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Abstract

Nitrogen (N) is a key element in terrestrial ecosystems as it influences both plant growth and plant interactions with the atmosphere. Accounting for carbon-nitrogen interactions has been found to alter future projections of the terrestrial carbon (C) cycle substantially. Dynamic vegetation models (DVMs) aim to accurately represent both natural vegetation and managed land, not only from a carbon cycle perspective but increasingly so also for a wider range of processes including crop yields. We present here the extended version of the DVM LPJ-GUESS that accounts for N limitation in crops to account for the effects of N fertilisation on yields and biogeochemical cycling.

The performance of this new implementation is evaluated against observations from N fertiliser trials and CO₂ enrichment experiments. LPJ-GUESS captures the observed response to both N and CO₂ fertilization on wheat biomass production, tissue C to N ratios (C : N) and phenology.

To test the model's applicability for larger regions, simulations are subsequently performed that cover the wheat-dominated regions of Western Europe. When compared to regional yield statistics, the inclusion of C–N dynamics in the model substantially increase the model performance compared to an earlier version of the model that does not account for these interactions. For these simulations, we also demonstrate an implementation of N fertilisation timing for areas where this information is not available. This feature is crucial when accounting for processes in managed ecosystems in large-scale models. Our results highlight the importance of accounting for C–N interactions when modelling agricultural ecosystems, and it is an important step towards accounting for the combined impacts of changes in climate, [CO₂] and land use on terrestrial biogeochemical cycles.

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1 Introduction

Nitrogen (N) plays an important role in plant productivity and physiology (Evans, 1989a) and is one of the main limiting nutrients for the functioning of ecosystems in many parts of the world (Grindlay, 1997; Gruber and Galloway, 2008; Vitousek et al., 2002), both in natural and agricultural ecosystems. Historically in agriculture, N limitation for crops has been overcome by the use of manure and N fixing legumes (Vitousek et al., 1997). Since the discovery of the Haber-Bosch process in the 1910's, humans have been able to effectively overcome N limitation by large scale production and application of reactive N in the form of mineral fertilisers (Vitousek et al., 1997).

The enhanced input of reactive N into agricultural ecosystems by fertiliser use, and deposition to the earth's surface of nitrous oxides which are by-products from combustion, has together with other technical developments more than doubled global food production during the 20th century (Tilman et al., 2001, 2002). However, enhanced N-input can also have detrimental effects on biodiversity and water quality, and lead to substantial emissions of N trace gases that affect air quality and climate (Galloway et al., 2004; Rockstrom et al., 2009; Tilman et al., 2002; Vitousek et al., 1997). Better understanding of N effects on yields, conjointly with other ecosystem processes, especially in a changing climate and CO₂ environment is therefore needed for a sustainable management of agricultural ecosystems, weighing enhanced productivity against detrimental side-effects.

N cycling by ecosystems is strongly interlinked with the carbon (C) cycle, which in turn has also undergone drastic changes during the 20th century (Ayres et al., 1994; Rockstrom et al., 2009; Vitousek et al., 1997), as the increased transport of C from the geo- and biosphere to the atmosphere through various human activities leads to an increase in carbon dioxide concentration ([CO₂]). Higher [CO₂] can have a positive effect on plant productivity, the reasons for this is that CO₂ is the main substrate in photosynthesis. Elevated concentrations relative to O₂ in the intercellular spaces of leaves are known to reduce photorespiration resulting from fixation of O₂

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by the enzyme Rubisco that catalyses the carboxylation step of photosynthesis (Long, 1991). In addition, enhanced levels of CO₂ result in increased water use efficiency in those plant species that lower stomatal conductance under elevated [CO₂], which limits transpirational water loss (Ainsworth and Rogers, 2007; Drake et al., 1997; Sun et al., 2014). However, CO₂ is also a greenhouse gas that leads to higher air temperatures which in turn can either increase or decrease plant productivity depending on the magnitude of the temperature increase. Several studies have assessed the effect that the already experienced environmental change has had on food production (e.g., Lobell et al., 2011; Olesen et al., 2011; Schlenker and Roberts, 2009; Tubiello and Ewert, 2002), and on the projected future changes, using crop models (e.g., Fischer et al., 2001; Rosenzweig and Tubiello, 2007; Rosenzweig et al., 2013). However, the magnitude of the CO₂ fertilisation of crop ecosystems is still under debate (Ainsworth et al., 2008; Rosenzweig et al., 2013; Sun et al., 2014).

A recent model intercomparison highlighted large uncertainties arising from treatment of warming effects vs. effects of CO₂ and N fertilisation on projections of global crop yields (Rosenzweig et al., 2013). In particular, differences between models, in the representation of a CO₂ fertilisation effect on productivity was highlighted as a key determinant of between-model differences, including globally applicable versions of traditional crop models (e.g. DAYCENT, Stehfest et al., 2007 and GEPIC, Liu et al., 2007), a crop management impact model (PEGASUS, Deryng et al., 2011) and also crop-enabled Dynamic Vegetation Models (DVMs) LPJmL (Bondeau et al., 2007) and LPJ-GUESS (Lindeskog et al., 2013).

For the simulation of crop productivity, traditional crop models typically rely on empirical scaling factors to modify the radiation-use efficiency based on measurements in CO₂ fertilisation experiments (Boote et al., 2013). A mechanistic representation of the CO₂ response (as well as other processes) has been argued to be critical when modelling crop responses to climate change (Yin, 2013), as recently shown for state-of-the-art crop models (Boote et al., 2013). In contrast to crop models, which are optimised to simulate yields, DVMs are tools for exploring and predicting the

coupled dynamics of ecosystem functioning, climate-carbon cycle interactions and biome distributions (Friedlingstein et al., 2013; McGuire et al., 2001; Prentice et al., 2007). In DVMs, photosynthesis and stomatal conductance are coupled and respond conjointly to changes in [CO₂] (Haxeltine and Prentice, 1996a). New developments in some DVMs in recent years are the inclusion of (1) land-use change and land management functionalities and (2) N cycling (cf., Arneth et al., 2010; Prentice et al., 2007; Smith et al., 2014; Thornton et al., 2002; Xu-Ri and Prentice, 2008).

The inclusion of N dynamics in DVMs has been found to alter future projections of climate and CO₂ interactions with the C cycle (Arneth et al., 2010; Friedlingstein et al., 2013; Thornton et al., 2009; Wårlind et al., 2014), while the land-use change functionality facilitates assessment of large scale patterns of changes in yields within a consistent model framework that can also address questions such as how management affects the land C sink (Bondeau et al., 2007; Lindeskog et al., 2013; Shevliakova et al., 2013). Important management options in this context include decisions on when to sow and harvest, irrigation, residue removal, presence of cover crops, tillage, or fertilisation. For the DVM LPJ-GUESS, including cropland and managed grasslands notably improved phenology when compared with satellite data (Lindeskog et al., 2013). In a study on land-use change in Africa for the 20th century, Lindeskog et al. (2013) found that the impact of implementing land-management decisions was of similar importance for the continental C budget as the effect of applying static vs. dynamic land use input data. Levis et al. (2012) showed that including an explicit representation of croplands in the Community Land Model changed both the patterns and amplitudes in the modelled climate compared to treating croplands as unmanaged grasslands. Still, only a few of today's DVMs account for crop processes and C–N coupling in crops (e.g. Arora, 2003; Drewniak et al., 2013), which is a prerequisite to account for fertiliser input, the associated effects it has on yields and the C cycle – and hence ecosystem fluxes affecting atmospheric composition and climate.

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Relationships between allocation to L, St, R and grains (Y) from the original allocation model of Penning de Vries et al. (1989) were established and fitted to a logistic growth function, a Richards curve (Richards, 1959), (Eq. 2):

$$f_i = a + \frac{b - a}{1 + e^{-c(DS-d)}} \quad (2)$$

5 where f_i is the daily allocation of assimilates to a plant organ relative to e.g. the shoot, a is the asymptote when $DS \rightarrow 0$, b is the upper asymptote when $DS \rightarrow \infty$, c the growth rate, and d is the DS of maximum growth.

Roots

The allocation to R (g_R) relative to the vegetative organs (g_V) (Eq. 3) is shown in Fig. 1a:

$$10 \frac{g_R}{g_V} = 0.52 + \frac{-0.47}{1 + e^{-7.63(DS-0.55)}} = f_1 \quad (3)$$

Leaves and stems

Reflecting the shift from L (g_L) to St (g_{St}) allocation during the initial part of the vegetative phase as outlined above, a relationship between the two organs were derived (Eq. 4) which is illustrated in Fig. 1b.

$$15 \frac{g_L}{g_L + g_{St}} = 0.88 + \frac{-0.79}{1 + e^{13.99(DS-0.65)}} = f_2 \quad (4)$$

Harvestable organs, grains

Finally a relationship of the allocation to grains (g_Y) as the fraction of the whole plant ($g_Y + g_V$) allocation (Eq. 5) was derived:

$$\frac{g_Y}{g_Y + g_V} = \frac{1}{1 + e^{-8.32(DS-1.15)}} = f_3 g_V = 1 - f_3 \quad (5)$$

Dynamic allocation

These relationships between the allocation to the different organs of the plant can be applied to favour allocation to one organ over others. Combining Eqs. (3)–(5) yields:

$$\begin{aligned}g_R &= f_1(1 - f_3) \\g_L &= f_2(1 - f_1)(1 - f_3) \\g_{St} &= (1 - f_2)(1 - f_1)(1 - f_3) \\g_Y &= f_3\end{aligned}\tag{6}$$

5 which is illustrated for winter wheat in Fig. 1b and for spring wheat in Fig. A1b.

Carbohydrate retranslocation

Crops store an easily mobilised reserve of carbohydrates in L, St and R (for some crops also tubers) (van Ittersum et al., 2003; Penning de Vries et al., 1989). To represent this in the model, a labile C pool is filled with a fraction of the C allocated to the stem, set here to 0.4 for wheat (Penning de Vries et al., 1989). During days when the daily assimilated C is lower than respiration costs (negative NPP), these sugars are used to compensate the loss (Seligman et al., 1975). Additionally, during the grain filling period the labile C pool is used to add to the grains and is reduced with a rate of 0.1 day^{-1} (Penning de Vries et al., 1989).

2.1.2 Daily nitrogen allocation

During the vegetative phase in which the leaves and roots are expanding, the plant seeks to maximise photosynthetic gain by having a leaf N content that optimises the carboxylation capacity (V_{\max}) (Hirose and Werger, 1987; Kull, 2002). Following Haxeltine and Prentice (1996a) and Smith et al. (2014) this is done by calculating the V_{\max} that maximises canopy-level net C assimilation given the current temperature, water status and biomass C : N.

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Leaf N content

Nitrogen associated with Rubisco, the key enzyme in photosynthesis, makes up more than 20 % of the total N in the leaves of wheat (Evans, 1989a), but N is also important for plant structural tissues (Anten et al., 1995; Hirose, 2005; Kull and Jarvis, 1995).

5 However, the vertical distribution of N in the canopy is not even. Higher [N] is usually found in the upper part of the canopy, where leaves experience the highest levels of irradiance (Hirose and Werger, 1987; Hollinger, 1996; Evans, 1989b), compared to the more shaded leaves below. The decline in leaf [N] with the increase in cumulative leaf area index (LAI) from top to bottom typically follows an exponential decrease with a N
10 extinction coefficient k_N that is related to the light extinction coefficient (k_L) as follows:

$$k_N = \beta_0 + \beta_1 k_L \quad (7)$$

where β_0 and β_1 are regression coefficients taken from Yin et al. (2003). Yin et al. (2000) derived a relationship between the LAI of an optimal N distribution in a crop canopy (Eq. 8) and k_N :

$$15 \quad LAI_N = \frac{1}{k_N} \ln \left(1 + k_N \frac{M_{N,L}}{N_b} \right) \quad (8)$$

where $M_{N,L}$ is the leaf N mass and N_b (Eq. 9) is the minimum N requirements for the leaf to function:

$$N_b = \frac{1}{C : N_{L,max}} SLA \quad (9)$$

20 where $C : N_{L,max}$ reflects the minimum N required for photosynthesis and SLA is the specific leaf area ($m^2 kg C^{-1}$).

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Root N content

The N requirement of the root follow that of the leaves through the functional balance concept (van Ittersum et al., 2003; Smith et al., 2014; Zaehle and Friend, 2010):

$$\frac{M_{N,L}}{M_{C,L}} \propto \frac{M_{N,R}}{M_{C,R}} \quad (10)$$

5 where $M_{N,L}$ denotes leaf N mass, $M_{C,L}$ leaf C mass, $M_{N,R}$ root N mass and $M_{C,R}$ root C mass. The theory behind the concept is that the activity of the roots (uptake and transport of water and nutrients) is proportional to that of the leaves (photosynthesis). A high photosynthesis rate in the leaves (high $[N]_L$) implies a corresponding relative $[N]$ in the roots to supply the demand of the leaves (Smith et al., 2014; Zaehle and Friend, 10 2010).

Plant N uptake

Following Smith et al. (2014), plants take up N from the mineral N pool in the soil on a daily time-step as the lesser of the plant demand vs. the amount of mineral N in the soil accessible for the plant. The latter depends on soil temperature and fine root biomass: see Smith et al. (2014) and Zaehle and Friend (2010) for details. For crops, we have expanded the soil N module so that the N available for uptake by the plant ($M_{N,avail}$) is related to the water content of the soil (Eq. 11), as proposed by Xu-Ri and Prentice (2008):

$$M_{N,avail} = \theta \varphi M_{N,soil} \quad (11)$$

20 where φ is the fraction of projected leaf coverage by the plant, $M_{N,soil}$ is the mineral N mass of the soil and θ is the mean water content of the soil profile.

2.1.3 Senescence

Senescence, the killing of cells, can be either genetically programmed and age dependent, or induced by stresses or environmental factors (Thomas and Stoddart, 1980). In the C-only original cropland version of LPJ-GUESS (Lindeskog et al., 2013), leaf senescence is a function of HU (see Sect. 2.1). We develop this further here with a dynamic response of plant senescence to its N status (Yin et al., 2000; Masclaux-Daubresse et al., 2010) and age (DS).

Leaf senescence

If the N status of the leaves is suboptimal, the plant tries to maximise the leaf N in the canopy by redirecting some of it from the shaded leaves towards those that are more sunlit (Hirose and Werger, 1987; Yin et al., 2000). This will eventually turn off the photosynthetic apparatus in the leaves from which all the non-structural N has been retranslocated (Thomas and Stoddart, 1980). Senescence of part of the canopy in the model is induced when the N-determined leaf area index LAI_N (Eq. 8) (Yin et al., 2000) is lower than the actual LAI (Eq. 12):

$$LAI = M_{C,L} SLA \quad (12)$$

where $M_{C,L}$ is the total C mass of the green leaves. For plants, senescence of leaves is not an instantaneous process. The time for the acclimation of the N content in crop leaves was estimated to be around 10 days (Seligman et al., 1975) which is within the range of what is observed for natural vegetation, 5–30 days (Kull, 2002). Implemented here is the proposed reduction of the leaf C mass as in Yin et al. (2000) $m_{C,sen}$ but with an inertia of 0.1 day^{-1} :

$$m_{C,sen} = 0.1 \frac{LAI - \min(LAI, LAI_N)}{SLA} \quad (13)$$

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The leaf C mass is then updated $M'_{C,L} = M_{C,L} - m_{C,sen}$ and N accordingly using the minimum N content of the leaves, $C:N_{L,max}$, $M'_{N,L} = M_{N,L} - m_{C,sen} C:N_{L,max}^{-1}$. The senesced C and N is then transferred to a pool of dead leaves with a high C:N, currently set to 100 (van Ittersum et al., 2003) and the residual N is translocated to then labile N pool. The N that is translocated to the labile N-pool due to senescence of the leaf is the leftover after maximising the C:N_L status:

$$m_{N,sen} = \begin{cases} M'_N - \frac{M'_{C,L}}{C:N_{L,opt}} & \text{for } C:N_L < C:N_{L,min} \\ 0 & \text{for } C:N_L \geq C:N_{L,min} \end{cases} \quad (14)$$

where $C:N_{L,opt}$ is the C:N below which a decrease has a small or no effect on photosynthesis which is estimated here as 3/4 of the range between $C:N_{L,max}^{-1}$ and $C:N_{L,min}^{-1}$.

In ageing leaves, observed enzyme efficiency is reduced. After anthesis, degradation of the enzyme Rubisco is higher than the de novo synthesis (Bertheloot et al., 2008). To reflect this in the model, a reduction of the leaf N content at rate of 0.1 day^{-1} (Bertheloot et al., 2008) starts at anthesis ($DS > 1$).

In order to avoid excessive allocation of C to the leaves while the plant experiences leaf-N deficit ($m_{C,sen} > 0$) during the vegetative phase, a rescaling of the factor that controls the flow of assimilates to the leaves (f_2 , Eq. 4) was implemented:

$$f'_2 = (f_2)^2, \text{ for } m_{C,sen} > 0 \quad (15)$$

Root senescence

Root senescence is still an unexplored area (Kunkle et al., 2009). In the absence of a full mechanistic understanding, the dynamics of the root in the model are assumed to be coupled to those of the leaves through the functional balance concept (Eq. 10).

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2.1.4 Seed development

During flowering and grain filling, a fraction of the assimilates is allocated to the grains, while the N transported to the grains comes primarily from the leaves (Seligman et al., 1975; van Keulen and Seligman, 1989). This is reflected in the model as a transport of N from the leaves, roots and the labile N pool. In the model the plant tries to meet the demand from the grain:

$$m_{N,Y,dem} = \frac{m_{C,Y}}{C:N_{L,min}} \quad (16)$$

primarily by reducing the labile N pool, $M_{N,labile}$.

Nitrogen retranslocation

If $m_{N,Y,dem}$ is larger than the labile N pool, the crop plant attempts to meet the unsatisfied N demand from the grains ($m'_{N,Y,dem} = m_{N,Y,dem} - M_{N,labile}$) by a N transport from the donor organs (leaves and roots). These donor organs have a resistance to let go of their N, r (Seligman et al., 1975), to account for the fact that N is needed for maintaining organ processes (e.g. photosynthesis and maintenance respiration):

$$r_j = \left(1 - \frac{C:N_{j,opt}^{-1} - C:N_j^{-1}}{C:N_{j,opt}^{-1} - C:N_{j,min}^{-1}} \right)^2, r \in [0, 1] \quad (17)$$

where j denotes the organ, L or R. The actual transport of N ($m_{N,retr}$) is calculated by summing the individual organs' relative portion of the total N demand from the grains after the labile pool has been emptied (Eq. 18). If the demand on the organ is larger than the available N, it is reduced to its minimum N content ($C:N_{j,max}$).

$$m_{N,j,retr} = \min \left(\frac{M_{C,j}}{C:N_{j,max}}, \frac{m'_{N,Y,dem}(1-r_j)}{1-r_L+1-r_R} \right) \quad (18)$$

During the initial part of the grain filling period, only leaves contribute to fulfilling the grain N demand. Once more than half of the assimilates goes to the grain ($DS > 1.15$, see Eq. 5), the model can utilize part of the plant root N as well to fulfill the N requirements of the grains.

2.1.5 Updated soil water parameters

Soils are characterized by their ability to store and provide water to the plants; a parameterization of these soil water characteristics based on fractions of grain sizes, available for the soils in the study area, was needed for this study. Soil water characteristics as used in LPJ-GUESS were derived from data on sand, silt and clay for the top soil layer taken from a map of soil mineral fractions. These fraction were then used as input to empirical relationships (Cosby et al., 1984, Table 3) for the following soil water characteristics: soil water pressure at saturation (Ψ_s), volumetric water content at saturation (θ_s) and a shape parameter describing the response of the water retention curve to changes in water content (b). These parameters were then used in Eq. (19) to derive the volumetric water content under specific conditions:

$$\Psi_i = \Psi_s \left(\frac{\theta_i}{\theta_s} \right)^b \quad \theta_i = \theta_s \left(\frac{\Psi_i}{\Psi_s} \right)^{-b} \quad (19)$$

where Ψ_i is the pressure head at the sought after conditions (e.g. pF = 4.2 at wilting point and pF = 2.0 at field capacity) and θ_i is the volumetric water content ($\text{m}^3 \text{m}^{-3}$) at e.g. field capacity.

The percolation coefficient K (Haxeltine and Prentice, 1996b; Gerten et al., 2004), an empirical parameter used in the model to derive the daily percolated water, was fitted against b values for 4 of the soil classes from Haxeltine and Prentice (1996b) (coarse, medium-coarse, medium, fine) and resulted in:

$$K = 5.49 - 0.22b \quad (20)$$

3 Experimental setups

The model's ability to simulate yields was evaluated using data from fertiliser trials from the Netherlands, a Free Air CO₂ Enrichment (FACE) experiment from Germany and regional yield statistics from European countries.

All simulations were performed using a 500 year spin-up using [CO₂] and repeatedly cycled detrended climate input for the first years of the historic climate data to build up pools of C and N. In the simulations with N dynamics turned on, monthly N deposition input from Lamarque et al. (2010) that varies decadal was used. The values were interpolated using bilinear interpolation from the original resolution (1.9° × 2.5°) to match the resolution of the climate data (0.5° × 0.5°) (Smith et al., 2014; Wårlind et al., 2014).

3.1 Fertiliser trials

To evaluate the model's ability to simulate phenology and yields, data from N fertiliser response trials with detailed measurements of dry mass and N mass allocation from the Netherlands (Groot and Verberne, 1991) were used. In the trials, winter wheat was grown with different fertiliser input in the years 1983–1985. The trials were conducted on three sites (The Eest, The Bouwing and PAGV), located in the central part of the Netherlands, see Fig. A2. At these locations, three different N treatments were carried out for two seasons (Table 1).

Based on an initial calibration of the model using leaf phenology data from Trial I, the parameters a and b in the allocation function f_2 (Eq. 4) were changed from 0.88 and 0.09 to 0.8 and 0.2 respectively. Daily climate data for the years 1979 to 1984 were downloaded from the Haarweg weather station, Wageningen University¹, located within 70 km from the sites. To initialise (spin up) N and C pools in the model, climate data for the year 1979 was repeated for 500 years, during the spin-up period a single application of 100 kg N ha⁻¹ y⁻¹ was applied on day 150 from the time of sowing. The

¹<http://www.met.wau.nl/haarwegdata/dayfiles/>, last access: 4 February 2014

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year before the trials started (1982 for Trials I, III and V and 1983 for Trials II, IV and VI) 200 kg N ha⁻¹ was applied (Table 1 in Groot and Verberne, 1991). As described in Sect. 2.1.5, fractions of sand, silt and clay from Table 1 were used to derive site specific soil water characteristics.

3.2 FACE experiment

The ability of the model to simulate the observed response to elevated [CO₂] treatment on yields and C:N of cropland ecosystems was tested using a FACE experiment (Weigel and Manderscheid, 2012) from an experimental site close to Braunschweig, Germany (10.83° E, 52.82° N), see Fig. A2. Between the years 1999 and 2005 the FACE experiment was carried out on a rotation of barley, ryegrass, sugar beet and winter wheat that was repeated once. At this point the N-enabled model is not equipped to model crop rotations or sugar beet. Also LPJ-GUESS does not model wheat and barley explicitly, but a temperate cereal (Bondeau et al., 2007; Lindeskog et al., 2013) represented by wheat in the model, therefore growth of cereals was simulated for all years.

Four different trials from the experiment were simulated, high (100% N) and low (50% N) N input with ambient and elevated [CO₂] (378/548 ppm), see Table 2 or Table 1 in Weigel and Manderscheid (2012) for more details. Due to the lack of information on the timing and amount of the individual fertiliser applications, these parameters were set using a similar approach as in Sect. 3.3 by choosing the N management that yielded the best model agreement. As climate input we used the WFDEI climate dataset (Weedon et al., 2012) which is a bias-corrected reanalysis dataset based on WATCH (Weedon et al., 2011) and Era Interim (Dee et al., 2011). During the spin up period (500 years), 30 years of detrended data (1979–2008) were used together with the ambient [CO₂] from 1979.

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3.3 Regional yields

To evaluate the model's ability to simulate wheat yields on a larger scale, 65 regions at the NUTS2 (Nomenclature of Territorial Units for Statistics in the EU; statistical administrative areas) level from north western mainland Europe and NUTS1 for southern England were selected based on their cereal fractions and yields taken from the EU statistics website, EUROSTAT². The regions and their administrative names are shown in Fig. A2 and the mean reported yields together with the number of years for which there where data for each region are listed in Table A3.

As climate input, WFDEI (Weedon et al., 2012), with a spatial resolution of $0.5^\circ \times 0.5^\circ$ was used. Spin-up with climate and $[\text{CO}_2]$ was performed as in the FACE experiment (see above). Soil characteristics (mineral size distributions) for the top layer (0.3 m) were derived from Batjes (2005) and used for the whole column (2 m). Simulated yields of spring and winter wheat were assigned to the regions by their relative proportion of the grid-cell area (a grid-cell can belong to more than one region). Fractions of each grid-cell covered by spring and winter wheat as well as the area equipped for irrigation were derived from the MIRCA data set (Portmann et al., 2010).

Timing of the fertiliser applications were selected based on the mean development stages for the three N applications listed in Table 1, (0.18, 0.49, 0.89). A common practice is to apply some or all of the fertiliser at the time of sowing (Mahler et al., 1994). The timing of the three applications was therefore changed to DS = 0, 0.5 and 0.9 respectively.

To test the effect of timing and amount of fertiliser applied, an experiment with 50 model permutations ($F_{T,A}$, timing (T) and application (A) varied), was conducted with five different fertiliser application rates (between $50 \text{ kg N ha}^{-1} \text{ y}^{-1}$ and $250 \text{ kg N ha}^{-1} \text{ y}^{-1}$). Fractions (0, 1/3, 2/3, 1) of the applied N were distributed at the development stages 0, 0.5, and 0.9, yielding 10 possible combinations.

²http://epp.eurostat.ec.europa.eu/portal/page/portal/agriculture/data/main_tables, last access: 6 May 2014

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The N managements (application rate and timing) that gave the best fit (lowest RMSE) were then selected for each region ($F_{\text{opt}(T,A)}$). To test whether a mean N management can be representative for the whole region, the mean timing and amount from $F_{\text{opt}(T,A)}$ were derived and simulated ($F_{t,a}$, timing (t) and application (a) fixed).

5 Additionally, to test the relative importance of timing and amount, an experiment with simulations where timing was fixed using the mean development stages as in $F_{t,a}$ together with varying input as in $F_{T,A}$ ($F_{t,A}$) and an experiment where timing was varied as in $F_{T,A}$ but with a fixed N application, were performed ($F_{T,a}$). Furthermore a simulation using a gridded data set of annual N input for wheat (Elliott et al., 2014) together with
10 the mean timing from $F_{t,a}$ was performed ($F_{t,i}$).

To test whether adding C–N dynamics in the model increased the overall model performance, simulations using the C only version of LPJ-GUESS were performed (F_C). In these simulations, C allocation was as described in Lindeskog et al. (2013).

A short description of the model setups used, together with their abbreviations, are listed in Table 3.

3.4 Statistical methods

In order to quantify the degree of agreement between simulations and the associated observations, two indices were calculated, the Willmott index of agreement (W_i , Eq. 21) (Willmott et al., 2012) and the root mean square error (RMSE) (Eq. 22). W_i is calculated
20 as:

$$W_i = \begin{cases} 1 - \frac{M}{cO} & \text{for } M \leq 0 \\ \frac{cO}{M} - 1 & \text{for } M > 0 \end{cases} \quad (21)$$

where M denotes the sum of absolute differences between the modelled and the observed mean and O is the sum of absolute differences between the observations and the observed mean and c is scaling constant here set to 2 (Willmott et al., 2012).
25 W_i is without unit and ranges from 1 to -1 , where 1 is a perfect agreement between the

modelled and observed variances and -1 means that there is a low or no agreement between the modelled and observed variances. RMSE is calculated as:

$$\text{RMSE} = \sqrt{\frac{\sum_{i=1}^n (o_i - m_i)^2}{n}} \quad (22)$$

where n is the number of observations, o is the observed value and m is the modelled value.

3.5 Conversion factors

To convert plant C to total dry matter, a conversion factor of 0.446 was used (Osaki et al., 1992). Dry weight was converted to wet weight (used in the regional statistics) by assuming a wet fraction of 0.15 in the grains (Fader et al., 2010).

4 Results

4.1 N fertiliser response

In the N fertiliser experiments from Groot and Verberne (1991), 18 trials with N input ranging from 0 to 240 kgN ha⁻¹ y⁻¹ applied at various crop development stages were performed, resulting in grain C production from 1 to 3.5 ton C ha⁻¹. During the growing-season, leaf C in the field trials increased until peaking around June, after which senescence commenced and leaf C decreased again (Fig. 2a–c). Simulations with LPJ-GUESS at these sites, and reproducing the applied fertiliser scheme broadly captured these seasonal dynamics, and the response to the different levels of N applications (Fig. 2a–c). Differences between simulated and observed leaf C values were largest towards the end of the growing-season (Fig. 2d), especially at the highest-fertilised trial sites and in the second growing-season. As seen from the example time

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series in Fig. 2a–c, rates of senescence in the simulations were too slow, compared to measurements, which resulted also in underestimated dead-leaf C (see Fig. A3a–b).

The model generally simulates the observed above-ground production of biomass (C and N) well at the sites, with more accuracy in the medium and high input trials (2 and 3) (Fig. 3c–d). C content in grains and above-ground biomass is captured reasonably well, with some underestimations for the lowest N trial (Fig. 3c). This picture was mostly similar also for simulated N content, as a consequence average C : N were not biased towards too high or too low values (Fig. 4a). The C : N of the grains (Fig. 4b) in response to differences in N treatment was better captured than the total C mass (Fig. 3c). Over the growing-season there is an underestimation of the N content in the grains, especially so for the low input treatments (Fig. 3a–b).

4.2 Response to elevated [CO₂]

At the Braunschweig FACE experimental site the mean observed yields under ambient [CO₂] (~ 378 ppm) were 8 and 6 ton ha⁻¹ for the sufficiently fertilised (100 % N) and the treatment receiving 50 % N respectively, whereas the simulated yields were 9 and 7 ton ha⁻¹, with the same pattern of higher simulated than observed yields also for the elevated [CO₂] (~ 548 ppm) treatments (Fig. 5).

Grain yields were simulated to rise by 19 % as a response to elevated [CO₂] for both the 100 and 50 % N treatments (Fig. 5). The observations show a similar response with a rise of 14 % ((9–19 %) for 100 % N and (5–24 %) for 50 % N), and neither simulations nor measurements did indicate a clear impact of N treatment on the CO₂ effect.

Under elevated [CO₂], increased C sequestration and yields were not balanced by grain N rising at the same rate as grain C, leading to enhanced grain C : N at elevated CO₂. In the observations, this increase was on average 16 % for both N treatments, whereas in the simulations the increase was 24 % (100 % N) and 20 % (50 % N) (Table 4).

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4.3 Regional wheat yields

In order to test model performance on spatial scales beyond field trials, regional modelled wheat yields were compared with yield statistics provided by EUROSTAT. The simulations were also set up to test the effects of different N management regimes (Table 3) in order to derive an implementation of fertiliser application that can be adopted for large-scale models even when exact information on fertiliser timing is not available.

To do so, from the 65 regions chosen from the EUROSTAT database, a set of 50 permutations of timing and amount of N application ($F_{T,A}$) was used to identify the management strategy resulting in the best agreement (lowest RMSE) with reported time series of yields ($F_{opt(T,A)}$). The optimised timing and associated amount of N input for each of the regions are listed in Table A3. This “optimised” simulation deviated only marginally (Fig. 6b) from the observed yields (Fig. 6a). The interannual variability in yields for individual regions was captured best for regions with a low productivity (model performance based on the Willmott index (W_i) and RMSE, Table A3), whereas the interannual variability for the more productive regions was captured less well.

In the optimised simulation ($F_{opt(T,A)}$), the mean N application rates for spring-sown wheat across the entire region were a total of $129 \text{ kg N ha}^{-1} \text{ y}^{-1}$, applied in fractions of 0.11, 0.50 and 0.39 at the three development stages described in Sect. 3.3, with the main application in mid-spring. For winter wheat, on average $172 \text{ kg N ha}^{-1} \text{ y}^{-1}$ were applied with fractions 0.08, 0.19 and 0.73 for the three development stages, with the main application in late spring or early summer.

For simulation $F_{t,l}$, the mean timing obtained from the optimisation was combined with a gridded data set of N application rates (Elliott et al., 2014), resulting in a reasonable agreement with the observed yield but with larger spread compared to $F_{opt(T,A)}$ (Fig. 6c). In particular, overestimations were found in parts of the Netherlands, Belgium and southwestern France, and a considerable underestimation in northern France. Some of the deviations between modelled and reported yields were likely

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due to a lack of spatial variability in the fertiliser data input, e.g., a constant value ($110 \text{ kg N ha}^{-1} \text{ y}^{-1}$) was applied for all regions in France (Table A3).

Despite of spread between the model and the observations for individual years, the temporal average of the optimised set showed a good agreement (Fig. 7). Even the simulation that applied the mean timing with reported fertiliser rates ($F_{t,l}$) showed a reasonable agreement, but generally overestimating the yields in low-productive areas, primarily because of a higher fertiliser application rate (regional mean N input of $188 \text{ kg N ha}^{-1} \text{ y}^{-1}$ for $F_{t,l}$, compared with $169 \text{ kg N ha}^{-1} \text{ y}^{-1}$ for $F_{\text{opt}(T,A)}$). Applying the same timing as in $F_{t,l}$ with the lower constant rate of $169 \text{ kg N ha}^{-1} \text{ y}^{-1}$ ($F_{t,a}$) resulted in a much better agreement for the mean response. However, both simulations ($F_{t,l}$ and $F_{t,a}$) have a smaller range of simulated yields from low-productive to high-productive areas than reported in the statistics data.

The spatial variation of the observations was captured well in all simulations except for those with maximised yields ($\max(F_{T,A})$) and the C-only version (F_C). As expected, optimised N management ($F_{\text{opt}(T,A)}$ and $F_{t,A}$) improved the fit of the model results to spatial variation in the data, but all the C–N enabled simulations except for $\max(F_{T,A})$ increased the agreement between the modelled and observed variance (Table 5). In order to address the spatial variability in timing and rates of fertiliser application, the optimised simulation ($F_{\text{opt}(T,A)}$, red line in Fig. 7) was compared with two additional optimisations. In the first of these ($F_{\text{opt}(t,A)}$), timing was prescribed using the same as for $F_{t,a}$ while application rates were varying. In the second optimisation ($F_{\text{opt}(T,a)}$), application rates were prescribed as for $F_{t,a}$ while timing was varying. Both optimisations gave better agreement with the reported yields than when only using a mean uniform N management over the region ($F_{t,a}$, Table 5), but optimising the application rates gave a considerably better fit than optimising the timing. This implies that it is more important to obtain data on application rates than on timing of the fertilisation.

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5 Discussion

Accounting for C–N dynamics in the crop version of LPJ-GUESS (Lindeskog et al., 2013) together with the new flexible allocation scheme resulted in good overall agreement when compared against site-scale observations and regional yields statistics. The simulated response to N management was also in line with the observed dynamic responses in a fertiliser trial and wheat grown under elevated [CO₂].

5.1 Model performance, fertiliser trials

Modelling the seasonality of growth, phenology, and the response to fertiliser is a prerequisite not only for model projections of crop yield responses to management in a changing environment, but also to aid assessments of management-related detrimental effects (Hawkesford, 2014; Lokupitiya et al., 2009). Models that operate on regional to global scales are not designed to be suitable tools for detailed local-scale decision-making on fertiliser use, but the improved representations of crop C–N coupling and phenology are necessary for simulating regional to global land use related surface-atmosphere exchange fluxes, to evaluate models against observations, and to contribute to analyses of the effects of land-use change in the climate system, including assessment of how multiple ecosystem-services are affected following land conversions (e.g., Kelley et al., 2013; Rounsevell et al., 2014). For these types of questions, a chief challenge remains in representing phenology and growth responses to fertiliser application and climate in a way that is suitable for large-scale models, but still reproduces realistic results (Lokupitiya et al., 2009; Boote et al., 2013).

In LPJ-GUESS, crop phenological events, and especially the growth of the leaves throughout the growing-season were captured (Fig. 2) and at the end of the growing-season, senescence was induced as a result of N retranslocation to grains from the leaves, albeit with a response that was a little too weak compared to the measurements (Fig. 2). The modelled mean harvest index ($HI = Y/(Y + V)$) of 0.57 was in line with the value obtained from observations (0.52; Fig. 3a,c). Modelled grain yields and above-

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ground biomass were on average only slightly lower than the observations, and the overall tissue as well as grain C:N also agreed well with the corresponding ratios derived from the measurements. But there was a discrepancy in the modelled C allocated to the grains during the early parts of the grain filling period that disappeared towards the end of the growing period (Fig. 3a).

When making these comparisons, the need to convert dry matter to mass of C, and vice versa, added a level of uncertainty that is not associated with modelled processes, since site-data often is reported as biomass (dry or wet). For instance, we used the published observations of [C] in the biomass of 44.6% (Osaki et al., 1992) when converting the experimental-site data. By contrast, in LPJ-GUESS a C content of 50% is assumed (Smith et al., 2014), which leads to slightly higher C density in modelled output compared to the observation-derived values.

Underlying the good agreement of the tissue C:N, was an underestimation of the absolute levels of both C and N in the grains at the end of the growing-season, which were underestimated by about 30% in many cases (Fig. 3a). The same pattern could also be seen for the above-ground C mass (Fig. 3c), suggesting that the productivity generally is too low in the model. One potential explanation for the underestimation of [C] in grains at the end of the growing period is C-retranslocation from leaves and roots to the grains during the growing-season, which has been observed, in forms of sugars (Osaki et al., 1991; Penning de Vries et al., 1989). Since in the current version of the model C supply originates solely from NPP, one potential source of carbon to grain filling therefore is missing. In addition, the model does not presently include other forms of molecular transport whereas the re-translocation of N from leaves to the grains is mostly in the form of amino-acids (van Keulen and Seligman, 1989) with a relatively low C:N (e.g. 4.0 in wheat Thornley, 1990; Osaki et al., 1991). Accounting for such an amino-acid transport would suggest that for every unit of N that is transported to the grain, four C would have to be supplied as well. This, too, cannot be captured by the current implementation that is based on allocation of the daily NPP.

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like GECROS (Yin and Van Laar, 2005) do so at higher temporal resolution. Next development phases in LPJ-GUESS will explore how to include these into the model.

5.2 Model performance, FACE comparison

In a recent intercomparison of crop models that can be applied globally, Rosenzweig et al. (2013) identified the CO₂ fertilisation response to be one of the major sources of uncertainty of how yields might change in a future environment. When disregarding advances in breeding, the CO₂ fertilisation response of crops (in particular: of the C₃ photosynthesis-type) is fundamental, as this response can counteract or at least dampen effects of climate change. The chief principles are related to the carboxylation reaction of Rubisco being stimulated by enhanced levels of CO₂, and by plants being able to operate at lower levels of stomatal conductance, thereby increasing the efficiency of gaining carbon per unit of water lost (Ainsworth and Rogers, 2007; Drake et al., 1997; Sun et al., 2014). The magnitude of the positive CO₂ response on yields will depend on the degree of leaf-level acclimation response, and how such an acclimation would translate to the whole-plant level (Ainsworth and Long, 2005; Drake et al., 1997; Smith and Dukes, 2013).

In existing crop models, the implemented CO₂ response is typically based on empirical relationships between an increase in [CO₂] and plant productivity, derived from e.g. FACE experiments (Boote et al., 2013; Rosenzweig et al., 2013). Adapting a more mechanistic representation of the CO₂ response by replacing a radiation-use efficiency formulation with a coupled photosynthesis and stomatal conductance description (as in LPJ-GUESS) increased the overall model performance of the DSSAT model and its ability to capture responses to the combined effects of different factors affecting plant productivity (Boote et al., 2013).

In the Rosenzweig et al. (2013) study, LPJ-GUESS showed a very strong yield response to enhanced levels of atmospheric CO₂. The model version used in that study did not include C–N interactions, and hence this strong response was expected, since the simulated underlying physiology was not constrained by N availability. With

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this constraint in place, LPJ-GUESS in the present study reproduced crop growth and productivity under elevated [CO₂] with different N fertiliser treatments, as well as responses in dry matter C : N observed at the different levels of CO₂, with C : N at the 100 % N treatment being somewhat above the observed values. A positive CO₂ effect on yields and C : N, as well as the higher variability between years was captured in treatments that received less N input. The results shown in Sect. 4.2 were also in line with observations from previous FACE experiments (Ainsworth and Long, 2005) that showed a mean increase of 14 % (–2 to 33 %) for wheat yields, compared to the modelled response of 20 and 24 % for the two different N treatments.

The modelled yields (ambient and elevated [CO₂], 50 and 100 % N) exceeded observations only slightly. This might be explained by insufficient information on the fertiliser management at the experimental plots but also by, for instance, a too high allocation to grains compared to other tissues. Moreover, under elevated [CO₂] a relative increase in root biomass (Pritchard and Rogers, 2000) often occurs. Currently, as discussed in the previous section, there are no explicit mechanisms implemented that would yield such a dynamic growth response. A step forward, that remains to be tested, would be to set a flexible root:shoot allocation via a modification of f_1 in response to water or N stress, see Sect. 2.1.1, which would result in such a response in situations when additional leaf C mass in response to elevated [CO₂] induced a N demand that cannot be met by soil uptake.

Moreover, as mentioned in Sect. 5.1, SLA in the model is treated as a constant, even though it has been observed to vary over the growing-season, and in response to elevated [CO₂] (Poorter et al., 2009). Ainsworth and Long (2005) found in a review of CO₂ effects on different plant traits that elevated [CO₂] was associated with a reduction in SLA, as the increase in leaf mass was not accompanied by a proportional increase in leaf area. These results are in line with the observed increases in leaf C : N under elevated CO₂ (Yin, 2002). Currently in the model the lower limit of leaf N (N_b) is a function of SLA (Eq. 9), and whether or not variable SLA would help to constrain the C : N response at variable N and CO₂ treatment remains to be tested. While some

studies have found elevated CO_2 to also change the chemical composition of the plants and thus the C:N (Yin, 2002), others (e.g., Gifford et al., 2000) found no evidence of changes in the C:N of the senesced leaves grown under higher $[\text{CO}_2]$ implying that the fixed C:N limits and in turn the N_b are valid also under elevated $[\text{CO}_2]$, but this remains to be explored.

5.3 Regional yields, model performance and implications for large scale modelling

The implementation of C–N dynamics improved the ability of LPJ-GUESS to simulate yields not only at local scale but also across larger regions, especially when all permutations of N managements were combined (Fig. 7). As expected, the comparison of the simulated yields with reported ones was best captured when considering time-averaged values (accounting only for the spatial variation) compared to the full temporal variability (difference between “mean” and “all” in Table 5). The discrepancy between results from the C–N and the C-only versions of the model was striking and clearly demonstrates the need to consider C–N interactions when modelling crop processes (Rosenzweig et al., 2013). In addition to the improved phenology and C–N coupling, which was seen also at the FACE site, on the regional scale the representation of soil texture proved to be an additional important aspect. By incorporating the WISE map of soil mineral fractions, we were able to increase the model performance from a W_i of 0.715 using the standard soil map in LPJ-GUESS simulations with fixed mineral fractions (Smith et al., 2014), to 0.807. With the more detailed soil information, the heterogeneity in the growth response from fertiliser applications due to differences in physical properties could be better captured.

Still, when applied across large spatial domains, there can be multiple reasons for a disagreement between modelled and observed variability that go beyond process representation linked to the basic physiology of C–N interactions. For instance, extreme heat or freezing, pests, or water logging of soils are frequent events detrimental for crop production (Reichstein et al., 2013). Effects of extreme weather events are difficult to

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account for, partially because of the smoothing effect of a daily time step, and also because aggregation averaging in the production of the gridded climate input data tends to remove weather extremes. Likewise, local management decisions that are not based on weather variability, and their effects on crops and environment, are difficult to capture with the current setup.

Several approaches to modelling N limitations in agricultural ecosystems over large region scales are available in the literature. In LPJmL (Fader et al., 2010), an implicit nutrient limitation on yields is considered by varying production parameters (LAI_{max} , HI, and α_a) to match country or region statistics from e.g. FAO (United Nations Food and Agriculture Organisation). This approach has the advantage that it can be applied without knowledge as to the management (fertilisation) practices that are common in a region, but lacks the possibility to assess effects of future changes in e.g. N fertiliser availability and changes in management. The crop model GEPIC (Liu et al., 2007) – like LPJmL (Bondeau et al., 2007) – has LAI_{max} and HI as input parameters but also includes N dynamics with empirical response functions as modifiers of productivity and yields. In contrast to LPJmL, GEPIC is based on a site-scale model approach which can be extended in space via a GIS interface that facilitates input of spatially explicit management, where available. WOFOST, a detailed crop-growth model that has recently been expanded to work at larger regions (Boogaard et al., 2013) has demonstrated skills in simulating local and regional yields with a mechanistic approach to modelling crop photosynthesis as well as physiology, but the model approach assumes a continuation of current management practices, and thus cannot be applied for future simulations.

LPJ-GUESS shares several aspects of the approaches of these models: the sowing algorithm (LPJmL Waha et al., 2011), temperature limits for different CFTs (GEPIC), and a large portion of the mechanistic formulations of crop physiology (WOFOST and GECROS are “School of de Wit” models, van Ittersum et al., 2003). Because of the dynamic PHU calculations (Lindeskog et al., 2013) and dynamic sowing and harvest calculations (Waha et al., 2011), LPJ-GUESS can be applied to all areas where suitable

temperature and soil moisture conditions allow wheat growth. In addition, we have shown here also that it is possible to find a suitable timing of N fertilisation on the regional-scale by relating the N application to those stages in the crop growing period when it is most needed. For globally applicable models this is an important result, since information on fertiliser application often includes total amounts per year, but typically lacks information about the seasonal distribution.

6 Conclusions

The approach chosen here to implement C–N dynamics in the crop module of LPJ-GUESS seeks to adopt mechanistic process implementations, which has been advocated in literature to be able to fully capture the effects of climate change on ecosystems. The modelling framework demonstrably responds realistically to different N fertiliser treatments and [CO₂] and produces results that are in line with observations from site-scale to a larger region.

These findings support the aim of this study, to find a level of complexity in the implementation of the N management that can be applied on larger regions, and that is ultimately also applicable under climate and other environmental changes. As long as spatially estimated total N applications are available, adopting mean treatment of timing of the N in the model that is based on the development stage appears sufficient for representing the mean and variance of regional yields.

Representing dynamic C–N interactions within a consistent terrestrial modelling framework provides the capacity to predict changes in global C and N pools and fluxes in historic or future land-use change scenarios, as well as to quantify and explore the effect of different managements on the global C and N budgets, considering hindcasts and projections of land-use change (e.g. Hurtt et al., 2011; Klein Goldewijk et al., 2011), climate change and historic or future N fertiliser application rates (e.g. Potter et al., 2010; Bouwman et al., 2013).

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Table 2. Description of the experiments carried at the Braunschweig research station in Germany and how it was modelled in LPJ-GUESS. For a more detailed description of the experiments see Table 1 in Weigel and Manderscheid (2012).

Management	Units	1999/2000 Barley*	2001/2002 Wheat	2002/2003 Barley*	2004/2005 Wheat
Sowing	Date	24.09.99	06.11.01	27.09.02	26.10.04
N-fert. (H/L)	kg ha ⁻¹	262/105	251/114	179/105	168/84
Final harvest	Date	26.06.00	31.07.02	25.06.03	27.07.05
[CO ₂] (amb./elev.)	ppm	373/549	377/548	378/547	378/549

* Modelled as wheat.

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Table 3. Description of the setups used in the comparison with regional statistics, with abbreviations used throughout the paper.

Setup	Description	Timing	N app.
$F_{T,A}$	50 permutations, with timing and application rate varied	varied	varied
$F_{opt(T,A)}$	optimised timing and rate based on model fit (RMSE) in comparison to regional yield statistics	opt.	opt.
$F_{t,a}$	mean timing and application rate over all regions from $F_{opt(T,A)}$	fixed	fixed
$F_{T,a}$	10 permutations with timing varied as in $F_{T,A}$, application rate from $F_{opt(T,A)}$	varied	fixed
$F_{t,A}$	5 permutations with timing from $F_{opt(T,A)}$, application rate from $F_{T,A}$	fixed	varied
$F_{t,l}$	Timing from $F_{opt(T,A)}$, application rate from (Elliott et al., 2014)	fixed	input
F_C	C only		

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Table 4. Comparison of modelled and observed C : N from a FACE experiment where wheat was grown in ambient CO₂ (~ 378 ppm) and elevated CO₂ (~ 548 ppm). The observed C : N where compiled using Tables 4 and 5 in Weigel and Manderscheid (2012), observed C values where derived from dry matter using the conversion described in Sect. 3.5. The range of the observed CO₂ effect is estimated from the standard errors listed in Tables 4 and 5 in Weigel and Manderscheid (2012).

	year	Ambient CO ₂		Elevated CO ₂		CO ₂ effect (%)	
		100 % N	50 % N	100 % N	50 % N	100 % N	50 % N
Modelled	2000	21.7	16.1	27.9	20.8	28	29
	2002	21.0	17.9	24.1	21.1	15	18
	2003	16.1	13.5	21.5	15.1	33	12
	2005	20.3	15.9	24.6	19.1	22	21
	mean	19.8	15.9	24.5	19.0	24	20
Observed	2000	13.2	16.2	16.3	19.1	23	18
	2002	13.0	14.4	13.6	17.9	5	24
	2003	12.8	15.5	14.9	17.4	16	12
	2005	12.7	17.5	15.2	19.4	20	11
	mean	12.9	15.9	15.0	18.5	16	16
	range					7–26	–3–40

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Table 5. Slopes, intercepts and R^2 values for regressions comparing the simulated yields using the model setups described in Table 3, against reported yields for the 65 NUTS2 level regions. RMSE values and Willmott index (W_i) are provided, the number of data points used to derive the statistics “all” were 1400 (all regions and years).

Setting	regression		R^2	RMSE	W_i
	slope	intercept			
$F_{\text{opt}(T,A)}$, mean	0.937	0.130	0.942	0.370	0.807
$F_{\text{opt}(t,A)}$, mean	0.820	0.805	0.801	0.588	0.721
$F_{\text{opt}(T,a)}$, mean	0.361	4.249	0.306	0.780	0.602
$F_{t,a}$, mean	0.228	4.510	0.082	1.243	0.353
$F_{t,l}$, mean	0.415	4.461	0.130	1.230	0.422
F_C , mean	-0.209	9.516	0.075	1.845	0.074
$\max(F_{\text{opt}(T,A)})$, mean	0.247	7.453	0.051	2.627	-0.343
$F_{\text{opt}(T,A)}$, all	0.412	3.737	0.163	1.598	0.448
$F_{t,l}$, all	0.185	6.128	0.022	2.199	0.269

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Table A1. The parameters for the factors f_1 , f_2 and f_3 (Eqs. 3–5) for spring and winter wheat.

parameter		spring	winter
f_1 :	a	0.62	0.53
	b	-0.02	0
	c	5.8	7.63
	d	0.55	0.55
f_2 :	a	0.86	0.8
	b	0.19	0.2
	c	28.65	13.99
	d	0.55	0.55
f_3 :	a	0	0
	b	1	1
	c	8.27	8.32
	d	1.1	1.15

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Table A2. A list of variables (in italics) and parameters used in the article with a short description and units.

variable	description	value	unit	reference
LAI	leaf area per ground area		m ² m ⁻²	
<i>M_{s,j}</i>	Mass of element <i>s</i> (C, N) in organ <i>j</i>		kg s m ⁻²	
<i>m_{s,j}</i>	Transport of element <i>s</i> (C, N) in organ <i>j</i>		kg s m ⁻² day ⁻¹	
C : N _{<i>j</i>} parameter	Carbon to nitrogen ratio of organ <i>j</i>		kg C kg ⁻¹ N ⁻¹	
C : N _{min,L}	Minimum C : N of the leaf	7	kg C kg ⁻¹ N ⁻¹	Penning de Vries et al. (1989)
C : N _{max,L}	Maximum C : N of the leaf	35	kg C kg ⁻¹ N ⁻¹	
SLA	Specific leaf area	45	m ² kg ⁻¹ C ⁻¹	Penning de Vries et al. (1989)
<i>d_{r,veg}</i>	development rate, vegetative phase	0.03	day ⁻¹	Wang and Engel (1998)
<i>d_{r,rep}</i>	development rate, reproductive phase	0.042	day ⁻¹	Wang and Engel (1998)
<i>N_p</i>	Minimum leaf N content	0.0011	kg N m ⁻²	
<i>β₀</i> & <i>β₁</i>	Regression coefficients <i>k_L</i> ~ <i>k_N</i>	0.01, 0.52		Yin et al. (2003)

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Table A3. Nitrogen fertiliser applications and timing used in the regional simulations resulting from optimising modelled yields against observations ($F_{opt(T,A)}$), see Sect. 3.3, together with the statistics (the 2 last columns). Number of years with reported yields for each region (n. y), fraction of the wheat area covered by winter variety (Ar.), fraction with spring variety: 1 – Ar., reported yields and AgGrid N input data for each region.

NUTS2	n. y	Ar.	Winter wheat			Spring wheat			AgGrid input kgNha ⁻¹	Yields		Statistics	
			N Timing, DS	0	0.5	N Timing, DS	0	0.5		Mod.	Rep.	RMSE	Willm.
BE10	25	0.97	0.00	0.00	100	0.00	1.00	50	282	6.41	6.52	2.34	0.48
BE21	31	0.81	0.00	0.00	250	0.00	1.00	50	257	5.50	5.73	1.30	0.45
BE22	31	0.95	0.33	0.33	250	0.00	1.00	50	271	7.21	7.43	1.94	0.36
BE23	31	0.91	0.00	0.00	150	0.00	1.00	50	263	6.79	6.98	1.63	0.46
BE24	19	0.97	0.00	0.00	200	0.00	1.00	50	282	7.72	7.84	1.45	0.05
BE25	31	0.97	0.33	0.00	250	0.00	0.00	250	139	6.64	7.49	2.14	0.23
BE31	19	0.97	0.67	0.00	150	0.33	0.00	200	282	7.90	8.26	1.44	-0.15
BE32	31	0.98	0.00	0.00	150	0.33	0.67	50	163	7.06	7.29	1.56	0.35
BE33	31	0.96	0.33	0.00	250	0.00	1.00	100	263	7.52	7.77	1.71	0.34
BE34	31	0.98	0.00	0.00	100	0.00	1.00	150	178	4.92	5.11	1.11	0.36
BE35	31	0.97	0.00	0.00	150	0.00	1.00	50	177	6.89	6.91	1.40	0.47
DE26	7	0.98	0.33	0.33	150	0.00	0.00	200	185	5.31	5.85	1.07	-0.16
DE41	3	0.96	0.00	0.00	250	0.33	0.00	250	166	5.60	5.63	1.17	0.55
DE50	7	0.97	0.00	0.00	100	0.33	0.00	250	185	5.23	5.88	1.57	0.35
DE60	19	0.98	0.00	1.00	200	0.67	0.00	50	185	6.54	6.94	1.92	-0.03
DE71	6	0.98	0.00	0.33	250	0.00	0.00	150	185	6.00	6.46	1.54	0.02
DE72	6	0.97	0.00	0.33	250	0.00	0.00	150	185	6.02	6.50	1.58	-0.03
DE73	6	0.97	0.00	0.33	250	0.00	1.00	50	185	6.49	6.68	1.50	0.07
DE80	15	0.97	0.00	0.00	200	0.00	0.00	250	183	6.25	6.73	1.23	0.25
DE91	7	0.98	0.00	0.67	200	0.00	0.67	100	185	6.69	7.18	1.79	0.22
DE92	7	0.98	0.00	0.00	200	0.00	0.00	200	185	6.70	7.29	2.13	0.12
DE93	7	0.97	0.00	1.00	150	0.00	1.00	50	185	6.26	6.55	1.76	0.18
DE94	7	0.96	0.00	0.00	100	0.00	0.00	200	211	6.00	6.64	1.67	0.30
DEA1	7	0.97	0.00	0.00	150	0.00	1.00	50	232	6.99	7.22	1.70	0.31
DEA2	7	0.97	0.00	1.00	150	0.00	1.00	50	208	7.67	7.59	1.57	0.36
DEA3	7	0.97	0.00	1.00	150	0.00	0.00	100	203	6.38	6.91	1.92	0.26
DEA4	7	0.98	0.33	0.67	150	0.00	0.67	150	185	6.38	6.99	2.23	0.18
DEA5	7	0.98	0.00	1.00	150	1.00	0.00	50	185	6.79	7.06	2.09	0.28
DEB1	7	0.98	0.00	0.33	100	1.00	0.00	50	185	5.52	5.78	1.23	0.15
DEB2	7	0.97	0.33	0.33	50	0.00	1.00	150	185	4.95	5.31	1.19	0.34
DEB3	7	0.98	0.00	0.33	200	0.00	1.00	50	185	5.69	5.68	1.06	0.23
DEC0	26	0.99	0.00	0.00	100	0.00	1.00	50	183	5.37	5.44	1.04	0.45
DEE3	2	0.98	0.33	0.67	250	0.00	0.33	250	185	6.97	7.84	0.90	-0.01
DEF0	26	0.97	0.00	1.00	250	0.00	1.00	50	184	7.81	7.87	2.00	-0.07

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Table A3. Continued.

NUTS2	n. y	Ar.	Winter wheat			Spring wheat			AgGrid		Yields		Statistics	
			N Timing, DS		kgNha ⁻¹	N Timing, DS		kgNha ⁻¹	input kgNha ⁻¹	Mod.	Rep.	RMSE	Willm.	
0	0.5	0	0.5											
FR10	28	1.00	0.00	0.00	200	0.00	1.00	50	110	7.15	7.29	1.41	0.21	
FR21	29	1.00	0.00	0.00	200	0.00	1.00	50	110	7.41	7.35	1.29	0.28	
FR22	29	1.00	0.00	0.00	200	0.33	0.67	50	110	7.32	7.60	1.58	0.21	
FR23	29	1.00	0.00	0.00	150	0.00	0.67	50	110	7.21	7.37	1.39	0.20	
FR24	29	0.99	0.00	0.00	100	0.00	1.00	50	110	6.20	6.32	1.14	0.34	
FR25	29	1.00	0.00	0.00	200	0.33	0.00	200	110	6.56	6.85	1.40	0.20	
FR26	29	1.00	0.00	0.00	100	0.33	0.00	250	110	5.61	6.02	1.18	0.27	
FR30	28	1.00	0.00	0.00	200	0.00	1.00	50	110	7.39	7.62	1.87	0.13	
FR41	29	1.00	0.00	0.00	200	0.00	1.00	50	114	5.90	6.03	1.33	0.37	
FR51	29	0.99	0.00	0.00	100	0.00	0.00	200	110	5.53	5.84	1.35	0.30	
FR52	29	0.97	0.00	0.00	100	0.00	1.00	50	110	6.22	6.22	1.22	0.38	
FR53	29	0.99	0.00	0.00	100	0.00	0.00	250	110	5.31	5.63	1.19	0.27	
FR61	29	0.96	0.00	0.67	100	0.00	1.00	50	110	4.94	4.96	1.38	0.14	
FR63	29	1.00	0.00	0.67	50	0.00	1.00	50	110	4.46	4.47	0.95	0.44	
FR72	29	1.00	0.33	0.00	100	0.33	0.00	250	110	5.20	5.51	1.11	0.32	
LU00	28	0.96	0.33	0.00	50	0.00	1.00	150	162	4.98	5.24	1.12	0.39	
NL11	31	0.85	0.00	0.00	150	0.00	0.00	250	257	7.22	7.45	1.70	0.13	
NL12	31	0.84	0.33	0.00	250	0.00	0.00	200	257	7.28	7.58	1.85	0.00	
NL13	31	0.87	0.00	0.00	100	0.00	1.00	50	257	6.18	6.32	1.18	0.18	
NL21	30	0.91	0.00	0.00	200	1.00	0.00	150	257	6.27	6.49	1.39	0.06	
NL22	30	0.91	0.33	0.00	250	0.00	0.00	200	257	7.15	7.50	2.06	0.10	
NL23	30	0.85	0.67	0.00	250	0.00	0.00	250	257	7.29	8.17	2.39	-0.20	
NL31	31	0.82	0.00	0.00	100	0.00	1.00	50	257	5.96	6.27	2.21	0.43	
NL32	31	0.82	0.00	0.00	250	0.00	0.67	50	257	7.37	7.93	1.83	-0.16	
NL33	31	0.83	0.00	0.00	250	0.00	0.00	200	257	7.63	8.21	1.93	-0.20	
NL34	31	0.86	0.00	0.00	250	0.00	0.00	200	257	7.96	8.31	1.76	-0.01	
NL41	31	0.86	0.33	0.33	250	0.00	0.00	200	257	7.39	7.89	2.01	-0.21	
NL42	31	0.94	0.00	0.00	200	0.00	0.00	200	257	6.81	7.31	1.54	0.12	
UKH	12	0.82	0.00	0.00	150	1.00	0.00	250	148	8.04	8.07	1.31	-0.46	
UKJ	11	0.82	0.00	0.00	200	0.00	0.00	250	148	7.65	7.75	1.10	-0.31	
UKK	29	0.81	0.00	0.00	150	0.00	1.00	150	148	6.62	6.71	1.32	0.10	

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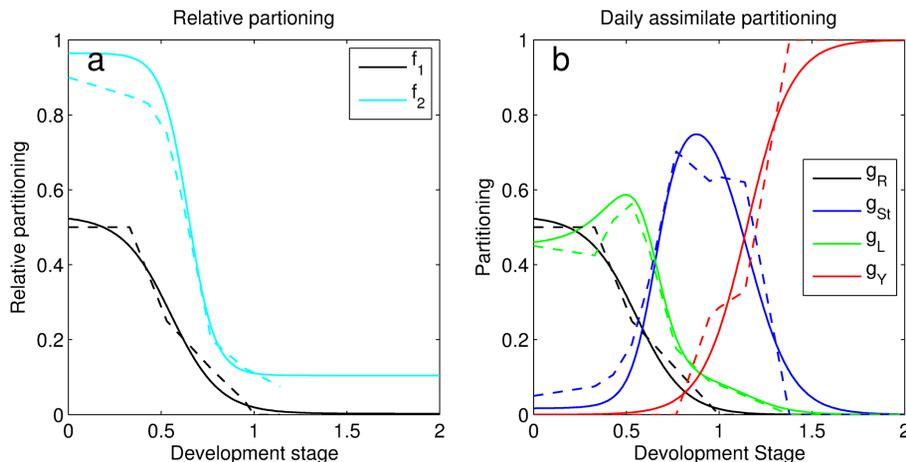


Figure 1. (a) The allocation to roots relative to vegetative organs (f_1) and the allocation to leaves relative to leaves and stem (f_2) for winter wheat. Dashed lines represent the allocation model from Penning de Vries et al. (1989) and solid lines are fitted Richards equations (Eqs. 3 and 4). (b) The resulting allocation scheme to roots (g_R), stem (g_{St}), leaves (g_L) and grains (g_Y) (solid lines) compared to data from Penning de Vries et al. (1989) (dashed lines) from equations in Eq. (6).

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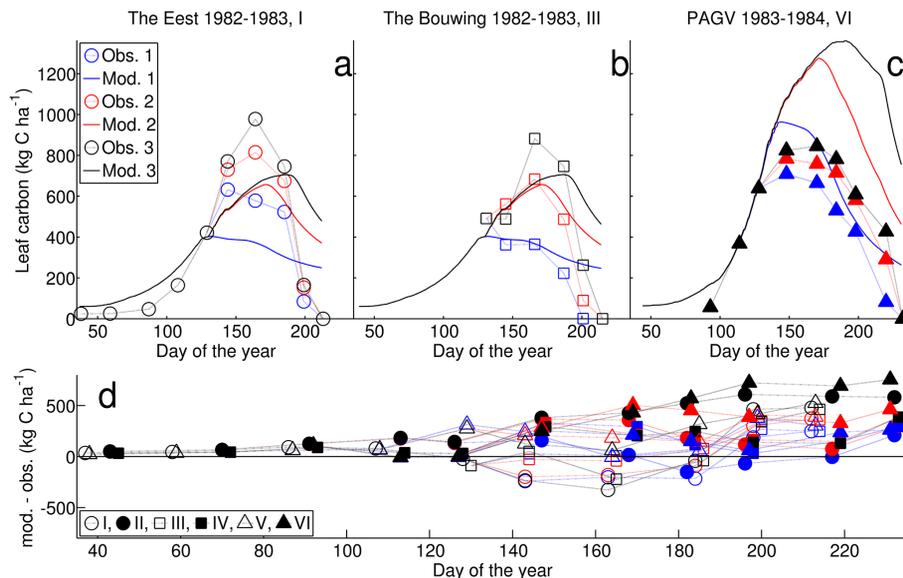


Figure 2. (a–c) Observed (thin lines) and simulated (thick lines) leaf C for the Eest and Bouwing for the season 1982–1983 and PAGV for the season 1983–1984, for three example plots with different levels of N fertiliser input. (d) The difference between observed and simulated leaf C for three different levels of fertiliser application for the Bouwing, the Eest and PAGV (Netherlands) for seasons 1982–1983 and 1983–1984 (Groot and Verberne, 1991). Blue symbols indicate lowest levels of fertilisation; red represent medium and black symbols a high N fertiliser input. Open symbols are for the season 1982–83, and closed symbols are for the season 1983–1984.

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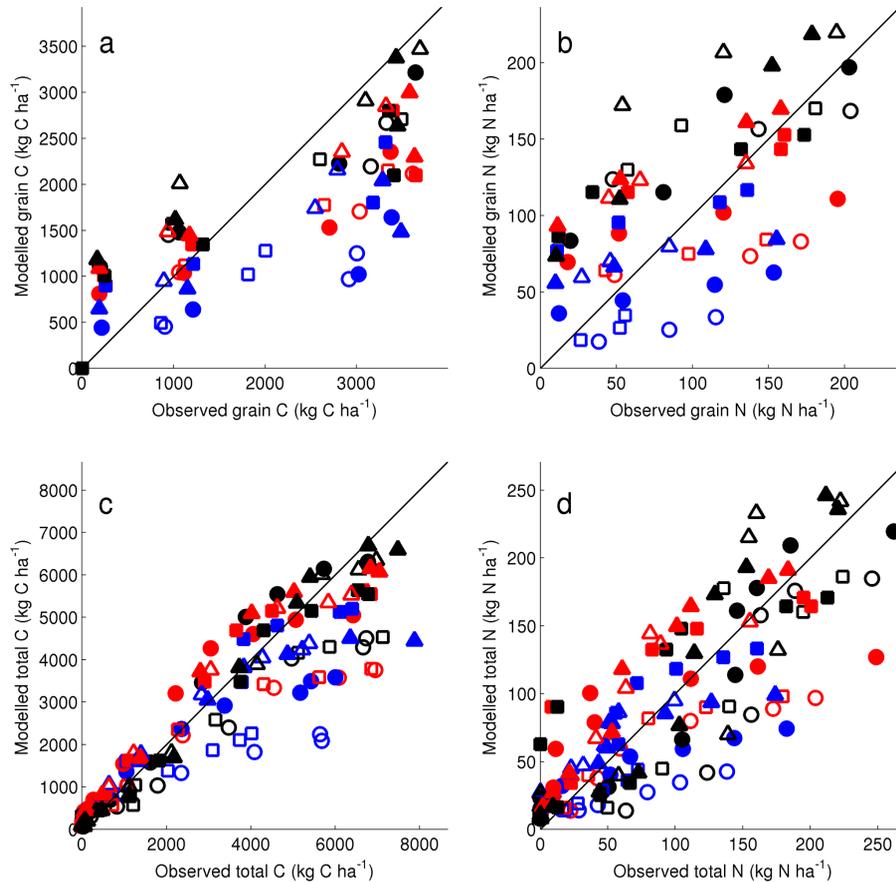


Figure 3. A comparison between modelled and observed grain C (**a**) and N (**b**), and total biomass C (**c**) and N (**d**) for the Eest, the Bouwing and PAGV, the Netherlands over the growing-seasons 1982–1983 and 1983–1984. Symbols the same as in Fig. 2 with blue symbols for low input of N fertiliser, red for a medium input of N and black for high N input.

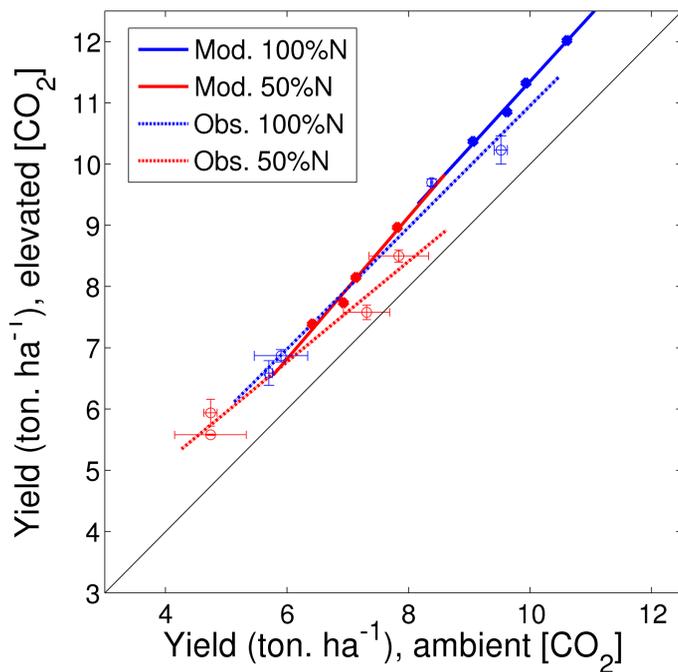


Figure 5. Effect of CO₂ fertilisation on observed and simulated grain yield, comparing wheat grain yields grown at elevated CO₂ (~ 548 ppm) with those grown at ambient CO₂ (~ 378 ppm). Simulated yields are depicted by solid lines and filled circles, observations are depicted by dashed lines and markers, shown for treatments with sufficient N fertiliser input (100 % N, blue), and treatments that received half of that amount (50 % N, red). Observations are from (Table 4 Weigel and Manderscheid, 2012).

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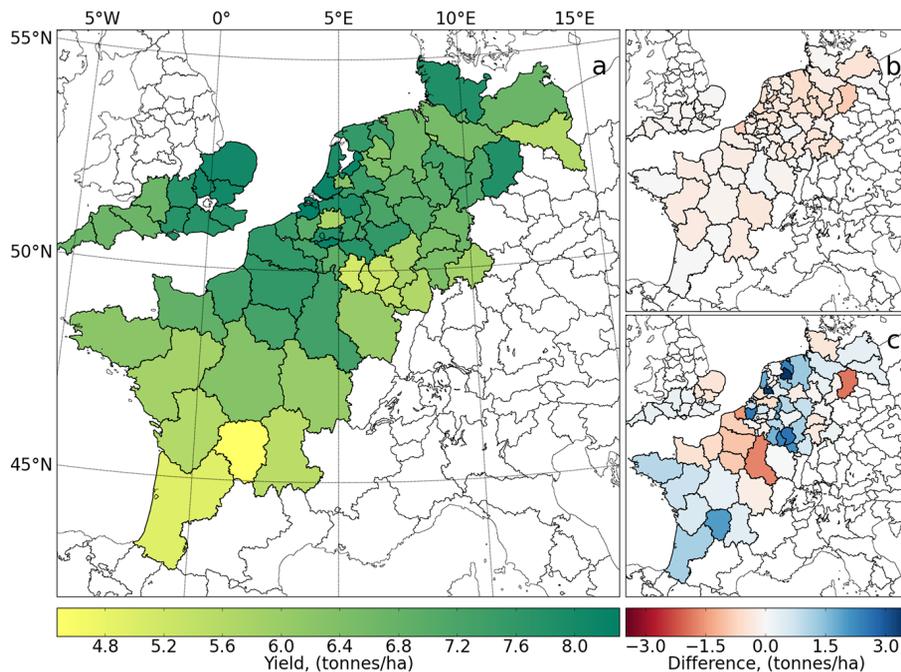


Figure 6. Reported regional yields from EUROSTAT (a), differences between simulated and reported yields for the $F_{opt(T,A)}$ setup (b) and the $F_{t,l}$ (c) simulations.

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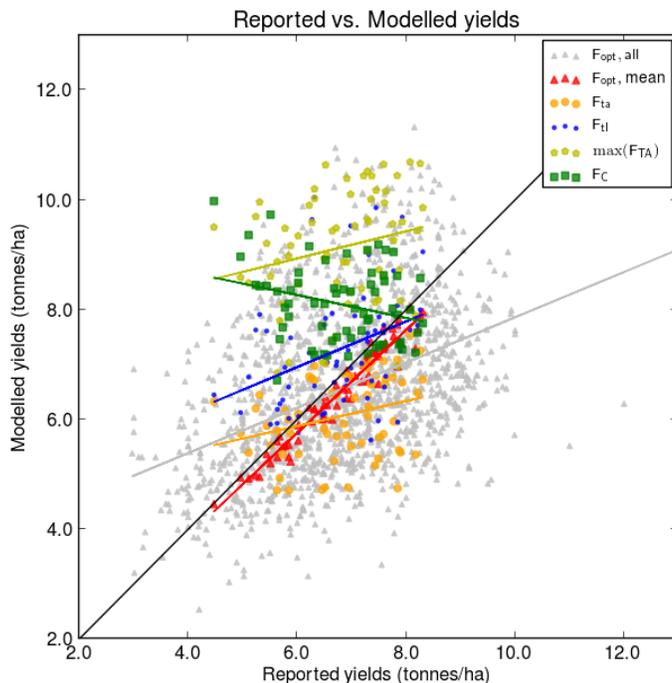


Figure 7. Reported vs. modelled yields for the 65 regions used in this study. Grey dots represent all available years for each region, with the fertiliser management that gave the best agreement with data for each region ($F_{opt(T,A)}$, all), the red dots are their means. Dark green markers show the mean for each region with the C-only version of the model (F_C), pale green represent the management that gave the maximum yields for each region ($\max(F_{T,A})$). Orange markers show the result from using a mean N management over the region, blue represent simulations using the same timing for each region but with a spatially explicit data set of N application (Elliott et al., 2014) ($F_{t,1}$). Lines are fitted linear regressions, see Table 5 for details. The number of years included for each region is listed in Table A3.

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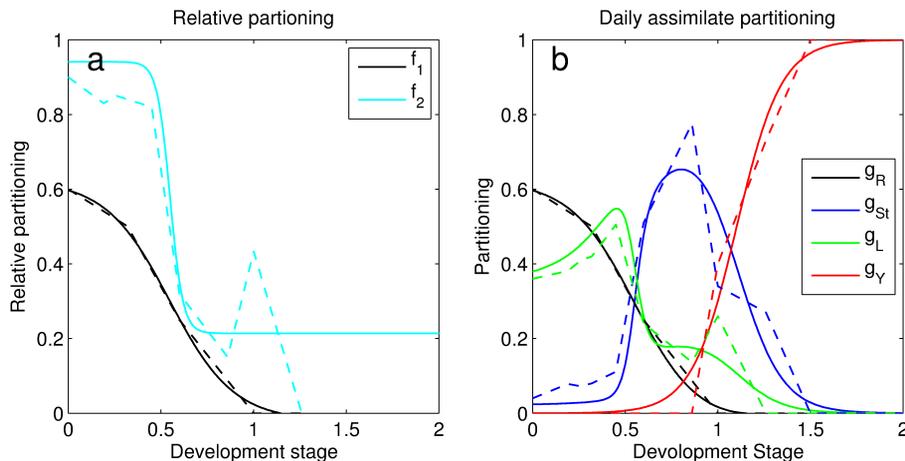


Figure A1. (a) The allocation to roots relative that to vegetative organs (f_1) and the allocation to leaves relative that to leaves and stem (f_2) for spring wheat. Dashed lines represent the allocation model from Penning de Vries et al. (1989) and solid lines are fitted Richards equations (Eqs. 3 and 4). **(b)** The resulting allocation scheme to roots (g_R), stem (g_{St}), leaves (g_L) and grains (g_Y) (solid lines) compared to data from Penning de Vries et al. (1989) (dashed lines) from equations in Eq. (6).

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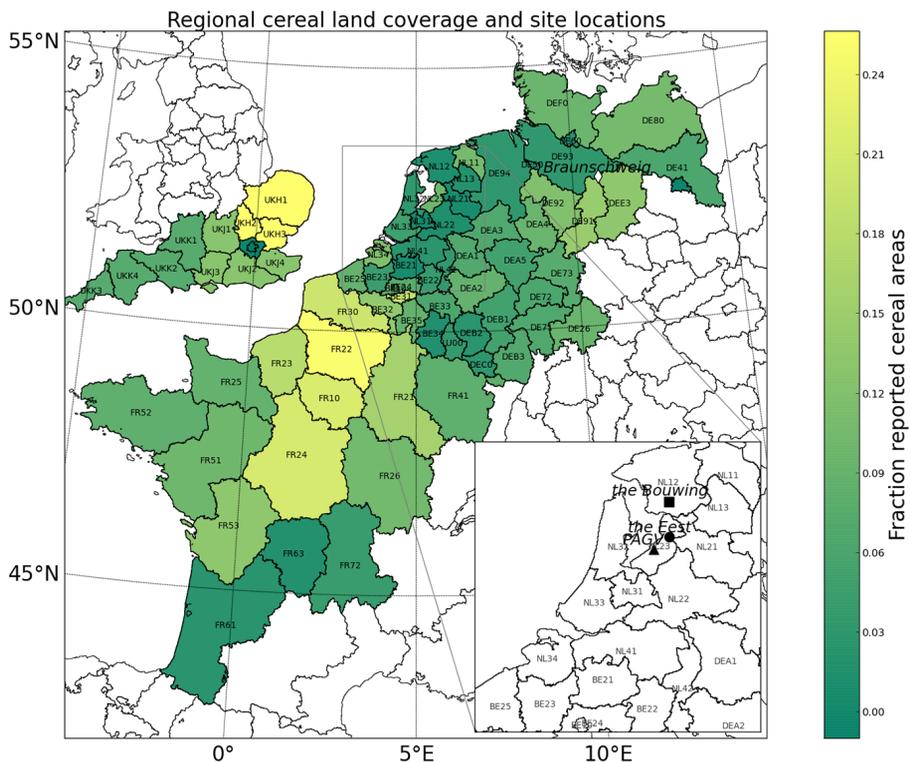


Figure A2. The fractions of cereal land in each selected region from EUROSTAT with region names as labels, also the locations of the trials described in Sect. 3.1 and the FACE experimental site.

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