

Complementary measures of soil texture, organic nitrogen accessibility and rhizosphere dynamics improve nitrogen supply prediction for short-cycle leafy vegetables

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Abstract

Accurate estimation of soil nitrogen (N) supply to plants is important for optimising fertiliser application, particularly for fast-growing, short-cycle crops with high N demand. Fertiliser recommendations for salad crops rely primarily on pre-sowing soil mineral N (SMN), which may not capture soil N supply via mineralisation during the cropping period. This study evaluated whether the plant N uptake by babyleaf spinach could be predicted by combining measures of soil N availability with soil properties. Six measures of soil N availability: KCl-extractable SMN, Total soil N, Anaerobically mineralizable N, Plant Root Simulator (PRS®)-N, Hydrolysable N and N contained in the free and lightly-occluded light fraction of SOM (FLOLF-N) were compared with plant N uptake across 15 soils. KCl-extractable SMN was a poor predictor of plant N uptake ($R^2_{\text{adj}} = -0.075$), while no individual N availability measure explained more than 28% of its variation. We found that sandy soils with relatively low organic matter could supply substantial quantities of plant-available N. Bayesian multiple regression identified a model including soil texture, PRS® and FLOLF-N that explained 77% of the variation in plant N uptake. These results suggest that predicting N supply for short-cycle crops may benefit from integrating rhizosphere inorganic N availability and N contained within physically accessible SOM fractions with the soil physical properties that control nutrient accessibility and transport.

1 Introduction

The global use of synthetic nitrogen (N) fertilisers has substantially increased agricultural productivity but has also contributed to the transgression of the planetary boundary for biogeochemical N cycling[1, 2]. The application of synthetic N fertilisers in excess of crop demand results in environmental losses of reactive N through nitrate leaching, ammonia volatilisation and nitrous oxide emissions[3, 4]. Sustainable nutrient management therefore depends on accurately estimating the amount of inorganic N supplied by the soil during crop growth and adjusting fertiliser inputs accordingly[5]. Inorganic N (ammonium NH_4^+ and nitrate NO_3^-) supplied by fertiliser inputs or mineralisation is immediately available for plant uptake. However, the inorganic N pool is a small and highly dynamic fraction of total soil N continuously undergoing depletion through plant uptake, microbial immobilisation, denitrification, and leaching[6], and resupply by mineralisation of organic matter. Consequently, a one-time measurement of inorganic soil mineral N (SMN) may provide an inadequate indication of the total N that will become available to a crop over its growing period. Improving estimates of soil N supply (SNS) could therefore ensure the calculated fertiliser recommendations better match crop N demand, reducing N losses from soils whilst maintaining yields[7].

The capacity of soils to supply mineral N through net mineralisation during the crop growth period depends not only on the size of potentially mineralizable N pools, but also on processes controlling their conversion into inorganic N. Net N mineralisation is influenced by substrate chemical quality, microbial activity, and environmental conditions including soil temperature and moisture[8, 9]. The physical organisation of soil organic matter (SOM) represents an additional, but less frequently considered, control on plant-available N[10]. Particulate organic matter (POM), consisting of ('light') relatively undecomposed plant material, is generally not stabilised through sorption to soil mineral surfaces and is therefore more accessible to microbial decomposition than mineral-associated organic matter (MAOM)[11]. Free and lightly-occluded light (intra-macroaggregate) fractions (FLOLF) of SOM are considered the most labile, as they are less physically protected and therefore more microbially accessible for decomposition[12]. Quantifying organic N within these fractions may indicate the pool of N potentially available through mineralisation over relatively short timescales [13, 14].

Total soil N provides a measure of the overall N pool but does not distinguish between fractions differing in accessibility or turnover. As a result, several approaches have been developed to estimate plant-available N beyond measurements of total N or SMN alone. Biological assays, such as anaerobic incubations, estimate potentially mineralisable N by quantifying inorganic N released through microbial activity[15, 16]. Chemical approaches, including acid-hydrolysable N provide an operational measure of the fraction of SON that is chemically labile and therefore potentially susceptible to microbial depolymerisation through enzymatic hydrolysis[17]. In contrast, ion exchange membranes such as Plant Root Simulator® (PRS®) probes integrate nutrient supply over time by continuously adsorbing mineral N under field conditions, providing a cumulative measure of realised N availability rather than a single time-point measurement[18]. Each of these methods

capture different components of the soil N supply system, ranging from immediately available inorganic N and potentially mineralisable organic N to chemically or physically accessible organic N and realised N supply over time.

Whilst previous studies have worked to improve fertiliser rate recommendations for cereal crops, there are knowledge gaps and uncertainty surrounding estimating fertiliser rate recommendations (for example using SNS calculations in the UK) for leafy salad crops, including babyleaf spinach[19, 20]. Salad crop systems experience frequent soil disturbance, high N residue incorporation, and multiple sequential short cropping cycles, requiring more adaptable approaches to SNS estimation[21]. Evidence from commercial babyleaf spinach production indicates that fertiliser N recovery can be relatively low, with reported recovery of approximately 60% and, under some conditions, as little as 40%[22] Such low recovery suggests that current approaches to matching fertiliser N supply with crop demand may not fully account for the dynamics of N availability during the short crop cycle. A single measure of SMN prior to sowing may not adequately represent the total quantity of N available to crops during the growing season[23, 24].

The methods described above provide information about soil N availability, but their relative ability to predict actual crop N uptake, particularly over the short growing period of babyleaf spinach, remains untested. Moreover, individual measurements may not capture the effects of soil physicochemical properties that regulate both nutrient supply and transport of inorganic N to the rhizosphere. Integrating measures of N availability with soil properties that influence N supply and transport, such as soil texture, could therefore provide a more complete representation of the factors governing plant N acquisition. Accounting for these factors may be particularly important for short-cycle crops such as babyleaf spinach, where rapid biomass accumulation and high N demand occur over a relatively short growing period.

The overall aim of this study was therefore to evaluate how well six selected measures of soil N availability (KCl-extractable SMN, potentially mineralisable N, hydrolysable N, FLOLF-N, and total N) predict plant N uptake by babyleaf spinach, with the goal of improving approaches to fertiliser recommendations. The specific objectives were to: (1) Quantify the relationship between these six measures and actual plant N uptake in babyleaf spinach; and, (2) Evaluate whether combining multiple N availability methods with soil properties (e.g., texture, pH) improves the prediction of actual plant N uptake. We hypothesised that: (1) Measurements that quantify available and potentially available fractions (e.g. SMN and hydrolysable N) will be stronger predictors of plant N uptake than measurements of total soil N; and (2) combining complementary measures of soil N availability with soil physicochemical properties would better predict plant N uptake by babyleaf spinach than any single predictor alone.

2 Results and Discussion

2.1 Soil physicochemical variability across the experimental soils

The fifteen soils selected for this study exhibited a broad range of physiochemical properties (Table 1) and nutrient management histories (see Supplementary Table S1 online), providing a diverse gradient for evaluating relationships between soil N availability indicators and plant N uptake. Soil pH ranged from 4.7 ± 0.012 (Garden) to 7.0 ± 0.074 (Gravel), with twelve of the fifteen soils falling between pH 5.9 and 7.05. This range is representative of UK agricultural mineral soils, which had a pH range of 4.86 to 8.38 in 2024[25] and is broadly consistent with conditions favourable for microbial N mineralisation, with reported optima of approximately pH 4.5–7.0 for bacteria and pH 4.5–8.3 for fungi[26, 27]. Electrical conductivity ranged from $984.0 \pm 23 \mu\text{S cm}^{-1}$ (KNAP) to $3,853 \pm 94 \mu\text{S cm}^{-1}$ (Clumps), while sand content ranged from $38 \pm 7\%$ (KNAP) to 62 ± 1.2 and $62 \pm 3.1\%$ (Straight and Gravel respectively), reflecting the predominantly light-textured soils preferred for babyleaf salad crops due to their free drainage and rapid warming in spring[28, 29]. Composted bark amended soil from plots at the Royal Horticultural Society (RHS) site at Wisley had the highest cation exchange capacity ($41 \pm 1.3 \text{ meq/ } 100\text{g}$), indicating a higher potential to retain NH_4^+ and to supply it for plant uptake.

Table 1

Physiochemical and biological properties of the fifteen soils used to evaluate methods for estimating plant-available N. Data are mean $\pm$ standard error. See Supplementary Table S1 online for further sample information.

Sample name	pH	Electrical conductivity ($\mu\text{S cm}^{-1}$)	Total soil N (mg kg^{-1})	C:N ratio	Combustible organic matter %	Sand %	Silt+Clay %	Cation Exchange Capacity (meq/100g)	Dehydrogenase activity ($\mu\text{g INTf/ g dry soil}$)
Straight	6.3 $\pm$ 0.017	1215 $\pm$ 25	2125 $\pm$ 130	11 $\pm$ 0.26	4.9 $\pm$ 0.022	62 $\pm$ 1.2	37 $\pm$ 1.2	14 $\pm$ 0.52	312 $\pm$ 110
Skew	6.1 $\pm$ 0.044	1325 $\pm$ 15	1760 $\pm$ 0	11 $\pm$ 0.057	4.4 $\pm$ 0.034	50 $\pm$ 5.5	47 $\pm$ 5.9	12 $\pm$ 1.5	217 $\pm$ 22
Gravel	7.0 $\pm$ 0.074	1661 $\pm$ 71	1755 $\pm$ 75	10 $\pm$ 0.23	4.3 $\pm$ 0.047	62 $\pm$ 3.1	32 $\pm$ 1.6	10 $\pm$ 0.60	274 $\pm$ 51
Broad	6.1 $\pm$ 0.020	1097 $\pm$ 15	2090 $\pm$ 100	10 $\pm$ 0.12	6.62 $\pm$ 0.39	46 $\pm$ 2.2	49 $\pm$ 3.2	14 $\pm$ 0.37	213 $\pm$ 19
Joe	6.3 $\pm$ 0.018	1462 $\pm$ 7.0	2625 $\pm$ 5.0	13 $\pm$ 0.051	6.7 $\pm$ 0.086	46 $\pm$ 5.9	47 $\pm$ 7.6	13 $\pm$ 0.37	183 $\pm$ 4.6
Brake	6.5 $\pm$ 0.0067	1208 $\pm$ 5.2	1275 $\pm$ 25	10 $\pm$ 0.032	3.1 $\pm$ 0.0082	39 $\pm$ 0.55	56 $\pm$ 0.97	10 $\pm$ 0.67	155 $\pm$ 4.1
KNAP	6.2 $\pm$ 0.026	984.0 $\pm$ 23	1405 $\pm$ 55	13 $\pm$ 0.14	3.0 $\pm$ 0.012	38 $\pm$ 7.0	58 $\pm$ 8.4	6.1 $\pm$ 0.54	304 $\pm$ 70
P3	6.4 $\pm$ 0.0067	1341 $\pm$ 34	1080 $\pm$ 20	9.6 $\pm$ 0.027	2.9 $\pm$ 0.021	52 $\pm$ 9.3	45 $\pm$ 11	7.7 $\pm$ 0.32	173 $\pm$ 9.3
Garden	4.7 $\pm$ 0.012	1355 $\pm$ 21	2320 $\pm$ 80	14 $\pm$ 0.079	5.6 $\pm$ 0.032	50 $\pm$ 5.0	43 $\pm$ 8.9	11 $\pm$ 0.71	256 $\pm$ 44
M + Cl	6.9 $\pm$ 0.0067	2433 $\pm$ 64	7870 $\pm$ 90	14 $\pm$ 0.046	18 $\pm$ 5.2	60 $\pm$ 1.6	39 $\pm$ 1.8	32 $\pm$ 2.0	285 $\pm$ 10
M + Co	7.0 $\pm$ 0.0058	2330 $\pm$ 31	9355 $\pm$ 340	12 $\pm$ 0.047	19 $\pm$ 0.20	58 $\pm$ 4.9	39 $\pm$ 7.6	40 $\pm$ 1.3	275 $\pm$ 9.9
B + Cl	5.2 $\pm$ 0.017	1629 $\pm$ 20	5460 $\pm$ 150	25 $\pm$ 0.43	20 $\pm$ 0.20	59 $\pm$ 4.5	38 $\pm$ 4.1	39 $\pm$ 3.2	268 $\pm$ 27
Bark	5.1 $\pm$ 0	1572 $\pm$ 17	5175 $\pm$ 15	24 $\pm$ 0.10	22 $\pm$ 1.3	55 $\pm$ 0.65	41 $\pm$ 1.0	41 $\pm$ 1.3	357 $\pm$ 23
Clumps	5.9 $\pm$ 0.097	3853 $\pm$ 94	3385 $\pm$ 75	9.9 $\pm$ 0.042	12 $\pm$ 6.3	57 $\pm$ 1.7	39 $\pm$ 3.9	15 $\pm$ 0.37	210 $\pm$ 9.9
Groves	6.9 $\pm$ 0.032	1992 $\pm$ 6.4	3425 $\pm$ 5.0	9.9 $\pm$ 0.021	6.3 $\pm$ 0.11	51 $\pm$ 11	46 $\pm$ 12	14 $\pm$ 0.16	217 $\pm$ 14

Notably, the soils exhibited a wide range of total N content, ranging from 1,080 $\pm$ 20 mg N kg^{-1} dry soil in P3 (a soil used for babyleaf spinach production) to 9,355 $\pm$ 340 mg N kg^{-1} soil in M + Co (a soil from RHS Wisley that was amended with mushroom compost). These differences in total N values reflect a wide variation in organic matter (and constituent organic N) inputs, nutrient management practices, soil texture and associated SOM stabilisation processes[30, 31]. Three of the four soils previously used for commercial babyleaf spinach production (Brake, KNAP and P3) had the lowest organic matter contents (3.12%, 3.02%, 2.94%, respectively), whereas soils from RHS Wisley had substantially greater organic matter contents (18.2–22.4%) and total N concentrations exceeding 5,175 mg N kg^{-1} dry soil. The C:N ratio ranged from 9.6 $\pm$ 0.027 in P3 to 25 $\pm$ 0.43 in B + Cl, reflecting differences in organic matter composition and stage of decomposition. Most soils had C:N ratios between 9.9 and 14.4, within the typical range reported for cultivated soils[32]. Overall, the selected soils represented substantial variation in both the size of soil N pools and the physicochemical properties controlling N

accessibility, mineralisation and transport. This range provided an appropriate basis for evaluating whether measurements of different N pools and soil properties could improve the prediction of babyleaf spinach N uptake.

2.2 Variation in spinach N uptake across soils with contrasting N availability

Spinach N uptake across the fifteen soils ranged from 16.7 to 82.7 kg N ha⁻¹ (Fig. 1). Weightman et al.[33] reported plant N uptake of 50 ± 34.6 kg N ha⁻¹ from non-fertilised spinach plots across three UK field sites, indicating that the glasshouse pot experiment in this study produced values representative of those observed under field conditions in the absence of fertiliser inputs. Fresh biomass yield in the pot experiment ranged from 3.82 ± 0.17 t ha⁻¹ for KNAP to 11.8 ± 3.18 t ha⁻¹ for Bark (Table 2), compared with 7.36 to 19.3 t ha⁻¹ reported by Weightman et al.[33] for unfertilised field-grown spinach. Differences in plant N uptake and yield between pot and field experiments are likely influenced by differences in rooting volume and environmental conditions. Nevertheless, the large variation in plant N uptake between soils demonstrates that inherent differences in soil properties strongly influenced the capacity of each soil to supply N during the short cultivation period.

Table 2				
Pot incubation details including soil water holding capacity, soil and water masses added to achieve a target hydrated mass of 3kg at 70% WHC, and harvesting information for spinach when at least four true leaves reached 8-10cm length. Mean ± SD (n = 3).				
Soil	WHC* (%)	Dry soil added to pot† (kg)	Time to harvest‡ (days)	Fresh yield (t ha ⁻¹)
Straight	50.7 ± 1.69	2.45	29 ± 4	10.5 ± 2.36
Skew	48.2 ± 0.956	2.46	27 ± 1	9.26 ± 1.89
Gravel	38.7 ± 1.21	2.45	30 ± 3	8.86 ± 1.61
Broad	51.9 ± 0.0136	2.40	28 ± 5	6.02 ± 0.61
Joe	60.9 ± 0.710	2.47	27 ± 2	10.6 ± 2.48
Brake	44.8 ± 0.893	2.44	33 ± 0	4.39 ± 0.29
KNAP	36.7 ± 0.736	2.48	33 ± 0	3.82 ± 0.17
P3	41.7 ± 0.967	2.46	30 ± 2	6.04 ± 0.40
Garden	50.6 ± 1.91	2.44	29 ± 0	7.44 ± 0.30
M + Cl	85.8 ± 1.37	2.35	25 ± 0	7.75 ± 0.26
M + Co	108.4 ± 0.848	2.39	25 ± 0	8.61 ± 0.19
B + Cl	118.3 ± 3.53	2.38	28 ± 2	9.26 ± 0.18
Bark	112.4 ± 12.1	2.37	26 ± 2	11.8 ± 3.18
Clumps	58.4 ± 1.05	2.44	29 ± 0	9.05 ± 1.33
Groves	60.5 ± 0.877	2.44	25 ± 0	7.75 ± 0.34
*Water Holding Capacity determined gravimetrically after saturation and free drainage				
†Air dried soil, adjusted weights for 3 kg ⁻¹ pot moist soil at 70% WHC				

KNAP and Brake (both soils used for commercial babyleaf spinach production) had the lowest mean plant N uptake of the fifteen soils (16.7 ± 2.7 and 22.67 ± 4.1 kg N ha⁻¹ respectively). These soils had relatively low organic matter content (KNAP 3.02% and Brake 3.12%), suggesting a limited pool of organic substrates available for mineralisation during crop growth. In

contrast, Straight and Bark had the highest mean plant N uptake (82.7 ± 23 and 81.2 ± 23 kg N ha⁻¹ respectively), despite differences in soil characteristics. Straight had relatively low organic matter content (4.91%), comparable to several soils with lower crop N uptake, whereas Bark had substantially greater organic matter (22.4%). These contrasting responses confirm that total soil N and organic matter quantity alone are insufficient to explain short-term N supply to crops.

2.3 Comparison of individual N availability measures against plant N uptake

The ability of six methods representing different components of soil N availability (1M KCl extraction of SMN, anaerobic mineralisable N, hydrolysable organic N, N content of free- and lightly occluded light fraction organic N (FLOLF-N), total soil N and PRS®) to predict spinach N uptake were evaluated using bivariate linear regression. Among the individual predictors, FLOLF-N provided the strongest relationship with spinach N uptake ($R^2_{\text{adj}} = 0.283$), closely followed by PRS® ($R^2_{\text{adj}} = 0.277$) and hydrolysable N ($R^2_{\text{adj}} = 0.247$) (Fig. 2, for further detail see Supplementary Table S3 online). These were the only measurements that showed statistically significant relationships with plant N uptake ($p < 0.05$). They each represent aspects of organic N accessibility and nutrient supply dynamics. Their stronger predictive performance compared with total soil N ($R^2_{\text{adj}} = 0.180$, $p = 0.064$) provides partial support for Hypothesis 1 that measurements of available and potentially available fractions of soil N would outperform measures of total soil N. However, these three predictors each explained less than one-third of the variation in crop N uptake, indicating that no single soil N pool or availability indicator fully captured the primary processes controlling N supply to the crop. Total soil N, anaerobic mineralisation (adjusted $R^2 = 0.163$) and KCl-extractable SMN (adjusted $R^2 = -0.075$, $p = 0.884$) did not provide statistically significant predictions of plant N uptake under these experimental conditions, suggesting that measurements of bulk N quantity, potential mineralisation capacity, or mineral N concentration alone were insufficient to explain the variation in crop N acquisition.

The limited predictive ability of the anaerobic mineralisation measurements likely reflects a mismatch between the processes quantified by this approach and the processes governing crop N acquisition. During the anaerobic incubation assay, conditions are established that reduce substrate diffusion constraints to microbial activity with soils maintained at saturation (water filled pore space > 100%). The assay is also conducted at a constant temperature of 30° C, providing favourable conditions for microbial activity[34]. These conditions accelerate short-term mineralisation compared to pot and field conditions[35]. In contrast, soils in the pot incubation experienced wet-dry cycling (70% WHC maintained every two days), likely causing the mineralisation rate to fluctuate over time due to diffusional constraints to microbial and enzymatic access to soil organic N[36]. Whilst measurement of total potentially mineralisable N over longer periods can be beneficial for estimating plant-available N for crops with longer growth periods[16], the short 25–33-day growth period of babyleaf spinach means that only a fraction of the total pool was mineralised and assimilated. Consequently, the artificial assay condition may overestimate the rate of mineralisation relative to the actual availability of N during the short growth period.

In addition to direct measurements of soil N availability, soil properties (texture, SOM, cation exchange capacity, electrical conductivity, water holding capacity, C:N ratio, pH and microbial activity) that may moderate N supply to plants were evaluated as potential predictors of spinach N uptake (see Supplementary Figure S1 online). These properties could influence N availability indirectly through their effects on organic matter chemical and physical protection[37], microbial process rates, soil moisture dynamics, nutrient retention, and plant uptake. Among these variables, soil texture (% sand) was the best individual predictor of plant N uptake, explaining 62% of the variation ($F(1,13) = 23.6$, $p = < 0.001$) (see Supplementary Figure S2 online). Therefore, a greater portion of the variation in plant N uptake was explained by % sand than any of the soil nitrogen methods. For every 1% increase in the proportion of sand particles in soil, plant N uptake increased by an estimated 3.06 mg N kg⁻¹ dry soil ($p < 0.001$, SE = 0.853) (see Supplementary Table S4 online). FLOLF mass ($R^2_{\text{adj}} = 0.31$) and total SOM content ($R^2_{\text{adj}} = 0.23$) were the next most influential predictors.

2.4 Soil mineral N, potentially mineralisable N, and N uptake efficiency

The poor predictive performance of KCl-extractable SMN is particularly relevant because mineral N measurements are a key component in the calculation of soil N supply to guide fertiliser recommendations[38]. However, this pot incubation suggests that relying solely on mineral N concentrations to estimate N availability during the crop growth period may be insufficient. We evaluated a multivariate linear regression model combining KCl extractable SMN and anaerobically mineralisable N. The combined model explained only 10.3% of variation in plant N uptake (see Supplementary Table S5 online), indicating that combining these two measures alone does not adequately capture the processes controlling crop N acquisition.

In unfertilised soils the main source of inorganic N is from mineralisation of OM, the OM content of soils is sometimes used as a proxy for the potentially mineralisable N in that soil. Currently, UK guidelines estimate that soils with < 4% OM content contribute 0 kg N ha⁻¹ from mineralisation when determining a SNS index[38]. In the current study, anaerobic mineralisation assays estimated potentially mineralisable N in soils with < 4% OM content (Brake, KNAP and P3) and < 7% OM (Straight, Skew, Gravel, Broad, Joe, Garden, Groves) (Table 1). Although these estimates represent mineralisation potential under favourable laboratory conditions, and are likely to exceed realised mineralisation under planted conditions, they demonstrate that relatively low organic matter soils can still contain measurable pools of mineralisable organic N. As UK arable and horticultural soils have a mean OM content of $6.19 \pm 4.65\%$ [25], the findings could have wide-scale implications for fertiliser recommendations as a proportion of agricultural soils may contain mineralisable N pools that are not fully captured by simple organic matter thresholds.

The SMN uptake efficiency, calculated as the proportion of the initial SMN pool recovered in spinach biomass at harvest, provides further evidence that soils with relatively low organic matter can still supply substantial quantities of plant-available N. Efficiency values exceeding 100% indicate that crop N uptake exceeded the initial SMN pool, implying an additional source of N; most plausibly mineralisation of SON (Fig. 3b). Six soils had SMN uptake efficiencies > 100% (Straight, Joe, P3, Bark, Clumps and Groves), including four soils with organic matter contents < 7% (Straight, Joe, P3 and Groves). This finding reinforces the idea that relatively low total SOM does not necessarily equate to low N supply potential, particularly over short crop cycles where rapid turnover of labile organic fractions may be important.

2.4 Bayesian model selection for predicting plant-available N using multiple covariates

Overall, the individual predictor analyses indicated that plant N uptake was associated not only with measurements of conceptually bioavailable N pools but also with soil properties that regulate substrate accessibility and rhizosphere nutrient supply. Bayesian model selection was therefore used to evaluate whether combining complementary measurements of N pools and their potential moderators improved prediction of spinach N uptake.

Bayesian model selection identified several models that substantially improved prediction, compared with individual predictors (Table 3). Under the assumption of equal prior model probabilities, the highest-ranked model (Model 1; posterior model odds (BF_M) = 40.3) included FLOLF-N, PRS[®] and soil texture. The second-ranked model (Model 2; BF_M = 24.486), which replaced FLOLF-N with total soil N, was less well supported by the data (BF_{10} = 0.608), indicating that the observed data were approximately 1.75 times more likely under Model 1 than under Model 2. The top five models each explained more than 73% of the variation in plant N uptake, representing a substantial improvement over the individual predictor models, in which no single variable explained more than 28.3% of the observed variation. These findings provide support for Hypothesis 2, demonstrating that combining complementary measures of N pools, transformation processes, and modifying soil properties substantially improves prediction of plant N uptake for short-cycle crops such as babyleaf spinach compared with any single predictor alone.

Table 3

Top-ranked Bayesian multiple linear regression models predicting plant N uptake based on N availability assays and soil physicochemical properties. Bayes Factor BF_{10} model comparison, compared with best model.

n	Model	P(M data)	BF_M	BF_{10}	R^2
1	Silt&clay + FLOLF-N + PRS®	0.002	40.309	1.000	0.769
2	Silt&clay + pH + PRS® + FLOLF	0.001	24.486	0.608	0.800
3	SoilN + Silt&clay + PRS®	0.001	22.979	0.571	0.738
4	Silt&clay + pH + FLOLF-N + PRS®	0.001	22.706	0.564	0.796
5	KCl + Silt&clay + pH + PRS® + FLOLF	0.001	22.131	0.550	0.845
Prior model probability P(M) 6.104×10^{-5} all models					

The posterior summary for the top model (Table 4) provided insight into the relative contribution of individual predictors through posterior inclusion probabilities ($P(\text{incl}|\text{data})$), representing the probability that a variable is included in the model considering the observed data. Soil texture (%clay + %silt) had the highest likelihood of inclusion (0.868), an increase from the prior value of 0.5, indicating strong evidence for its relevance. This was further supported by the model averaged posterior summary (see Supplementary Table S6 online), where soil texture had the highest probability of inclusion (0.868) and a Bayes inclusion factor ($BF_{\text{inclusion}}$) of 6.567, indicating substantial evidence for its contribution to explaining variation in plant N uptake. PRS® also showed increased support after observing the data, with its inclusion probability increasing from 0.5 to 0.569 and a $BF_{\text{inclusion}}$ of 1.319, providing moderate evidence for its contribution.

Table 4

Posterior summary of coefficients for best model (Model 1, Table 3). Ordered by $BF_{\text{inclusion}}$.

Coefficient	P(incl)	P(excl)	P(incl data)	P(excl data)	$BF_{\text{inclusion}}$
Intercept	1	0	1	0	1
Silt&clay	0.5	0.5	0.868	0.132	6.567
PRS®	0.5	0.5	0.569	0.431	1.319
FLOLF-N	0.5	0.5	0.433	0.567	0.763
95% Credible Interval					
	Mean	SD	Lower	Upper	
	13.155	0.684	11.689	14.622	
	-0.388	0.104	-0.611	-0.166	
	0.006	0.002	0.002	0.01	
	-0.005	0.002	-0.009	-8.369×10^{-4}	

In contrast, FLOLF-N showed weaker independent support after accounting for other predictors, with its inclusion probability decreasing from 0.5 to 0.433 ($BF_{\text{inclusion}} = 0.763$). However, FLOLF-N remained included in the highest ranked model and showed a negative posterior coefficient, with a 95% credible interval entirely below zero (-0.009 to -8.369×10^{-4} , Table 4) indicating evidence for a negative association with plant N uptake when considered alongside soil texture and PRS®. Soil texture (%clay + %silt) also exhibited a negative association with plant N uptake, with a 95% credible interval of -0.611 to

-0.166 (Table 4). As this interval does not include zero, it indicates strong evidence for a negative effect, although the width of the interval suggests uncertainty about the magnitude.

2.5 Mechanisms controlling plant-available N for babyleaf spinach

The Bayesian regression analysis identified soil texture as the strongest predictor of spinach N uptake, with the percentage of clay and silt content showing a negative association with plant N uptake in the highest-ranked model. This finding is consistent with the individual-predictor analysis, in which sand content was the strongest single predictor of plant N uptake, although the two analyses represented soil texture using different measures. The influence of soil texture on plant N uptake is likely related to its effects on both the generation of plant-available N through mineralisation and the subsequent transport of inorganic N to the root system. Sandy soils typically have larger pore sizes and greater pore connectivity than fine-textured soils, facilitating the movement of dissolved nutrients, microbial communities and extracellular enzymes involved in organic matter decomposition[39]. In contrast, clay-rich soils possess a greater surface area and more reactive mineral surfaces, promoting organo-mineral associations and physical protection of organic matter within microaggregates[40, 41]. This reduces microbial accessibility to particulate organic matter and slows mineralisation. Consistent with this mechanism, Geisseler et al. [42] demonstrated that although clay soils contained greater total N than sandy loams (12.8 versus 9.0 g kg⁻¹), the proportion of total N mineralised over 10 weeks was lower in clay soils (1.9%) than sandy loams (3.1%). Larger pore sizes in sandy soils may also promote more dynamic wet–dry cycles, stimulating N release through microbial biomass turnover[43].

Soil physical controls may be particularly important for babyleaf spinach because rapid biomass accumulation within a short growing period requires efficient transfer of inorganic N to the root system. In soil, nitrate movement occurs predominantly through mass flow of soil solution driven by plant transpiration[44], and greater pore connectivity in sandy soils may enhance this process. Increased mass flow favours plant N uptake relative to microbial competition for available N[45]. High expression levels of NO₃⁻ transporters contribute towards spinach crops being NO₃⁻ accumulating, suggesting the primary source of inorganic N uptake by spinach is NO₃⁻ rather than NH₄⁺[46–48]. In this study, NO₃⁻ was the dominant inorganic N form measured before sowing (14.32 ± 1.23 mg NO₃⁻-N kg⁻¹ dry soil compared with 1.23 ± 0.96 mg NH₄⁺-N kg⁻¹, data not shown), while NH₄⁺ remained below detection limits in PRS® measurements after the 14-day burial period. Larger pore sizes in sandy soils also facilitate plant root branching and lateral expansion of roots into new areas of undepleted N reserves[49–51]. As spinach is generally considered non-or weakly mycorrhizal, efficient access to soil solution N through direct root uptake is likely to be important[52].

As a single predictor, PRS® explained 27.7% variation in plant N uptake. Although this was relatively modest given that PRS® directly measures the availability of inorganic N to a root-like sink, its importance increased when evaluated alongside complementary predictors and had the second highest posterior support for inclusion in Model 1. Unlike incubation-based approaches that estimate the potential supply of N through mineralisation under controlled conditions, PRS® integrates the effects of mineralisation, microbial immobilisation, nutrient transport and environmental constraints on inorganic N availability over time. Being *in-situ* during the pot incubation, PRS® reflect the dynamic moisture and temperature conditions experienced during crop growth, potentially giving a more realistic estimate of N supply over time compared with anaerobic incubation assays[36]. Mineralisation rates are non-linear and influenced by soil properties and environmental conditions, meaning that estimates obtained under standardised incubation conditions may not fully reflect N supply under the fluctuating conditions experienced by a growing crop[53]. In this study the deployment of PRS® probes occurred during the crop growing period, which is not feasible for the pre-sowing fertiliser rate recommendations. Pre-sowing PRS® analysis of short-term N supply could potentially be combined with weather-based modelling to account for environmental fluctuations during crop growth and their influence on N availability[54].

The improved explanatory power obtained by combining complementary predictors in Model 1 is consistent with previous studies showing that no single measurement adequately captures soil N availability. Gallagher & Bartholomew[55] demonstrated, using multiple regression analysis, that combining methods for predicting N availability explained more

variance than using single methods. Although multivariate models generally have greater explanatory power than single-predictor regressions, the improvement observed here is biologically meaningful because the selected predictors in Model 1 represent complementary controls over N availability, integrating the size and accessibility of organic N pools (FLOLF-N), the physical environment governing substrate accessibility and nutrient transport (soil texture), and realised inorganic N supply under prevailing environmental conditions (PRS®). The combination of predictors identified in Model 1 is also consistent with previous empirical studies. Dessureault-Rompré et al.[9] found that 67–70% of the variation in mineralisable N across 56 Canadian agricultural soils could be explained by a model including soil texture, an organic matter fraction (organic N or POM-C) and climatic variables (daily air and soil temperature, precipitation and evapotranspiration). Similarly, Model 1 retained soil texture and an active organic matter fraction, while PRS® measurements, which integrate the effects of soil moisture, temperature and biological activity on inorganic N supply, may partially capture the environmental influences represented explicitly by the climate variables in the Canadian study. Individual components of the present model have also been identified previously as indicators of short-term N supply. Sharifi et al.[18] reported that PRS® probes explained 60% of the variance in potato N uptake in a 31-day period. Overall, these findings reinforce the findings of this study, confirming the importance of integrating biologically active SOM fractions and *in-situ* nutrient flux measurements when determining the crop availability of N in soils.

Our results have important implications for fertiliser recommendations for short-cycle salad crops. Current UK guidance for salads is based primarily on measurements of soil mineral N and does not explicitly account for differences in soil texture or the contribution of biologically active OM fractions to short-term N supply. In addition, soils containing less than 4% OM are assumed within the guidance to contribute negligible amounts of mineralised N, despite evidence from this study that soils with relatively low total organic matter can make considerable contributions to plant N uptake. Incorporating soil texture, measures of active organic matter (such as FLOLF-N), and time-integrated estimates of inorganic N supply (such as PRS®) alongside existing field assessment methods could improve prediction of crop N availability during the 25–33 day growth period of babyleaf spinach. Such an approach has the potential to improve fertiliser recommendations and increase nitrogen use efficiency while reducing the risk of unnecessary fertiliser application and associated environmental losses.

3 Conclusion

No single measurement of soil N availability or soil physicochemical property explained more than 55% of the variation in plant N uptake by babyleaf spinach. Among the six methods evaluated for estimating plant-available N, no individual assay explained more than 28% of the observed variation, despite some of these methods (e.g. KCl extraction and anaerobic mineralisation) underpinning current estimates of soil N supply in commercial practice. Bayesian multiple regression identified a model combining soil texture, FLOLF-N, and PRS® measurements that explained 77% of the variation in plant N uptake by babyleaf spinach across 15 soils with contrasting physical and chemical characteristics. Soil texture (%clay + %silt) was consistently the strongest predictor, indicating that soil physical properties regulate N availability alongside the size and turnover of biologically active N pools. Together, these findings support the view that plant N uptake in babyleaf spinach is governed by interactions between soil physical properties, the accessibility of organic matter for mineralisation, and the dynamic supply of inorganic N under field conditions.

4 Methods

4.1 Soil selection, sampling and preparation

Fifteen soils were collected from sites across southern England (UK) to encompass a wide range of soil N fertility through variation in N amendment regimes and land use history (see Supplementary Table S1 online) and physiochemical properties (Table 1). Four soils (Joe, Brake, KNAP, P3) had previously been used for babyleaf spinach production, while the remaining soils represented a diversity of crop rotations, amendment strategies, and management intensities, including sites with ornamental horticulture, arable crops, and perennial grass systems.

At each sampling location, four sampling points were randomly selected. At each point 2.5kg of soil was collected from the 0-20cm depth using a hand trowel, giving a 10kg composite sample for each sampling location. The hand trowel was cleaned between sample locations to avoid cross contamination. Large organic matter (e.g. coarse plant root fragments) and visible soil fauna were removed during sampling. Samples were stored at 4°C until analysis (1M KCl extractable NO_3^- and NH_4^+ ; anaerobic incubation). A 1kg portion of each soil sample was air dried for 2–4 days at 40°C, then sieved at 2mm and stored in airtight containers for subsequent physiochemical and plant N uptake analysis.

4.2 Controlled pot experiment to quantify spinach N uptake

A pot experiment consisting of the 15 soils (Table 1) in 15 cm diameter pots was established with 3 replicates per soil type. Air-dried soil was weighed into each pot in variable amounts such that, after rehydration to 70% water holding capacity (WHC), the total soil mass was 3.0 kg (Table 2). Soils were rehydrated with ultrapure water, equilibrated for 24 h, and then sown with six seeds of *Spinacia oleracea* L. cv. Montego at a depth of 2 cm and equal spacing. Following emergence, seedlings were thinned to three plants per pot, allowing for the reported germination rate of approximately 80% for this cultivar. Plants were grown in a glasshouse (Reading, UK) during August without supplementary lighting or heating. Pots were maintained at 70% WHC by gravimetric watering every second day for four weeks.

To ensure that N was the only limiting macronutrient, all pots received phosphorus, potassium and magnesium according to RB209 recommendations for leafy salad crops grown on soils with P, K and Mg indices of 0–1. Fertilisers were applied at rates equivalent to 200 kg P ha⁻¹ as superphosphate (1.41g pot⁻¹ P₂O₅; Miracle-Gro®), 225 Kg K ha⁻¹ as sulphate of potash (1.59 g pot⁻¹ K₂O; Westland) and 100 kg Mg ha⁻¹ as kieserite heptahydrate (1.8g pot⁻¹ MgO₄S·7H₂O; Fisher Scientific).

Plants were harvested when at least four true leaves reached 8-10cm in length, corresponding to the commercial harvest stage for babyleaf spinach. Plant growth rates varied between soils, so pots were harvested individually when this developmental stage was reached rather than harvesting all pots on a fixed date. Aboveground biomass (leaf tissue plus 3 cm of stem) was harvested to mimic commercial babyleaf spinach harvesting practices. Fresh biomass was recorded and converted to an equivalent yield (t ha⁻¹) before samples were dried at 60°C for 48 h and reweighed to determine dry biomass.

Dried plant material was stored in a desiccator before being ground to a fine powder using a Pulverisette 14 Rotary Mill (1 min at 16,000 rpm). Subsamples (5 ± 0.5 mg) of ground plant material were weighed into tin capsules and analysed in triplicate for total C and N by dry combustion (FLASH 2000 C/N analyser; Thermo Scientific, Waltham, MA, USA). An in-house QC plant material (1.48% N, 40.16% C) traceable to GBW07412 was included with each batch, giving recoveries of 93.2% for N and 98.7% for C. Total plant N uptake per pot (mg N pot⁻¹) was calculated by multiplying aboveground dry biomass by plant N concentration. Plant N uptake was then expressed on a soil basis (mg N kg⁻¹ dry soil) by dividing the total N accumulated in each pot by the dry mass of soil in that pot. For comparison with field-scale studies, plant N uptake was also expressed as kg N ha⁻¹. Conversion from mg N kg⁻¹ dry soil assumed a bulk density of 1.3 g cm⁻³ and a soil depth of 30 cm.

4.3 Soil N availability assays and predictors of spinach N uptake

4.3.1 Total soil N

A sub-sample (10 ± 1g) of sieved (< 2 mm) air-dried soil was ground to a fine powder using a ball mill (Fritsch) and 10 mg subsamples were weighed into tin capsules before triplicate analysis for total soil N (and C) by dry combustion (FLASH 2000 C/N analyser) alongside an in-house QC soil material (0.33% N, 3.52% C) that is traceable to GBW07412, giving recoveries of 96.62% for N and 94.35% for C.

4.3.2 KCl extractable soil mineral N

Fresh soil (40 g; 5 mm sieved) was extracted with 200 ml of 1M KCl in plastic bottles. Samples were agitated for 1 h at 20°C on a horizontal shaker (180rpm). Extracts were filtered through a GF/A filter paper and stored at 4°C until analysis for NH_4^+ -N

and $(\text{NO}_3^- + \text{NO}_2^-)\text{-N}$ using a continuous flow analyser (Skalar SAN++). Calibration curves were constructed using $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ standards prepared in a 1 M KCl matrix. Plant uptake efficiency of soil mineral N was calculated as the proportion of measured soil mineral N that was recovered in spinach biomass. This was calculated by dividing plant N uptake (kg N ha^{-1}) by the initial SMN pool (1M KCl extractable $\text{NH}_4^+\text{-N} + \text{NO}_3^-\text{-N}$; kg N ha^{-1}) and expressing the value as a percentage.

4.3.3 Anaerobic incubation mineralisable N

Potentially mineralisable N was determined using a 14-day anaerobic incubation assay adapted from established methods [56]. For each soil, six 40 g subsamples of fresh, 4 mm-sieved soil were prepared. Three subsamples were extracted immediately to determine baseline 1 M KCl-extractable inorganic N ($\text{NO}_3^-\text{-N}$ and $\text{NH}_4^+\text{-N}$), following the method described above (section 4.3.2). The remaining three subsamples were flooded with 100 ml ultra-pure water (18.2 M Ω ·cm purity) in 150 ml conical flasks. To create anaerobic conditions, flasks were sealed with Suba-seals and flushed with N_2 gas for 2 minutes using hypodermic needles connected to a N_2 gas supply (19G inlet needle and 21G outlet needle). Samples were incubated in the dark at 30°C for 14 days, after which mineral N was extracted using KCl. To account for the dilution effect of the initial water addition, 100 ml of 2M KCl was added to each flask, resulting in a final extraction concentration of 1 M KCl. Extracts were analysed for $\text{NO}_3^-\text{-N}$ and $\text{NH}_4^+\text{-N}$ using a Skalar SAN++ continuous flow analyser as described above (Section 4.3.2). Anaerobically mineralisable N (mg N kg^{-1} dry soil) was calculated as the increase in extractable $\text{NH}_4^+\text{-N}$ during incubation by subtracting the initial $\text{NH}_4^+\text{-N}$ concentration from the post-incubation concentration.

4.3.4 Plant root simulators[®] (PRS[®])

PRS[®] probes (WesternAg Innovations Inc, Saskatoon, Canada)[57] were installed one week post sowing and remained in the soil for 14 days during plant growth. One anion exchange membrane (AEM) probe and one cation exchange membrane (CEM) probe were installed into each pot. As three replicate pots were used for each soil treatment, the corresponding three AEMs and three CEMs were analysed together to give a composite measurement for each soil treatment. A blunt knife was used to create a narrow insertion space equivalent to the dimensions of the probes, which were then inserted vertically into the soil. The surrounding soil was gently compacted ensure sufficient contact between the probes and the soil matrix. After removal from the soil, the probes were rinsed with ultrapure water to remove adhering soil particles. For soils with higher clay content, a soft brush was used where necessary, taking care to avoid damaging the membranes. Probes were stored moist in sealed plastic bags at 4°C before transportation to WesternAg Innovations Inc. for analysis. The maximum adsorption capacities for PRS[®] probes reported by Western Ag Innovations Inc. are 1050 and 3668 $\mu\text{g 10 cm}^2$ for NO_3^- and NH_4^+ [58], respectively; these limits were not reached during this study.

4.3.5 Physical isolation and analysis of the free and lightly occluded light organic fraction

Isolation of the free and lightly occluded light SOM fractions was based on the method of Plaza et al.[59], modified to incorporate the collection of both free and lightly occluded light fractions (FLOLF) together, following Zimmermann et al.[60]. Air dried soil (15 g, < 2 mm) was added to 80 ml of Sodium polytungstate (SPT; density 1.8 g cm^{-3})[61] and samples were dispersed using a calibrated probe-type ultrasonic disruptor at an output energy of 22 J ml^{-1} , sufficient to disrupt macroaggregates and release lightly occluded particulate organic matter. Following sonication, samples were transferred to 250 ml polypropylene centrifuge tubes and centrifuged at 2,500 g for 60 min. The resulting supernatant was filtered using a Buchner funnel through pre-weighed GF/A filter paper under vacuum. The light fraction residue on the filter paper was washed with ultrapure water to remove residual SPT, then transferred to pre-weighed petri dishes and dried at 70°C overnight before determining fraction mass gravimetrically. The recovered SPT was recycled using an activated charcoal column following Six et al.[62].

The dried FLOLF material retained on the filter paper was finely ground using a domestic coffee grinder (Asda, UK) before analysis of total N and C using dry combustion, following method described in section 4.3.1 The in-house QC plant material (traceable to GBW07412) returned recoveries of 97.1% for N and 95.04% for C.

4.3.6 Hydrolysable soil organic N

Hydrolysable soil organic N was determined according to the method of Ramnarine et al.[17]. Air-dried soil (1.5 g, 2 mm sieved) was weighed into Pyrex glass boiling tubes and 15 ml of 6 M HCl was added (soil-to-solution ratio 1:10, w/v) whilst gently agitating with a glass rod. Tubes were covered with glass bubbles and left overnight at room temperature to cold digest. The tubes were then placed in a cold water bath and the temperature increased in 10°C increments every 20 mins until reaching 95°C and maintained at this temperature for 8 hours. After hydrolysis, samples were allowed to cool overnight. A 12 ml aliquot of the hydrolysate was pipetted to a 50 ml beaker and neutralised by gradual addition of 6 M NaOH in 1 ml aliquots. The neutralised sample was transferred to polypropylene centrifuge tubes and centrifuged at 14,000rpm for 20 minutes. The supernatant was filtered through a 0.45 µm syringe filter and then analysed for dissolved organic N, total N and C on a Shimadzu TOC-V with a TN module.

4.4 Soil physiochemical properties

4.4.1 pH and Electrical conductivity

Soil pH and electrical conductivity (EC) were measured in a 1:2.5 soil:water (m/v) ratio suspension. Air-dried, 2 mm sieved soil (10 g) was shaken with 25 ml ultrapure water for 15 min. The pH meter was calibrated with pH 4, 7 and 9 buffers depending on expected soil acidity, and pH was recorded after ~ 30 s equilibration. EC was measured on the same extract using a conductivity meter verified against a 1411 µS cm⁻¹ standard.

4.4.2 Soil organic matter by combustion

Organic matter content was determined by loss on ignition. 10g oven-dried soil (105°C to constant mass), in pre-weighed crucibles, was combusted in a muffle furnace at 500°C overnight. Crucibles were cooled in a desiccator to room temperature and reweighed. Organic matter (%) was calculated from the mass lost during ignition.

4.4.3 Soil texture

Soil texture, particle size was determined using a Malvern Mastersizer 3000 hydro laser granulometer with 10g 2mm sieved air-dried soil.

4.4.4 Cation exchange capacity

CEC was measured using ammonium-acetate saturation and NaCl displacement[63]. 5g of 2mm air-dried soil were packed into a pre-leached syringe column containing cotton wool and saturated with ammonium acetate for 16 h. The column was then leached at a controlled flow (~ 14 drops min⁻¹) with ammonium ethanoate, followed by IMS and finally 1 M NaCl to displace adsorbed NH₄⁺. Leachate was analysed by Skalar San ++ autoanalysis to estimate CEC.

4.4.5 Dehydrogenase activity

Dehydrogenase activity was determined using an iodonitrotetrazolium chloride (INT) reduction assay[64]. For each soil type, 1g of field moist, 2mm sieved soil was weighed in triplicate into autoclaved glass McCartney bottles, and 4ml of a 0.2% (w/v) INT solution was added. The caps were screwed on and tightened by hand and then incubated in the dark for 48hrs at 25°C. After incubation, 10ml N, N-dimethyl formamide: ethanol (1:1, v/v) extractant was added and bottles incubated in the dark for a further 1 hr with agitation (horizontal shaker at 50 rpm). A 1.2ml aliquot of soil suspension was then transferred from the bottle into a 1.5ml microcentrifuge tube and centrifuged at 11,600 g for 5mins. A sub sample was transferred to a 96 well plate and absorbance was measured at 464nm (OD_{464nm}) using a SpectroMax spectrophotometer. A calibration curve was made using working solutions of Iodonitrotetrazolium formazan (INTF (0–25 µg/ml)). Sterile controls consisted of soil that had been autoclaved at 121°C for 20mins for 3 consecutive days.

4.4.6 Water holding capacity

Water holding capacity (WHC) was determined gravimetrically. Approximately 50 g of air-dried soil was saturated in water for 6–12 h, then allowed to drain under cover for 12–16 h. A subsample of the drained soil was weighed, dried at 105°C to constant mass, cooled in a desiccator, and reweighed. WHC (%) was calculated as the difference between the mass of the drained soil and the mass of the oven-dry soil, divided by the mass of the oven-dry soil, and multiplied by 100.

4.5 Data analysis

Simple linear regression was used to evaluate the relationship between each measure of soil N availability and plant N uptake. Prior to analysis, data were log₁₀ transformed to improve normality and homogeneity of residuals. Linear regression was conducted in R version 4.3.0 using the packages `library(ggplot2)`, `library(ggpubr)`, `library(scales)`, `library(grid)`.

Bayesian multiple linear regression was subsequently used to determine whether combining measures of soil N availability with soil physicochemical properties improved the prediction of plant N uptake. Bayesian regression was selected because the number of candidate predictor variables ($n = 16$) was large relative to the available sample size ($n = 15$), and preliminary stepwise regression procedures produced unstable and inconsistent models. Bayesian model estimation was implemented in JASP (version 0.19.0) using Bayesian adaptive sampling (BAS)[65] with default Jeffreys-Zellner-Siow (JZS) priors (r-scale of 0.354), 10,000,000 iterations and 10,000 posterior samples for estimation of credible intervals.

Declarations

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Author Contribution

E.B wrote the original draft and L.S and T.S reviewed and edited the manuscript.

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Data Availability

The datasets generated and/or analysed during the current study are available in the Mendeley Data repository, <https://data.mendeley.com/datasets/mchfxk6kdc/1>.

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Figures

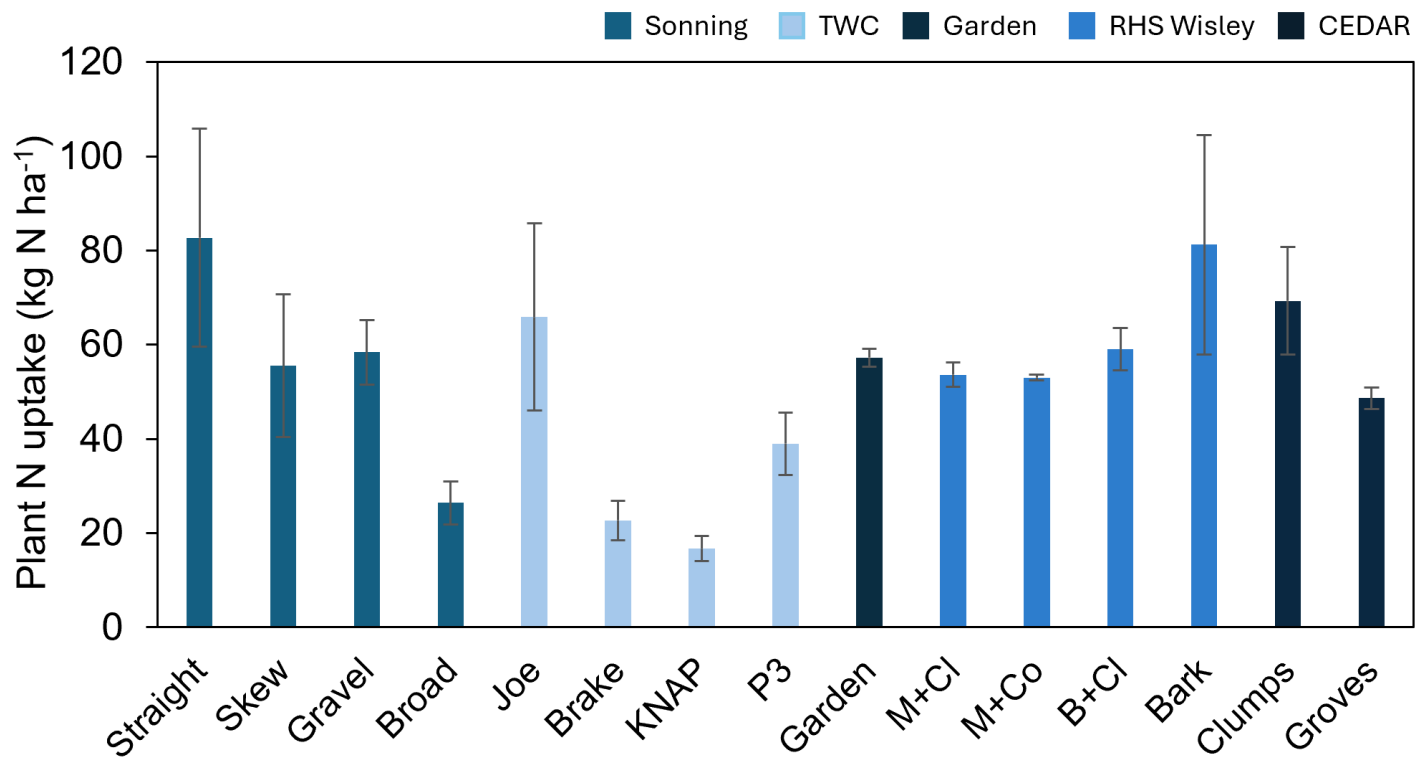


Figure 1

Plant N uptake (kg N ha^{-1}) by babyleaf spinach grown in fifteen soils under glasshouse conditions. Bars represent means ($n=3$) and error bars show $\pm$ SE. Bars are coloured depending on sample location. See Supplementary Table S1 online for sample information.

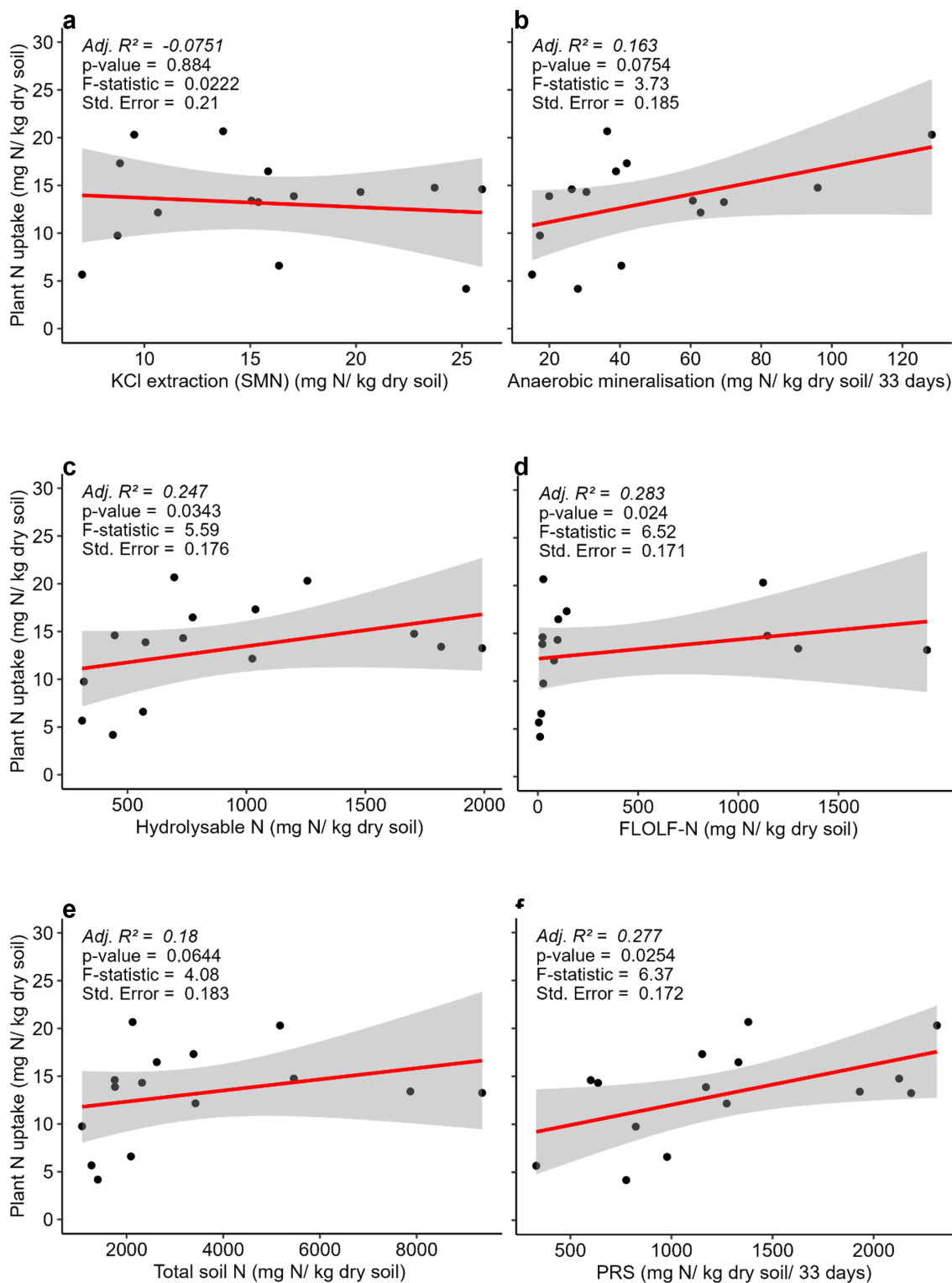


Figure 2

Simple linear regression analysis with plant N uptake (mg/ kg dry soil) as the dependant variable and six different methods for measuring pools of soil N. Linear regression line shown in red, confidence intervals (95%) shown in grey. Mean (n = 3) value for each of the fifteen soils shown. Results shown on plot are of Log10 transformed data regression analysis.

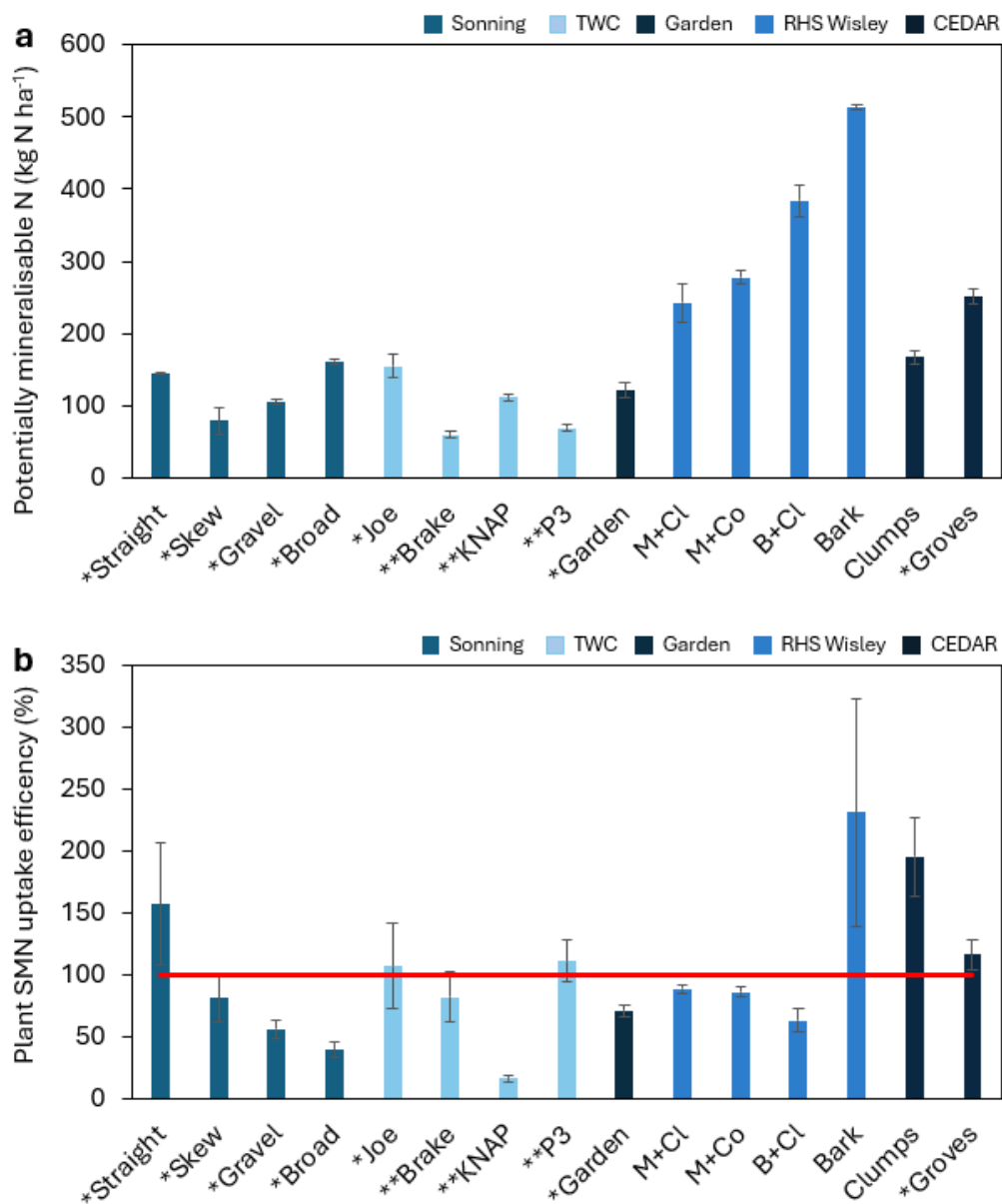


Figure 3

(a) Potentially mineralisable N (kg N ha⁻¹) as estimated by anaerobic incubation assay and **(b)** plant SMN uptake efficiency (%) representing the percentage of initial SMN recovered in spinach biomass. Mean values plotted, error bars represent standard error (n = 3). Asterisks indicate soils with SOM contents <4% (**) and <7% (*). Colour differences denote soil groups defined in Supplementary Table S1. The red line (panel b) represents a SMN uptake efficiency of 100%; values above this line indicate that plant N uptake exceeded the initial SMN pool and therefore must have been supported, at least in part, by additional N supply during the experiment, potentially through mineralisation of soil organic N.

Supplementary Files

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