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Will breeding for nitrogen use efficient crops lead to nitrogen use efficient cropping systems?: a simulation study of G×E×M interactions

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Abstract The benefits of improving nitrogen use efficiency (NUE) in crops are typically studied through the performance of the individual crop. However, in order to increase yields in a sustainable way, improving NUE of the *cropping systems* must be the aim. We did a model simulation study to investigate how improvement of NUE traits of individual crops affects the succeeding crops and the NUE of the crop rotation. Based on experimental results parameterization was altered for different types of improved NUE in the EU-Rotate_N model, e.g. through higher N harvest index, reduced litter loss or improved root depth penetration rate. The different ways of improving NUE have different effects on the cropping system, affecting either N uptake, the ability of the crop to hold on to N already taken up, or the fraction of crop N being harvested. Due to the different modes of action, the model simulations show that these changes in NUE traits will also have different effects on N leaching loss and on N availability and N loss in the following years. Simulations also show that the effect of genotypes with improved NUE depend on environment and crop management. This is true for the improved crop itself and when its effect is analyzed for the whole cropping system. The environmental conditions, crop choices and management will all affect the fate of the N left in the soil, and whether this will contribute mainly to leaching loss or be used for production in later crops. As an example, increasing pre-crop fertilization was shown to affect the leaching after the following oilseed rape crop with up to 50 kg N ha^{-1} taken up before it was lost to the environment when pre-crop fertilization as well as root depth penetration rate was high. All in all, the simulations illustrate the concept of NUE as the result of interactions between genotype, environment and crop management (G×E×M).

Keywords EU_Rotate · NUE · Oilseed rape · Wheat · Model simulations · Leaching

Introduction

Lowering the fertilizer input to agricultural cropping systems, while increasing the yield, is one of the keys to meet future demands for sustainable food production. Nitrogen (N) is an important macronutrient for plants, but is costly to supply and it can affect the surrounding environment negatively. It has been estimated that up to 50–70 % of N applied to the cropping system is lost (Hodge et al. 2000). Thus, in order to limit these losses and create sustainable cropping systems with high productivity with reduced inputs of N, the nitrogen use efficiency (NUE) of the

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crops as well as the cropping systems has to be improved. This can be achieved through breeding and improved crop and soil management.

When determining NUE of a crop, several definitions have been applied over the years (Fageria et al. 2008; Good et al. 2004). Thus, when discussing improvements in NUE or comparing results, it is obviously necessary to state clearly how NUE is defined. The definitions generally differ in a few basic ways e.g. whether determined as agronomic efficiency (grain yield per unit of N applied), as physiological efficiency (total biomass per unit of N uptake) or as uptake efficiency (N taken up per unit N available). However, the fate of the N not taken up by the crop is not considered when determining individual crop NUE. At the cropping system level, the fate of the N is a pivotal question affecting cropping system NUE. The N can (1) be taken up and harvested with the crop, (2) be taken up but left in the field with the crop residues, or (3) be left in the soil as it was not taken up by the crop. When nutrients are not harvested, they are subject to use by later crops or to loss, in the case of N mainly through leaching or denitrification. Considering the cropping system, it is less important that the single crop maximize its use of the available nutrients. As long as the nutrients are not lost from the field, they may be used by later crops. Therefore the loss processes become highly important when considering NUE at the cropping system level. The physiological efficiency is of course still important as for single crop NUE, but on the larger scale, the reuse of the same nutrients by successive crops represents a further element of physiological efficiency. Thus, while at the single crop level, a high nutrient harvest index is a component of high NUE, at the cropping system level, the highest efficiency is reached if the nutrient is used by the crop, but then still left in the field for subsequent crops to use again. Calculating the NUE of a cropping system as an exact number is therefore not possible, but should be assessed through the different components of NUE.

When breeding for improved NUE, focus is generally on one specific trait in the crop, and in molecular genetics the focus on single genes often neglects the possibility of compensation by other genes and processes during the plant growth cycle (Boote et al. 2013). Increased NUE can be measured on single crop level, or even on single plant level as it is often done in laboratory or greenhouse studies where external conditions can be controlled (Habash et al. 2001; Hirel et al. 2001). The improvement of NUE of individual crops is desirable, but in crop production the effect on the crops should not be seen in isolation, as they are a part of a cropping system where genotype (G), environment (E) and management (M) will affect the outcome, both of the crop itself and of the crops in the following years. The effect on single crop level can more easily be determined, whereas effect on cropping system level is difficult to measure. First of all it is resource intensive and time consuming, but more importantly the outcome of changes in succeeding years in cropping system NUE are typically small, e.g. a reduced leaching of just a few kg N ha^{-1}, which will normally be below the detection limit due to experimental variability. Thus, in order not just to interpret the effect on single crops but on the entire cropping system, crop models that take G×E×M interactions into account could be employed as a valuable tool.

Research on improving NUE has been done extensively during the last decades (Bingham et al. 2012; Cormier et al. 2013), and has been approached by improving agronomic practices as well as genetic modification (Good et al. 2004; Hirel et al. 2007). One way to improve NUE is by improving N uptake from the soil. This can be done e.g. by improving the actual uptake mechanisms from soil to root or by altering root architecture resulting in more branched roots or deeper rooting, bringing the roots into contact with more soil N (Garnett et al. 2009). Improved NUE could also be a result of improved remobilization of N from leaves and stem to seeds (Masclaux-Daubresse et al. 2010) or reduced litter loss during the growing season (Malagoli et al. 2005). But, it is important to stress that NUE is not a single trait in the crop that can be bred for. NUE of a crop and a cropping system can be affected by a range of traits, and is also dependent on interactions with the environmental conditions and the agronomic management of the crop.

Crop models have the advantage of being able to test the improved crop in different simulated environments and under different management practices. Including catch crops in the cropping system to reduce leaching losses (Thorup-Kristensen et al. 2003), choice of crop sowing date (Islam and Garcia 2012) and N fertilization according to plant demand and yearly variation in availability (Guillard et al. 1999; Hirel et al. 2001) are all examples of agronomic practices that affect the NUE of the system significantly. The improvement of NUE through breeding will typically be much smaller than improvements obtained by management if compared directly. However, if the improved trait is incorporated in lines distributed over larger agricultural regions, it will have a significant impact on the overall N use and loss.

Improving NUE by increased N uptake from the soil will have a direct and positive effect on the environment by reducing leaching losses, while the effect on subsequent crops might be small. Improving NUE by reducing the N left in organic material in the field might on the other hand affect the following crops negatively as less N will be mineralized from the soil. Thus, different ways of obtaining increased NUE on single crop level is expected to lead to different effects on the cropping system level.

Simulating N leaching loss and the effect of variable rooting depths present a special problem. The movement of N through the soil can be quite well simulated by various models, and calculating the movement across a depth defined as the bottom of the rooting zone can be done. But it is not easy to decide the depth of the rooting zone, and especially not when working with crops with different rooting depths and even trying to simulate the effect of genotypes with different rooting depths. In most models the leaching loss is calculated as N movement to below ~1 m, for various reasons including the fact that many experimental studies do the same. However, as many common crops have roots to more than 1 m depth, and take up N from below that depth, there is a need to correct the model simulated N leaching loss for the N uptake from below the depth used for calculation of leaching loss.

The objective of the model simulations was to examine the effect of genetically increased crop NUE at the cropping system level, with the hypotheses that: (1) different ways of improving crop NUE will have different effects at the cropping system level—sometimes counteracting the effect of the individual crops, (2) the effect at cropping system level is highly dependent on the environment/management applied to the system and (3) agronomic practices might under certain circumstances improve the NUE of the cropping system more than the results of breeding.

Materials and methods

In this study, we examined the effect of changing parameters affecting NUE in two major winter crops; oilseed rape and wheat. The parameters chosen for this study were root penetration rate for both crops, litter loss for oilseed rape, and the ratio between N in straw and N in grain for wheat affecting the nitrogen harvest index (NHI). These three parameters affect different aspects of NUE. Root penetration rate affect the crop ability to take up N, leaf litter loss affect the crop ability to hold on to the N already taken up, and NHI affect the crop ability to translocate its N content into the harvest product. Model simulations were conducted by the use of the EU-Rotate_N model (Rahn et al. 2010), and parameter changes were based on experimental data from 2 years of field trials with oilseed rape and wheat. The EU-Rotate_N model has a well-developed root component compared to many other crop-soil models (Pedersen et al. 2010) and has been validated to experimental data on root density and soil N uptake. It is therefore appropriate for use in studying effects of improved crop NUE.

Model

The EU-Rotate_N model is an integrated soil–plant–atmosphere model based on a number of modules simulating plant and soil processes including plant growth above and belowground, as well as N mineralization and uptake. The model runs on a daily basis using daily weather such as temperature, rainfall, potential evapotranspiration and irradiation, and data on soil properties, crop residues, fertilization and crop management. In brief, the model include an aboveground crop development and N demand module (Greenwood et al. 1996; Greenwood 2001), a soil organic matter, soil microbial biomass and decomposition module from the Daisy model (Hansen et al. 1991), a water balance module (Brisson et al. 2003) and a root module (Pedersen et al. 2010).

Crop rotations

The simulations are based on crop rotations running over 8 years. The first 3 years of the simulated rotation are used for initialization of the model to activate SOM pools in the soil (Hansen et al., 2012), followed by 5 years of rotation used for studying our research questions. The initialization phase was made with 3 years of spring barley crops, the first year with an undersown clover grass cover crop. The 5 years of rotation used for the study consisted of (1) winter oilseed rape, (2) winter wheat, (3) spring barley, (4) winter wheat and (5) winter oilseed rape. The initialization crops were chosen in order to create a situation with deep N available in the soil before the oilseed rape crop. The rotation represents a rotation that could be seen under Danish conditions, but the overall aim of the rotation was to test scenarios where the fate of N in the cropping system varied.

In the first set of simulations (simulation 1), the effect of different genotype traits on NUE of the first oilseed rape crop in the rotation was examined on the crop itself as well as on the following crops. The effect of varying pre-crop fertilization (simulation 2) and the yearly variation (simulation 3) was examined as well. Scenario inputs are shown in Table 1. Varying NUE was created by changes in root depth penetration rate or in the rate of leaf litter loss from the crop. In the second set of simulations two parameters were altered on the first wheat crop in the rotation; root penetration rate or the ratio of N in grain/N in straw used for calculating the N harvest index. Simulations were carried out, examining the effect of genotype differences by varying parameter values as well as environmental conditions such as pre-crop fertilization (simulation 4), soil types (simulation 5), climatic conditions (simulation 6), and effects of management such as use of catch crops (simulation 7) and sowing date (simulation 8). Scenario inputs are shown in Table 1. The simulated effects of different sowing dates and the use of catch crops were evaluated against wheat genotypes with different root depth penetration rates.

Parameter values altered

We worked with three model parameters to mimic genotypic differences in selected traits affecting NUE in different ways. The three parameters were (1) root depth penetration rate, (2) leaf litter loss rate and (3) a parameter controlling the ratio of [N] in straw/[N] in grain. The range of parameter values we used in the simulations reflects large genotypic variation as a response to plant breeding. A change in e.g. litter loss rate from 0.4 to 0.3 % is a large step, and it is not realistic to select for such a change in the breeding of the next set of genotypes to be released for agriculture. However, the values were chosen to study potential long term gain by continuous breeding for these traits.

In oilseed rape two parameters, root penetration rate and leaf litter loss rate, were altered. Simulations were carried out with root penetration rates of 0.001, 0.0015 and **0.002** m day^{-1} °C^{-1}, and daily litter loss percentages of 0.3, 0.4 and **0.5** %. In winter wheat, root penetration rates of 0.001, **0.00125** and 0.0015 m day^{-1} C^{-1} was applied and a variation in ratio of [N] in straw/[N] in grain of 0.25, **0.3** and 0.35. Estimates of current cultivar values are shown in bold.

Table 1 Conditions used for the eight overall model simulations

Simulation no.	Pre-crop fertilization (kg N ha^{-1})	Crop fertilization (kg N ha^{-1})	Avg. yearly precipitation (mm year^{-1})	Soil type (mm year^{-1})	Catch crops (mm year^{-1})	Test crop sowing date (mm year^{-1})
Winter oilseed rape						
1	0/250	110/180	781	Loamy	None	17/9
2	0/50/100/125/150/175/200/250	110/250	781	Loamy	None	17/9
3	0/250	250	Variable	Loamy	None	17/9
Winter wheat						
4	0/250	175	781	Loamy	None	17/9
5	250 and 350*	175	781	Sandy	None	17/9
6	250 and 350	175	991	Loamy	None	17/9
7	250 and 350	175	781	Loamy	Fodder radish	17/9
8	250 and 350	175	781	Loamy	None	24/8, 3/9, 17/9, 2/10

In the first three simulations, root penetration rate and litter loss rate was altered for the first winter oilseed rape crop in the rotation, and in the following five simulations root penetration rate as well as ratio of N in straw/N in grain was altered in the following winter wheat crop

* 250 kg N ha^{-1} for the two barley crops, 350 kg N ha^{-1} for the oilseed rape crop

Root penetration rate [vertical root penetration rate parameter (k_{rz})] is used in the model to calculate the root penetration depth (R_z) as follows:

$$R_z = \left\{ \begin{array}{ll} \mathrm{R}_{z-\min} & ; \sum DD \le DD_{lag} \\ \sum((DD - DD_{lag})k_{rz}) + \mathrm{R}_{z-\min} & ; \sum DD > DD_{lag} \\ R_{z-\max} & ; \sum DD - DD_{lag}k_{rz} + \mathrm{R}_{z-\min} > R_{z-\max} \end{array} \right\}, \quad (1)$$

where DD is day-degrees, DD_{lag} is the lag phase for initiating root growth, $R_{z\text{- max}}$ is the maximum rooting depth and $\mathrm{R}_{z\text{-min}}$ the rooting depth at sowing or planting. The differences generated in rooting depth will subsequently affect the simulated amount of N taken up from different soil depths.

Differences in litter loss rates control the percentages of plant biomass and N which are lost back to the soil on a daily basis. The litter loss rate determine the fraction of plant biomass lost per day, and plant N is lost as well according to the [N] in the plant. Litter loss therefore reduces the total plant N content, which will be lower than the accumulated plant N uptake. The material lost from the plant is added to the uppermost soil layer affecting the ongoing organic matter turnover and N mineralization or immobilization there. The N ratio is simply used at the date of harvest, in order to calculate the N concentrations and N amounts in the harvested product and in the crop residues:

$$[\mathrm{N}]\mathrm{straw} = [\mathrm{N}]\mathrm{grain} * \mathrm{Nratio}, \quad (2)$$

where [N]straw is the N concentration in the straw, [N]grain is the N concentration in the grain, and Nratio is the parameter value given for N partitioning.

$$\mathrm{Ngrain} = [\mathrm{N}]\mathrm{grain} * \mathrm{DM\_grain}, \quad (3)$$

where Ngrain is the amount of N in the harvested grain, calculated in kg N ha^{-1}, and DM_grain is the simulated grain yield in kg DM ha^{-1}.

$$\mathrm{Nstraw} = [\mathrm{N}]\mathrm{straw} * \mathrm{DM\_straw}, \quad (4)$$

where Nstraw is the amount of N in the straw, calculated in kg N ha^{-1}, and DM_straw is the simulated amount of straw in kg DM ha^{-1}.

NUE components

Three components of NUE were studied; (1) leaching loss, which will decrease NUE, (2) harvested N, which will increase NUE and (3) soil organic matter N content (SOM-N), which will have variable effect on NUE depending on when the SOM_N is mineralized. Harvested N and SOM-N content were determined at harvest of the crops, whereas leaching losses were determined from crop establishment, until establishment of the next crop. However, when crops were followed by an autumn sown crop, the leaching loss was determined from establishment until April 1 in the following year. This is done as the effect of a crop on N leaching loss continues in the months after its harvest with most leaching during fall and winter. To avoid overlap, leaching after the winter crops were then calculated from spring to spring. With the EU-Rotate_N model N leaching is calculated as leaching below 0.9 m (gross leaching, Fig. 1), but crop N uptake from below 0.9 m is also calculated, and this is subtracted from the gross leaching in order to calculate net leaching loss, as illustrated in Fig. 1. If the previous crop left plenty of N in the soil some will move downwards and accumulate in deeper soil layers. If the current crop is deep rooted the uptake from below 0.9 m can in periods exceed the amount leached below 0.9 m resulting in periods where negative net leaching is observed (Fig. 1). As crop rooting depths differ there is no optimal leaching depth to be determined, and net leaching must be calculated as described if the fate of N throughout the crop rotation should be described.

Climatic data

The model simulations were carried out using weather data collected during 25 years from 1983 to 2008 at Aarslev research station, Denmark (see Pedersen et al.

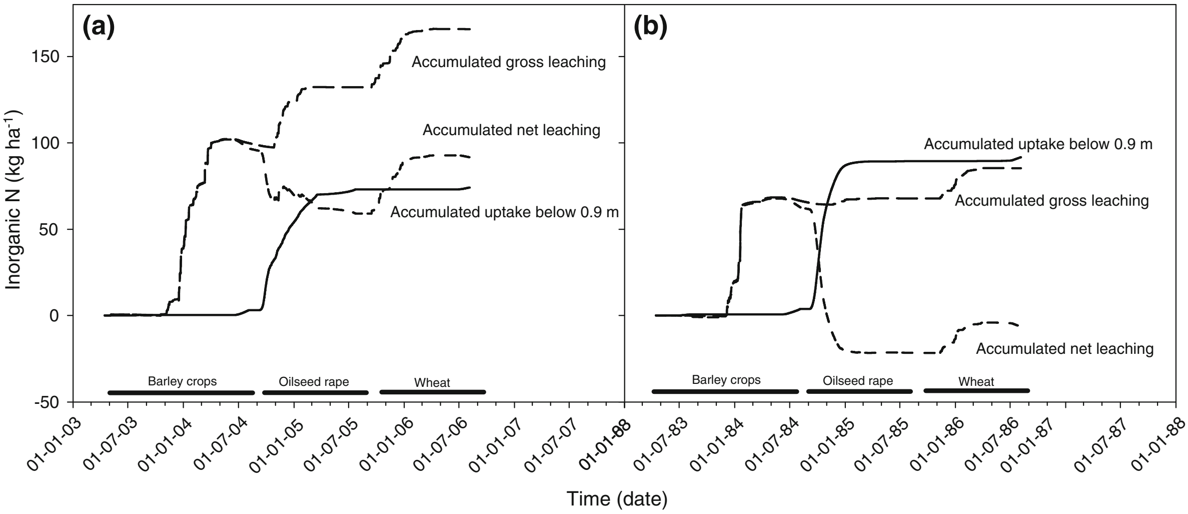


Fig. 1 Example of the relationship between N leached and N taken up from below 0.9 m. Accumulated uptake below 0.9 m, accumulated gross leaching and accumulated net leaching is shown in a crop rotation where the oilseed crop had a root penetration rate of 0.002 m $\mathrm{day}^{-1}{}^{\circ}\mathrm{C}^{-1}$. Pre-crop fertilization and fertilization for the oilseed rape crop were high (250 kg N ha^{-1}). The example is simulated with two different weather conditions (**a**, **b**)

2009). To study the effect of different yearly weather conditions, the 8-year simulations were run starting at different years, e.g. starting with the first barley crop in 1983, in 1984 and so on, creating a total of 18 different sets of weather conditions for simulating the crop rotations. This allowed us to analyze average NUE effects across years with different weather conditions as well as to analyze the variation and effects of specific weather conditions on NUE. In order to compare different regions with varying rainfall, we used the same weather file, but increased the rainfall to match a wetter region of Denmark (average 991 mm precipitation per year vs. 781 mm at Aarslev). The daily precipitation data from one region were increased based on the difference in average monthly precipitation between the two sites. Thereby only the amount of precipitation differed, whereas rainfall pattern and other weather conditions were maintained (Pedersen et al. 2009).

Most simulations were conducted using a sandy loam soil containing 11 % clay and 52 % sand in the top 0.5 m layer and 18–19 % clay and 48–49 % sand in the deeper soil layers. However, to simulate the effect of growing the crops on a sandy soil for some simulations this was changed to 5 % clay and 62 % sand in top 0.5 m layer and 5 % clay and 58–59 % sand in the deeper layers (simulation 5, Table 1).

Management

Simulations were made with different crop management (N fertilizer level, sowing date and the use of catch crops), in order to analyze interaction between crop management and genotype effects (Table 1). In the first rotation the simulations were conducted with varying N fertilization to the oilseed rape crop and the two preceding spring barley crops (Table 1, simulations 1 and 2). Wheat was simulated with medium level of N fertilizer, and either high or low pre-crop fertilization was applied to the preceding barley and oilseed rape (Table 1, simulation 4).

Most wheat simulations were done using a sandy loam soil and with a normal sowing date for Danish conditions (17/9). Effects of environmental conditions were also studied by using a sandy soil for the simulation (simulation 5), and with increased yearly precipitation (simulation 6). Examples of management effects were studied by including fodder radish as a catch crop after the winter wheat (simulation 7) (Table 1), and by making simulations with four different sowing dates of the winter wheat crop, two early, a normal and a late sowing date (24/8, 3/9, 17/9 and 2/10) (simulation 8).

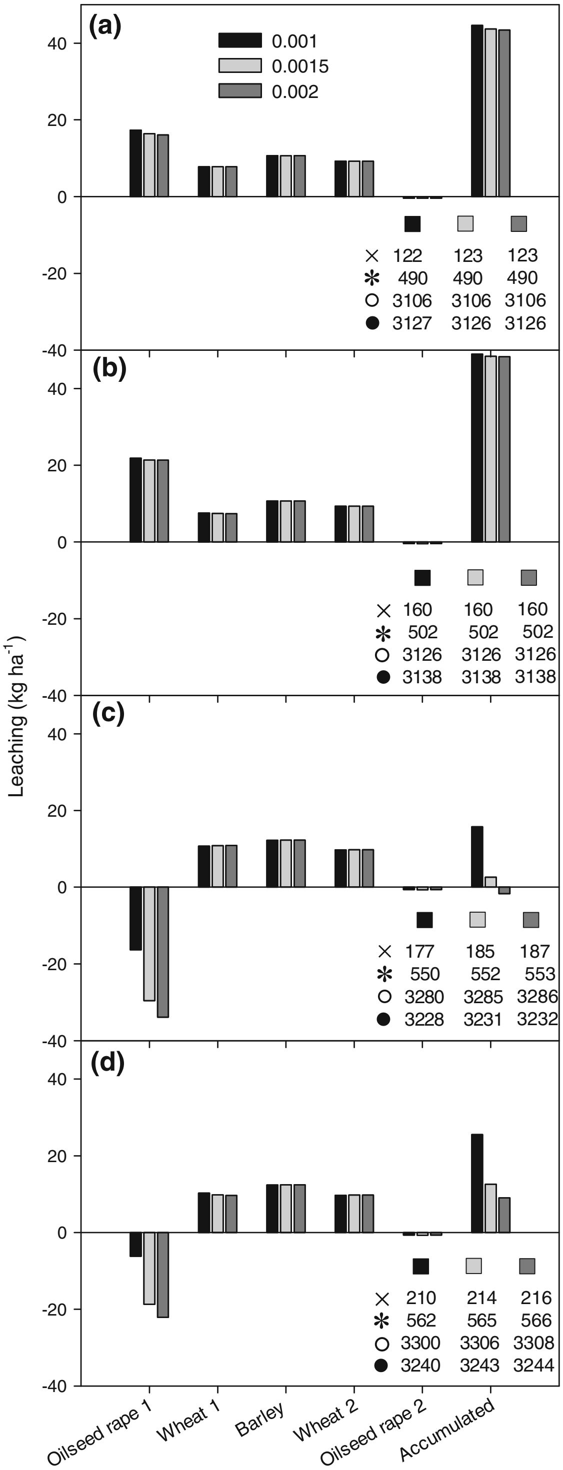


Fig. 2 Net leaching after each of the crops in a crop rotation ▶ where the oilseed rape crop had varying root penetration rates (0.001, 0.0015 and 0.002 m day^{-1}°C^{-1}) as well as accumulated leaching after all crops shown (simulation 1). **a** Low pre-crop fertilization (0 kg N ha^{-1}) and low (110 kg N ha^{-1}) oilseed rape fertilization. **b** Low pre-crop fertilization (0 kg N ha^{-1}) and medium (180 kg N ha^{-1}) oilseed rape fertilization. **c** High pre-crop fertilization (250 kg N ha^{-1}) and low (110 kg N ha^{-1}) oilseed rape fertilization. **d** High pre-crop fertilization (250 kg N ha^{-1}) and medium (180 kg N ha^{-1}) oilseed rape fertilization. *Times* harvested nitrogen (N) after oilseed rape, *asterisks* harvested N after following crops, *open circle* organic N in soil after oilseed rape, and *filled circle* organic N in soil after following crops

Experimental data

In this study, model simulations were used to study the effect of increased NUE due to single crop traits at the cropping system level. The EU-Rotate_N model has previously been validated to experimental data on aboveground biomass (Nendel et al. 2013) and on root density and soil N uptake (Pedersen et al. 2010). However, the effects on cropping system level might be small and would be difficult to measure in direct experiments where variation in experimental data could shadow the effects. Validation of the model to experimental data was therefore not the aim in this study, which leaves the results to be somewhat hypothetical. However, the parameter values used were based on experimental data. In 2011 and 2012 field experiments with different cultivars of oilseed rape was grown at different N levels. Roots were studied by 3 m long minirhizotrons inserted into the soil in an angle of 30° (Kristensen and Thorup-Kristensen 2004). Rooting depth and root intensity were determined three times during the growing season. In addition, leaf litter loss was determined during 2 week periods six times during the growing season.

Experimental values for litter loss rate and root penetration rate was determined, and the alternative values for these two parameters were chosen to differ significantly from the experimentally determined values.

Different cultivars of winter wheat were grown in field experiments in 2011 and 2012 as well. The cultivars were grown under different N fertilization and with varying sowing date. Root growth was determined six times during the growing season by the use of minirhizotrons and yield and N harvest index (HI) were determined at harvest. The results from these experiments were used to verify the average parameter values affecting NUE of winter wheat to be used in the model simulations and from which significantly different parameter values were chosen to simulate effects of genotypic differences.

Results

The results of altering parameter values in the EU-Rotate_N model, to represent genotypic differences in NUE, are presented for the crop itself and for the crops grown in the following years in the field. This is done as differences in 1 year will continue to affect field N dynamics in the subsequent years. Effects on the cropping system as a whole will therefore differ from the single crop effect observed in the first year. The fate of N through the cropping system, i.e. the losses of N due to leaching, the harvested N and the N remaining in the soil as organic N are all NUE components and was used to reflect the effect on NUE. Leaching loss of N is not well defined as it has to be calculated as N leaching below a specific soil depth although rooting depths varies between species. Leaching is often measured or simulated as leaching below 1.0 or 0.9 m, but some crops have deeper roots and also take up N from below this depth. In our simulations this is the case for oilseed rape as well as for winter wheat.

Root penetration rate

Sensitivity of the predicted values of the NUE components (leaching, harvested N and SOM-N)

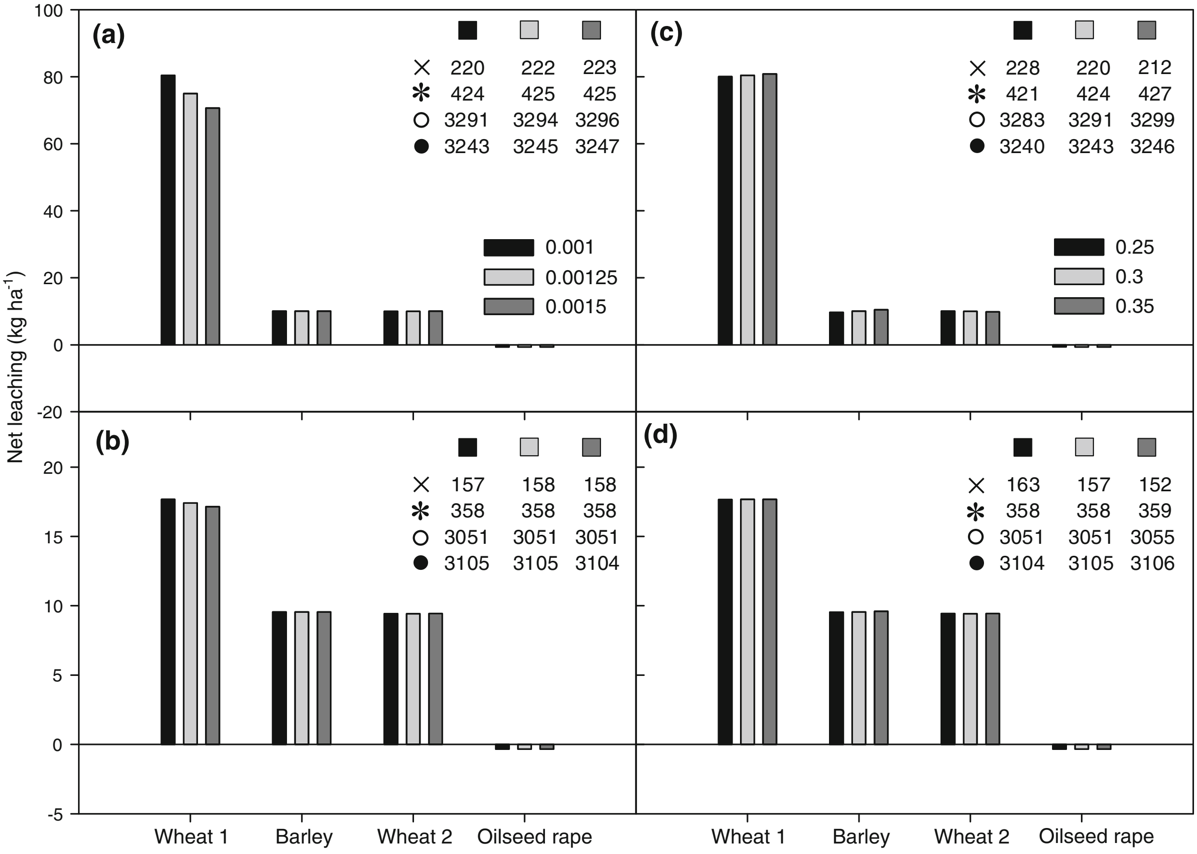
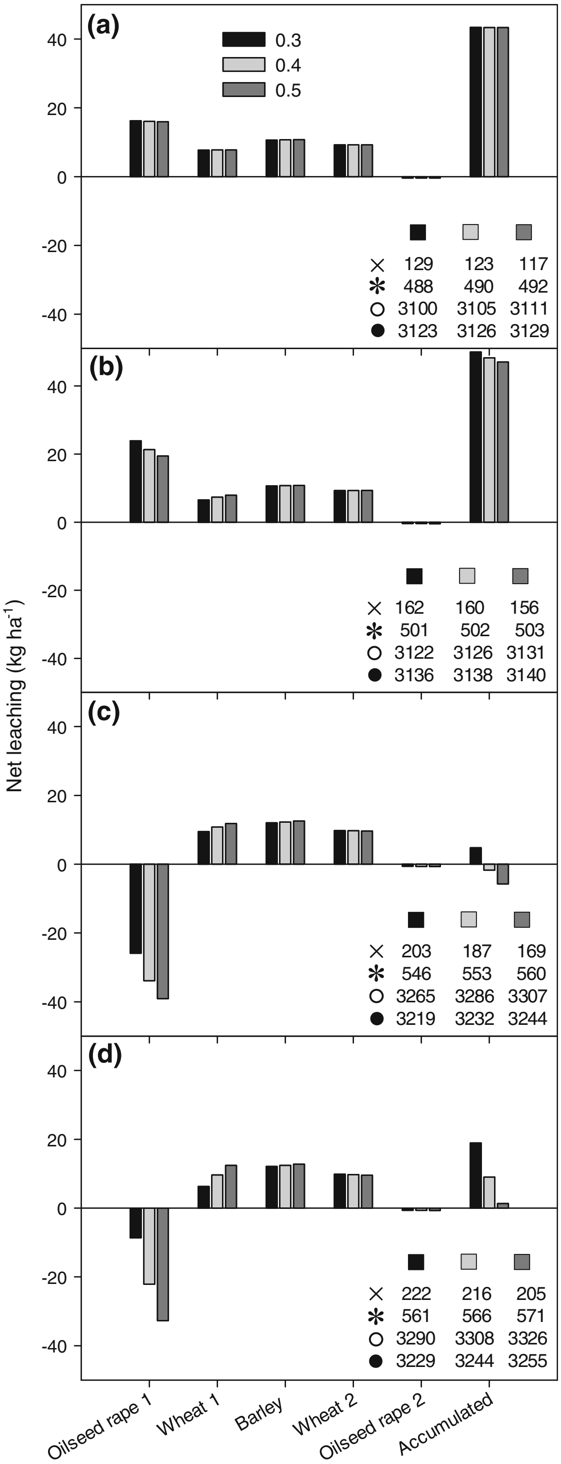


Fig. 3 Net leaching after each of the crops in a crop rotation where the winter wheat crop had varying root penetration rates (0.001, 0.00125 and 0.0015 m day^{-1}°C^{-1}) (**a**, **b**), and net leaching after each of the crops in a crop rotation where the winter wheat crop had a varying ratio of N in grain/N in straw (**c**, **d**) (simulation 4). The winter wheat crop was fertilized with medium (175 kg N ha^{-1}) level fertilizer. **a** High pre-crop fertilization (250 kg N ha^{-1}), **b** low pre-crop fertilization (0 kg N ha^{-1}), **c** high pre-crop fertilization (250 kg N ha^{-1}), and **d** low pre-crop fertilization (0 kg N ha^{-1}). *Times* harvested nitrogen (N) after winter wheat, *asterisks* harvested N after following crops, *open circle* organic N in soil after winter wheat, and *filled circle* organic N in soil after following crops



◀**Fig. 4** Net leaching after each of the crops in a crop rotation where the oilseed rape crop had varying litter loss percentages (0.3, 0.4 and 0.5) as well as accumulated leaching after all crops shown (simulation 1). **a** Low pre-crop fertilization (0 kg N ha^{-1}) and low (110 kg N ha^{-1}) oilseed rape fertilization. **b** Low pre-crop fertilization (0 kg N ha^{-1}) and medium (180 kg N ha^{-1}) oilseed rape fertilization. **c** High pre-crop fertilization (250 kg N ha^{-1}) and low (110 kg N ha^{-1}) oilseed rape fertilization. **d** High pre-crop fertilization (250 kg N ha^{-1}) and medium (180 kg N ha^{-1}) oilseed rape fertilization. *Times* harvested nitrogen (N) after oilseed rape, *asterisks* harvested N after following crops, *open circle* organic N in soil after oilseed rape, and *filled circle* organic N in soil after following crops

towards the changes in plant parameters varies depending on the environment or the management applied to the system. Increasing root penetration rate of winter oilseed rape (simulation 1, Fig. 2) and winter wheat (simulation 4, Fig. 3) was shown to reduce the net leaching loss during crop growth and in the following winter season, with little effect on leaching during the following years in the crop rotation (Figs. 2, 3). The effect of altering root penetration rate is highly dependent on other factors, especially on the pre-crop fertilization conditions, i.e. how much N is left in the soil to be taken up by deeper roots. When the preceding barley is given 250 kg N ha^{-1} the net leaching after both oilseed rape and wheat become negative, as much nitrate-N is available below the leaching depth, and the crops can take up more of this deep N than what is lost by leaching after harvest. While the depth penetration rate has little effect on N leaching when the pre-crop N fertilization was low, doubling the depth penetration rate of oilseed rape reduced leaching by c. 20 kg N ha^{-1} when the pre-crop N fertilization was high (Fig. 2). With low pre-crop N fertilization no effect is seen on N harvest or SOM-N content, whereas an increase in both components is determined when high N fertilization is given to the barley pre-crop.

Several components can be chosen to describe the effect of the altered parameters on NUE. We chose leaching, harvested N and SOM-N as NUE components. Whether the altered parameters leads the components to strengthen or counteract the impact of each other, will determine the overall effect on NUE. Increasing root penetration depth led to reduced net leaching, preserving a pool of N that would otherwise have been lost to the environment (Figs. 2, 3). The increased N uptake lead to more N in the plant material and thus more N harvested and less N left in the soil as organic N. Hence, on the single crop level increasing root depth penetration rate had a positive effect on all the processes affected.

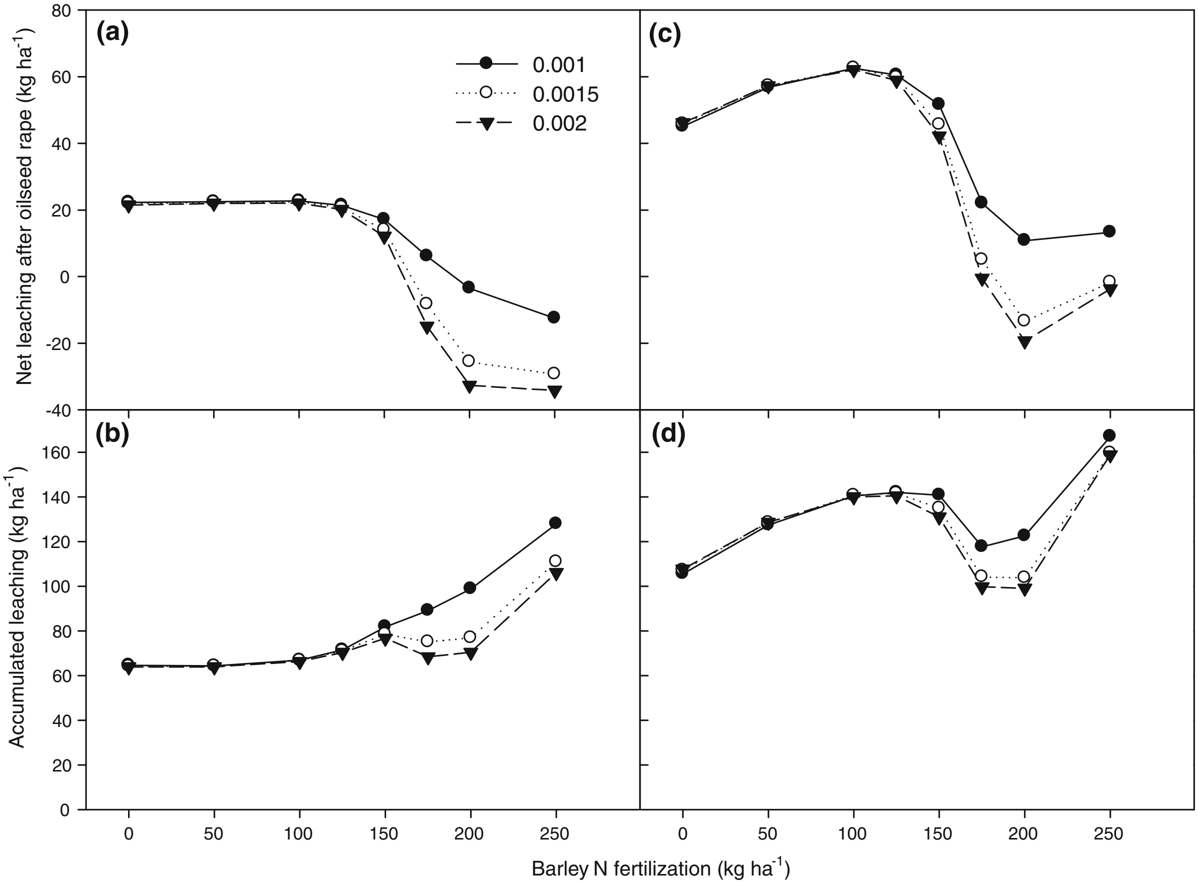


Fig. 5 Effect of pre-crop fertilization on net leaching after oilseed rape with varying root penetration rates (0.001, 0.0015 and 0.002 m day^{-1}°C^{-1}) (**a**, **c**) as well as accumulated leaching after the crop rotation (**b**, **d**) (simulation 2). Oilseed rape fertilization: **a** low (110 kg N ha^{-1}), **b** high (250 kg N ha^{-1}), **c** low (110 kg N ha^{-1}), and **d** high (250 kg N ha^{-1})

Litter loss rate

A somewhat different development is seen in simulations where NUE is improved by reducing the litter loss from the oilseed rape crop (simulation 1, Fig. 4). With low pre-crop and crop fertilization levels, leaching is not sensitive to altered litter loss rates. However, when the oilseed rape fertilization and/or the pre-crop fertilization are increased, leaching does become sensitive to the rate of litter loss (Fig. 4b–d). Plants with reduced litter loss have reduced overall biomass production, and thus a reduced N demand and uptake, leading to more N left in the soil for potential leaching after harvest. When the N content in the soil is increased through pre-crop effects or direct fertilization the effect becomes stronger (Fig. 4c, d). The following year the opposite effect is observed; leaching after the oilseed rape with high litter loss increases, as the leaf matter added to the soil continue to contribute to N mineralization. Irrespective of the fertilization levels, more N is harvested in the oilseed rape when less biomass is lost. However, more inorganic N is also left in the soil due to the reduced N demand. This will contribute to leaching as well as crop uptake in the following years.

While increased root depth penetration rate contributes to NUE in all aspects, the effect of reduced leaf litter loss is found to be more complicated. Effects are mainly seen when N availability is medium or high due to pre-crop effects or direct fertilization.

N harvest index

A change in the N harvest index only has a slight effect on leaching, with more leached with decreases in NHI, since more N is left in straw (simulation 4, Fig. 3). As

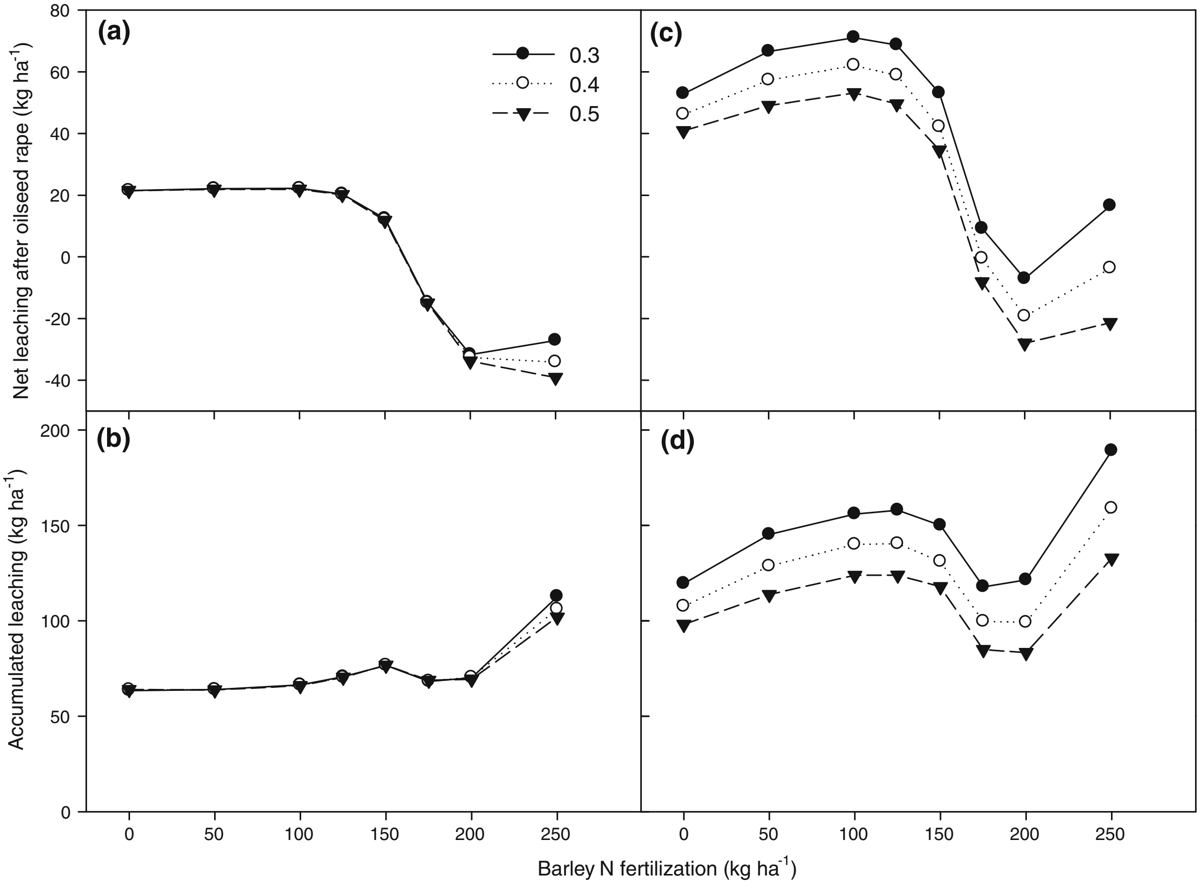


Fig. 6 Effect of pre-crop fertilization on net leaching after oilseed rape with varying litter loss percentages (0.3, 0.4 and 0.5) (**a**, **c**) as well as accumulated leaching after the crop rotation (**b**, **d**) (simulation 2). Oilseed rape fertilization: **a**, **c** low (110 kg N ha^{-1}), **b**, **d** high (250 kg N ha^{-1})

changes in NHI primarily affects the N removed from the field or the N left as organic N in the soil, the effect on leaching losses were low. Nevertheless, the effect of genotypic variations on leaching was shown to increase when pre-crop fertilization was high (Fig. 3c) and the same trend was seen in the crop the succeeding year. Increasing the NHI will obviously lead to increased N harvest, while the SOM-N content will decrease as less N is left in the straw. Under high fertilization conditions organic N in the soil is still lower at the end of the crop rotation when less N is left in the straw, indicating that the effect will continue in the future crops to come.

Increasing NHI improved NUE of the individual crop but the reduced SOM-N will affect the N uptake of the following crops, as less N will be mineralized. This will also result in reduced leaching the subsequent years.

Pre-crop fertilization

Sensitivity of net leaching to the genotypic variations is shown to be highly influenced by the fertilization applied. With low pre-crop fertilization and low fertilization to the main crop the sensitivity of net leaching to the genotypic variations was low (simulation 2, Figs. 5, 6) and neither increased rooting depth nor decreased litter loss affected leaching losses up to pre-crop fertilization of at least 125 kg N ha^{-1} (Fig. 5a, b) or even higher (Fig. 6a, b). Net leaching increased with increased fertilization especially in the plants with higher root penetration rate, as more is left in the deep soil layers after a highly fertilized pre-crop leading to increases in the amount of N taken up from these layers. However, overall accumulated leaching during the crop rotation will increase with increasing pre-crop fertilization (Fig. 5b).

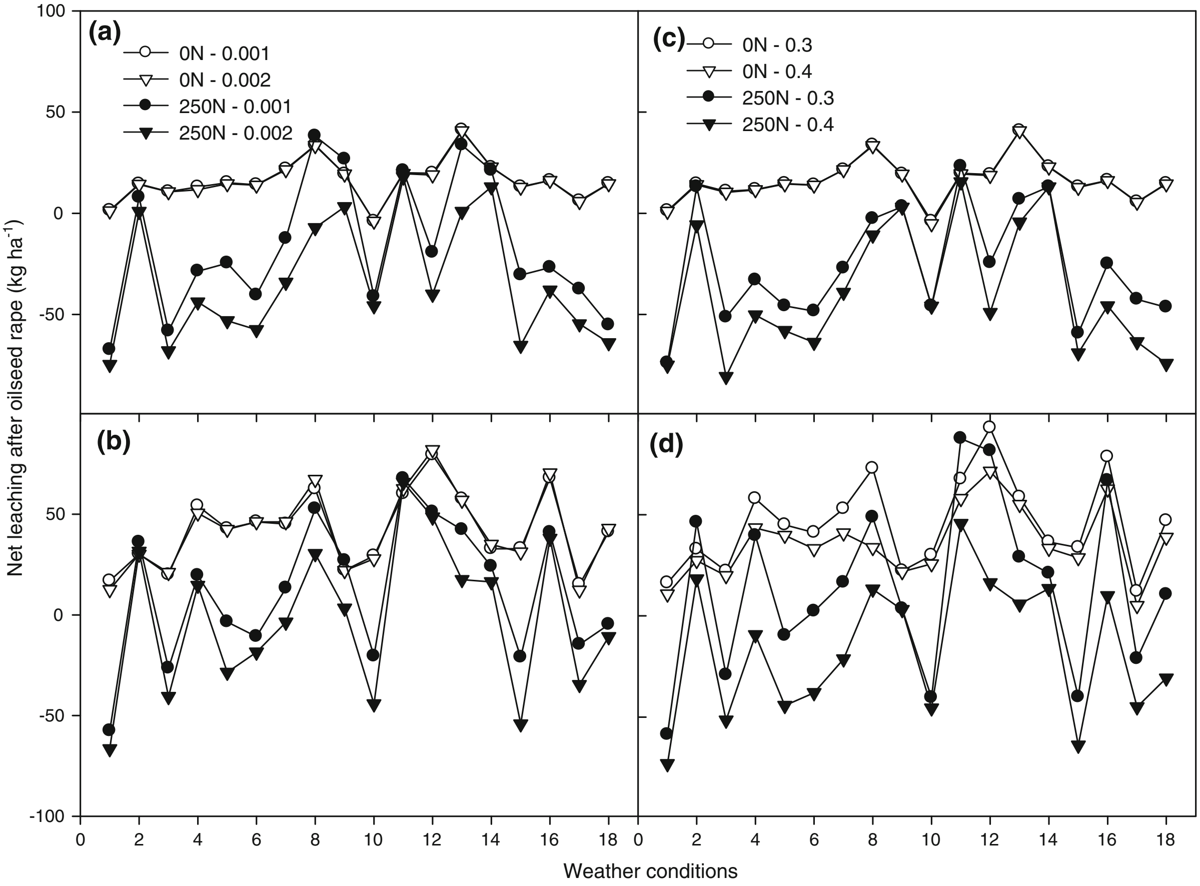


Fig. 7 Yearly variation in net leaching after oilseed rape with differing root penetration rates (0.001 and 0.002 m day^{-1}°C^{-1}) (**a**, **b**) and differing litter loss percentages (0.3 and 0.4) (**c**, **d**) (simulation 3). Weather conditions are constructed from 25 years climatic data resulting in 18 9-year periods. Oilseed rape fertilization: **a**, **c** low (110 kg N ha^{-1}) and **b**, **d** high (250 kg N ha^{-1})

Increasing the fertilizer level to the oilseed rape crop, results in more leaching losses as well (Figs. 5c, 6c) at all pre-crop fertilization levels. Especially the effect of changing litter loss rates increases with increasing fertilizer application as the lower biomass loss leads to lower N demand and therefore more is leached, when high fertilizer levels are applied (Fig. 6c, d).

Influence of environment

The model simulations showed that the predicted NUE components, net leaching, harvested N and organic N in soil, are more sensitive to environmental conditions than to genotypic variations. Differences in weather conditions such as temperature and precipitation, affects the leaching pattern significantly (simulation 3, Fig. 7). Leaching will especially be affected by precipitation under high fertilization conditions. In some years the weather conditions result in no difference between the genotypes, whereas in other years significant differences between the genotypes are seen (Fig. 7). Selecting single years where the effect of genotypes on leaching were either high or low (Figs. 8, 9), revealed the large differences in leaching and uptake below 0.9 m under otherwise similar conditions. When considering differences in root penetration rates it is clear that it is especially the uptake below 0.9 m that differentiates genotypes with varying root penetration rates more than the amount leached (Fig. 8) as increased root penetration rate will lead to higher sub-soil uptake. On the contrary, when

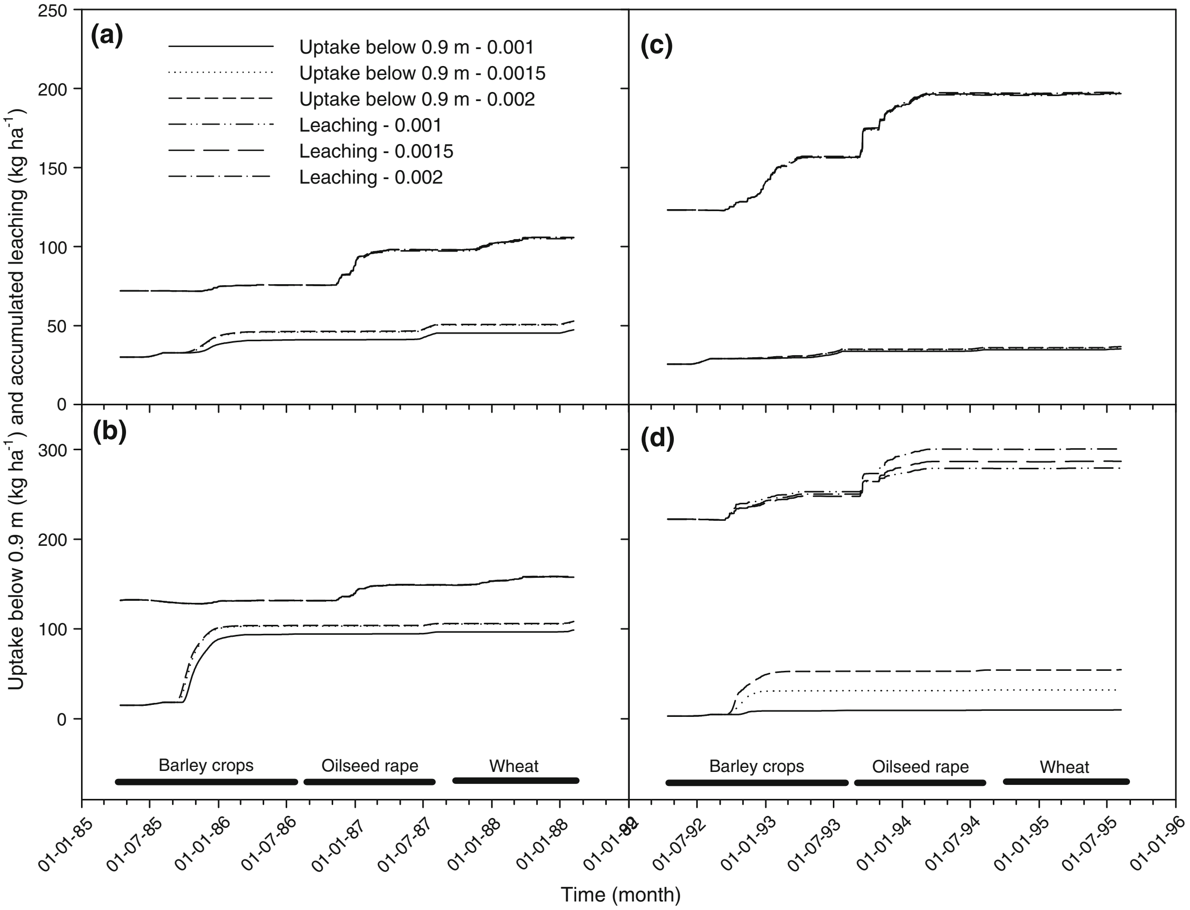


Fig. 8 Variation in leaching and uptake below 0.9 m of oilseed rape with varying root penetration rates (0.001, 0.0015 and 0.002 m day^{-1}°C^{-1}) during selected weather conditions (simulation 3). **a**, **b** Weather condition 1, **c**, **d** weather condition 8. Oilseed rape fertilization: high (250 kg N ha^{-1}) and pre-crop fertilization: **a**, **c** low (0 kg N ha^{-1}), **b**, **d** high (250 kg N ha^{-1})

considering differences in litter loss rates it is mainly the leaching losses that differentiate the genotypes with varying litter loss rates (Fig. 9). Thus, the amount of N taken up or leached varies considerably between years and will in some years increase the genotype differences and in others shadow the effect.

More permanent conditions such as climatic zones with differing average yearly precipitation and different soil types will also interfere with the effect of improved NUE by genotypic variation. Comparing a loamy soil to a sandy soil and an area with higher annual precipitation (simulation 5 and 6, Figs. 10, 11) it was clear that net leaching increased on the sandy soil and in the higher precipitation area. Leaching is especially high on the sandy soil (Figs. 10b, 11b), but the sensitivity of leaching to different litter loss rates was low on sandy soils (Fig. 11b). In contrast, the sensitivity increased under high precipitation conditions (Fig. 11c) resulting in larger differences between the genotypes.

Agronomic practices

In a model simulation the effect of growing a catch crop after wheat and before barley was compared to no crop cover during winter (simulation 7, Fig. 12). The effect of changing root penetration rates on leaching decreased when including a catch crop in the rotation. The leaching losses after wheat followed by fodder radish was shown to be more than halved compared to bare soil after the wheat. In total more organic N is also added to the soil after a crop rotation including a catch

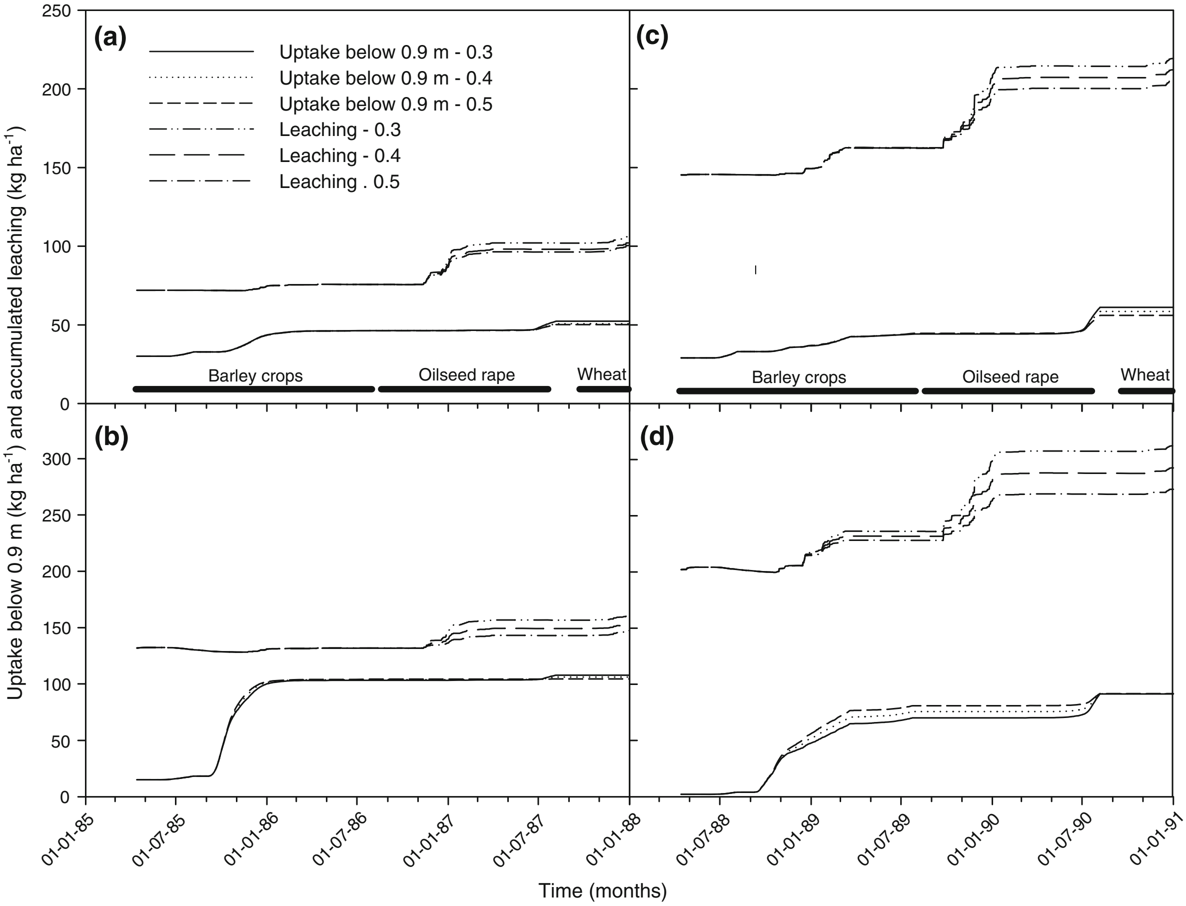


Fig. 9 Variation in leaching and uptake below 0.9 m of oilseed rape with varying litter loss percentages (0.3, 0.4, and 0.5) during selected weather conditions (simulation 3). **a**, **b** Weather condition 1, **c**, **d** weather condition 4. Oilseed rape fertilization: high (250 kg N ha^{-1}) and pre-crop fertilization: **a**, **c** low (0 kg N ha^{-1}), **b**, **d** high (250 kg N ha^{-1})

crop. Depending on when the organic N is mineralized it can either lead to more leaching after the crop or to more available N for the following crop.

Another effective agronomic practice is the modification of sowing dates e.g. by earlier sowing of winter wheat. We simulated wheat sown at four different autumn dates and the results showed that early sowing clearly reduces the leaching losses with up to c. 30 kg N ha^{-1} difference between the earliest sowing date and the normal sowing date (simulation 8, Fig. 13). This effect is enlarged with increasing root penetration rate. Less N is harvested after wheat when sown early, but more organic N is left in the soil. The effect of changing root penetration rates on leaching is low at the latest sowing date. At this point all genotypes will reach the deep soil layers too late to take up what was leached from the previous crop. The quantitative effects of both agronomic practices studied here were found to be clearly larger than the effects of the genotypic differences in NUE, with the highest differences in leaching of c. 10 kg N ha^{-1}.

Discussion

Improved NUE at the cropping system level is achieved with improved crop genotypes, in combination with crop management and optimization of crop rotation factors (Thorup-Kristensen 2006; Thorup-Kristensen et al. 2012). Improving NUE, not only of individual crops (Good et al. 2004) but of cropping systems, is a necessity to meet the demands for high productivity without increasing inputs.

Whether determined at the crop or the cropping system level, high NUE refers to a high productivity per unit nutrient available. However NUE at the cropping system level must be determined somewhat differently from NUE of a single crop. With the single crop, we analyze the crop use of available nutrients, but not the loss of nutrients from the system. When determining the NUE of cropping systems the fate of N in the system becomes important. If not lost, the N can stay in available or unavailable forms for the following crops. The N can remain as easily available nitrate in the topsoil or as less available nitrate in deeper soil layers. In addition, it can remain as N in easily decomposable crop residues or in more recalcitrant forms such as N in soil organic matter, which can be stored in the soil and only become available slowly over the next many years.

Determining cropping system NUE effects of single measures such as improved genotypes is challenging, since the effects are spread over several years and interact with many other aspects of the environment, crop management and crop rotation decisions. Model simulations are therefore an important tool to study NUE at the cropping system level, offering broader analysis of the effects to complement the more scattered experimental results at this level.

Additive effects or counteraction

The hypothesis that different ways of improving crop NUE in one crop would affect cropping systems differently, potentially leading to counteracting effects on NUE within the crop and in the following years was confirmed by the simulations, leading to a reduced overall effect on cropping system level.

With variable litter loss rates it was shown that NUE components counteracted each other, both within and between years. Reducing leaf litter loss reduced the overall N demand by the plant, leaving more N for seed production and thereby increased NUE, but also leaving more mineral N in the soil adding to leaching loss risk. So already within the first season, reduced leaf litter loss had opposing effects on NUE, and on top of this, it added less to soil organic matter N content, thereby reducing the amount of N becoming available for the succeeding crops through mineralization. Reducing litter loss rates is probably a valid approach to increasing the NUE of oilseed rape. However, it should be kept in mind, that the overall gain in cropping system NUE is less than the apparent direct effect which can be measured on the crop. Further, to obtain the best effect, it must be integrated with other agricultural practices, such as reducing N fertilization according to the reduced N demand, and understanding that it will make oilseed rape a less valuable pre-crop for other crops in the rotation, maybe increasing the amount of N fertilizer which has to be applied to the succeeding crops.

Thus, reduced litter loss improved NUE through increased N harvest in the crop, and again with small increases in N uptake in following crops, but reduced system NUE through increased N leaching losses in the autumn/winter season following the oilseed rape crop. Increased root penetration rate on the other hand, improved NUE through increased N harvest as well as through reduced N leaching loss the first autumn/winter season. In this case, plants with high root penetration rate reach deep layers fast and take up N that would otherwise have been lost to the environment. In the following years small increases in crop N uptake were also seen, as more N was left in crop residues. This contributed to overall increase in cropping system NUE. However, increased soil organic N could also lead to increased risk of leaching when the organic N is mineralized.

Thus, improved NUE measured on one crop and parameter may lead to misleading conclusions on the actual NUE improvement as: (1) improvement in N uptake in a crop one year may reduce N availability in the following years, and (2) improvements may be seen in one NUE component with opposite effects on other NUE components affected.

Environment and management

The effect of genotypic changes in NUE at cropping system level was also shown to be dependent on the environment and management of the crops as hypothesized. It was clear from the simulations that a NUE trait is not equally important under different environments.

The effect of variable root depth penetration rates was primarily important when significant amounts of N were present in deeper soil layers. Under conditions of potential high leaching, e.g. on a sandy soil or in areas with high precipitation, leaching of inorganic N will occur rapidly (Askegaard et al. 2005) and high root penetration rates will be necessary to ‘catch’ the N

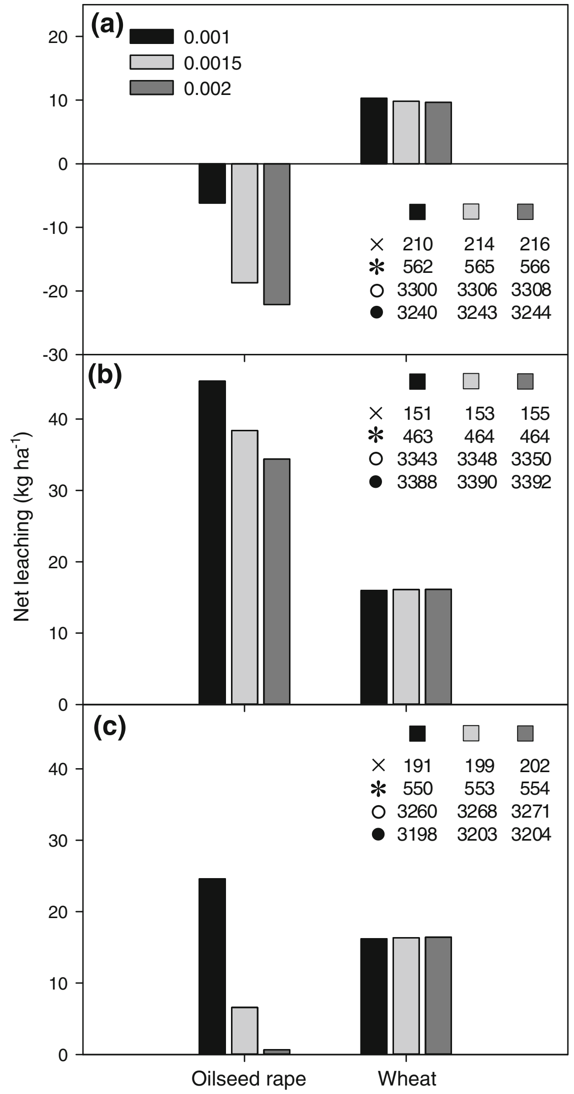


Fig. 10 Net leaching after oilseed rape with varying root penetration rates (0.001, 0.0015 and 0.002 m day^{-1}°C^{-1}) and the following winter wheat crop when grown on **a** a loamy soil, **b** a sandy soil and **c** under conditions with high annual precipitation (simulation 5 and 6). *Times* harvested nitrogen (N) after oilseed rape, *asterisks* Harvested N after following crops, *open circle* organic N in soil after oilseed rape, and *filled circle* organic N in soil after following crops

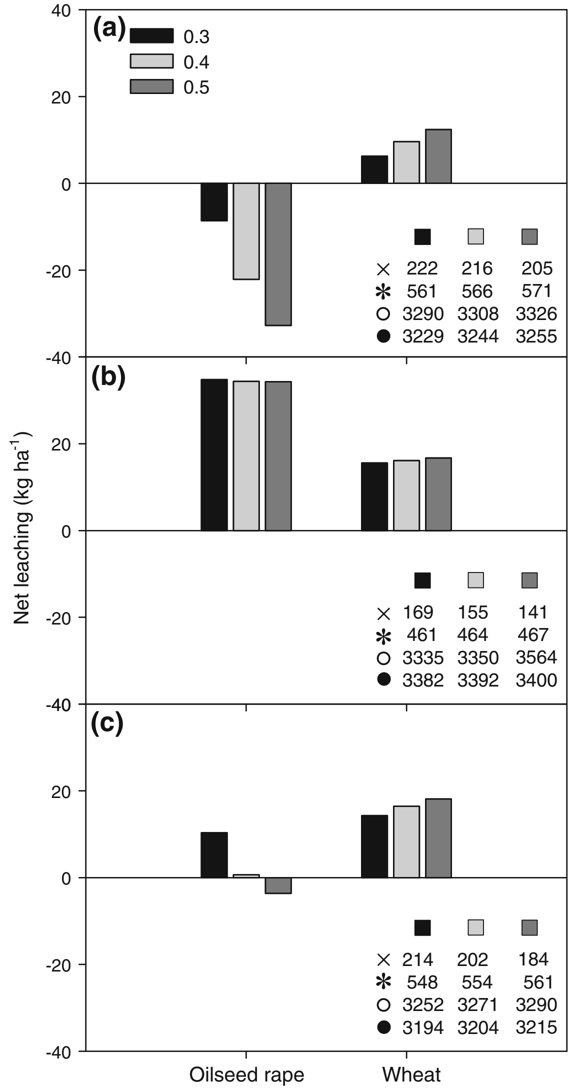


Fig. 11 Net leaching after oilseed rape with varying litter loss percentages (0.3, 0.4, and 0.5) and the following winter wheat crop when grown on **a** a loamy soil, **b** a sandy soil and **c** under conditions with high annual precipitation (simulation 5 and 6). *Times* harvested nitrogen (N) after oilseed rape, *asterisks* Harvested N after following crops, *open circle* organic N in soil after oilseed rape, and *filled circle* organic N in soil after following crops

before it is beyond the rooting depth of the crop (Fig. 10b, c). Combining low precipitation with high soil water holding capacity may lead to the opposite situation, where inorganic N will remain in the upper soil layers reducing the importance of deep rooting for N uptake. However, in situations in between these extremes, common for many temperate areas, N will often leach deep into the soil, though staying within reach of deep rooted crops.

Downward leaching is not in itself a loss process, if roots are present in deeper soil layers the leached N will only be lost if it leaches beyond the root zone (Thorup-Kristensen 2006). As the higher pre-crop fertilization leaves substantial amounts of N below

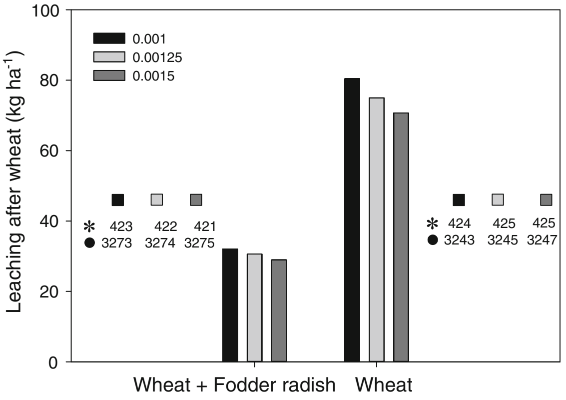


Fig. 12 The effect of sowing a catch crop (fodder radish) after winter wheat on net leaching after the crop compared to bare soil (simulation 7). The effect was determined on winter wheat with varying root penetration rates (0.001, 0.00125 and 0.0015 m day^{-1} °C^{-1}). *Asterisks* harvested N after following crops, and *filled circle* organic N in soil after following crops

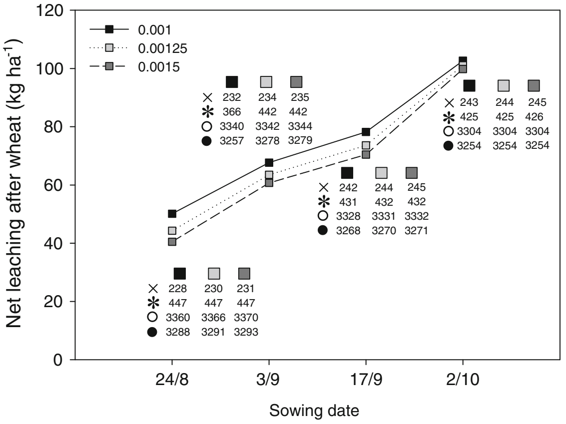


Fig. 13 The effect of sowing date on net leaching after winter wheat with varying root penetration rates (0.001, 0.00125 and 0.0015 m day^{-1} °C^{-1}) (simulation 8). *Times* harvested nitrogen (N) after oilseed rape, *asterisks* Harvested N after following crops, *open circle* organic N in soil after oilseed rape, and *filled circle* organic N in soil after following crops

0.9 m it enables deep rooted crops to take up part of the N from these soil layers that would otherwise have been lost to the environment. Oilseed rape is efficient in 'cleaning up' after high fertilization of previous crops as it has a deep root system and can take up large amounts of N (Barraclough 1989). However, too high pre-crop fertilization levels will initially lead to more leaching losses continuing until the oilseed rape crop develop its deep roots, allowing it to take up N from below the designated leaching depth. Despite the fact that oilseed rape generally show a high N balance surplus (high N fertilization compared to N removal by harvest (Rathke et al. 2006), it is still very efficient in taking up N after high fertilization conditions due to the deep rooting and high N demand for its above-ground growth (Lemaire et al. 2007, 2008). Experimentally, yields of winter oilseed rape have been found to be dependent on the pre-crops. When grown after peas, which leave significant amounts of N in the soil, yields were higher than when following a cereal crop (Rathke et al. 2005). Winter oilseed rape itself also has a positive effect when sown as pre-crop to cereals, both due to the function as break-crop for diseases, but also because of the relatively high amounts of N left in the soil after winter oilseed rape (Kirkegaard et al. 1997; Rathke et al. 2006).

Leaching after oilseed rape with different litter loss rates was shown to be almost equally large when grown on sandy soils, as downward movement of available N will occur fast and be lost from the root zone. The most important factor for varietal differences in yield of oilseed rape under low N conditions was shown to be the N uptake mainly after flowering (Berry et al. 2010; Schulte auf'm Erley et al. 2011), in accordance with the fact that N taken up late will have a reduced risk of being lost through litter loss. Other studies where litter loss was taken directly into account showed that NUE genotypes of oilseed rape were characterized by high root growth in the vegetative phase, combined with slow aboveground growth and N uptake until beginning of flowering (Ulas et al. 2012). In addition, N uptake after flowering was more important for NUE than N remobilization from vegetative biomass in oilseed rape at both high and low N supplies (Ulas et al. 2013). Bogard et al. (2010) also found that post-anthesis uptake in winter wheat was the main process accounting for grain protein deviation (deviation from the regression line between grain yield and grain protein concentration) which was a useful trait to improve grain yield and grain protein concentration simultaneously.

Year to year variation in precipitation and leaching strongly affect the leaching, yields and quality of crops, and yearly weather variation will lead to variable conditions for crop traits to affect crop NUE. The 18 different sets of weather conditions clearly revealed that this is the case. In some years no sensitivity was seen to variable genotypes, while in other years strong sensitivity was observed. It is practically impossible to predict the yearly variation but important to be aware that it might control the effect of the NUE related crop traits. This fact stresses the importance of taking plants into the field and run trials for a number of years and/or a number of sites to include a relevant range of environmental conditions for more general conclusions to be drawn.

Yearly variation in leaching also means that the total soil N supply for the crop will vary strongly from year to year. If a standard fertilizer dose is applied as is common practice, some years the total supply will be well above optimum supply, leading to inefficient use and increased risk of subsequent N loss.

Agronomic practice versus breeding

Finally, we made an attempt to compare effects of agronomic practice to breeding. Comparing the two directly is not possible, as both can be approached in many ways, and selected examples were therefore compared. Agronomic practice and breeding do not exclude each other, both approaches are needed and important, and can be applied simultaneously. However, they are very different in nature and in what aspects of NUE may be improved. The simulations revealed that the effect of improved agronomic management will be much larger than the effect of genetic improvement, here effects of catch crops or earlier sowing of wheat were approx. five times as high as the effect of genetically increased root depth penetration rates, even though a large genetic improvement was assumed, but this exact comparison is related to the specific simulations chosen in this study.

Including catch crops in the crop rotation was shown to have a positive effect on the net leaching after the crop, as has been shown in many studies (e.g. Askegaard et al. 2005), and the effect was high compared to reductions in leaching due to genotypic variation in root penetration rates or litter loss rates. Catch crops grown to reduce nitrate leaching do also affect the N supply for succeeding crop in the rotation. However, the effect on the following crop is again highly dependent on management factors such as incorporation time of the catch crop and also the specific weather conditions that year (Thorup-Kristensen and Dresbøll 2010).

Changing the autumn sowing date of winter wheat to an earlier date made the winter wheat have some of the same effect as a catch crop with a 50 % reduction in net leaching between the earliest and latest sowing dates, as it has also been seen previously from experimental data (Thorup-Kristensen et al. 2009).

Catch crops and earlier sowing of main crops are just examples of practices that would affect the NUE and combining different practices might even further reduce the losses from the system. However, most agronomic practices have drawbacks as well. Too early sowing can result in problems with weeds and increase winter vulnerability of the plants and sowing catch crops is more labor intensive and is a practice that should be repeated every year by the farmer in contrast to traits built into new genotypes.

Another important agronomic practice is adapting fertilization to yearly variation in soil N supply and plant N demand. Using methods such as pre-sidedress soil nitrate test (PSNT) which use a measure of soil NO_3-N concentrations and provide site- and year specific N recommendations, was shown to decrease leaching from a sandy loam soil (Guillard et al. 1999). Delaying the last fertilizer application to after flowering would also increase the NUE (Bogard et al. 2010).

The variations in NUE made possible by breeding were generally in the order of only a few kg N ha^{-1} up to about 30 kg N ha^{-1} per year according to the model simulations. Even though this might seem as a moderate improvement the results are higher than what can be expected from breeding in the near future, as we chose large differences in crop parameter values to emphasize the impact of breeding for NUE. Thus, realistically the outcome of breeding will be significantly lower than the obtained differences in these model simulations, at least within the next 10 years or more. However, breeding for traits that improves NUE will lead to significant results if the improved traits are incorporated into many lines and grown over large areas every year. An increase in rooting depth of just 0.1 m could make a very significant contribution to NUE if applied to most of the European wheat area.

Examining the genetic improvement of French winter wheat cultivars released during 46 years Brancourt-Hulmel et al. (2003) found that yields had increased significantly (on average 126 kg ha^{-1} $year^{-1}$) and mainly through reduction of height. Cultivars with shorter straw had higher harvest index and more consistent yields. Another important change was increased kernel number (on average 115 year^{-1}) without reduced kernel weight. The modern cultivars had increased NHI and were shown to use the N more efficiently than old cultivars for grain production. It is generally accepted that improved dry matter partitioning, i.e. higher HI is the main reason for improved yield in modern dwarf or semi-dwarf genotypes rather than increased N uptake or greater total dry matter production (Barraclough et al. 2010).

It has been claimed that the genetic gains in wheat yield have slowed down in the last decades. However, in a study comparing CIMMYT spring wheat lines from 1977 to 2008 it was shown that genetic gains in yield were still observed especially related to earliness of heading, cooler canopies and increases in stay-green. These parameters are associated with heat and drought adaptation and are related to root systems able to take up water from deep soil layers (Lopes et al. 2012). Thus, various parameters have been improved through breeding during the last decades though increased yield has also led to a decrease in grain protein concentration (Bogard et al. 2010). The continued breeding gain show that while yearly gains from genetic improvements are relatively small, they continue to accumulate over years giving a large total contribution to agricultural NUE.

Simulations revealed that sensitivity of crop and cropping system NUE components to genotypic differences in NUE traits was highly dependent on external factors such as fertilization level, precipitation and soil type. Crop genotype can to some extent affect the loss processes, through their uptake, the amount and quality of their crop residues and by their rooting depth. However, even the most efficient crop genotype cannot prevent release of nutrients outside of the growing season, or prevent that it is lost by leaching, denitrification or erosion. Such processes may on the other hand be affected by agronomy in choosing different crops, cropping practices or e.g. adding catch crops, thereby changing the duration and timing of periods where the field is left without crops.

Conclusion

NUE is not a well-defined trait that can be measured and selected for when breeding new cultivars. Even the term is not well defined itself on cropping system level, and the NUE of a crop is not only the result of its genetics, but also of its genetics interacting with environmental conditions and agricultural management, as shown by many of the simulated examples. Traits such as root growth, the N uptake from soil to plant, transport and remobilization of N in the plant, harvest index, N harvest index and litter loss are just some of the factors that influence NUE. When developing strategies for breeding for improved NUE, it is therefore important to consider the system in a holistic manner.

Whether improving NUE by traditional breeding or by genetic modifications model simulations have shown clearly that single crop evaluation is not sufficient as effects on crop level will affect the succeeding crops in the rotation as well. It should also be considered whether the improvements are relevant under the relevant environmental and management conditions.

Breeding is important and a necessary step towards more NUE cropping systems, but, there are aspects of the NUE problem which cannot be approached by breeding, but only by agronomy, just the fact that most leaching loss occur during autumn and winter where there is little or no crop growth activity stresses this point. Breeding may contribute in an indirect way to solve this problem, not by breeding for improved NUE of the crop, but by helping to shorten the periods with bare soil e.g. breeding for genotypes suited for earlier sowing as in the simulated wheat example or by breeding for improved catch crops.

There are other aspects of NUE where agronomy offer better opportunities in the short term, while improvements through breeding will have to accumulate over longer time in order to achieve similar improvements.

Model simulations are a powerful tool to examine the effect of G×E×M on single crop growth and NUE as well as effects on NUE at the cropping system level. However, modelling is of course not the only and superior approach to work with G×E×M, but should be combined with experimentation. However, there are aspects where experimentation is so difficult and effects are so small that attempts to measure them will normally drown in experimental variation, and modelling may be the only realistic chance to estimate such effects. Though, without direct validation of the model output against measured data on the effect of the altered parameters on yield, crop or soil N, the simulated results should be considered as guidelines more than exact values.

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