Max. root zone extension rate: 0.01-0.05 m d^{-1} f_{crop}: 0.4 - 1.0 f_{leaf}: 0.4 - 0.9	Leached N	1991, 1992	x	x	x	x
Incorporation date	19 Nov, 19 dec; 18 Jan, 17 Feb, 19 Mar; sowing date next crop 19 Mar, 18 Apr, 18 May; rooting depth next crop 0.3 – 0.6 – 1.0 m; duration of growth 30 – 60 – 90 d	N available to next crop	1991, 1992, 1974	x	x	x	x

or temperature (above 0 °C) in the first 30 or 60 days after both sowing dates with N150. We did this by linear regression. We consider the initial period after sowing the most important for catch crop performance because radiation and temperature levels are still relatively high, and decline strongly during autumn, and because high precipitation upon sowing, may result in leaching of N before the catch crop is established and starts to act as a sink for soil N.

N availability

N availability to catch crops can vary in different ways. Firstly, the N present in the soil profile at sowing may vary. Secondly, the mineralization rate of soil organic nitrogen is different from one soil to another. Lastly, N can be supplied with fertilizers. The effect of N present in the soil at sowing was examined in combination with variation of weather data, by comparing results of N50 and N150 (see Table 2). Here, we explored the capacity of catch crops to use N mineralized during their growth. Moreover, we examined the effect of N application at sowing on leached N. The N mineralized in the first three months after sowing (in the current model about 26 kg N ha^{-1}) was increased by 30 and 60 kg N ha^{-1}, by increasing the decomposition rate of soil organic matter.

In agricultural practice intermediate, non-commercial crops are being planted in late summer or autumn, not only for the sake of catching N, but for purposes such as the reduction of wind erosion, the production of fresh organic matter to be incorporated into the soil or the reduction of the number of plant pathogenic nematodes in soil. Fertilizer N is often applied to such crops. The N dressing may, however, increase leaching of N as well. To evaluate the overall effect, N dressings of 30 of 60 kg N ha^{-1} at sowing were tested.

All simulations were performed with 50 kg N ha^{-1} present in soil at sowing (N50) of a rye catch crop, for sowing on 11 Aug (S1) and 20 Sep (S2). Years were chosen which showed one of the highest and the lowest reduction of leached N by the catch crop in the analysis of effects of weather conditions. For S1, these were 1991 and 1992. For S2, these were 1984 and 1989.

Sowing date

From the above scenarios, and from literature (e.g. Vos, 1992; Vos & Van der Putten, 1997), it is clear that catch crop N uptake and hence, reduction of N leaching by the catch crop, decreases with later sowing of the crop. The effect of sowing time on catch crop N uptake was tested with the model for low residual N (50 kg N ha^{-1}; N50), and for high residual N (150 kg N ha^{-1}; N150), present in soil on 11 Aug (day 223). Sowing dates were chosen every fifth day from 11 Aug until 15 Oct (day 288), in 1991 and 1992. Moreover, N uptake by the catch crop was simulated at N150 in combination with a split N application of 100 kg N ha^{-1} in four doses, the first supplied at sowing and the others at 14 d intervals. This very high N availability was used to test the potential N uptake of the catch crop. This scenario was run for 30 years and results were compared with the literature data.

Seed rate

In the model, the leaf area at germination was proportional to the amount of seed used. Therefore, the seed rate was important for the rates of leaf expansion and light interception at the start of the growing season, and, consequently, for the growth rate and the rate of N storage in catch crop biomass. The cost of seed is a substantial part of the total costs of catch crop cultivation, and the recommended seed rates vary with catch crop species (e.g. fodder radish 25 kg ha^{-1}; winter rye 180 kg ha^{-1}). It is therefore interesting to see how strongly the amount of seed influences the reduction in leached N by a catch crop. The seed rate of rye was varied in the simulation, set at levels of 50, 100, 150, 200 and 250 kg ha^{-1}, for crops sown on 11 Aug (S1) and 20 Sep (S2) in 1991 and 1992, with 50 or 150 kg N ha^{-1} in soil at sowing (N50 and N150, respectively).

Crop characteristics

The sensitivity analysis revealed a few crop characteristics that strongly determined the catch crop N uptake and the reduction of N leaching. Firstly, rooting depth appeared important when soil N availability was limiting growth. When radiation intensity was low and N accumulation was poor, catch crop performance was also sensitive to parameters determining light interception and CO_2 assimilation. Some of these parameters may differ considerably from one species or cultivar to another, or, like rooting depth, may be improved by prevention or remediation of obstructions for root growth in soil. Therefore, we tested the effect of variation in these parameters. Maximum rooting depth (rd_{max}) was varied from 0.2 to 1.0 m and the maximum root zone extension rate from 0.01 to 0.05 m day^{-1}, realistic values for rye (Thorup-Kristensen, 2001). The crop factor (f_{crop}), determining the relation between the effective light saturated CO_2 assimilation rate of the canopy and that of young, full-grown leaves, was varied from 0.4 to 1.0. The fraction of assimilates allocated to leaves (f_{leaf}), which was important for leaf expansion at the start of the growing season, was varied from 0.5 to 0.9. These parameters were tested for sowing on 11 Aug (S1) and 20 Sep (S2) in 1991 and 1992, with 50 or 150 kg N ha^{-1} in soil at sowing (N50 and N150, see Table 2).

Incorporation date

The optimum date for incorporation of a catch crop into the soil depends on a number of factors, e.g. trafficability and workability of the soil throughout the winter, effects on transfer of pests and diseases from one crop to the next, effects on soil biology, etc. Here we focused on finding the optimum incorporation date for conservation of N in the soil – plant system and supply of N to the succeeding crop. Even then the optimum incorporation may depend on a number of factors. These are 1. the biomass and N content of the catch crop; 2. the N leaching rate, which is a function of soil properties and weather conditions; 3. the sowing date, rooting depth and the duration of N uptake of the succeeding crop. 4. the rate of N mineralization from the catch crop biomass.

To test the effect of a different biomass and N content of the catch crop, simulations were performed with the model of rye catch crops sown on 11 Aug (S1) and 20 Sep (S2) in 1991 and 1992, with 50 or 150 kg N ha^{-1} in soil at sowing (N50 and N150, see Table 2). The crops were incorporated in soil at different dates, at 30 d intervals: 19 Nov, 19 Dec, and in the next year 18 Jan, 17 Feb and 19 Mar (day numbers 323, 353, 383, 413 and 443 counted from 1 Jan in the year of sowing of the catch crop). Precipitation between 19 Nov and 18 Mar was 203 and 231 mm, in 1991-92 and 1992-

93, respectively, close to the 1970-2000 average of 238 mm. For comparison, the optimal dates were also calculated for a wet winter period, 1974-75, with 308 mm precipitation. The succeeding crop was assumed to be able to use all N in the soil in 0 to 30, 60 or 100 cm depth at its sowing on 19 Mar, 18 Apr or 18 May, plus the N mineralized from the catch crop during the first 60, 90 or 120 d of growth after sowing. As for all other scenarios, a sandy soil profile was assumed, similar as in the validation described in Chapter 7. The mineralization of N from the catch crop biomass was calculated as described in Chapter 6.

The incorporation date was calculated for which the N supply to the succeeding crop was at maximum for various combinations of sowing date of the catch crop, N availability to the catch crop, rooting depth and duration of N uptake of the succeeding

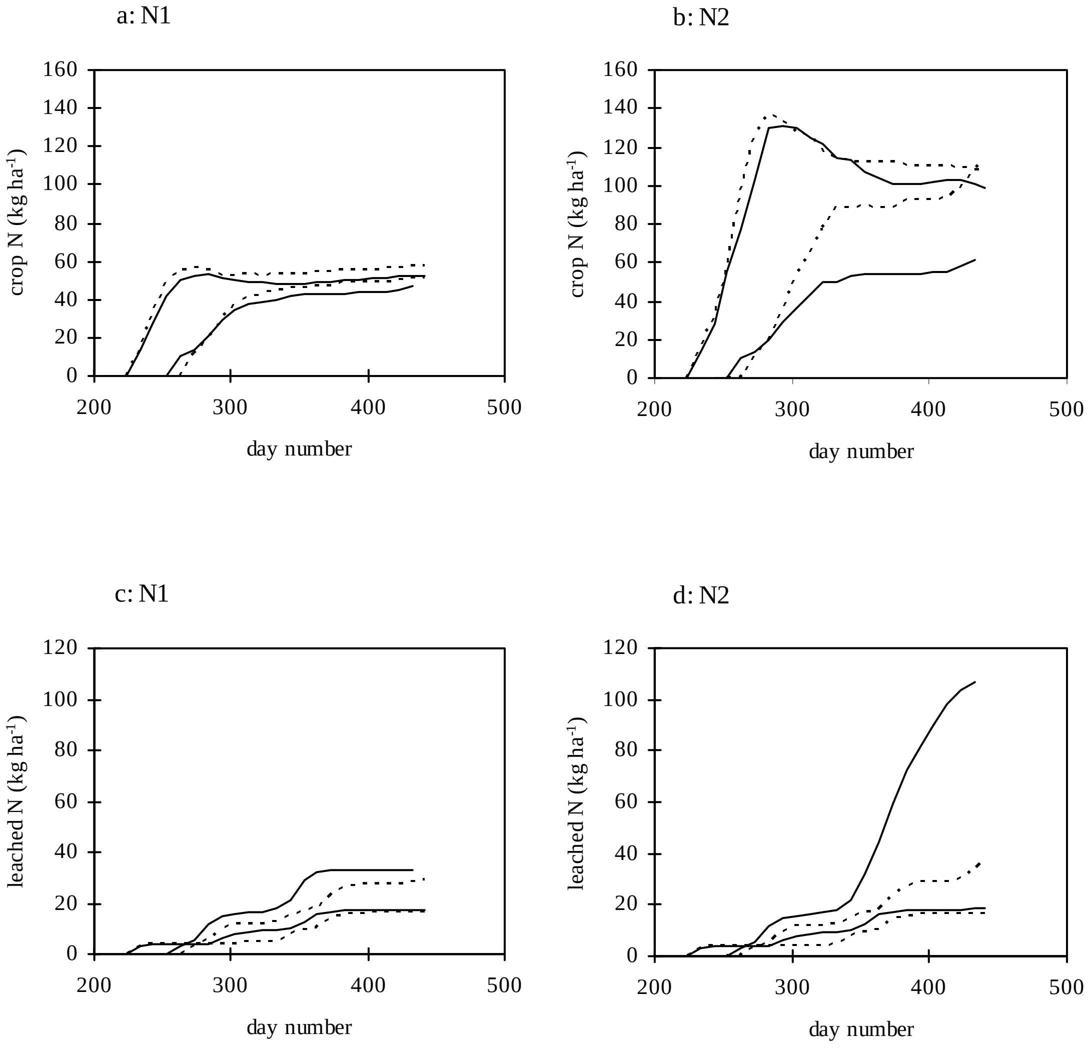


Figure 1. Simulated time courses of crop N content (Figures a and b) and amount of leached N below 1 m depth (Figures c and d), for crops sown on 11 August and 20 September in 1978 (full lines) and 1995 (dotted lines) with low and high N availability (N1: figures a and c; and N2: figures b and d, respectively).

crop. This was done by fitting a quadratic function to the 1991-1992 averages of the N available to the succeeding crop at the different incorporation dates. The date at which the function was at its maximum was determined. Analysis of variance was performed on these calculated optimal incorporation dates.

Results

Simulation with standard parameter values

Crop N content and the amount of leached N are shown in Figure 1, calculated using the standard parameter sets. Crop N content and the amount of leached N did not differ much between years at N1 (the maximum difference in leached N was 11 kg ha^{-1}), whereas large differences among years were calculated at N2, especially at the late sowing date (maximum difference of 70 kg ha^{-1} in leached N). Apparently, at N1 the amount of N in soil largely determined crop N uptake and the amount of N leached. This implies that radiation and temperature conditions were favorable enough in both years to

Table 3. Changes in the simulated amount of leached N on day 441, in kg N ha^{-1}, caused by 10% variation in input parameters. Absolute values of changes caused by increase and decrease in parameter values are averaged, the sign of the value is that occurring with increase in the parameter value. Data are shown for simulation with low (N1) and high (N2) N supply, early (S1) and late (S2) sowing with weather data of 1978-79 (low radiation and temperature) and 1995-96 (high radiation and temperature).). Simulated leached N with standard parameters is shown in the first row (in kg N ha^{-1}, italics). Changes greater than 2 kg N ha^{-1} are printed bold.

	N1				N2			
	S1		S2		S1		S2	
	1978	1995	1978	1995	1978	1995	1978	1995
standard	*17.2*	*16.7*	*33.2*	*28.7*	*18.5*	*16.7*	*106.4*	*37.4*
K_{dif}	0.0	0.0	–0.1	–0.1	0.0	–0.1	**–2.7**	–1.0
f_{crop}	0.0	0.0	–0.1	–0.1	–0.8	0.0	**–5.6**	–1.8
m_l, m_s and m_r	0.0	0.0	0.0	0.0	0.7	0.0	**2.5**	0.8
c_{LE}	0.0	0.0	0.0	0.0	–0.2	0.0	–0.3	–0.5
rd_{max}	**–2.8**	**–2.8**	**–2.3**	**–2.8**	**–2.8**	**–2.9**	–0.2	–1.8
f_{leaf}	0.0	0.0	–0.1	–0.1	–0.6	0.0	**–5.4**	–1.4
LS_{leaf}	0.0	0.0	0.0	0.0	–0.4	0.0	–0.7	–0.3
$C_{N,max,0}$ and $C_{N,max,\infty}$	0.0	0.0	0.0	0.0	**–2.4**	0.0	**–4.8**	**–2.5**
$C_{N,min,L,0}$	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
$C_{N,min,A,0}$	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
$F_{max,t}$	0.0	0.0	–0.1	0.0	–0.1	0.0	–0.1	–0.1

Table 4. Changes in the simulated amount of N in living crop biomass in November (day 323), in kg N ha^{-1}, caused by 10% variation in input parameters. Absolute values of changes caused by increase and decrease in parameter values are averaged, the sign of the value is that occurring with increase in the parameter value. Data are shown for simulation with low (N1) and high (N2) N supply, early (S1) and late (S2) sowing with weather data of 1978-79 (low radiation and temperature) and 1995-96 (high radiation and temperature). Simulated N in living crop biomass with standard parameters is shown in the first row (in kg N ha^{-1}, italics). Changes greater than 2 kg N ha^{-1} are printed bold.

	N1				N2			
	S1		S2		S1		S2	
	1978	1995	1978	1995	1978	1995	1978	1995
standard	*48.9*	*52.7*	*37.5*	*43.3*	*121.2*	*117.8*	*44.1*	*78.4*
K_{dif}	0.2	0.6	0.2	0.1	0.0	–0.1	**2.1**	1.8
f_{crop}	0.8	0.9	0.4	0.0	1.9	1.8	**4.6**	**6.0**
m_l, m_s and m_r	–0.3	–0.3	–0.1	0.0	–1.3	–1.2	–1.7	**–2.1**
c_{LE}	–.05	–0.6	0.0	0.0	–1.3	–1.4	0.1	0.8
rd_{max}	**2.0**	**2.1**	1.8	**2.5**	**2.1**	**2.1**	0.1	0.4
f_{leaf}	0.5	0.9	0.3	0.0	0.6	0.4	**4.1**	**5.3**
LS_{leaf}	1.7	1.9	0.5	0.8	**5.0**	**5.4**	0.8	1.7
$C_{N,max,0}$ and $C_{N,max,\infty}$	0.8	0.6	1.2	0.9	**4.9**	**2.5**	**4.4**	**6.4**
$C_{N,min,L,0}$	0.0	0.1	0.0	0.0	0.1	0.1	0.0	0.0
$C_{N,min,A,0}$	–0.1	–0.1	0.0	0.0	0.0	–0.1	0.0	0.0
$F_{max,t}$	0.0	–0.1	0.1	0.0	–0.7	–0.7	0.3	0.8

allow an uptake of N larger than the N supplied in soil. Beyond mid January (day 380) both crop N content and leached N hardly increased anymore. Apparently, there was no N available anymore in the soil profile (calculated as 2 – 5 kg ha^{-1} in 0-100 cm depth), and mineralization was slow (calculated as 1-2 kg N ha^{-1} between day 383 and day 441).

At N2, weather conditions strongly affected simulated crop N content and leached N at S2. With this late sowing, there was a large benefit of the higher radiation and temperature in 1995, compared to 1978. In general, sowing date effects on crop N and, hence, on leached N were larger at N2 than at N1. With the higher availability of N in soil, the weather conditions became more important determinants of the fraction of available N that could be absorbed by the catch crop. At S2, leached N increased until the end of the simulation (mid March). At that moment there was still 15 kg N ha^{-1} in the soil profile in 1978 and 25 kg N ha^{-1} in 1995. Most of this N was located at greater depth, below the 60 cm deep rooted zone. This N would leach if drainage down the profile continued after mid March.

Table 5. Changes in the simulated amount of N in living crop biomass in March (day 413), in kg N ha^{-1}, caused by 10% variation in input parameters. Absolute values of effects of increase and decrease in parameter values are averaged, the sign of the value is that occurring with increase in the parameter value. Data are shown for simulation with low (N1) and high (N2) N supply, early (S1) and late (S2) sowing with weather data of 1978-79 (low radiation and temperature) and 1995-96 (high radiation and temperature). Simulated N in living crop biomass with standard parameters is shown in the first row (in kg N ha^{-1}, italics). Changes greater than 2 kg N ha^{-1} are printed bold.

	N1				N2			
	S1		S2		S1		S2	
	1978	1995	1978	1995	1978	1995	1978	1995
standard	*51.7*	*56.1*	*44.1*	*49.6*	*102.7*	*109.8*	*55.0*	*93.4*
K_{dif}	0.4	0.7	0.1	0.0	–0.4	0.1	**2.7**	1.5
f_{crop}	1.2	1.3	0.1	–0.2	**4.5**	1.9	**5.8**	**6.5**
m_l, m_s and m_r	–0.5	–0.6	–0.1	0.0	**–4.9**	–1.3	**–2.8**	**–3.6**
c_{LE}	–0.6	–0.8	0.0	0.0	–0.3	–1.4	0.3	1.4
rd_{max}	1.6	1.8	**2.2**	**2.7**	**0.4**	**1.8**	–0.1	0.1
f_{leaf}	1.3	1.5	0.0	–0.5	**3.0**	0.6	**5.5**	**5.0**
LS_{leaf}	1.9	1.8	1.4	1.5	**7.5**	**4.8**	**2.6**	**3.8**
$C_{N,max,0}$ and $C_{N,max,\infty}$	0.6	0.5	0.9	0.8	**8.8**	**2.5**	**5.8**	**9.6**
$C_{N,min,L,0}$	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
$C_{N,min,A,0}$	–0.1	–0.2	0.0	0.0	–0.1	–0.1	0.0	0.0
$F_{max,t}$	0.1	–0.1	0.2	0.0	–0.2	–0.7	0.2	0.4

Sensitivity analysis

In general, model results were not very sensitive to changes in input parameters. Maximum deviations from the 'standard'-output were 5.9 kg N ha^{-1} for leached N and -7.8 and -10.1 kg N ha^{-1} for crop N on day 323 and 413, respectively. In percentages, maximum deviations were 22% for leached N and 11% for crop N on both dates.

Effects of variation in input parameters are shown for the amount of leached N in March (Table 3), crop N content in mid November (Table 4) and crop N content in mid February (Table 5). The absolute values of the results of positive and negative deviations from the default parameter values were averaged, and the sign (positive or negative) indicates the direction of the effect for increase in parameter values.

Also here results at N1 differed from those at N2. At N1, maximum rooting depth (rd_{max}) was the only parameter influencing leached N (Table 3). N deficiency was limiting uptake, as was already clear from comparison of N1 and N2 in Figure 1. Apparently, the most effective way to alleviate the N shortage was to grow deeper roots. The extra N uptake led to a decreased amount of N leached until March. At N2, deeper root growth was also effective for increasing N uptake at S1 in 1995, but in the colder and darker year 1978 other crop characteristics were important as well.

Especially increase in the maximum N percentage in the leaves, (by change in $C_{N,max,0}$ and $C_{N,max,\infty}$) decreased leached N (Table 3). This indicates that the capacity for storage of N in biomass had become a determining factor when the crop was sown late in an autumn with low radiation conditions. At high N supply and with late sowing, changes in the light interception coefficient (K_{dif}), the crop factor for CO_2 assimilation (f_{crop}), the maintenance respiration coefficients (m_l, m_s and m_r) and the partitioning fraction for leaves (f_{leaf}) also affected leached N, and most strongly in the darker and colder season 1978-79. All these parameters influence the radiation use efficiency of the crop. They were apparently the most influential determinants of the reduction of leaching by catch crops when soil N was amply present and radiation was limited, as was the case with late sowing and low radiation per day.

The parameters important for the reduction of leaching also affected the N content in living crop biomass (Tables 4 (Crop N in November) and 5 (Crop N in March)). Moreover, increase in leaf lifespan (LS_{leaf}) led to a higher N content in living biomass. This was most evident for the crop N content in March (Table 5). For November, this effect was stronger for S1 than for S2, which indicates that leaf turnover was still low in November for the later sown crops. Changes in leaf lifespan did not affect simulated leached N, because mineralization and subsequent leaching of N from dead crop material were not calculated in the model.

There were some parameters in the sensitivity analysis that hardly affected crop N or leached N in any of the tests. For instance, $F_{max,t}$, determining the uptake capacity of the roots, had almost no effect. This implies that the uptake capacity was almost always larger than the N demand or the N availability. Also, there was little effect of changes in $C_{N,min,L,0}$ and $C_{N,min,A,0}$, the minimum N percentages for leaf expansion and for

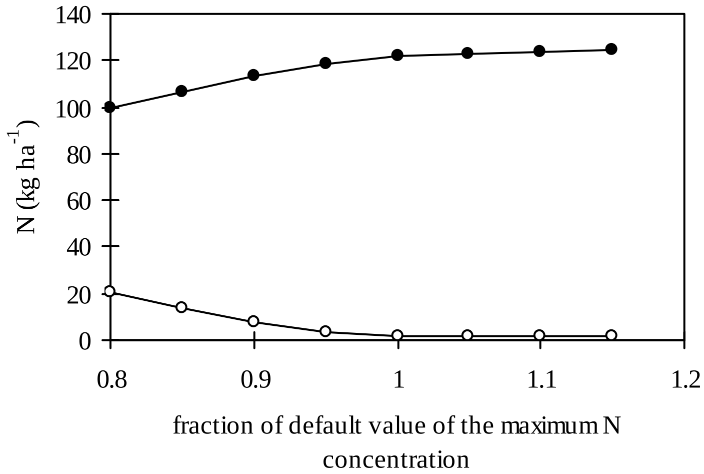


Figure 2. Simulated crop (closed dots) and root zone (open dots) N content on day 323 (19 November) as a function of the maximum N percentage in the crop, determined by the parameters $C_{N,max,0}$ and $C_{N,max,\infty}$.

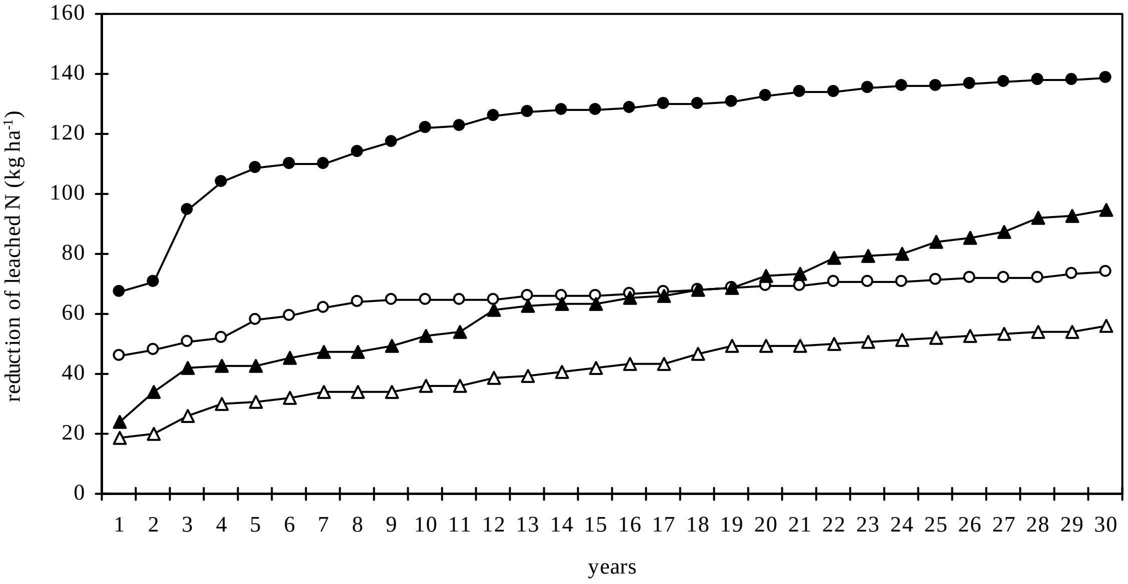


Figure 3. Simulated reduction in the amount of leached N on 16 March by catch crop cultivation, compared to fallow. Results are shown for two sowing times and two N availability levels, for catch crops sown in the years 1970 – 1999. Values per year are ordered from small to large. Dots: sowing 11 August; triangles: sowing on 20 September. Open symbols: 50 kg N ha^{-1} in soil at sowing; closed symbols: 150 kg N ha^{-1} in soil at sowing.

assimilation, respectively. This can be explained by the observation that N percentages tended to be closer to the maximum than to the minimum, so that a small shift in the minimum percentages at which certain processes can proceed was not likely to have large effects.

The only strong non-linearity in the response of the amounts of leached N and of crop N content in November was found after variation of the maximum N percentage in the leaves (by change in $C_{N,max,0}$ and $C_{N,max,\infty}$) and of the crop factor for CO_2 assimilation (f_{crop}) for the first sowing at N2 in 1978: decreased values of the maximum N percentage and of f_{crop} have a much larger effect than increased parameter values. This can be explained by a shift from a situation of growth which was not limited by N supply to one with limiting N supply, as shown for variation of the max N percentage in Figure 2: Root zone N in November decreased to near zero at increase of $C_{N,max,0}$ and $C_{N,max,\infty}$ to above the default value.

Scenario study

Weather conditions

Averaged over 30 simulated years, when no catch crop was grown and simulation started on 11 Aug (S1), 85 ± 6 kg N ha^{-1} leached when initially 50 kg N ha^{-1} was present in soil (N50) and 184 ± 9 kg N ha^{-1} leached when initially 150 kg N ha^{-1} was present in soil (N150). When simulation started on 20 Sep, 68 ± 6 kg N ha^{-1} leached at N50 and 167 ± 9 kg N ha^{-1} leached at N150. The reduction in leaching by catch crop cultivation in 30 years is shown in Figure 3. The data show that with early sowing and low residual N (S1N50), variation in reduction of leached N from one year to another was relatively small. This implies that weather conditions did not strongly influence the crop N uptake or the reduction of leached N in this situation. With increase in residual N (to N 150) or shortening of the growing season by later sowing (S2), weather conditions became more determining for crop N and leached N. The distribution of reduction of leached N over the years was not symmetric. For S1N150 there were two years in which the reduction of leached N was much lower than the average (more than twice the standard deviation). These were years with a high amount of precipitation is the first month after sowing. In 90% of the years, the reduction of leached N at S1N150 was higher than 100 kg N ha^{-1}, but in the other years, the effectiveness of the catch crop could be markedly less. The same asymmetry occurred in the distribution of the other simulated treatments, although less pronounced.

The reduction of leaching decreased for larger cumulative precipitation and increased with larger cumulative radiation for both S1 and S2 and, at S2, with temperature sum in the first 30 days after sowing. The coefficient of determination, R^2, was highest for the precipitation sum in the first 30 days after S1 (Table 6), indicating that the leaching of N just after sowing of the catch crop might reduce the possibility for the crop to catch N and conserve it over winter, even if the radiation sum was sufficiently high for growth and nitrogen accumulation by the catch crop. At S2, sums of radiation and of precipitation had about equal values of R^2. Temperature sum explained much less variation, indicating that in this time of the year a low temperature was mostly not limiting the capacity of the catch crop to reduce N leaching.

Both at S1 and S2 radiation sums were negatively correlated with precipitation sums ($R^2 = 0.30 – 0.44$), so that it was not clear whether the correlations with reduction of leached N by the catch crop were caused by radiation or by precipitation. To check whether both radiation and precipitation were significant for reduction of leaching, we combined weather data sets for simulation:

- the precipitation data in the first 30 days after sowing were used of years with high precipitation sums and low reduction of leached N
- the remaining weather data were used of years with high radiation sums in the first 30 days after sowing and a high reduction of leached N.

Results for N150 are shown in Table 7. Reduction of leached N by the catch crop calculated with combined weather data sets was in between that calculated for years with high and with low reduction of leaching. This means that increased precipitation in the first 30 days after sowing had a strong effect on N leaching rate, decreasing the opportunity for the catch crop to take up N before it had leached. Still, a difference remained with the years with both a high precipitation sum and a low radiation sum. A

Table 6. R^2 values of the correlation of reduction of leached N with either precipitation sum, global radiation sum or temperature sum above 0 °C. Simulated reduction of leached N was used of catch crops sown at 11 August (S1) or 20 September (S2) in the years 1970-1999, with 150 kg ha^{-1} mineral N present in soil at sowing (N150, see table 2).

	sum in 30 days after sowing			sum in 60 days after sowing		
	precipitation	radiation	temperature	precipitation	radiation	temperature
S1	0.53	0.18	n.s.	0.26	0.14	n.s.
S2	0.49	0.48	0.12	0.41	0.46	n.s.

Table 7. Sums of global radiation and precipitation in 30 d after sowing and simulated reduction of leached N by the catch crop at N150 (150 kg ha^{-1} of residual N present at sowing) for: a. years with a high reduction of leached N; b. years with a low reduction of leached N; c. combined weather data: precipitation sums in the first 30 d after sowing from years with low reduction of leached N (b) with remaining weather data of years with a high reduction of leached N (a). Thus, the bold printed radiation and precipitation data were used to produce the bold printed reduction of leached N.

	years with high reduction of leached N				years with low reduction of leached N				combination
	a	a, c	a	a	b	b	b, c	b	c
		Radiation sum ($J\ m^{-2}$)	Precipi-tation (mm)	reduction leached N (kg ha^{-1})		Radiation sum ($J\ m^{-2}$)	Precipi-tation (mm)	reduction leached N (kg ha^{-1})	reduction leached N (kg N ha^{-1})
S1	1976	$4.4 * 10^8$	32	138	1977	$3.2 * 10^8$	123	68	102
					1992	$3.1 * 10^8$	178	71	98
	1991	$4.2 * 10^8$	6	136	1977	$3.2 * 10^8$	123	68	89
					1992	$3.1 * 10^8$	178	71	96
S2	1989	$2.1 * 10^8$	47	95	1974	$1.7 * 10^8$	103	34	64
					1984	$1.3 * 10^8$	113	24	55
	1999	$2.0 * 10^8$	49	93	1974	$1.7 * 10^8$	103	34	62
					1984	$1.3 * 10^8$	113	24	52

high radiation sum was thus beneficial to the catch crop's growth and N accumulation and, hence, ability to reduce leaching, even with a high precipitation sum and high N leaching rate in the first 30 d after sowing. In conclusion, both radiation and precipitation separately affected the reduction of leached N by catch crops.

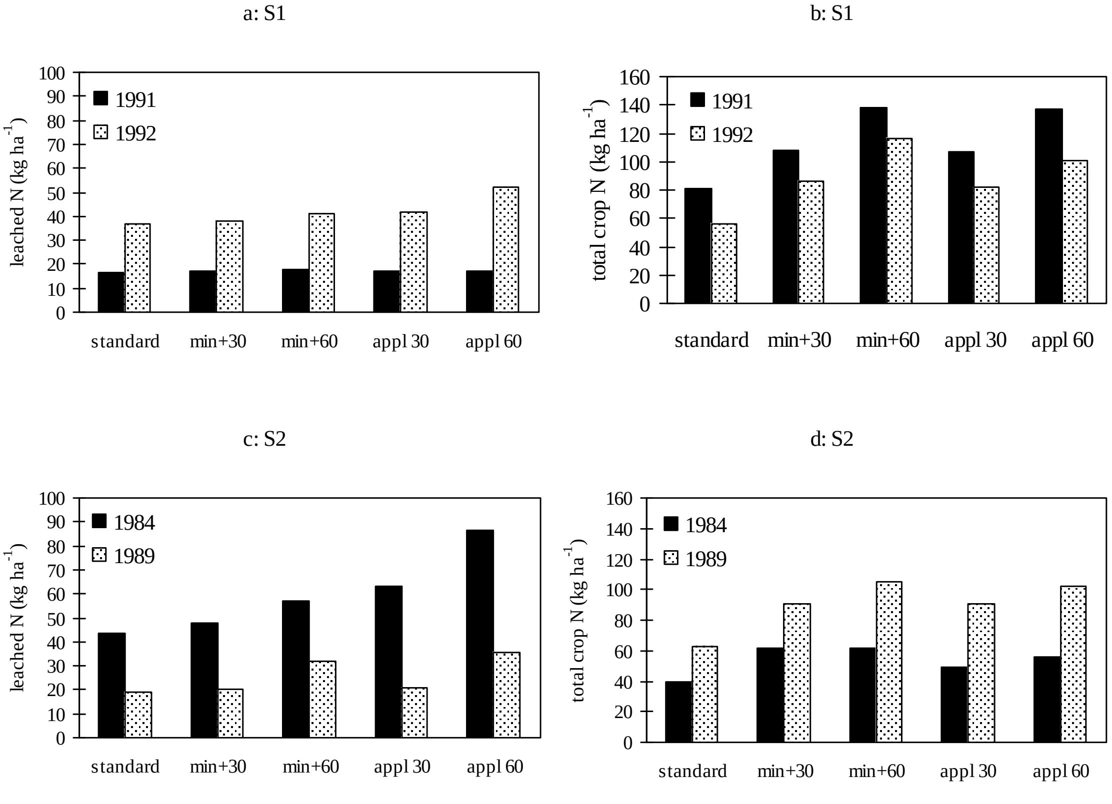
N availability

For 1991 (a year when catch cropping resulted in a large reduction of leached N) and sowing on 11 Aug (S1), none of the changes in N availability increased the amount of leached N in March by more than 1 kg ha^{-1} (Figure 4a). This was explained by extra N uptake by the catch crop. Three months after sowing 97-100 % of the extra mineralized N and 87-93 % of the applied N was taken up by the crop. In 1992 (a year with a low reduction of leached N by the catch crop) leached N increased by 1-4 kg N ha^{-1} as a result of higher mineralization and by 5-15 kg N ha^{-1} when N was applied at sowing

(Figure 4b). Recovery of N three months after sowing was 91-92 % for the extra mineralized N and 75-84 % for the applied N. Application at sowing led to higher leaching and lower recovery than increased mineralization, which could be explained by the high precipitation sum in the first 30 d after sowing and N application in this year (Table 7).

With the catch crop sown on 20 Sep (S2), 30 kg N ha^{-1} extra by either mineralization or by application increased leached N considerably (by 4 - 20 kg ha^{-1}) only in 1984 (a year with a high reduction of leached N by the catch crop) (Figure 4c), whereas 60 kg N ha^{-1} extra increased the amount of leached N in all scenarios (by 13 - 43 kg ha^{-1}). This was related to the uptake of N by the catch crop (Figure 4d). For S2, recoveries of mineralized and applied N in the crop at three months after sowing were much lower than for S1: 28-74 % in 1984 and 66-94 % in 1989. Recoveries were lower for applied than for mineralized N and lower at 60 than at 30 kg N ha^{-1}.

In conclusion, application of 30 kg N ha^{-1}, in addition to 50 kg N ha^{-1} present in soil at sowing (N50), only led to an increase in leached N if sowing was late and if there was a


a: S1

b: S1

c: S2

d: S2

Figure 4. Simulated leached N on 16 March (figures a and c) and total crop N content at three months after sowing (figures b and d) for different N availability scenarios. Scenarios are: standard (50 kg N ha^{-1} in soil at sowing); 'min+30' and 'min+60', respectively: 30 and 60 kg N ha^{-1} extra mineralized in 3 months after sowing; 'app 30' and 'app 60', respectively: 30 and 60 kg N ha^{-1} applied at sowing. For scenarios with sowing on 11 august (S1), simulations were run for crops sown in 1991 and 1992 (figures a and b); for sowing on 20 September, the years 1984 and 1989 were chosen (figures c and d).

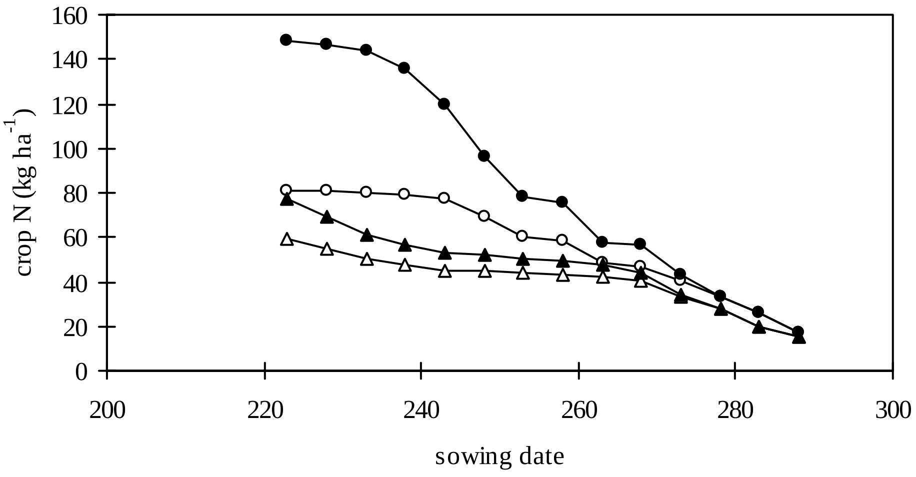


Figure 5. Simulated total crop N content on 19 November (day nr 323) after sowing on different dates in 1991 (dots) and 1992 (triangles). Simulations were run with 50 (N50; open symbols) or 150 (N150; closed symbols) kg N ha^{-1} in soil at sowing.

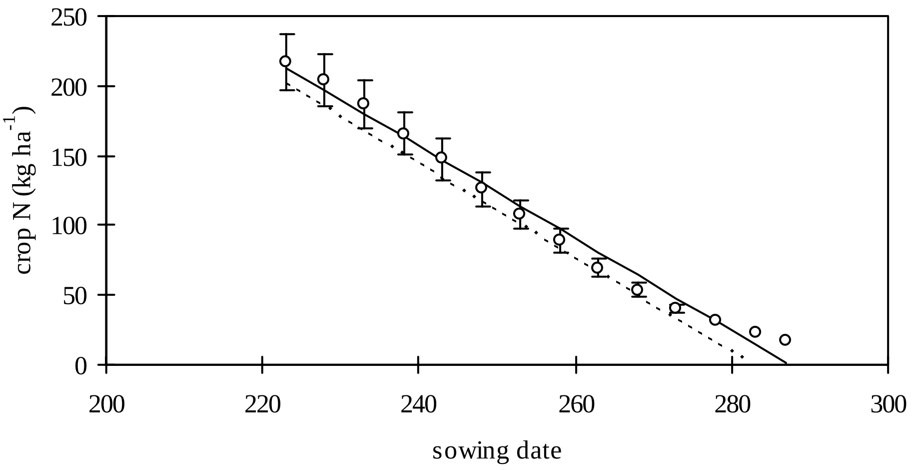


Figure 6. Simulated rye catch crop N content on 19 November (day nr 323). Average result of simulation with weather data of 1970-1999 and ample N supply (dots), as a function of sowing date, and linerar regression line (full line) çompared with result of Vos and Van der Putten (1997; dotted line).

high precipitation sum soon after sowing. Application of 60 kg N ha^{-1} increased leaching for sowing on 20 Sep (S2), and, in years with weather conditions unfavorable for catch crop effectiveness, also for sowing on 11 Aug (S1). The catch crop recovered a larger part of the nitrogen when the extra N was not applied at sowing but mineralized after sowing. This was most strongly so with sowing on 20 Sep (S2).

Sowing date

Simulations of 1991 and 1992 show that with 150 kg N ha^{-1} present in the soil at sowing (N150), there was a strong effect of sowing date, whereas with 50 kg N ha^{-1} in

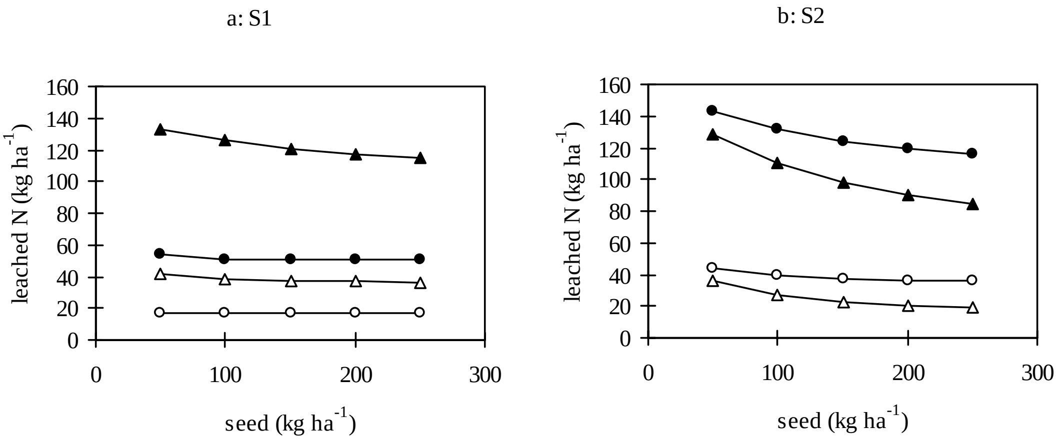


Figure 7. Simulated amount of leached N on 16 March as a function of the amount of seed applied for a winter rye catch crop. Figure a: sowing on 11 August (S1); Figure b: sowing on 20 September (S2). Dots: crop sown in 1991; triangles: crop sown in 1992 Open symbols, N50: 50 kg N ha^{-1} in soil at sowing; closed symbols, N150: 150 kg N ha^{-1} in soil at sowing.

the soil (N50), the effect was less (Figure 5). The relation differed between years: With the high precipitation in 1992, even early sowing was not effective for catching all available soil N. The potential crop N uptake at different sowing dates, averaged over 30 years, strongly declined with later sowing by about 3.3 kg N ha^{-1} day^{-1} (Figure 6). This relation almost coincided with that of Vos & Van der Putten (1997) (Figure 6), deducted from experiments of catch crops with ample N supply.

Seed rate

The differences in leached N between seed rates of 50 and 250 kg ha^{-1} varied from 0 to 44 kg N ha^{-1} (Figure 7). This effect on leached N was related to differences in crop N uptake (data not shown). The differences in results from one seed rate to another increased with N availability and with later sowing, and the effect was larger in 1992 than in 1991. Again, a good start of the crop, with good light interception was most important when there was a large amount of N to be ‘caught’ by the catch crop, or when radiation was limited, due to late sowing or a low radiation sum (combined with high precipitation) in a particular year.

Crop characteristics

The amount of leached N decreased strongly with increase of the maximum rooting depth in all scenarios (Figure 8). Increase in rooting depth had most effect on leached N for sowing on 11 Aug (S1) with 150 kg N ha^{-1} in the soil at sowing (N150), and the effect was stronger in 1991 than in the wetter year 1992, in which N leaching occurred earlier in the season. Variation in the extension rate of the root zone had effect only

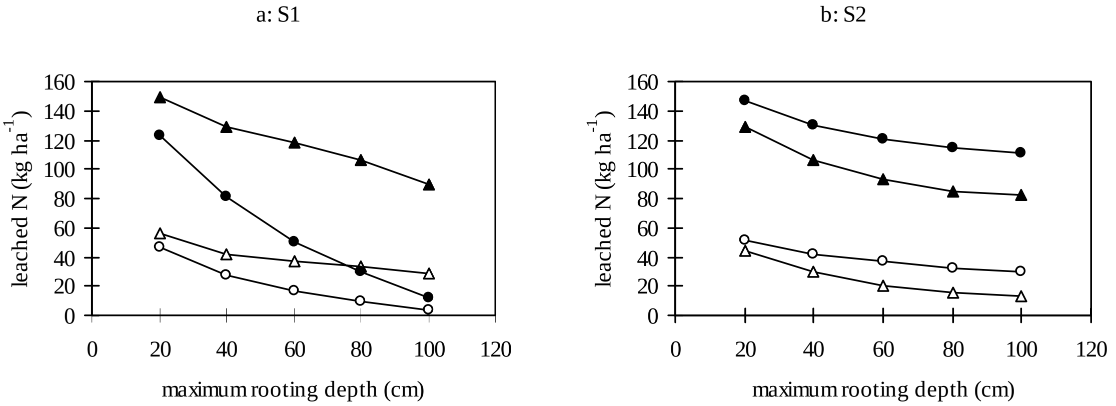


Figure 8. Simulated amount of leached N on 16 March as a function of the maximum rooting depth of a winter rye catch crop. Figure a: sowing on 11 August (S1); Figure b: sowing on 20 September (S2). Symbols as in figure 7.

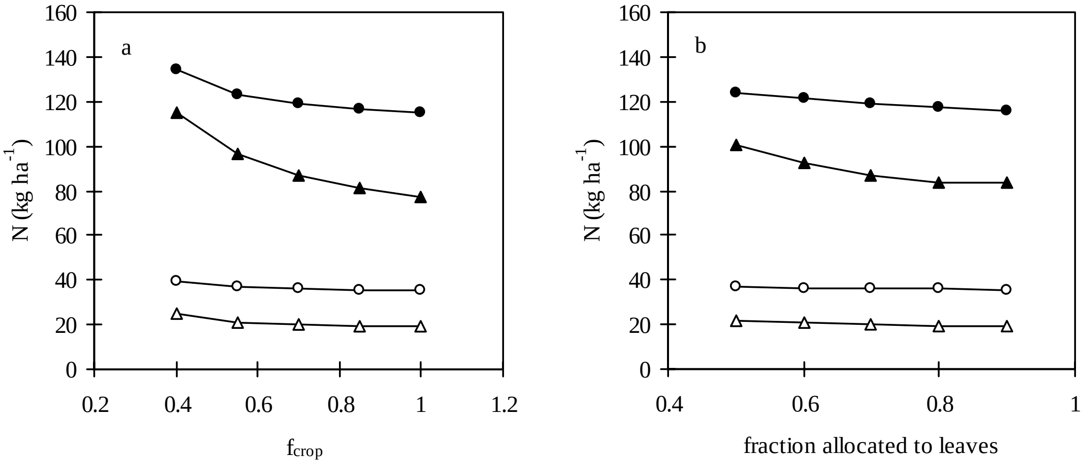


Figure 9. Simulated amount of leached N on 16 March as a function of (a) the crop factor for CO_2 assimilation and (b) the fraction of assimilates partitioned to leaves of a winter rye catch crop sown on 20 September. Symbols as in Figure 7.

when it was lowered from 0.02 to 0.01 m day^{-1}: leached N increased by 2 to 11 kg ha^{-1} for S1 and by 7 to 21 kg ha^{-1} for sowing on 20 Sep (S2). At higher values of the root zone extension rate, the effect on leached N was lower than 2 kg ha^{-1} in most cases.

The changes in the crop factor and in the fraction of assimilates allocated to leaves had the largest effect for sowing on 20 Sep (S2) with 150 kg N ha^{-1} in the soil at sowing(N150) (Figures 9). This indicates that in this situation radiation was the most determining factor for producing sufficient biomass to store this amount of nitrogen.

Incorporation date

For catch crops sown in 1991 and 1992, simulated leached N on 18 Mar decreased by 4 tot 12 kg N ha^{-1} when incorporation was postponed from 19 Nov to 18 Mar (Figure

10). Most of the difference occurred when postponing incorporation from 19 Nov to 19 Dec.

For the maximum N availability to the succeeding crop after catch crop cultivation, the calculated optimum incorporation date was mostly between 19 Nov and 18 Mar. An example is shown in Figure 11, with a succeeding crop sown on 18 Apr, exploiting the N available in 0 – 0.6 m depth and taking up N for 90 d from sowing. For a catch crop sown on 11 Aug (S1) with 150 kg N ha^{-1} in the soil at sowing (N150) the optimum incorporation date was on 18 Feb (day nr. 414). For the other catch crop treatments it was earlier, on 9 and 11 Jan (day numbers 374 and 376) for catch crops sown on 20 Sep (S2) with 150 and 50 kg N ha^{-1} in the soil at sowing (N150 and N50) and on 23 Jan for sowing at S1 with N50.

The R^2 of the quadratic curves fitted to the data was 0.98 on average, and the lowest R^2 was 0.92. Averaged over all scenarios, 18 January (day nr. 383) was the optimal incorporation date. The sowing date and depth of N uptake of the succeeding crop were the most strongly determining factors for the optimal incorporation date (Figure 12). These resulted in average optima on 18 December (day 352) for sowing on 19 Mar and 100 cm rooting depth, to 25 February (day 421) for sowing on 18 May and 30 cm rooting depth. When only the sowing date of the next crop was taken into account, the catch crop was best incorporated at 89 d before sowing, on average. Moreover, a catch crop sown early, on 11 Aug, (S1) was optimally incorporated 19 d later than a catch crop sown on 20 Sep (S2). The duration of N uptake by the succeeding crop had a smaller effect: for N uptake during 120 d, incorporation was optimally 10 d later than for N uptake during 60 d.(all with F-probability <0.001). The N availability to the catch crop had no significant effect on the optimal incorporation date. A part of the two-way and three-way interactions between the factors (also including the N availability to the catch crop) had significant effects.

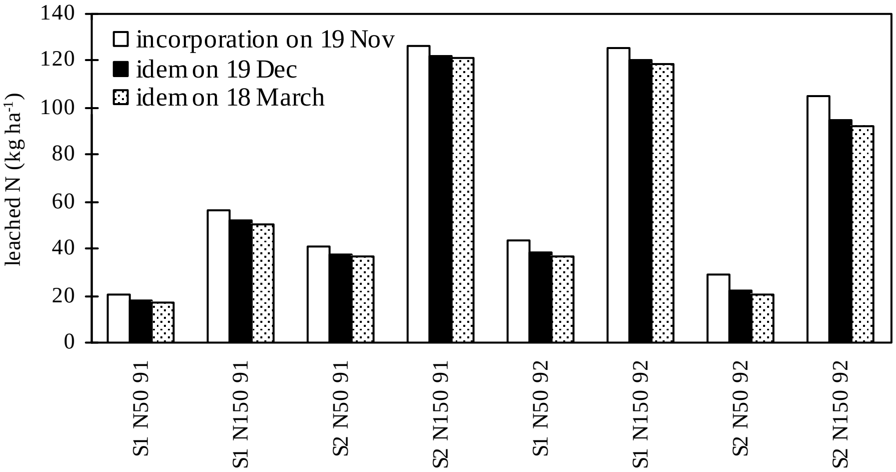


Figure 10. Simulated amount of leached N on 18 March for different dates of incorporation of a catch crop. Data are shown for crops sown on 11 august (S1) and 20 September (S2) in 1991 and 1992, with 50 or 150 kg N ha^{-1} in soil at sowing (N50 and N150, respectively).

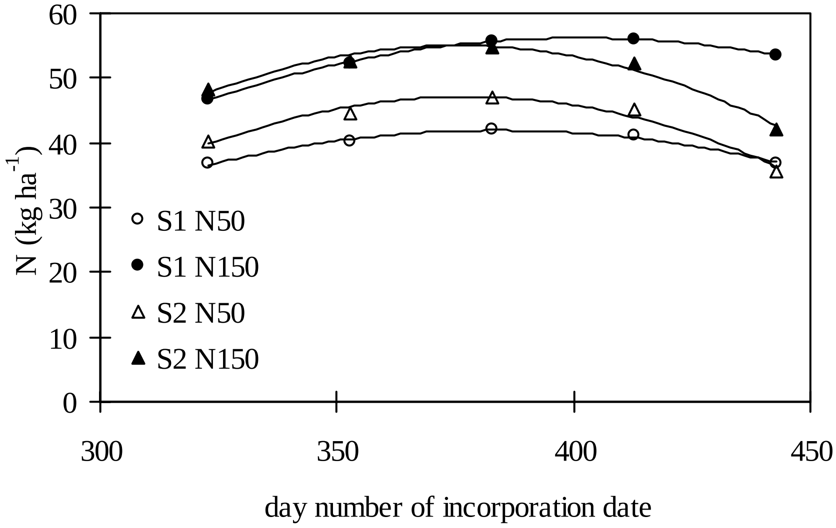


Figure 11. Simulated amount of N available after catch crop cultivation, for a succeeding crop sown on 18 April, which could take up N from 60 cm soil depth for 90 days, as a function of catch crop incorporation date (day numbers calculated from 1 January in the year of sowing of the catch crop). The catch crop was sown on 11 August (S1) and 20 September (S2) and supplied with 50 (N50) or 150 (N150) kg N ha^{-1} in soil at sowing.

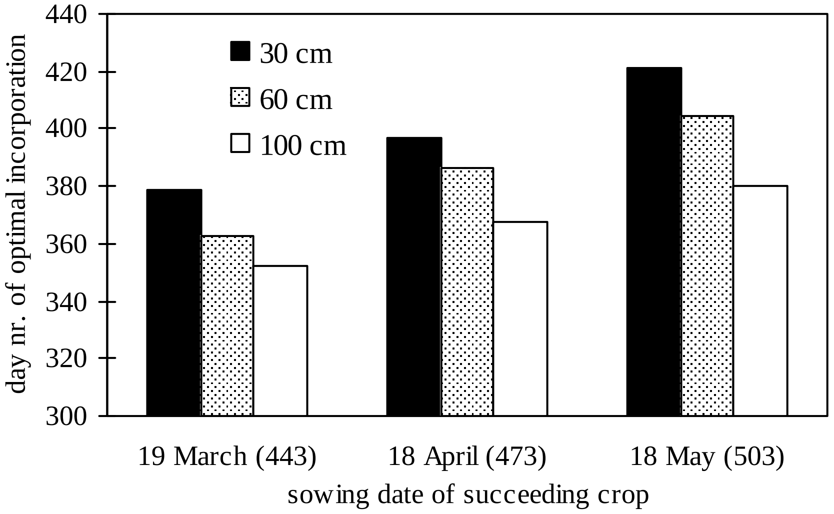


Figure 12. Simulated optimal incorporation date for a catch crop, for various sowing dates of the succeeding crop, with various depths of soil exploration by the succeeding crop: 30, 60 or 100 cm. Day numbers were calculated from 1 January in the year of sowing of the catch crop.

Incorporating 30 days earlier or later than the optimal date lowered the N available to the succeeding crop by 2 ± 1 kg N ha^{-1} on average, which equaled 4 ± 1 % of the available N when the incorporation time was optimal. A change of 60 days from the optimal date resulted in 7 ± 2 kg N ha^{-1} less available to the next crop, which was a decrease by 14 ± 5 %. This implies that an exact timing of catch crop incorporation was not the most important factor for successful use of catch crop N, at least in winters with moderate leaching, like 1991-92 and 1992-93.

For the wet winter of 1974-75, the average incorporation date was 25 Jan, one week later than for 1991-92 and 1992-93. The effect of incorporating later or earlier than the optimal date had the same effect on the absolute amount of N available for the succeeding crop in all years, only, 1974-75 it was a larger part of the available N (4 ± 2 % for a 30 d change in incorporation date and 18 ± 8 % for a 60 d change), because the amount of available N was lower in this year. In this year, a catch crop sown on 11 Aug was optimally incorporated 34 d later than on sown on 20 Sep, a larger difference than in 1991-92 and 1992-93 (19 d). Thus the differences in optimal timing of incorporation between a year with average precipitation and a year with high precipitation are rather small.

Discussion

Sensitivity analysis

The aim of the sensitivity analysis was to evaluate which crop parameters in the model mainly determine N uptake by a catch crop and the associated reduction of N leaching. Theoretically, a larger N accumulation capacity could be achieved by 1. increased rooting depth for a better interception of leaching N; 2. a larger production of biomass per unit incident radiation; 3. a higher N concentration in the biomass; 4. maintenance of the standing, N containing biomass over winter.

In the sensitivity analysis, maximum rooting depth (rd_{max}) significantly determined N accumulation and leached N when N was limiting growth: exploring a greater soil volume was effective to diminish N shortage. When N was limiting, maximum rooting depth was the only parameter to which leached N was sensitive. Increasing rooting depth is thus in many cases the most important way to improve the performance of a catch crop. This may be achieved by selecting a deep-rooting catch crop (e.g. fodder radish (Kristensen and Thorup-Kristensen, 2004)), and loosening of soil layers that impede root growth.

Changes in the maintenance coefficients (m_l, m_s and m_r), the crop factor for CO_2 assimilation (f_{crop}) and the partitioning factor for leaves (f_{leaf}) affected crop N considerably at N2. Lowering m_l, m_s and m_r, and increasing f_{crop} and f_{leaf} enhanced a faster production of (N-containing) biomass, by an increase in the rate of assimilation (f_{crop}), a lower use of assimilates for maintenance processes (m_l, m_s and m_r) and by a faster production of the light intercepting and assimilating canopy (f_{leaf}). In 1978, with low radiation, also changes in K_{dif} affected crop N at S2N2, stressing the importance of light interception in this situation. All these factors affect the efficiency of the interception and use of the incoming radiation, which may be increased in several ways. F_{leaf} and K_{dif} are important for a fast development of light intercepting leaf area, and may differ from one crop species to another, as do associated characteristics like specific leaf area (Chapter 7; Vos & Van der Putten, 1997). Changes in the leaf expansion coefficient (c_{LE}) had some effect at S1N150 in 1995 only, which indicated that a limited leaf expansion (dependent on temperature) was important at high radiation and high N supply. These crop characteristics may be managed by choice of catch crop species and, within species, by breeding. Crops with a slow development of leaf area or a low K_{dif} may take up more N when the seed rate is increased (see scenario study). A high CO_2 assimilation rate of the canopy, here manipulated by F_{crop}, may be achieved by choosing a crop in which the most productive, young leaves are located at the top of the canopy and intercept most light (Chapter 4). Changing the assimilate requirements for maintenance respiration (m_l, m_s and m_r) is not very well possible, considering the sparseness of data and understanding of respiration in various crops (see below).

A other way to improve catch crop effectiveness may be selecting a crop with a high N percentage in the biomass: the amount of leached N is, when soil N at sowing was high (N150), sensitive to changes in $C_{N,max,0}$ and $C_{N,max,\infty}$. In other studies, differences in N percentage in aboveground biomass from one species to another seem to be small (Greenwood *et al.*, 1990). Here, only a small difference was found in leaf N concentrations between winter rye and fodder radish (Chapter 7). As the N concentration in roots is normally lower than in shoots, crops with a high shoot/root ratio may have a high N concentration averaged over their total biomass.

Finally, maintaining biomass over winter has some effect on catch crop performance. Changes in LS_{leaf} affected crop N when N in the soil at sowing was high (N150). For leached N (Table 3), LS_{leaf} was not an important determining factor, because mineralization and subsequent leaching of N from dead crop material were not calculated in the model. In reality, there may be some mineralization of catch crop N during winter (Vos & Van der Putten, 1997), but it seems unlikely that this N will leach below 100 cm depth during the same winter period.

In conclusion, the simulated crop N contents and the amount of leached N are most sensitive to changes in parameters determining rooting depth, the efficiency of use of incident radiation and crop N concentration, whereas maintaining biomass over winter may also have some effect.

The relevant parameters and processes must be well known and modeled in order to predict well the effects of a rye catch crop on leached N. Other crop growth determinants, like the leaf expansion coefficient, the uptake capacity of the roots, and the lower boundaries of N responses of leaf expansion and assimilation, are less important.

Measurements and predictions of the crop parameters will always be subject to uncertainties due to natural variation in crop material and imperfect measurement methods. The rooting depth (rd_{max}) of a crop can generally be measured with an uncertainty of only a few centimeters, but is dependent on soil conditions (e.g.

compaction, depth of groundwater). The crop factor for CO_2 assimilation, f_{crop}, determines the level of the light saturated crop CO_2 assimilation rate. To calculate f_{crop}, CO_2 assimilation rates have to be measured both on individual leaves and on crop canopies, and these measurements both contain inaccuracies. Moreover, f_{crop} may change during growth when the percentage of older, less productive leaves increases (Chapter 4). Therefore, the uncertainty in this parameter may be considerable. The maintenance requirements of the crop were derived from data for spring wheat (Van Keulen & Seligman, 1987), but with adaptations for roots and sheaths, derived from other crop species (Bouma *et al.*, 1996. Van der Werf *et al.*, 1988). The coefficients are, therefore, not very precisely known. The rate of maintenance respiration of roots is one of the most uncertain factors in SUCROS based crop growth simulation models (Metselaar, 1999). The estimate of maintenance respiration rates of leaves and sheaths are more determining (because of higher biomass), and better known. Nitrogen concentrations in the crop can, in general, be measured accurately.

We conclude that there is a number of parameters in the model that determines model performance, that cannot be determined accurately: f_{crop}, m_l, m_s and m_r . Because of this, the model will not be able to simulate crop N uptake perfectly. However, generally the effects of parameter changes were small, so that an adequate simulation of a rye catch crop can be achieved, as was also shown in Chapter 7. For improving predictions, simplification of the model might help. Especially factors determining radiation use efficiency (CO_2 assimilation and respiration) might be modeled in less detail and, for respiration, might be determined experimentally.

Scenario study

In general, the results of the sensitivity analysis and the scenario studies show that effects of changes in conditions or parameters on catch crop performance increased with increase in soil N availability and decrease with the length of the growing season and the radiation that could be used by the catch crop. N accumulation by the catch crop is essentially governed by two opposing processes: crop growth, determined by radiation, and N leaching from the root zone. Therefore, the outcome of the scenarios is determined by the ratio of the amount of radiation available to the catch crop and the amount of N that can be caught before it has leached. This can be seen in the study of weather conditions: effects of variation in weather on reduction of leaching by the crop were larger with 150 kg N ha^{-1} in soil (N150) than with 50 kg N ha^{-1} in soil (N50), and for N50, larger with sowing on 20 Sep (S2) than on 11 Aug (S1) (Figure 3). Also the correlations between amounts of precipitation or radiation on the one hand, and reduction of leaching on the other hand confirm that catch crop effectiveness depends on the ratio of the rates of growth and N uptake, determined by radiation, and the rate of leaching, determined by the precipitation surplus. In the calculations with different sowing dates, crop N initially decreased little when sowing was postponed, until a ‘critical’ sowing date was reached, after which radiation became more and more limiting for N accumulation (Figure 5, data 1991).

The scenarios with extra N availability by mineralization or application show that, in general, the extra N could be taken up by the catch crop when it was sown on 11 Aug (S1), unless part of it was leached immediately after sowing, as happened in the simulation with the weather data of 1992. But even in this extremely wet year, most of the applied or mineralized N was taken up by the crop, which had, after this earlier sowing, plenty of radiation available to catch N. At S2, higher N availability led to increased leaching, especially in a wet year (1984, Figure 4). Here, the amount of radiation was, apparently, not sufficient to catch all extra N. This can also be concluded from the scenarios with different sowing dates: at S2 (day nr 263, 20 Sep) a catch crop could, on average, take up 69 kg N ha^{-1} (Figure 6).

The potential crop N uptake strongly declined with later sowing by 3.3 kg N ha^{-1} day^{-1} (Figure 6). This was almost the same as found experimentally by Vos & Van der Putten (1997).

Seed rate was only of importance at late sowing (S2, Figure 7). At this sowing time a fast development of leaf area intercepting radiation was beneficial for N accumulation. With early sowing, a later canopy expansion was not hampering N accumulation, and seed rate could be lower without loss of catch crop effectiveness. A similar effect could be seen for changes in the fraction of assimilates partitioned to leaves (f_{leaf}), also a determinant of leaf expansion (Figure 9b): this was only of importance with late sowing and high N availability.

The crop factor for CO_2 assimilation was only important at high N supply, at both sowing times. Rooting depth was determining N uptake in all scenario’s (Figure 8). This can be explained by uptake of N available in the subsoil, already leached to this depth around sowing time. If there is more N in the subsoil, the effect of deeper rooting was larger (at N150 larger than at N50).

The optimal timing of incorporation was not strongly determined by the weather conditions or management of the catch crop. It was more dependent on the next crop, which may take up N mineralized from the catch crop. Depending on sowing date and soil exploration by the next crop, the optimal date for incorporation of a catch crop shifted from mid December to the end of February, calculated with the moderate leaching rates in the winters of 1991-92 and 1992-93. Deviations of 30 days from the optimal date had only a small effect on the N available to the next crop. Therefore, this may be interpreted as follows: depending on the properties and management of the next crop, the catch crop may best be incorporated in soil before winter (November – December) or after winter (February - March).

Conclusions

The capacity of a catch crop to reduce N leaching depends on its N uptake. We conclude that the potential N uptake of a rye catch crop is rather high, over 200 kg N per ha (present in soil at sowing, applied or mineralized during growth), when it is sown before mid August. Postponement of sowing decreases the potential N uptake, in the simulations by 3.3 kg N ha^{-1} d^{-1}. This potential N uptake is determined by the amount of radiation that can be used for growth, several factors determining the amount of biomass produced per unit incident radiation, and the concentration of N in the produced biomass.

In practice, the N uptake capacity of the catch crop often exceeds the N availability in the root zone. The soil depth explored by catch crop roots and the amount of precipitation in the first period (e.g. one month) after sowing determine how much of the available N will be taken up, and how much will leach. When the catch crop is sown relatively late and the N availability is high, the N uptake capacity of the crop exceeds the N availability. Then the uptake capacity, determined by growth and N concentration in biomass, is more determining catch crop effectiveness than the exploration of the soil.

Optimal timing of incorporation of a catch crop, for maximum N availability to a succeeding crop was, on average, mid January. The optimal incorporation date is later for later sowing and for deeper soil exploration by the succeeding crop. Deviation of incorporation time from the optimum, by 30 or 60 d, decreases N available to the succeeding crop only rather weakly, by 2 and 7 kg ha^{-1}, respectively. This implies that an exact timing of catch crop incorporation is not an important factor for successful use of catch crop N.

Chapter 9

General discussion

Introduction

In this study a quantitative analysis of the growth and N uptake of catch crops and their effect on N leaching was performed, with two aims:

1. to explain variation in catch crop N uptake and reduction of leaching by catch crops;
2. to identify desirable catch crop characteristics for selection and breeding and catch crop cultivation strategies to minimize N losses from the crop-soil system.

To reach this aim, an explanatory catch crop and soil N model was developed, parameterized, tested and used in scenario studies. Several experiments were conducted for parameterization of the model. Here, a summary and discussion is presented of the conclusions reached in the study, about the factors explaining the variation, desirable catch crop characteristics and effective cultivation strategies. The possibilities for application of these results are evaluated. Finally the research method is examined and unanswered questions regarding catch crop effectiveness are commented on.

Answers to the research questions

1. Variation in catch crop N uptake and reduction of N leaching explained

Variation in N uptake by catch crops and their effect on N leaching is explained by a number of factors. First, sowing date determines the capacity of the catch crop to take up N. Under Dutch weather conditions, the simulated capacity of a catch crop to take up N is over 200 kg N ha^{-1} if it is sown in the first half of August. For rye, it decreases on average by 3.3 kg N ha^{-1} per day postponement of sowing (Chapter 8), which was also found experimentally by Vos & Van der Putten (1997). Sowing date determines the length of period of time until weather conditions become practically prohibitive of growth, and through that, the amount of radiation, the day length and the temperature to which the catch crop is exposed. Of these, radiation is a strong determinant of the reduction of leaching by the catch crop (Chapter 8).

Precipitation in the first month after sowing is, especially with early sowing (August), explaining still more variation in reduction of leaching than radiation. Precipitation determines the N leaching rate, which determines, together with rooting depth, whether soil N is available to the catch crop before it has leached. This indicates that catch crop growth is often limited by a low N supply, as was also concluded by Thorup-Kristensen *et al.* (2003).

Thus, N availability is another factor explaining the variation in N uptake. Low N availability may be caused by several factors. First, residual N after the harvest of the main crop plus N mineralized during growth are often lower than the catch crop N uptake capacity. Secondly, a part of the available N may be lost by leaching soon after sowing of the catch crop. This is indicated by the significance of precipitation after sowing for reduction of leached N. The effect of precipitation will be stronger when rooting depth of the crop is shallower.

Moreover, there are effects that are not treated in this study because they are supposed to be only incidentally determining for catch crop performance. These are: a bad crop establishment due to drought or severe rainfall, growth reduction by pests and diseases (e.g. brown rust in rye, caterpillars in fodder radish) and early frost killing of the crop before N uptake is maximal, in case of frost sensitive catch crops (e.g. white mustard, Phacelia).

In conclusion, variation in catch crop N uptake is mainly explained by the variation in the N availability (determined by soil, previous crop, precipitation and rooting depth) when availability is smaller than the N uptake capacity, which occurs often. It is mainly explained by radiation (determined by sowing date and weather conditions) available to the crop when N availability is larger than the N uptake capacity. The model may be used to examine which factors determine catch crop N-uptake in a specific situation. With this information catch crop management may be improved.

2. Desirable catch crop characteristics and effective cultivation strategies identified

Desirable characteristics for a crop that should reduce N leaching thus depend on the proportion of N availability and the N uptake capacity of the crop. If N supply is smaller than the potential N uptake, deep rooting will increase the N-uptake by a catch crop. This is confirmed by experiments (Thorup-Kristensen, 2001; Kristensen & Thorup-Kristensen, 2004), where N-depletion of the soil was correlated with rooting depth of a catch crop. Other features are then relatively unimportant (Chapter 8). Generally, cruciferous catch crops have deeper roots and increase their rooting depth faster than Gramineae (Thorup-Kristensen, 2001, Thorup-Kristensen *et al.*, 2003).

If N availability is larger than the N uptake capacity, desirable crop characteristics include fast production of leaf area, a high amount of biomass produced per unit intercepted radiation and a high N concentration in the biomass. These characteristics enhance uptake of a maximum amount of N per unit incoming radiation. In this situation, deep rooting may still be advantageous to catch N in case high precipitation causes fast leaching of the available N.

Once a catch crop with desirable characteristics is chosen, sowing as early as possible is the most important strategy in catch crop management. With early sowing, roots grow deeper and the N uptake capacity is larger and the chance that N is taken up before it has leached is larger than with late sowing. When early sowing is not possible, increase in seed rate, and hence the number of plants per unit area may increase the N uptake.
A difference in seed rate might partly explain, for example, the difference in growth and N uptake between forage rape and winter rye with later sowing (Vos & Van der Putten, 1997). Sown on 21 August or 7 September a forage rape has, with 25 kg seed ha^{-1}, an N uptake equal to or higher than that of winter rye, with 180 kg seed ha^{-1}. This can be attributed to a higher leaf weight ratio, thereby a faster interception of radiation, and probably higher canopy CO_2 assimilation capacity in forage rape (with young leaves at the top of the canopy – analogous to fodder radish – Chapter 4). With sowing on 28 September, winter rye took up more N than forage rape. At this sowing time, with lower radiation, the fast interception of radiation by forage rape could probably not counterbalance the fast start of growth of rye with the much higher seed rate. An other factor explaining the lower N uptake of fodder radish with late sowing is a lower specific leaf area (m^2 kg^{-1}) (Vos & Van der Putten, 1997), which was not included in the model.
Also undersowing the catch crop in the main crop may give the catch crop a good start after the harvest of the main crop. Then other crop characteristics become important as well: the catch crop should not diminish the yield of the main crop (see Karlsson-Strese *et al.*, 1996).

On average, incorporation in mid January is optimal for maximum N availability for the next crop on a sandy soil, but incorporating a month later or earlier has only a small effect on the N availability (Chapter 8). This seems in contradiction to experimental results showing that a few weeks difference in incorporation date may seriously change N taken up by the next crop (Thorup-Kristensen, 1996; Thorup-Kristensen *et al.*, 2003). This discrepancy can be explained by the choice of incorporation dates in experiments: these are often far from optimal, in autumn or in spring. Further from the optimal date, effects of advance or delay of incorporation are larger. The workability of arable land in January may be insufficient for catch crop incorporation. If so, the catch crop is generally incorporated best as late as possible in autumn or as early as possible at the end of winter or the beginning of spring. The optimal incorporation date is earlier when the sowing time of succeeding crop is earlier in the season and deeper rooting. Likewise, it is later for late sown succeeding crops and shallower rooting. For a sandy soils it is a practical rule that the optimal incorporation date is at three months before sowing of the next crop. Deviating from this rule will have only small effect, so that it may also be formulated: incorporating tow to four months before sowing o the next crop is optimal (Chapter 8). Thus, preceding sowing in March, the catch crop should be incorporated just before winter (November-December). For a next crop sown in May, incorporation is best as soon as possible after winter, if working the land in winter is not possible.

Most of these conclusions were derived from Chapter 8, which deals with winter rye only. Because the processes which were described in the model also govern growth of other crop species, the conclusions can be also applied to other catch crops, except for the information about exact amounts of N and the exact dates of incorporation.

3. Other new insights

Besides answers to the research questions, the study yielded information that may also be applied in other situations. Firstly, the maximum CO_2 assimilation rate in autumn and winter was measured for winter rye and fodder radish. This rate appeared much higher than was generally assumed for crops in growth models, based on measurements on plants not acclimated to autumn and winter weather conditions (Chapter 2). In literature, there is much information about the acclimation of CO_2 assimilation to changing seasons in plant species in forests and nature areas (e.g. Ellsworth, 2000; Burkle, 2003)), but little is available for agricultural crops. Secondly, rates of N-mineralization of plant material were measured at temperatures normally occurring in soil in winter. N-mineralization at low temperature proceeded faster than is often assumed in soil N models, which are based on measurements at higher temperatures (Chapter 6). Later this was confirmed by research of Magid *et al.* (2001). Thirdly, various crop characteristics of winter rye and fodder radish were measured. Especially for fodder radish, these data are scarce. Data on CO_2 assimilation and leaf appearance of this crop have not been published before. Lastly, a detailed model of catch crop growth and N dynamics (in crop and soil) was made (Chapter 7). The model includes several new process descriptions. To improve simulation of CO_2 assimilation during autumn and winter, the maximum CO_2 assimilation rate is modelled dependent on radiation during leaf growth. Besides, structural aboveground growth is described as a function of assimilate availability and temperature. Moreover, low N concentrations in biomass affect both CO_2 assimilation and structural growth processes. Because low N concentrations and low temperature limit the growth of only the aboveground plant parts, also the simulated shoot root ratio is influenced by these. Leaf aging is related to temperature in a new way in two model elements: (1) the leaf lifespan, calculated in degree days, based on the experiment in Chapter 2, and (2) the relation between temperature sum after emergence and the maximum N concentration in leaves, based on data of Vos and Van der Putten (1997). Finally, a simple but satisfactory description of soil temperature was developed that could work with the time step of one day. This was done by calculating the amplitude of the yearly soil temperature cycle and its phase shift relative to air temperature, using soil physical data. In this way, an explicit physical description of the heat diffusion equation, with a small time coefficient (e.g. Leffelaar, 1993), could be avoided.

Application

The results of the study can be used for different purposes. First, they may serve to improve information about catch crop management for growers: choice of the crop, sowing, soil preparation, incorporation. Secondly, the quantification of N accumulation by a catch crop may be used in strategic planning of fertilization on the field level. Also, the model may be applied in design of government policy for reduction of N leaching.

Catch crop management

The general outline for the application of the research for catch crop management is given above, with the answer to the second research question. Here, this information is, where, possible, applied in practical recommendations.

For catch crop management, several recommendations can be derived from the study.

Firstly, catch crops should be sown as early in the season as possible. Earlier sown catch crops have a better chance to catch N before it is leached (Chapter 8). Secondly, the best catch crop species should be chosen. Timmer *et al.* (2003), give a number of criteria to determine the choice of a green manure species in general, of which the aim of the cultivation (here reduction of N-leaching) is only one. Other criteria are sowing time, fitness for undersowing in preceding main crop or sowing after harvest of the main crop, the degree of compatibility with other crops in the rotation and resistance to soil herbicides. Focusing here on reduction of N-leaching by crops sown after the harvest of the main crop, desired crop characteristics depend on whether catch crop growth will be mainly determined by N-limitation or by incoming radiation. This may be done by comparing N-uptake capacity with N-availability. For Dutch conditions the N-uptake capacity can be estimated with that of winter rye:

N uptake capacity (kg ha^{-1}) = 949 (kg ha^{-1}) –3.3 (kg ha^{-1} d^{-1}) × Y (d),

where Y is the day number of the sowing date (between 220 and 275), calculated from 1 Jan (day nr 1). The N availability will, however, generally not be known exactly at the moment the catch crop species is chosen. Therefore, the best catch crops will be those which have both a fast development of light intercepting leaf area and deep rooting. Crucifer crops like fodder radish and forage rape have these characteristics (Chapter 7; Thorup-Kristensen *et al.*, 2003). For late sowing, a high seed rate is advantageous for a fast development of the light intercepting canopy, enhancing growth and N-uptake. For planting later than mid September, however, winter rye performed better than cruciferous species (Vos & van der Putten, 1997). This may be caused by a higher seed rate for rye, and a higher specific leaf area in autumn conditions. Thirdly, root growth should be unhampered. Traffic at harvest of a crop often compacts the topsoil. Removing this compaction before sowing of the catch crop will generally improve the reduction of N leaching. A catch crop, used for reduction of N leaching, should not be fertilized with N to improve growth, because this may increase N leaching. If the crop is also used for another purpose (e.g. organic matter production, suppression of nematodes), a high biomass production is advantageous. With sowing earlier than September, soil mineral N may be increased by fertilizers up to 80 N kg ha^{-1} with only a small risk of increased N leaching (Chapter 8). Furthermore, a catch crop on a sandy soil is best incorporated three months before sowing of the next crop, as also discussed above. On soils less prone to leaching, like loamy or clayey soils, incorporation may be earlier (Thorup-Kristensen & Nielsen, 1998). Lastly, if the succeeding crop is sown late (May) and/or shallowly rooting (e.g. 30 cm), a winter-hardy catch crop, not frost-killed before winter, is best. Leaving a frost-killed crop (e.g. white mustard, oats, fodder radish) on the field may also lead to (too) early N-release by mineralization from frost-killed leaves on the soil surface (Dejoux *et al.*, 2000).

Estimation of the effect of catch crops on N-leaching

To estimate the effect of catch crops on N leaching, we first look at the reduction in leached N in the autumn and winter in which the catch crop is grown. Especially at high N availability to the catch crop, this reduction can be large. It was 80-140 kg N ha^{-1} for sowing in August (Chapter 8), and may be more when soil mineral N is high. The effectiveness of the catch crop will generally depend on the sowing time, which is mainly determined by the harvest time of the preceding crop.

In the long term, N losses will only be mitigated by reduction of the surplus on the N balance of the soil-crop system. This is mostly done by lowering the N input while maintaining the output of N with the harvested crop. Therefore, it is better to look at the net fertilizer value of the catch crop to estimate its effect on the N-efficiency of the soil-crop system. This was not determined in this study, but data (not shown) in Chapter 8 indicate that the amount of N available to the next crop is much less variable than the N uptake or the reduction of leaching by the catch crop. The model developed in this study could be used for this in further research.

Experimentally, Schröder *et al.* (1996) determined the fertilizer value of (late sown) catch crops in a 6 year experiment with continuous silage maize followed by catch crop. Over the six years, the fertilizer value (compared with artificial fertilizer) was 38 kg N ha^{-1} for a rye catch crop (122 % of the aboveground N), and 22 kg N ha^{-1} for ryegrass (65 % of the aboveground N). Vos and Van der Putten (2001) determined that 61 % of incorporated catch crop N could replace fertilizer N.

Evaluation

Methods

To reach the aims of the study, an explanatory simulation model was developed. Detailed experiments were performed to examine model processes for which no good description was available from literature. For validation of the model, several experiments were used, some carried out in this study (separate validation of the sub-model describing N-mineralization from catch crop biomass; separate validation of the sub-model for transport of water and N in soil), some taken from the literature (field experiments to validate the whole model). Here the suitability of the model and the experiments are evaluated.

The model integrates all available quantitative knowledge about growth processes in winter rye and fodder radish grown as catch crops with the insight in crop growth processes in general, as comprised in SUCROS (Goudriaan & Van Laar, 1994) and related models (Van Keulen & Seligman, 1987; Groot & De Willigen, 1991). In this way, we could explain variation in catch crop growth and N-uptake and examine which crop characteristics are important for catch crop effectiveness as well as possible. With the validated model, we could run widely varying scenarios with different weather data, to explore the effects of weather, crop characteristics and management on the reduction of N leaching by catch crops. This gives more insight in the effectiveness of catch crops than analysis of experiments only. Therefore, use of an explanatory model has been an efficient way to answer the questions of this study.

A rather detailed crop model was developed: SUCROS combined with crop N sub-models and a description of seasonal and temperature effects on growth processes (CO_2 assimilation, respiration, leaf expansion). This level of detail was chosen to assess the importance of crop characteristics. This has led to a large input data requirement, which was problematic for fodder radish. Therefore a part of the growth processes were parameterized with data of the related crop forage rape. Validation of the fodder radish model was done with data of one field experiment only. The the model overestimated N-uptake by this crop, most strongly at early sowing and low N supply. Therefore the sensitivity analysis and scenario study were conducted with the rye model only. Less detailed data would have been necessary when a simpler model would have been used. For instance a model could have been used which calculates production of biomass with a radiation use efficiency (RUE) (e.g. LINTUL; Spitters, 1990) as an alternative for SUCROS. SUCROS calculates biomass production in separate descriptions of light interception and CO_2 assimilation at different heights in the canopy, of maintenance respiration of several plant parts and of conversion factors of assimilates for different plant parts. With a simpler model, the effects of growth limitation by a low N availability in summer, autumn and winter (with strongly variable radiation and temperature) on RUE should have been modelled. When the crop biomass is high and radiation is low in winter, a large part of the assimilates may be used for maintenance. Therefore, the carbohydrate use for maintenance respiration should affect RUE strongly. Without insight in the underlying processes it may be rather difficult to construct such a model and apply it in widely divergent situations. Then it would have been hard to identify crop characteristics affecting the success of the catch crop, and thus to answer the research questions. These arguments have lead to the choice for extending the SUCROS model for this study.

Results from all experiments in this study were used to construct and parameterize the model. The experiment on leaf growth and CO_2 assimilation of winter rye and fodder radish in autumn and winter (Chapter 2) yielded essential information for modelling CO_2 assimilation in both crops and valuable data for modelling rye leaf expansion. For fodder radish, leaf expansion could not be described with the data, because leaf size was not well enough recorded, and it was much more variable than in rye. Measuring leaf size as well as leaf appearance might have improved the data for this aim.

The experiment designed to determine the N uptake capacity of the roots at low temperatures (Chapter 3) yielded model parameters to which the model output appeared insensitive. There are some explanations for this. Low soil temperature generally coincides with low growth rates, and thus with a low N demand. Also, low soil temperatures occur mainly in the winter, whereas catch crop N uptake takes place mainly in the first months after sowing: August, September and October. In these months, soil temperature is still high compared to air temperature, due to the time needed for cooling the soil. In winter there is often N from turnover of crop material available for newly grown biomass, so that N uptake hardly takes place. Lastly, in winter the catch crop has already formed a large root length, which makes a limitation of N uptake by the uptake capacity of the roots unlikely. This information has become available in this study, but was not clear beforehand.

The Rhizolab experiments with fodder radish and winter rye gave indispensable insight in the canopy CO_2 assimilation (Chapter 4). Also, the data of soil mineral N and water in the fallow compartments in the first experiment (Chapter 5) were very useful for testing the soil model. The root data (Chapter 5), however, have been used only to determine the maximum rate of growth of the root zone in the model. A large part of the root data were not used for development of the model, nor for its validation. This was because root distribution in the Rhizolab – with a uniform 0-100 cm layer of topsoil – differed too much from root growth in the field (Vos *et al.*, 1998).

Lastly, the determination of N-mineralization from catch crop material at low temperature (Chapter 6) was very useful for describing this process in the model and calculating the availability of N for a succeeding crop. In hindsight, an extra field experiment with fodder radish would have been desirable for a better parameterization of the model for this crop species. Also, more soil mineral N data in the validation experiments would have improved the model validation, because the relations between soil mineral N, N uptake and N leaching could have been tested better.

Remaining questions

Necessarily, the research was focussed on crop growth determined by weather conditions, crop characteristics and nitrogen availability only. Some aspects of weather determining catch crop effectiveness were not yet well investigated, nor were they included in this study. Firstly, the sensitivity of the crop to frost is not well understood. Catch crop species differ in their winter-hardiness (e.g. Timmer *et al.*, 2003; Thorup-Kristensen, 1994). However, we could not find enough data on cold acclimation and frost resistance of catch crops to include this process in a catch crop model. This crop characteristic may, however, be important for prevention of N loss in winter, as discussed above. Secondly, crop establishment can, in practise, be variable, mainly due to drought or extreme precipitation after sowing or soil compaction. This is a source of uncertainty if catch crops are used to reduce leaching, but it was not yet modelled. I consider variation in crop establishment and winter-hardiness the most important remaining sources of uncertainty in catch crop effectiveness.

Also there are factors other than weather conditions and N determining catch crop growth. Pests and diseases may reduce growth rate and thereby N uptake, but generally these effects are not considered seriously reducing catch crop growth (Timmer *et al.*, 2003). Shortage of nutrients other than N might occur, but have not been investigated yet. In general, amounts of these nutrients in soils in the Netherlands are estimated sufficient for unlimited growth.

Effects of catch crops on losses of nutrients other than N have seldom been investigated (e.g. Eriksen & Thorup-Kristensen, 2002; Vos & Van der Putten, 2004). Catch crops might be very helpful in decreasing P losses, as well as N-losses from the soil-crop system (Thorup-Kristensen *et al.*, 2003). Catch crop cultivation may thus be a useful practice to approach the water quality standards set by the Water Framework Directive (Ligtvoet *et al.*, 2006).

For further increase of N-efficiency, one could harvest catch crops for use as fodder, instead of incorporating them in the soil. By harvesting, all N in aboveground parts could be used efficiently, which may increase the efficiency of use of this N from 61-65% (Schröder *et al.*, 1996; Vos & Van der Putten, 2001) to close to 100%. It is to be expected that in the long term N losses will generally be reduced more strongly when a catch crop is harvested, than when the catch crop is incorporated in soil, in which case a part of catch crop N may still leach in the winters following incorporation.

Nederlandse samenvatting

Inleiding

Bemesting met stikstof (N) is een effectieve en, in geïndustrialiseerde landen, goedkope maatregel om productie van landbouwgewassen te verhogen. Daarom wordt stikstofbemesting in ruime mate toegepast, waardoor aanzienlijke verliezen van stikstof uit de landbouw naar de omgeving kunnen optreden. Deze verliezen hebben een negatief effect op de leefomstandigheden van mensen, flora en fauna, b.v. door verhoogde nitraatconcentraties in drinkwater, eutrofiëring van biotopen die van nature voedselarm zijn en uitstoot van het broeikasgas N_2O. Daarbij komt dat de energiebehoefte van de industriële productie van stikstofmeststoffen hoog is: 39 MJ per kg N. Daarom zijn minimalisering van de verliezen en verhoging van de doelmatigheid en doeltreffendheid van de N-bemesting in toenemende mate doelen van onderzoek geworden.

Stikstofverliezen uit de landbouw treden op in de vorm van gasvormige emissies vanwege ammoniakvervluchtiging en denitrificatie uit stallen, toegediende mest en de bodem, en daarnaast in de vorm van nitraatuitspoeling naar grond- en oppervlaktewater. Uitspoeling uit de bewortelde bovengrond en denitrificatie uit de bodem zijn verantwoordelijk voor een aanzienlijk deel van de N-verliezen. Uitspoelingsverliezen zijn vooral problematisch op zandgrond met een diepe grondwaterspiegel, waar van nature weinig N denitrificeert. Hierbij wordt de maximumwaarde van 50 mg nitraat per liter grondwater, zoals gesteld door de Europese Nitraatrichtlijn, in Nederland veelvuldig overschreden.

N-uitspoeling treedt vooral op in herfst en winter, als er meer neerslag is dan verdamping van water. Op braakliggend land is er veel uitspoeling, door de afwezigheid van verdamping en N-opname door een gewas. Uitspoeling van N kan op verschillende manieren verminderd worden. Ten eerste kan de stikstofgebruiksefficiëntie van gewassen verhoogd worden, waardoor er bij oogst minder N in de grond overblijft. Deze strategie is niet altijd effectief: voor sommige gewassen moet voor een optimale opbrengst ruimschoots meer N toegediend worden dan er opgenomen wordt. Daarnaast laten sommige gewassen veel N in gewasresten achter, die na mineralisatie in de herfst verloren kan gaan. Ten tweede kan uitspoeling en denitrificatie na de oogst van de hoofdgewassen verlaagd worden door immobilisatie in organisch materiaal met een hoge C/N verhouding (bv. stro), of, vaak veel effectiever, door teelt van stikstofvanggewassen na de oogst van het hoofdgewas.

Stikstofvanggewassen kunnen tot zo’n 200 kg N per ha opnemen, afhankelijk van de gewassoort, de zaaidatum, de hoeveelheid N in de grond en de weersomstandigheden. Vlak voor of na de winter kan het vanggewas geoogst worden als voedergewas of ondergewerkt worden. Na inwerken in de grond begint de mineralisatie van N uit het gewasmateriaal, zodat, met een goede timing, deze stikstof weer ten goede kan komen aan het volggewas, zodat de N-bemesting hiervoor verlaagd kan worden. Het effect van vanggewassen op N-uitspoeling en op de N-voorziening van het volggewas is al vaak in veldexperimenten onderzocht. Hieruit blijkt een grote variatie in de effectiviteit van het vanggewas, die toegeschreven wordt aan verschillen in zonnestraling en temperatuur tijdens de groei van het gewas, aan wortelontwikkeling en aan variatie in de hoeveelheid N die voor het vanggewas beschikbaar is. Er bestaat echter geen systematische, kwantitatieve analyse van de mogelijkheden om met vanggewassen de N-uitspoeling te verlagen, afhankelijk van de weersomstandigheden en gewaseigenschappen. Het doel van deze studie is om door een dergelijke analyse (1) de variatie in de N-opname van vanggewassen en het effect op de N-uitspoeling te verklaren en (2) te bepalen wat wenselijke eigenschappen en teeltstrategieën zijn voor vanggewassen, gericht op minimale N-verliezen.

Hiervoor is een simulatiemodel ontwikkeld dat de groei en N-opname van vanggewassen (winterrogge en bladrammenas) en de dynamiek van water en stikstof in de bodem beschrijft. Het model had betekking op de vanggewassen winterrogge (*Secale cereale*) en bladrammenas (*Raphanus sativus*). Het is gebruikt om de effecten van gewaseigenschappen en groeiomstandigheden op de N-opname en N-uitspoeling te evalueren.Hiervoor is de gewasgroei en N-huishouding in herfst en winter gemodelleerd, bij temperaturen en stralingsniveaus die veel lager zijn dan die waarvoor andere gewasgroeimodellen ontwikkeld zijn. Voor de modelontwikkeling zijn een aantal experimenten uitgevoerd om de snelheden van een aantal groeiprocessen (CO_2 assimilatie, blad- en wortelexpansie, N-opname op wortelniveau) en bodemprocessen (N-mineralisatie uit gewasmateriaal in de grond, transport van water en stikstof in de grond) vast te stellen. Verder zijn er gegevens uit de literatuur gebruikt.

CO_2-assimilatie en de bladdynamiek

Om de CO_2-assimilatie en de bladdynamiek van winterrogge en bladrammenas geteeld als vanggewas (augustus – april) te meten is een potexperiment uitgevoerd bij twee stikstofniveaus (hoofdstuk 2). Hierbij werd een vaste relatie gevonden tussen de temperatuur en de bladverschijning bij deze gewassen, en bij rogge ook tussen de temperatuur en het verschijnen van spruiten. De spruitvorming bij rogge en de bladverschijning bij bladrammenas werden ook beïnvloed door de N-voorziening. De levensduur van het blad was te beschrijven met een temperatuursom vanaf verschijnen van het blad. Voor bladrammenas had deze een vaste waarde, bij rogge nam deze af in de loop van het groeiseizoen en met toename van de N-voorziening. De lichtverzadigde CO_2-assimilatiesnelheid (A_{max}) in jong blad was ongeveer 1.2 mg CO_2 m^{-2} blad s^{-1} in september en 0.5 mg CO_2 m^{-2} blad s^{-1} later in het seizoen, onafhankelijk van gewas en N-niveau en de temperatuur tijdens de meting. Er was wel een correlatie met het stralingsniveau of de temperatuur tijdens de ontwikkeling van het blad. De CO_2 assimilatiesnelheid bleek niet limiterend voor de groei: bij alle metingen (september – maart) bevatte het blad fluctuerende concentraties wateroplosbare koolhydraten.

Maximale nitraatopnamesnelheid van de wortels

Om de nitraatopnamecapaciteit van de wortels van winterrogge en bladrammenas bij lage temperaturen vast te stellen werden deze gewassen in de kas geteeld op potten met voedingsoplossing (hoofdstuk 3). De maximale nitraatopnamesnelheid van de wortels werd gemeten bij een worteltemperatuur van 3, 10 en 17 °C, bij een hogere luchttemperatuur.. Dit gebeurde na een onderbreking van het stikstofaanbod in de voedingsoplossing, zodat de planten behoefte hadden aan stikstof. Nitraat werd tijdens de meting in een voldoende hoge concentratie aangeboden, zodat de opnamesnelheid hier niet door beperkt werd.De nitraatopnamecapaciteit van de wortels nam sterk toe met de temperatuur tussen 3 en 10 °C en nam nog iets toe tussen 10 en 17 °C. De opnamesnelheid varieerde van 0.068 ± 0.010 tot 0.24 ± 0.05 μmol m^{-1} h^{-1} voor rogge en van 0.068 ± 0.025 tot 0.28 ± 0.14 μmol m^{-1} h^{-1} voor bladrammenas. Ook nam in een van de twee experimenten de specifieke wortellengte van de gewassen toe met de temperatuur, en in beide experimenten nam de spruit-wortelverhouding af bij toename van de temperatuur. Dit wijst er op dat de groei van de wortels geremd werd bij lage temperatuur.

CO_2-assimilatie op gewasniveau

Om de CO_2 assimilatie en wortelgroei van rogge en bladrammenas, en de dynamiek van N en water in zandgrond te meten werden twee experimenten (één met bladrammenas, één met rogge) uitgevoerd in het Rhizolab (hoofdstukken 4 en 5). Hierbij werden de gewassen geteeld op lysimeters (1.25 m × 1.25 m en 1.7 m diep) met apparatuur om de wortels op verschillende diepten te kunnen fotograferen. Bij bladrammenas werd de irrigatie gevarieerd en bij rogge de N-gift. De CO_2 uitwisseling van de gewassen werd gemeten bij verschillende temperaturen in een aantal intervallen in de periode van oktober tot maart. Ook werden een aantal bodemprocessen in twee onbeplante lysimeters gevolgd. De maximale CO_2-assimilatiesnelheden voor bladrammenas en rogge in oktober waren 1.1 en 0.9 mg CO_2 m^{-2} grondoppervlak s^{-1}, bij respectievelijk bladrammenas en rogge, bij ongeveer 200 W m^{-2} geabsorbeerde fotosynthetisch actieve straling (PAR). Later in de herfst en in de winter was dit 0.6 mg CO_2 m^{-2} grondoppervlak s^{-1}, bij 100 W m^{-2} PAR voor beide gewassen en 0.6 mg CO_2 m^{-2} grondoppervlak s^{-1} voor rogge in maart bij 220 W m^{-2} PAR. De CO_2–assimilatiesnelheid werd niet beinvloed door de temperatuur tussen 4 en 16 °C. Door inverse modellering met de assimilatiemodules van SUCROS werd per meetperiode en per lysimeter de effectieve A_{max} van het bladoppervlak bepaald. Deze werd vergeleken met de A_{max}-waarden die in de potproef (hoofdstuk 2) op bladniveau gemeten was, met behulp van de daar bepaalde correlatie tussen de stralingsintensiteit tijdens de bladontwikkeling en de A_{max} op bladniveau. Voor bladrammenas was de A_{max} op blad- en gewasniveau gelijk, maar voor rogge was de A_{max} op gewasniveau lager, waarschijnlijk omdat bij dit gewas meer oud blad, met een lagere A_{max} dan jong blad, bovenin het gewas licht onderschept. Bij bladrammenas onderschept het jonge blad het meeste licht.

N-dynamiek in de bodem

De gewassen namen in de Rhizolabproeven 200 tot 300 kg N per ha op, waarvan aan het eind van het groeiseizoen (maart) een aanzienlijk deel (37 - 48%) in dood blad aanwezig was (hoofdstuk 5). De reductie van N uitspoeling was gelijk aan de N-opname. De N-concentratie in de grond werd door het gewas verlaagd, eerst in de bovengrond, en later verder naar beneden. De nitraat-N-concentratie in bodemvocht werd met 49 tot 85 mg l^{-1} (62 - 99%) verlaagd door het vanggewas. Bij toename van de irrigatiesnelheid (1 – 3 mm per dag) werd de N concentratie in het uitgespoelde water lager, maar de totale hoeveelheid uitgespoelde N hoger. De mineralisatie van N uit een in de bodem ingewerkt vanggewas werd gemeten bij temperaturen tussen 1 en 15 °C (hoofdstuk 6). Hiervoor werden de bovengrondse delen en de wortels van rogge apart geïncubeerd in zandgrond. Periodiek werden de concentraties van ammonium-N en nitraat-N in de grond bepaald. Na 10 weken was bij 1 °C 20% van de organische N uit het gewasmateriaal gemineraliseerd, waaruit blijkt dat de mineralisatie bij deze lage temperatuur niet verwaarloosbaar is. Bij 15 °C was dit 39% voor N uit de bovengrondse delen en 35% voor N uit de wortels. Het temperatuureffect op de mineralisatiesnelheid kon beschreven worden met een Arrhenius-curve. Er is een simulatiemodel ontwikkeld waarin afbraak van organische stof, mineralisatie en nitrificatie beschreven worden als enkelvoudige processen met een eerste-orde-kinetiek. Het model is geparameteriseerd met gegevens uit de uitgevoerde incubatie, en gevalideerd met een onafhankelijk veldexperiment (temperatuur 3-20 °C). Hierbij werd de mineralisatie in de eerste weken onderschat, en later in de tijd goed gesimuleerd.

Modelontwikkeling en -toetsing

Op basis van gegevens uit de hier beschreven proeven en de literatuur is een simulatiemodel ontwikkeld waarmee de onderzoeksvragen beantwoord konden worden (hoofdstuk 7). Het gewasmodel is gebaseerd op SUCROS en aangepast om de groei van rogge en bladrammenas te simuleren bij lage temperatuur en stralingsintensiteit en bij lage N beschikbaarheid, zoals die voorkomen tijdens de groei van een vanggewas. In het model was A_{max} een functie van de stralingsintensiteit tijdens de bladontwikkeling. Boven 5 °C was A_{max} niet afhankelijk van de temperatuur. Bladexpansie, afhankelijk van de beschikbaarheid van N en koolhydraten en van de temperatuur, bepaalde de structurele groei. Koolhydraten hoopten in het gemodelleerde gewas op als er geen vraag naar was voor onderhoudsademhaling of groei. Blad, bladscheden en stengels stierven af na een vaste levensduur (in °C d). Transport van water in de grond werd gemodelleerd met behulp van met een ‘tipping bucket’ waterbalansmodel, aangepast met een drainagecoëfficient die bepaalde welk deel van het bodemvocht binnen een dag kon draineren naar een diepere bodemlaag. Stikstofuitspoeling werd gesimuleerd met de ‘complete mixing’ theorie. Mineralisatie van gewasmateriaal werd gemodelleerd zoals hierboven vermeld. Het model is getoetst met gegevens uit de Rhizolabproeven en veldexperimenten. Het model overschatte de N-uitspoeling ten opzichte van de percolatie van water. Hiervoor werd geen verklaring gevonden. De N-inhoud van het gewas werd vrij goed voorspeld als er ruimschoots N beschikbaar was, maar bij N-gelimiteerde groei werden de gemeten waarden soms onderschat en soms overschat door het model. Dat kwam ten dele door een imperfecte simulatie van de N-huishouding van de grond, maar ook door een overschatting van de N-opname bij lage N-beschikbaarheid. Hoewel de exacte hoeveelheden N in gewas en grond dus niet altijd goed gesimuleerd werden, volgden de gesimuleerde waarden het gemeten tijdsverloop van N in gewas en uitgespoelde N goed. Daarom werd het model geschikt geacht voor verkenningen naar het effect van gewaseigenschappen, teeltmaatregelen, weersomstandigheden en N-beschikbaarheid op de N-opname van vanggewassen en op de N-uitspoeling. Omdat de simulaties voor rogge beter waren dan voor bladrammenas, werd het roggemodel gebruikt voor een gevoeligheidsanalyse en een scenariostudie.

Gevoeligheidsanalyse en scenariostudie

Bij de gevoeligheidsanalyse werd voor elk gewasgroeiproces in het model een parameter geselecteerd, die met –10% en +10% gevarieerd werd (binnen het biologisch relevante bereik van de parameterwaarden). Het effect van die variatie op N-opname en N-uitspoeling werd berekend. Hieruit bleek dat bij een beperkte N-beschikbaarheid de opname en de uitspoeling vooral gevoelig zijn voor de bewortelde diepte. Bij een ruime beschikbaarheid van N was de modeluitkomst daarnaast ook gevoelig voor variatie van parameters die bepalen hoeveel N opgenomen kan worden per eenheid inkomende straling: de A_{max}, de fractie van assimilaten die de bladgroei ten goede komt, de coefficiënten die het niveau van de onderhoudsademhaling bepalen en het maximale N-gehalte in gewasmateriaal.

Bij de scenariostudie bleek dat het effect van de weersomstandigheden op de N-opname en de N-uitspoeling toenamen naarmate het gewas later in het seizoen gezaaid werd, en naarmate de N-beschikbaarheid in de grond hoger was. Zowel de straling als de neerslag in de eerste maand na planten hadden een effect op de vermindering van de uitspoeling, vergeleken met die in onbeteeld land. Bij toename van de stralingssom werd de uitspoeling meer gereduceerd, bij toename van de neerslag werd de uitspoeling juis minder gereduceerd door het vanggewas. Uitstellen van zaai vanaf midden-augustus verminderde de N-opnamecapaciteit van het vanggewas met 3.3 kg N ha^{-1} per dag. Een gift van 30 kg N per ha, bij 50 kg N aanwezig in de grond, verhoogde de uitspoeling alleen aanzienlijk bij late zaai (20 september) in een jaar met veel neerslag na zaai. Een gift van 60 kg N per ha verhoogde de uitspoeling aanzienlijk bij zaai op 20 september, maar ook, onder ongunstige weersomstandigheden, bij zaai op 11 augustus. Verhoging van de hoeveelheid zaaizaad had een aanzienlijk effect op de N inhoud van het gewas bij zaai op 20 september, maar niet bij zaai op 11 augustus, waarbij door een langer groeiseizoen met hogere stralingsintensiteit er altijd genoeg groei plaatsvond om de beschikbare N op te nemen. Het vanggewas kan, voor een maximale N-beschikbaarheid voor het volggewas, het best half januari ondergewerkt worden. Een maand eerder of later onderwerken heeft echter slechts een klein ongunstig effect.

Conclusie

Er wordt geconcludeerd dat de vermindering van N uitspoeling door vanggewassen bepaald wordt door:

- de hoeveelheid N in de grond;
- de N-uitspoelingssnelheid, bepaald door het neerslagoverschot;
- het vermogen van het vanggewas om N op te nemen voor die is uitgespoeld, bepaald door de straling en gewaseigenschappen.

Als de N-beschikbaarheid limiterend is voor de groei, bepalen de neerslag en de worteldiepte hoeveel N opgenomen kan worden voordat die uitgespoeld is. Als er meer N in de grond beschikbaar is dan het gewas kan vastleggen in biomassa, zijn (1) de straling, (2) de gewaseigenschappen die bepalen hoeveel biomassa gevormd wordt per eenheid inkomende straling en (3) het N-gehalte in de biomassa bepalend voor de omvang van vermindering van de N-uitspoeling door een vanggewas. Het moment van onderwerken is relatief onbelangrijk voor vasthouden van N in het bodem-gewassysteem en beschikbaarheid van N voor het volggewas.

De mogelijkheden om met vanggewassen de N-verliezen te verminderen zijn aanzienlijk. De teeltkundige maatregelen voor die vanggewassen kunnen worden afgestemd op een zo groot mogelijk effect voor de N-benutting op gewassysteemniveau.

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Curriculum Vitae

Anne Marie van Dam is op 18 november 1967 geboren in Delft. Zij behaalde in 1986 haar VWO diploma bij het Stedelijk Gymnasium te Leiden. In dat jaar begon zij haar studie Bodemkunde aan Wageningen Universiteit (toen Landbouwuniversiteit Wageningen). Zij koos binnen deze studie de richting Bodemvruchtbaarheid en Plantenvoeding en deed afstudeervakken in de Bodemvruchtbaarheid, de Theoretische Productie-ecologie en de Alternatieve Landbouw. In 1992 studeerde zij met lof af, en begon zij als assistent in opleiding aan haar promotieonderzoek bij de vakgroep Theoretische Productie-ecologie. Vanaf 1997 werkt zij als onderzoeker bodem, water en bemesting bij Praktijkonderzoek Plant en Omgeving, sector Bloembollen, Boomkwekerij en Fruit, voorheen het Laboratorium voor Bloembollenonderzoek, te Lisse. Daarnaast heeft zij dit proefschrift afgerond.