150 years of macronutrient change in unfertilized UK ecosystems: Observations vs simulations

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HIGHLIGHTS

- Tested models are needed to understand plant-soil C N and P change & untangle drivers.
- Two long-term experiments are used to test the N14CP model and to uncouple drivers.
- N deposition is shown to have a large effect on the Geescroft Wilderness experiment.
- Biomass removal has reduced the effect of N deposition at the Park Grass experiment.
- These conclusions can be interpreted more widely in northern grasslands and forests.

GRAPHICAL ABSTRACT
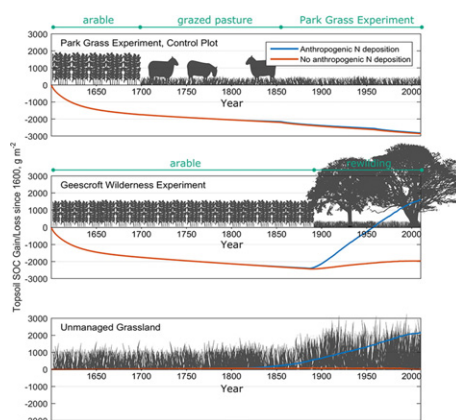
ABSTRACT

Understanding changes in plant-soil C, N and P using data alone is difficult due to the linkages between carbon, nitrogen and phosphorus cycles (C, N and P), and multiple changing long-term drivers (e.g. climate, land-use, and atmospheric N deposition). Hence, dynamic models are a vital tool for disentangling these drivers, helping us understand the dominant processes and drivers and predict future change. However, it is essential that models are tested against data if their outputs are to be concluded upon with confidence. Here, a simulation of C, N and P cycles using the N14CP model was compared with time-series observations of C, N and P in soils and biomass from the Rothamsted Research long-term experiments spanning 150 years, providing an unprecedented temporal integrated test of such a model. N14CP reproduced broad trends in soil organic matter (SOM) C, N and P, vegetation biomass and N and P leaching. Subsequently, the model was used to decouple the effects of land management and elevated nitrogen deposition in these experiments. Elevated N deposition over the last 150 years is shown to have increased net primary productivity (NPP) 4.5-fold and total carbon sequestration 5-fold at the Geescroft Wilderness experiment, which was re-wilded to woodland in 1886. In contrast, the model predicts that for cropped grassland conditions at the Park Grass site, elevated N deposition has very little effect on SOM, as increases in NPP are diverted from the soil. More broadly, these results suggest that N deposition is likely to have had a large effect on SOM and NPP in northern temperate and boreal semi-natural grasslands and forests.

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1. Introduction

The last two centuries have seen large-scale long-term perturbations of the carbon, nitrogen and phosphorus cycles as a result of elevated nitrogen deposition, land-use change, and agricultural intensification. Understanding the long-term plant-soil systems response to changing carbon, nitrogen and phosphorus (C, N and P) cycles is important given the timescale of this anthropogenic disturbance, and the centennial to millennial residence times of soil organic matter that our current understanding suggests (Mills et al., 2014).

The N14CP model was designed to represent linked plant-soil carbon, nitrogen and phosphorus cycling for temperate, boreal, semi-natural ecosystems (including broadleaf and coniferous forests, grassland and heathland habitat types) over these time scales (Davies et al., 2015), having been run from the start of the Holocene to simulate soil nutrient pool development. The model has been calibrated and tested against 88 northern European sites with single time point observations of soil carbon, nitrogen and phosphorus, dissolved fluxes and radiocarbon. The aim was to provide a single non-site-specific parameterisation using these 88 sites so that the resultant model is generalizable for temperate, boreal semi-natural ecosystems, rather than being restricted to the site of calibration only. A non-site-specific parameterisation is necessary for models that are to be applied at larger scales (where data-based calibration will not be possible) to provide us with regional, national or global insights into the consequences of land-use change and anthropogenic disturbances of C, N and P cycles. This prior work, in effect, provided a space-for-time test of the model, as N deposition, climate and pH varied between sites and sampling points with dates ranging from 1979 to 2013. Whilst this provided the most robust constraining exercise of such a model to date given the number of sites used and the diversity of the observation types to which the model was compared, the temporal response of any particular site to elevated N deposition could not be examined as the soil data were limited to single time points.

The Rothamsted Experiments (Johnston et al., 2009; Macdonald et al., 2015; Rothamsted, 2006) offer a rare opportunity to test the N14CP model against long-term soil carbon, nitrogen and biomass time series, with experiments spanning the period from the mid-19th Century to the present day, and providing data on the responses of the plant-soil system to management and changes in atmospheric deposition, especially that of N. Here, selected treatments from two of the Rothamsted Long-Term Experiments are simulated using the N14CP model: the Park Grass control plot (Silvertown et al., 2006) and the Geescroft Wilderness experiments (Poulton et al., 2003), as these two treatments are unfertilized, making them suitable for examination with N14CP, and they provide two contrasting land-use change tests of this model. The Park Grass control plot has been unfertilized grassland since 1856 and Geescroft is an unmanaged arable site which returned to trees in the 1880s.

Whilst soil models have been applied to these experiments previously (e.g. Smith et al., 1997), the focus in this earlier work was largely on soil carbon pools and concentrations, and there has been relatively little account taken of plant growth and its dependence on N. Where soil N has been considered in addition to soil C, it seems that N deposition has either been neglected completely, or that the large changes in N deposition over the observation period have not been considered. No models consider the links between C and N cycles to those of P. Indeed, to the authors' knowledge, the simulations presented here comprise the first long-term simulation of C, N and P cycles compared to a long-term time-series of observations.

The aims here are two-fold. First, we tested the N14CP model against measured changes in the two ecosystems, driving the model with the best information about site history, climate, atmospheric deposition, and management. Second, we used hypothetical management and deposition scenarios to uncouple these drivers, so as to quantify their separate effects. The variables considered comprised net primary production (NPP), plant biomass, plant topsoil pools of C, N and P (0–15 cm), and bulk soil radiocarbon.

2. Methodology

2.1. N14CP model summary

A full description of the N14CP model can be found in Davies et al. (2015), where the multi-site calibration of this model is also described. The resultant parameterisation is used in this present work. Fig. 1 gives a schematic of the model. The model is run from the start of soil formation (12,000 years BP) so that pools of macronutrients build up over time. N14CP simulates on a quarterly time-step stoichiometrically linked C, N and P pools representing nutrients in plant biomass, coarse decomposing litter, and soil organic matter (SOM) in two layers representing the first 15 cm and everything below this depth. The SOM is divided into three compartments (fast, slow and passive) with turnover rates of ~2–1000 years. In addition to these linked C, N and P pools, a pool of weatherable P is simulated and P sorption to soil surfaces is included in the topsoil and subsoil layers. As the model name suggests, radiocarbon ^{14}C is also tracked within the model, providing an additional means to evaluate the SOM turnover rates and litterfall inputs. In the simulations, C, N and P are transferred between these pools or lost as dissolved and gaseous outputs due to plant growth and litterfall, decomposition, denitrification, weathering, P sorption/desorption, and N and P immobilisation.

Following Liebeg's law of the minimum, net primary productivity (NPP) is assumed to depend of one of a number of potentially limiting factors, those considered here being: temperature, precipitation or N or P availability. Limitation by CO_2 is neglected here, as the sites examined are unfertilized and most likely N or P limited rather than C limited. Vegetation is represented on a plant functional type (PFT) basis, with each PFT having different stoichiometric C, N and P growth requirements and litterfall characteristics. The PFTs used here are grass and broadleaf deciduous forest, and the generic plant properties are taken from Tipping et al. (2012). The vegetation biomass is split into two compartments: one representing coarse woody plant tissues, and the other fine soft plant tissues, which is assumed to be divided 50:50 between above and below ground.

Available N for plant growth derives from decomposition of the SOM and the coarse litter pool, atmospheric N deposition, and N fixation. Decomposition of the coarse litter pool and SOM compartments is represented by a first order process, modified by temperature. Decomposed C in the coarse litter pool is assumed to be lost as CO_2, and N and P contribute to the plant available N and P pool in soil water. Carbon deriving from decomposition of the SOM is partitioned into dissolved organic C and CO_2. Nutrients N and P resulting from decomposition are partitioned into organic and inorganic dissolved forms, and the inorganic N undergoes temperature dependent denitrification. The N fixation rate is also dependent on temperature, but is also related to the availability of P, and down-regulated by N deposition. Available P for plant growth derives from P weathering, P deposition, P from
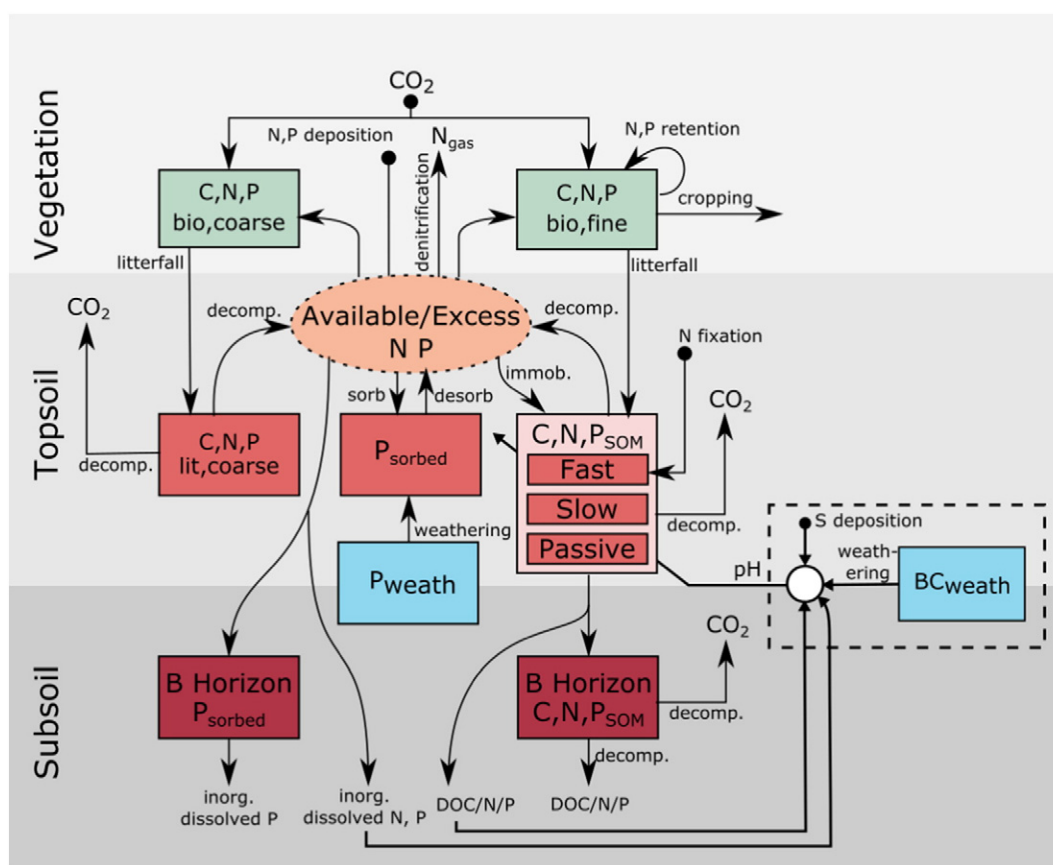
Fig. 1. Schematic of the N14CP model.

decomposition and desorption, and P which can be accessed by extracellular phosphatase enzymes. Excess N and P post-growth are either immobilized into the SOM or leached in inorganic forms, in addition to dissolved organic C, N and P (DOC, DON, DOP) which result from decompositon.

An annual estimate of soil pH is made based on atmospheric additions of N, sulphate and base cations (BCs), weathering inputs of BCs, fluxes of DOC and inorganic N (which is treated as nitrate), and soil pCO_2. The pH is used to modify the decomposition and immobilisation rates.

All model parameters, and plant stoichiometries, were kept at the generalised values found in Davies et al. (2015). Two site variables were estimated. The starting pool of weatherable base cations was estimated from soil pH measurements for 2002 and 1999 for Park Grass and Geescroft Wilderness respectively, using the same methodology as Davies et al. (2015). Doing so involved a back-calculation of the BC_{weath0} pool by calculating the present day flux of BCs needed to produce the modern day observed pH, taking into account typical DOC and inorganic N leaching rates and N and S deposition at the site. A backwards projection was then made based on the known climate and deposition history to produce the BC initial condition. The weatherable phosphorus pool (P_{weath0}) was estimated by adjusting it to match as well as possible the observed organic P soil pools. It was assumed that the two sites, given their proximity and shared soil classification, have the same value of P_{weath0}. The value of P_{weath0} was adjusted to minimize the sum of absolute errors between modelled topsoil SOP and measured topsoil SOP, resulting in a P_{weath0} of 600 gP m^{-2}.

We assumed that the formation of currently-observed top soil and immediate subsoil started at 10,000 BCE as the periglacial sites started to warm after the last Ice Age. Thus, the simulated pools of C N and P began to accumulate at that point in time. The model was run driven by land-use histories for the Park Grass and Geescroft sites (described

in Sections 2.2 and 2.3 respectively), climate and deposition data described in Section 2.4, and the resulting outputs compared with experimental observations detailed in Section 2.5.

2.2. Park Grass land-use history

The Park Grass Continuous Hay Experiment was established in 1856 on a 2.8 ha area. Prior to this, the area is thought to have been used as grazed pasture since 1700, and for arable cropping in the 17th century (Rothamsted Research, 2015). The management of the site pre-1600 is more uncertain: there is evidence of medieval tillage at the site, and Rothamsted fields were first cleared and cultivated in Roman times, but the extent of these activities and their continuity are unknown. Hence, for modelling purposes the site is assumed to be long-term grassland prior to 1600. The history used within the model is summarised in Table 1.

The experiment investigates various fertilizer and liming treatments, however the plot of interest here is the un-limed and un-fertilized control plot 3d, which carries a mixed sward. The site was cut annually in June between 1856 and 1874, with sheep grazing of re-growth after the crop. From 1875, the site was cut twice annually usually in June and October, although some year's regrowth was insufficient for a second cut. After the first cut material is left on the site to make hay and return seed, whereas the second cut is removed immediately. The plots were originally cut by scythe, and then horse-drawn and tractor-drawn mowers. Since 1960, the second cut (and only the second cut) has been made with a forage harvester, which removes more of the above ground vegetation compared with the mower. The forage harvester is also used on a small section of the plot in the first cut post-1960 for the purposes of measuring the yield, but for the remainder of the plot is mowed in the traditional manner.

Table 1
Scenario descriptions for Park Grass and Geescroft Wilderness sites. Land-use scenarios based on the experimental conditions and alternate land-uses are combined with two deposition scenarios to create 10 scenarios that are examined in the model simulations in order to decouple the effects of N deposition and land-use management on these sites. The "real" land-use scenarios are shown by *, others were run to isolate different effects (see Section 2.6).

Land-use scenario	Deposition scenario	
	Anthropogenic N deposition between 1800 and 2010	No anthropogenic N deposition between 1800 and 2010
Park Grass		
Experiment land-use history: 1600–1700 unfertilized arable, 1700–1856 grazed pasture, 1856 to 1960 two mown annual cuts, 1960–2010 second harvest forager cut.	PG1a*	PG1b
Continued grazing: 1600–1700 unfertilized arable, 1700–2010 grazed pasture.	PG2a	PG2b
Natural: 1600–2010 undisturbed grassland	PG3a	PG3b
Geescroft wilderness		
Experiment land-use history: 1600–1886 unfertilized arable. 1886–2010 broadleaf deciduous.	GW1a*	GW1b
Continued arable: 1600–2010 unfertilized arable.	GW2a	GW2b

Assumptions needed to be made regarding the removal of vegetation by grazing, arable cropping and cutting during the experiment for the model. Cutting practice has changed over the course of the Park Grass experiment, as described above, hence, these changes were acknowledged within the modelling. Two vegetation cuts were performed within the model: one at the end of quarter 2 and another at the end of quarter 3. Pre-1960, the second cut was less systematic, with some years having no second crop. However, most commonly a second cut was taken, and it was assumed within the model that this was always the case. It was assumed that scything, horse-drawn and tractor drawn mowing cut the vegetation to the same extent. The forage harvester removes significantly more vegetation compared with these methods. Data collected over 3 years (Macdonald, 2015) at the Park Grass site informs a power law regression between forage harvested yields and mown yields ($r^2 = 0.9$), such that mown yield is $0.02*(forage harvester yield)^{1.7}$ in gC m^{-2}. The forage harvester does not cut the total above ground biomass: a stubble remains, the fraction of which is dependent on the herbage height. In low growth years the stubble is thought to be as much as 50% of the total above ground biomass, whilst in years with better growth, a larger percent of the biomass is accessible (Macdonald, 2015). Hence, to estimate the stubble for modelling purposes, the minimum yield from data collected at the site since 1856 (0.13 t of dry mass per ha) was assumed to be equal to the inaccessible portion of the above ground biomass (i.e. 6.5 gC m^{-2}, assuming that half of the dry weight is carbon). In the model, the above ground biomass (50% of total biomass given the assumption in the model's plant stoichiometries that the above and below ground biomass is split 50:50) minus the inaccessible stubble is removed for forage harvested cuts.

Arable cropping pre-1700 is assumed to remove the same amount of vegetation as the mowing method, once annually at the end of quarter 3.

Grazing animals are assumed to consume on average 60% of the above ground biomass (Ball and Ryden, 1984; Lemaire and Chapman, 1996). It is assumed that 75% of the C ingested by the animal is either respired or accumulated, with 25% being indigestible and returned to the soil (Soussana et al., 2010). For N and P it is assumed that 25% is accumulated by the animals, with the remaining 75% being returned to the soil system (Ball and Ryden, 1984; Haygarth et al., 1998; Jarvis, 1993; Tyson et al., 1990).

2.3. Geescroft Wilderness land-use history

The Geescroft Wilderness is a small area of land (1.27 ha), which was fenced off in 1886 and allowed to revert to deciduous woodland. The area is thought to have been in arable cultivation since at least 1623 when the site was mapped, and is known to have been used for arable field trials between 1847 and 1878 (Rothamsted Research, 2015). As with Park Grass, pre-1600 site management is uncertain and as such it is assumed here that the two sites have a shared history prior to this as a long-term grassland. Arable cropping at Geescroft is assumed to remove the same amount of vegetation as mowing, as described in Section 2.2. The site has been monitored since being fenced off in 1878 and trees were observed to be establishing on the site in 1913 (Harmer et al., 2001). Given this relatively rapid colonisation by woody species, the land-use type was switched to trees in the model on commencement of rewilding in 1878. The land-use history used within the model for the Geescroft Wilderness is summarised in Table 1.

2.4. Climate, atmospheric deposition and atmospheric radiocarbon

Mean quarterly temperature and precipitation are used within the model to define the maximum NPP over a quarter. Temperature also controls decomposition, fixation and immobilisation process rates. Daily precipitation data from 1856 to 2012 and daily temperature data from 1878 to 2012 collected at the Rothamsted site were aggregated to quarterly values and used to drive the model. Prior to 1856, the long term average quarterly precipitation was used, and pre-1878 the long-term quarterly temperature was adjusted using a temporal anomaly following Davis et al. (2003).

Estimates of N and sulphur deposition generated by the CBED model were used to drive N14CP (Smith et al., 2000), providing average estimates for wooded and non-fertilized grasslands for 2006–2010 of
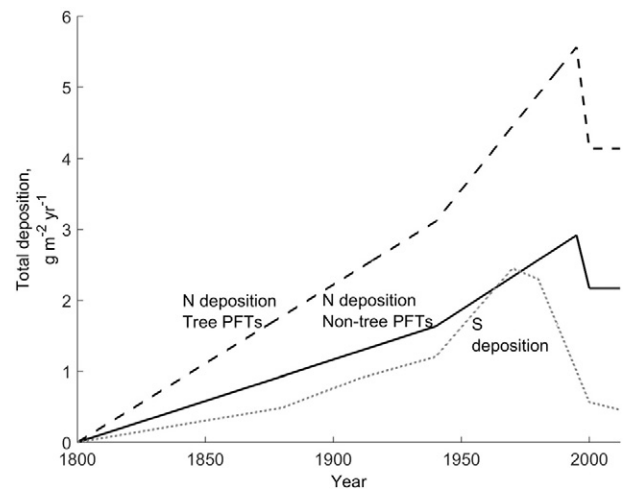

Fig. 2. Total nitrogen and sulphur deposition time series for driving the model based on a temporal anomaly (Schöpp et al., 2003) and local N and S deposition modelled estimates by CBED (Smith et al., 2000).

2.17 gN m^{-2} and 4.14 gN m^{-2} per annum respectively for this location. A deposition temporal trend for Europe defined by Schöpp et al. (2003) is combined with both of these estimates to provide the deposition time series shown in Fig. 2. Observations of N deposition exist for the Rothamsted site. Goulding et al. (1998) estimate a total annual deposition in 1996 for a fertilized arable crop of 4.33 gN m^{-2} yr^{-1}. However, estimates do not exist for non-fertilized areas or for woodlands at the site, and hence the modelled outputs are used.

Pre-industrial (pre-1800) N and S deposition rates are assumed to be zero for the purposes of these simulations (Fig. 2). Given the agricultural nature of the surrounding area, the deposition at the sites pre-1800 is likely to be non-zero, however, the magnitude of that deposition is highly uncertain. As down regulation of N fixation is included in the model formulation, N deposition does not have an effect on the model unless it is in excess of the fixation rate, which is ~0.3 gN m^{-2} yr^{-1} in this case. Hence, the zero N deposition rate assumption is equivalent to an assumption of ≤0.3 gN m^{-2} yr^{-1}.

Atmospheric deposition of P was not included as gains and losses are likely to be similar and there is no reliable means to estimate the net value at a given site (cf. Tipping et al. (2014)) found no systematic variation of P deposition across Europe. Therefore inputs and losses of P between semi-natural ecosystems and the atmosphere are likely be approximately equal. Base cation deposition is set in line with estimates as described by Davies et al. (2015).

Atmospheric radiocarbon values were obtained from Levin and Kromer (2004), as described by Davies et al. (2015). They cover the period 12,000 BP to the present, including 20th Century enrichment in "bomb carbon".

2.5. Long-term experiment observations

The Park Grass and the Geescroft Wilderness share the same soil type, which is a brown earth silty loan overlaying clay drift (Batcombe Series in the England and Wales classification), which is a brown earth silty loam overlaying clay drift. The soils at the sites have been sampled over the experiment's duration at least to 23 cm with some samples being taken to 82 cm. Observations of soil C and N and radiocarbon from these samples were collated for the two sites spanning the period 1870 to 1999 for the Park Grass and 1886 to 1999 for Geescroft (Hopkins et al., 2009; Jenkinson et al., 1992; Jenkinson et al., 2008; Poulton, 1996; Poulton et al., 2003). Power law depth trends were fitted to observations of C and N where data at multiple depths were available, in order to interpolate the measurements to the 15 cm depth used by the model.

Several observations of organic P content (determined by the method of Williams et al., 1960) are available for Geescroft, taken from areas of the site that are known not to have received fertilizers (Jenkinson, 1971). We also used new organic phosphorus measurements for cores from the Park Grass site spanning the period 1984–2005, carried out by Blackwell (2015) as described in Turner and Blackwell (2013). This involves extraction with NaOH-EDTA solution followed by ^{31}P NMR analysis of different organic P forms. For both sets of organic P measurements, results for a soil depth of 23 cm were proportioned to 15 cm for use with the N14CP model, and soil organic P pools were estimated by combining the organic P concentrations with reported bulk densities.

Hay yield data are available for the Park Grass Experiment between 1856 and 2012. The post-1960 measurements for the first annual cut, which were made using a forage harvester, have been adjusted to represent the actual biomass removal by the mowing method based on a period of dual measurements with mowing and forage harvesting techniques. Above-ground biomass estimates are also available for the Geescroft Wilderness sites in 1965 and 1999, made by Poulton et al. (2003).

Inorganic N and P leaching data are also available for the Park Grass site as collected from the Environmental Change Network (Rennie et al.,

2015). Leachate concentrations of NO_3-N, NH_4-N and PO4-P have been monitored collected between 1994 and 2012 on approximately fortnightly basis. By combining these with average annual rainfall and potential evapotranspiration at the site, mean fluxes of inorganic N and PO_4-P were estimated for comparison with the model.

2.6. Hypothetical past scenarios

As can be seen from the preceding sections, land management and N deposition have not been static over the course of the Rothamsted long-term experiments, and therefore, change in observed variables cannot be attributed to a single driver. Hence, additional scenarios were explored to decouple the effects of N deposition and land management as summarised in Table 1. For Park Grass, in addition to the land-use change based on the actual experiment (Section 2.2, termed scenario PG1a), two further scenarios are examined. A scenario where the site continues to be grazed rather than converted to the cropped grassland experiment (PG2) is examined; and a scenario where the site was never grazed or cropped is considered (PG3). For the Geescroft Wilderness, in addition to the re-wilding history informed by the experimental description (Section 2.3, scenario GW1a in Table 1), a second land-use scenario (GW2) is examined where the site remains under arable management. These land-use scenarios are combined with two N deposition scenarios, where a) N deposition is elevated post 1800 as per the assumptions in Section 2.4 and b) where no N deposition occurs.

3. Results

The modelled topsoil SOC, SON and SOP pools, biomass pools and fluxes, and soil radiocarbon results for the Park Grass and Geescroft Wilderness experiments and scenarios described in Table 1 are given in Figs. 3–7. Experimental observations (adjusted to 0-15 cm), are also given in these figures, and we first compare them against default scenarios PG1a and GW1a (Table 1).

The model underestimates SOC and SON pools at Park Grass (Fig. 3, top row PG1a), but overestimates SOC and SON for Geescroft Wilderness (Fig. 3, third row GW1a). This arises because the model could not reproduce, on the basis of the assumed site histories (Table 1), the appreciable differences in SOC and SON pools that were observed in the late 1800s. That the modelled C and N pools are too large at one site and too small at the other is therefore the best result that could be expected given a lack of information on historical land management differences and other input drivers. For example, more information regarding pre-1800 N deposition may be critical in determining differences.

The model's temporal SOC and SON dynamics during the 20th Century agree reasonably well with the trends in observations, with Park Grass having decreasing soil C and N and Geescroft Wilderness gains in soil C and N pools (Fig. 3). Between the start of the Park Grass experiment in 1856 and the last observation point in 1999, the observed SOC and SON pools fall by 14% and 12% respectively, and the model produces 16% and 11% declines. For Geescroft Wilderness, the model predicts rises in SOC and SON of approximately 100% and 40% between 1883 and 1999, as compared with the observed increases of 126% and 30%.

Topsoil radiocarbon observations and simulations are given in Fig. 4. The Geescroft Wilderness experiment simulation (GW1, solid line third row) reproduces the observed ^{14}C well. However, the model simulates only a small increase in topsoil ^{14}C at the Park Grass site in response to bomb carbon, smaller than the observed increases (Fig. 4, black solid line, top row).

Comparing modelled crop yields to observations for Park Grass (Fig. 5, PG1a), it can be seen that the model produces crop estimates within the range of measured yields, but with less inter-annual variability. The model suggests that NPP and in turn biomass removal have been enhanced by N deposition, just sufficiently to overcome the resultant nutrient availability reduction caused by cutting the vegetation and
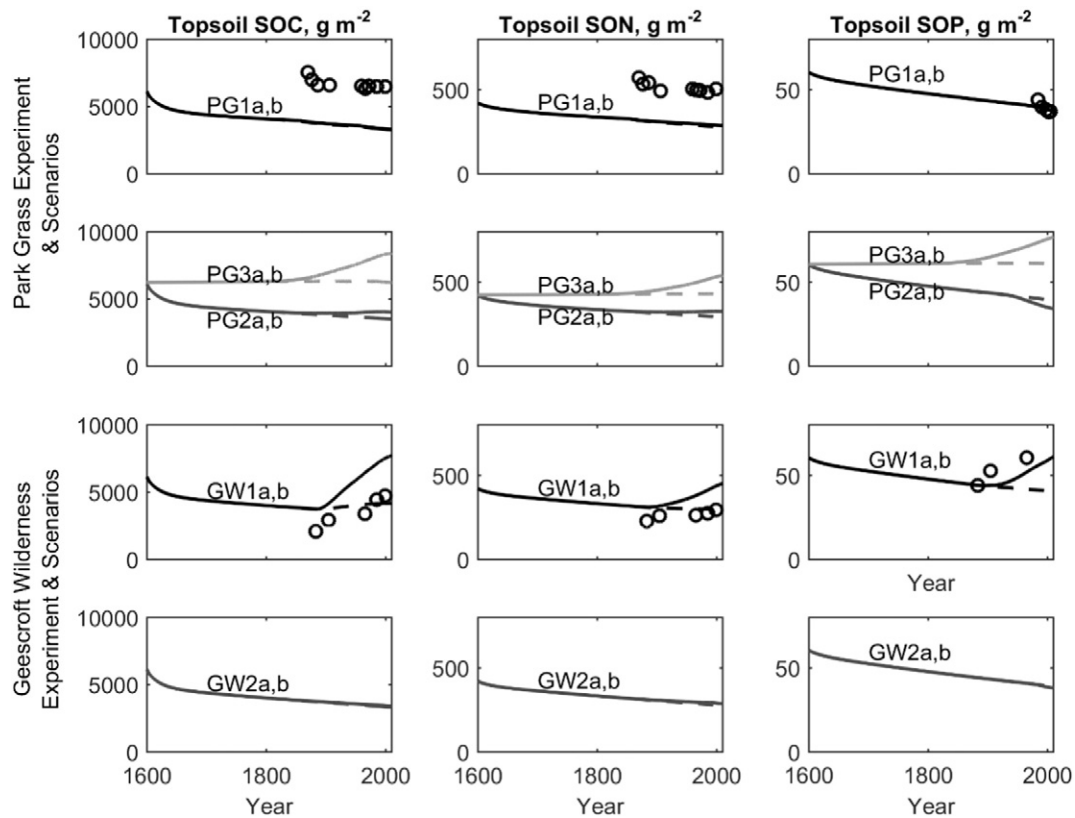
Fig. 3. Simulated topsoil SOC, SON and SOP from 1600 to 2010 for the Park Grass experiment 0–15 cm (PG1, top row), alternative land management scenarios where the site is continually grazed or is undisturbed grassland (PG2 and PG3 respectively, second row), and for the Geescroft Wilderness experiment (GW1, third row) and alternative land management scenario where the site is not rewilded (GW2, bottom row). Scenarios with and without anthropogenic N deposition are given by the solid and dashed lines respectively. Experiment observations (adjusted to 15 cm soil depth) are denoted by circles for comparison with the PG1a and GW1a model outputs, denoted by black solid lines in rows 1 and 3.

diverting N and P from the soil system. For Geescroft, the model produces biomass values in agreement with the observed values (Fig. 6).

The observed flux of inorganic N (nitrate) at the Park Grass site between 1994 and 2012 is low in comparison to measurements at other grassland sites. In the dataset previously used to calibrate and test N14CP (Davies et al., 2015), the mean flux for grassland sites was 0.38 gN m^{-2} yr^{-1}, with a maximum of 1.15 g-N m^{-2} yr^{-1}, whereas Park Grass has a mean and median of 0.03 and 0.01 g-N m^{-2} yr^{-1} respectively. The modelled inorganic N flux of zero for this period, therefore, can be considered to be consistent with the relatively low inorganic N leaching observed at the site. The mean observed PO4-P flux at Park Grass was 0.03 g-P m^{-2} yr^{-1}, which compares favourably with the simulated mean inorganic P flux of 0.021 g-P m^{-2} yr^{-1}.

3.1. The effects of nitrogen deposition, land-use change and management at Park Grass

Simulations of the Park Grass experiment under the two deposition scenarios (PG1a and PG1b) result in little effect of N deposition on the soil C and N pools under the cropping regime in place at Park Grass (Fig. 3). This is because the extra NPP due to increased N availability from deposition, which would have led to increased C and N inputs to the soil, is assumed to have been removed by cropping (Fig. 5), diverting C, N and P from the soil. The NPP and biomass decline in the scenario with no N deposition (PG1b), whilst increases are simulated when N deposition is included (PG1a), due to the fertilization effect of the additional N.

If the site had been ungrazed grassland since 1600 (PG3), then as shown in Figs. 3 and 5, increased N deposition (PG3a) would have produced large increases in NPP, biomass, and soil organic C, N and P, compared to the hypothetical scenario with no increased N deposition (PG3b). Simulated plant biomass and NPP increases by approximately

125% between 1800 and 2000 in the undisturbed grassland simulations and topsoil organic C and N increase by 2034 gC m^{-2} and 105 gN m^{-2}. Under N deposition, SOP also increases, as the extra N allows the plants to access more P from the inorganic (sorbed) pool.

Under the hypothetical grazed scenarios (PG2a and b), NPP and peak biomass are lower than in the ungrazed cases (Fig. 5), because significant N and P are removed from the system. Consequently soil C and N pools are also lower than the ungrazed case (Fig. 3), but higher than the cropped scenario (PG1a and B) as a proportion of the N and P grazed is returned to the soil from the animals. The effect of N deposition is seen, with higher values of NPP and biomass, and slightly higher soil C and N pools in scenario PG2a than PG2b, but the effects are not as prominent as the undisturbed grassland case (PG3). Under these scenarios, SOP declines, due to removal from the system, and N deposition accelerates the loss.

The net changes in topsoil organic matter pools in the simulation scenarios between 1600 and 2010 are summarised in Fig. 7. The total loss of soil carbon due to grazing and cropping in the Park Grass experiment since 1600 in the simulation is 2830 gC m^{-2} equating to a 45% loss over that period. However, comparing the soil carbon at the experimental site to the soil carbon that would have been sequestered in an undisturbed grassland increases this to a 2.5 fold reduction in soil carbon, or an effective loss of ~5000 gC m^{-2} between the undisturbed and the managed site.

3.2. The effects of nitrogen deposition and land-use change at Geescroft Wilderness

Based on the Geescroft Wilderness experiment (GW1a) simulation and the hypothetical experiment with no increase in N deposition (GW1b), it is evident that increases in soil C, N and organic P at the
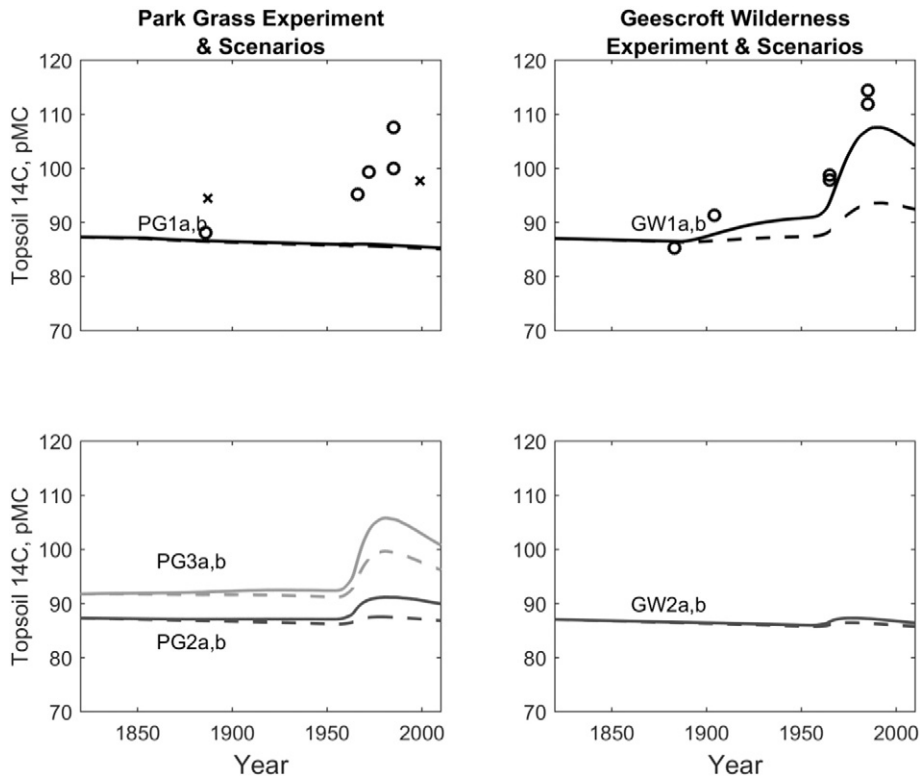
Fig. 4. Radiocarbon simulations and observations in percent modern Carbon (pMC) for the Park Grass experiment and land use scenarios (left column), and the Geescroft Wilderness experiment and alternate land use scenario (right column). Scenarios with and without anthropogenic N deposition are given by the solid and dashed lines respectively. Experiment observations are denoted by markers for comparison with the PG1a and GW1a model outputs, denoted by black solid lines in rows 1 and 3. In the top pane, observed radiocarbon data from Jenkinson et al. (2008) is denoted by an 'x' and Jenkinson et al. (1992) by an 'o'.

site since rewilding are in large part attributable to N deposition (Fig. 3). Succession to trees without added N deposition gives an SOC gain of 445 gC m^{-2} from 1886 to 2010, but approximately 8.5 times more

carbon is sequestered under the elevated N deposition scenario (3774 gC m^{-2}). Plant biomass and NPP are also over 4.5 times higher in 2010 in the anthropogenic N deposition scenario compared to a no
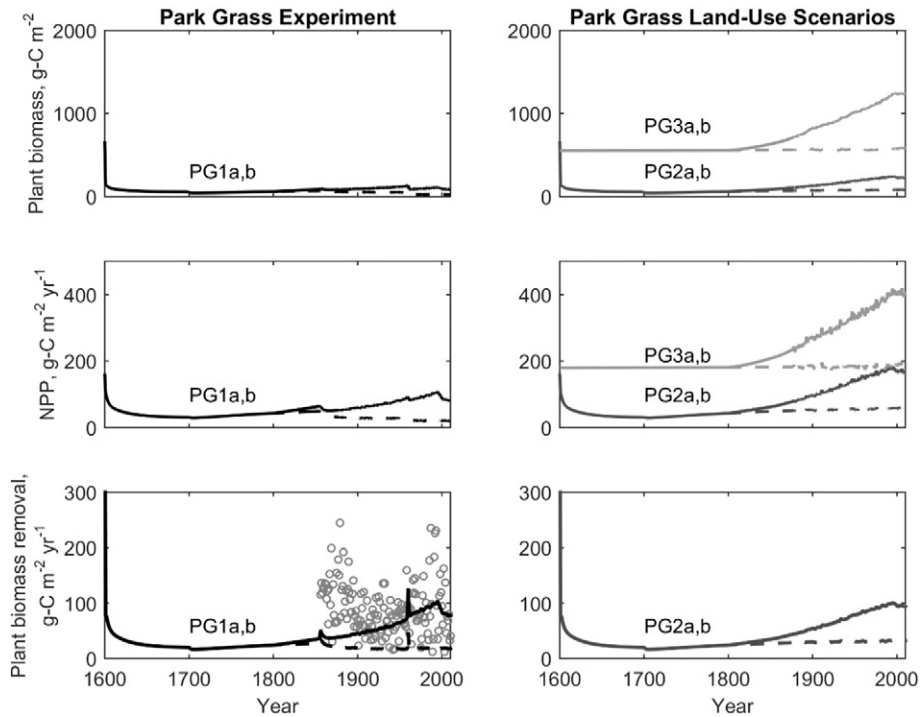

Fig. 5. Simulated annual peak plant biomass, net primary productivity and biomass removal through grazing and cropping for the Park Grass experiment (left column) and hypothetical management scenarios (right column), where the site is under continual grazing (PG2) or undisturbed grassland (PG3). Solid lines denote simulations with actual N deposition change, and dashed lines show results for simulations with no increase in N deposition (hypothetical). Circle markers represent plant biomass removal measurements from the experiment.
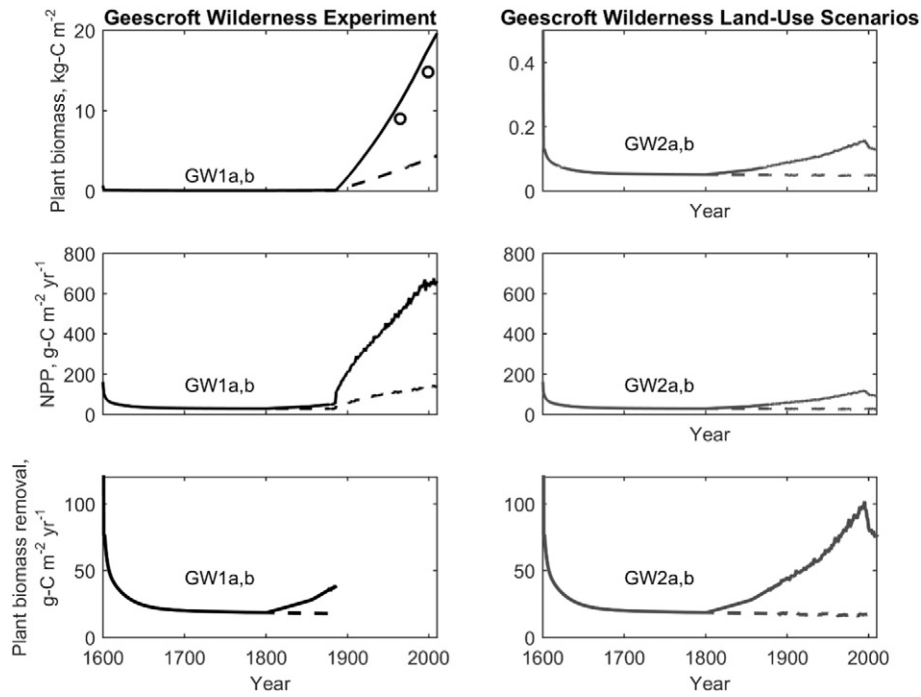
Fig. 6. Simulated plant biomass, net primary productivity and biomass removal through grazing and cropping for the Geescroft Wilderness experiment (left column) and other land-use scenarios (right column) where the site is under continually cropped (GW2). Solid lines denote simulations with anthropogenic elevation of N deposition and dashed lines simulations with no increase in N deposition.

deposition scenario. The increase in total plant-soil C (in biomass, topsoil and subsoil compartments) over the lifetime of the experiment is 5 times higher under N deposition (GW1a), compared with the no deposition scenario (GW1b).

Similar to the undisturbed grassland scenario (PG3a), rewilding at Geescroft under elevated N deposition (GW1a) resulted in increased SOP (Fig. 3), due to the uptake of P by the plants and the creation of more litter, at the expense of the P sorbed pool.
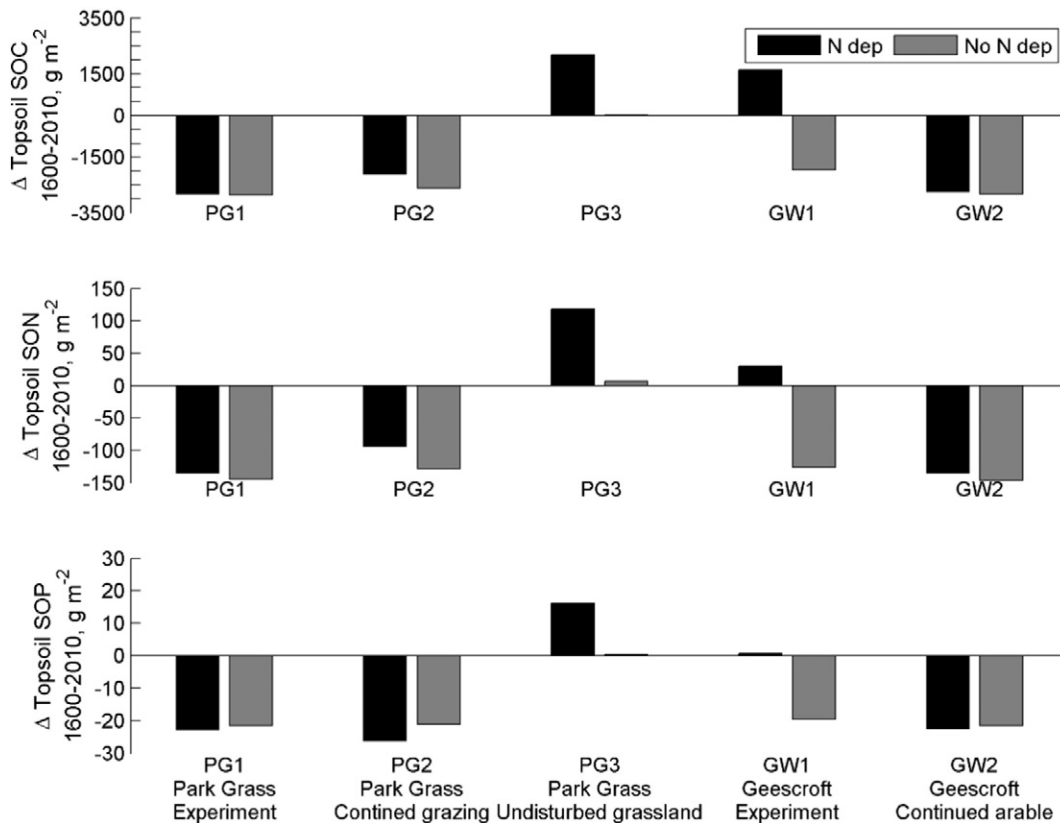

Fig. 7. Simulated changes in topsoil SOM pools over the period 1600 to 2010 for the Park Grass and Geescroft Wilderness sites and hypothetical deposition and land management scenarios as described in Section 2.6.

The calculated increase is in line with the available observations (Fig. 3).

Continued unfertilized arable management at Geescroft, as explored by hypothetical land-use history GW2, shows a similar trajectory to the Park Grass experiment (PG1), which is unsurprising given similar assumptions are made regarding cropping. Park Grass SOC and SON have a sharper decline however due to the twice annual cropping, and the use of the forage harvester for crop two which removes further biomass from the system.

4. Discussion

4.1. Nutrient response to N deposition and land management change

The N14CP model suggests significant effects of N deposition on the productivity of the Park Grass site (Fig. 5), as actually managed, but a weaker effect on soil C and N pools (Fig. 3). This arises because the removal of biomass acts to prevent the accumulation of atmospherically-deposited N. If the model is run without biomass removal, or grazing, then the extra input of N causes increases in NPP, biomass and soil C and N (Figs. 3 and 5), compared with pre-disturbance levels. The hypothetical simulations of grazing (scenarios PG2a and b) yield intermediate responses. At Geescroft, NPP would have increased even in the absence of N deposition (scenario GW1b), as trees generate more biomass carbon per unit available N and/or P, but the extra N from deposition leads to a much greater increase (scenario GW1a). A strong NPP response to N deposition in forested ecosystems was also simulated in the Northern European sites examined in Davies et al. (2015), which were in line with measured increases in forest biomass for the region (de Vries et al., 2009). Increases in forest NPP in response to elevated N deposition are also supported by the observations of Kahle (2008) and Quinn Thomas et al. (2010).

The model results suggest that N could potentially influence the behaviour of P over the period of observation. Since the sites are N-limited, extra plant growth caused by N fertilization can cause P to be transferred from the adsorbed inorganic pool first to plant biomass and then to SOP. This is strongly seen for Geescroft (Fig. 3), but the removal of N and P by cropping at Park Grass meant that the effect did not operate here. Interestingly, had we not calibrated the value of P_{weath0} for these sites, and used a default value of 204 gP m^{-2} found in Davies et al. (2015), the simulated pool of sorbed inorganic P at Geescroft would have been appreciably smaller, and as a result the SOP pool would have decreased as P is enzymatically liberated from the SOP to support increased plant growth under elevated N. In effect, threshold behaviour is seen where above a certain level of soil system P, elevated N drives increases in SOP, and below this threshold, decreases in SOP occur. The difference in results from site-specific and default P_{weath0} underlines the conclusion of Davies et al. (2015) that weatherable P is a key determinant of long-term ecosystem behaviour.

4.2. Comparison with previous modelling efforts

These valuable data sets have previously been analysed as part of a multi-model comparison exercise (Smith et al., 1997) in which 9 models were compared. All were applied to the control plot on Park Grass site, while 7 were used to simulate Geescroft Wilderness. The focus of this earlier work was on soil carbon pools and concentrations, and the only models to address nutrient effects (N only) and plant growth were the Hurley Pasture (HP) and Edinburgh Forest (EF) models (Arah et al., 1997), and the Century model (Kelly et al., 1997). Of these only the Century modelling took N deposition into account, but the report suggests that it was assumed constant over the simulation period (1876–1990), whereas in fact it varied considerably (Fig. 1). Therefore, results from this previous exercise cannot meaningfully be compared to those reported here.

Jenkinson et al. (1992) applied the RothC model to both the Park Grass and Geescroft Wilderness sites, optimising C input to the soil (assumed constant over the ~150-year simulation period) in order to fit observed values of soil C pools and soil ^{14}C data. For Geescroft the deduced NPP (equal to soil input) was 250 gC m^{-2} yr^{-1} which is roughly the same as the average value obtained with N14CP during the period following abandonment (Fig. 6, left-middle). However, the NPP for the Park Grass site reported by Jenkinson et al. (1992) was 400 gC m^{-2} yr^{-1}, of which 25% was assumed to be removed in harvest based on yield data, so that the input to soil was 300 gC m^{-2} yr^{-1}. This NPP value is considerably higher than our estimates of c. 100 gC m^{-2} yr^{-1} (Fig. 5, left-middle). We suggest two reasons for this discrepancy. Firstly, the N14CP model likely underestimates the NPP at Park Grass, as shown by the tendency of the modelled biomass removal to be lower than observed values (Fig. 5, left-bottom). Mean plant biomass removal was 90 gC m^{-2} yr^{-1}, whereas the model predicts 62 gC m^{-2} yr^{-1}. This may arise due to our underestimation of soil N, and consequently N availability, and because our general model fails to take account of local, non-modelled, factors that can lead to large inter-site variations in NPP for grass species (cf. Milne et al., 2002). Secondly, the NPP value reported by (Jenkinson et al., 1992) depended greatly on radiocarbon values that showed a large acquisition of "bomb carbon" by the soil during the second half of the 20th century. In subsequent work, Jenkinson et al. (2008) revised some of the Park Grass soil radiocarbon data, which they considered had been compromised by the presence of coal. In particular, a pre-bomb value of 79.9 pMC was revised to 94.5 pMC. Had the latter value been used in the simulations reported by Jenkinson et al. (1992), a lower average input of C to the soil would have been calculated, and hence a lower NPP estimated. Between them these two factors probably explain much of the disagreement between the RothC and N14CP results for Park Grass.

4.3. Radiocarbon at Park Grass

Whilst the ^{14}C predictions at the Geescroft Wilderness match the observations well (Fig. 4), the modelled results at Park Grass do not align with the observations. The measured enrichment in ^{14}C at the Park Grass site would be very difficult to reproduce with the N14CP model, given that measured SOC is declining in the topsoil and that cropping diverts new carbon from the soil. Reducing the removal of vegetation cropped, so that more new carbon enters the soil, would not improve the results, as indicated by PG3a, which represents an undisturbed grassland. The ^{14}C values produced by PG3a are more in line with the measurements, but the reduction in cropping increases the SOC (Fig. 3) and this is not witnessed at Park Grass.

One interpretation of the ^{14}C measurements might be that old soil carbon is somehow being lost from the site, in addition to the loss of new carbon fixed within the sward via cropping. However, the magnitude of loss of SOC is consistent with the removal of biomass C, so if this was the case greater declines in SOC might be expected.

The model could possibly reproduce both the SOC and the ^{14}C if the turnover rates of the SOM pools were calibrated to the Park Grass site. The modelled ^{14}C is too low at the start of the measurement period, suggesting that a different composition of fast, slow and passive C pools would be needed to meet this value. Site-specific calibration would defeat the purpose of this study, however, which is in part to test a generalised model under varying land use change conditions, using the long-term datasets of Park Grass and Geescroft Wilderness. Hence, it can be concluded that whilst net primary productivity, SOC, SON and SOP trends can be broadly represented, the measured SOC and ^{14}C at this Park Grass cannot be explained by the model, and that the consideration of multiple ecosystem variables is a strong test of a model.

4.4. Assessment and future possibilities

We deliberately refrained from site-specific calibration of the N14CP model in this work, because it is intended to be used as a simulation and forecasting tool, with readily available driving data (annual climate, atmospheric deposition, vegetation history). We allowed ourselves one calibration, that of the initial weatherable P pool using SOP data, in light of previous experience (Davies et al., 2015) which showed how this initialising variable has a strong influence on ecosystem development. The lack of site-specific calibration will partly explain why the model does not produce soil C and N pools in close agreement with the observations, unlike for example the C-models of Section 4.2, which were either initialised or spun-up to the late 19th Century soil pool values. Another contrast that can be made with the earlier C modelling is that it paid little or no attention to the role of N and P in controlling production, whereas N14CP places considerable stress on these nutrient elements.

Judged on the basis of the correspondence or otherwise between the measured data points and the model simulations in Figs. 3–6, we can argue that N14CP provides a good first approximation to reality with respect to multiple variables of interest. The main exception is the radio-carbon data for the Park Grass soils, discussed in Section 4.3. Discrepancies between measured and modelled variables produced by the present analysis may be useful in assessing uncertainty in the model's predictions at the UK scale, which is its primary purpose.

The two sites studied here provide two rare examples of long-term monitored semi-natural sites. One other possible site to analyse in the UK is the control plot at Palace Leas, Northumberland (Hopkins et al., 2009), while the Calhoun Forest experimental site in the US is another (Richter and Markewitz, 2001). Extending the modelling to incorporate the effects of added fertilizer would yield more possibilities for assessment. It would also be beneficial if other ecosystem models could be applied to these experiments such that the breadth of output variables available spanning C, N and P in soil, plant and water fluxes are simultaneously compared.

5. Conclusions

Soil C, N and P pools, plant biomass, and N and P leaching measurements at the Park Grass experiment (harvested grassland) and Geescroft Wilderness experiment (arable land re-wilded to woodland) have been approximately predicted by the N14CP model, using a non-site-specific version of the model driven by climate, increasing atmospheric deposition, and site management history.

For the Park Grass control plot, the model shows that coevolution of ecosystem C, N and P over the last 150 years has been strongly affected by the removal of nutrients in harvested biomass. N deposition change over this period partially compensated removal of N, supporting NPP and peak biomass. However, the effect of N deposition on soil C, N and P was marginal due to the removal of biomass.

In contrast, at Geescroft the model suggested that the growth of trees and increased storage of soil C, N and organic P have been strongly affected by N deposition; without it, carbon sequestration in the plant-soil ecosystem, since rewilding began in 1878, would have been 5 times lower.

The behaviour of P in the model at Geescroft is significantly affected by the greater availability of N due to deposition, with transfer of P from the inorganic sorbed pool to the plant biomass and the SOP pool. The results provide further evidence of the importance of weatherable P in soil parent material for determining ecosystem development.

As the N14CP model uses a non-site specific parameterisation, these results may be interpreted beyond the site-scale. Accordingly, the results suggest that N deposition is likely to have had a large effect on SOM and NPP in semi-natural grassland and forested ecosystems across temperate and boreal ecosystems in the northern hemisphere. For unfertilized cropped and grazed systems in the same region, the model suggests that whilst yields may have been supported in part by elevated N deposition, declines in SOM due to biomass removal have not been significantly counteracted by increased N availability from atmospheric N deposition.

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