Sulphur nutrition and the sulphur cycle

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Over the last decade, sulphur deficiency has increased substantially in many crops in the UK, and is predicted to increase further because the decreasing trend in S emissions is expected to continue. Sulphur is important not only for crop yields but also for crop quality. Sulphur deficiency can also result in greater losses of nitrogen to the environment. To predict where S deficiency is likely to occur and to recommend optimised uses of S fertilisers requires a detailed understanding of the S cycling in soil-crop systems. A better understanding of the molecular physiology of crop S nutrition is imperative for improving S utilisation efficiency and crop quality.

Sulphur

Sulphur is an essential nutrient for all living organisms. However, S deficiency was rare before the 1990s, due to the presence of S in fertilisers and atmospheric deposition. Over the last decade the S balance has shifted toward deficit as a result of decreased S pollution, increased use of non S-containing fertilisers and increased crop yields. Long-term monitoring of S deposition at both Rothamsted and Woburn allowed us to detect the early signs of a potential S deficiency at the beginning of the 1990s **(Fig. 25)**. Since then our research on S has intensified, encompassing both fundamental and applied aspects of crop S nutrition and the S cycling.

At the fundamental level, our research aims to elucidate the molecular mechanisms of S acquisition and utilisation by crop plants, and to understand and model the S cycling in agricultural systems. At the applied level, our research aims to provide farmers with information about where and when S deficiency may occur and how to treat it.

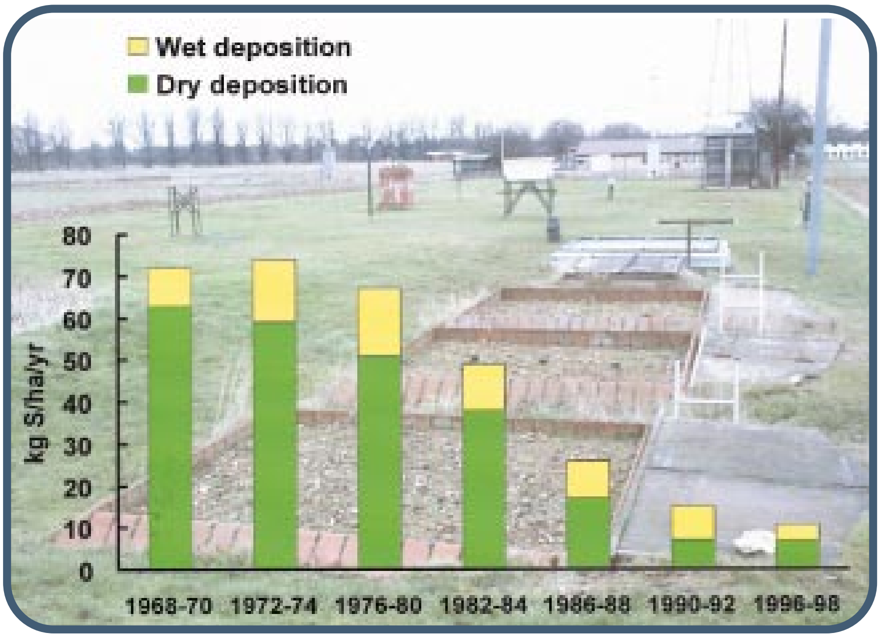

Fig. 25. Rapid decrease in the sulphur inputs from atmospheric deposition at Woburn

Long-term sulphur cycling

Sulphur in soils and biota is derived from the weathering of S-bearing minerals in rocks and from atmospheric deposition. In the UK, SO_2 emissions reached a peak in the early 1970s, and have since decreased rapidly due to adoption of pollution control measures. We found that the stable S isotopic ratio ($\delta^{34}S$) in the archived plant and soil samples from the Rothamsted Classical Experiments provides a finger print of past S pollution. $\delta^{34}S$ of wheat grain and herbage from the control plots of the Broadbalk and Park Grass experiments mirrored the pattern of national SO_2 emissions **(Fig. 26)**. Using the stable S isotope data, we estimate that between 30% and 40% of the S now in topsoil at Rothamsted is derived from atmospheric deposition.

Results from the Rothamsted Classical Experiments show that different land uses have a large impact on S cycling in soils, which is driven mainly by soil organic C cycling. However, S deficiency may have a feedback effect on both C and N cycling. We are now using triple labelling with the stable isotopes ^{34}S, ^{13}C and ^{15}N to investigate the interactions between the three elements. This study is aimed at providing quantitative information for a better integration of the S cycling with C and N cycling.

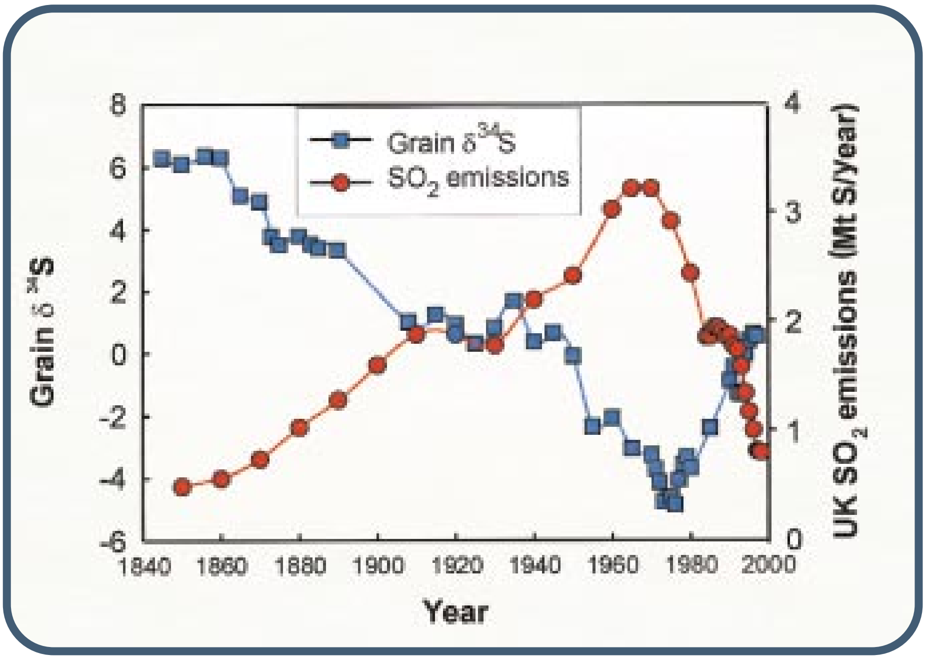

Fig. 26. Sulphur isotope ratios in the wheat grain from the Broadbalk Experiment mirror SO_2 emissions in the UK

Yield and quality responses to sulphur

Sulphur deficiency has increased considerably over the last decade, particularly in oilseed rape but also in cereals **(Fig. 27)**. Our computer model predicts that currently about 50% and 30% of the British land area are potentially deficient in S for oilseed rape and cereals, respectively. Field experiments show that yield losses due to S deficiency can be up to 70% in oilseed rape and up to 50% in cereals.

Sulphur in wheat is important for breadmaking quality. In a collaborative project with Campden & Chorleywood Food Research Association, ADAS and Newcastle University, we found that quality responses to S were more common than yield responses. Increasing S concentration in wheat grain was associated with increased dough extensibility and loaf volume **(Fig. 28).** We also showed that loaf volume correlated more closely with grain S than with grain N concentration. The effects of S on the quality of other crops, such as malting barley and legumes, are being investigated.

Optimised use of sulphur fertilisers

There are various types of S fertilisers that farmers can use to treat S deficient crops. In a field study using lysimeters, we found that the S fertilisers in the sulphate form were prone to leaching, and there was little residual value from fertilisers applied in previous years. Annual applications of >50 kg S ha^{-1} as sulphate for more than 150 years in the Broadbalk Experiment have not resulted in an accumulation of S in the soil. Inputs of sulphate in excess of crop uptake were lost mainly through leaching.

Fertilisers in the form of elemental S need to be oxidised to sulphate in soils before they are available for plant uptake. Particle size of the elemental S is the most important factor controlling S oxidation. Our research shows that certain types of elemental S are oxidised too slowly in soils to provide sufficient amount of available S to arable crops.

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Diagnosis of sulphur deficiency

We are developing a reliable plant diagnostic test to detect S deficiency as early in the growth season as possible. This will enable farmers to take remedial action if it is necessary. Many S-containing pools in plants respond to changes in the external S supply, but their concentrations fluctuate depending on growth rate and the developmental state of the plants, making them impractical as indicators of deficiency.

We have shown that the peak area ratio of malate to sulphate in plants is a reliable indicator of S deficiency. A ratio >1 indicates S deficiency, whereas a ratio ≤ than 1 indicates sufficiency. Both compounds are extracted simultaneously and measured in a single analysis by ion chromatography. No calibration is needed, which reduces the chance of errors and misdiagnosis. In wheat, 90% of the S-deficient plots were correctly identified early in the growth season (GS 30) by using the malate:sulphate ratio, whereas at this same growth stage only 17% were correctly dentified using the N:S ratio.

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A family of genes involved in sulphate uptake and utilisation

Sulphate is taken up from soil and distributed around the plant by a family of membrane-bound sulphate transporters. At Rothamsted, sulphate transporters have been cloned from a range of agriculturally important plant species including wheat, barley, maize, oilseed rape, potato and tomato. Studies showing the location of expression and functional analysis of cloned transporters suggest specific roles for identified sub-groups of the

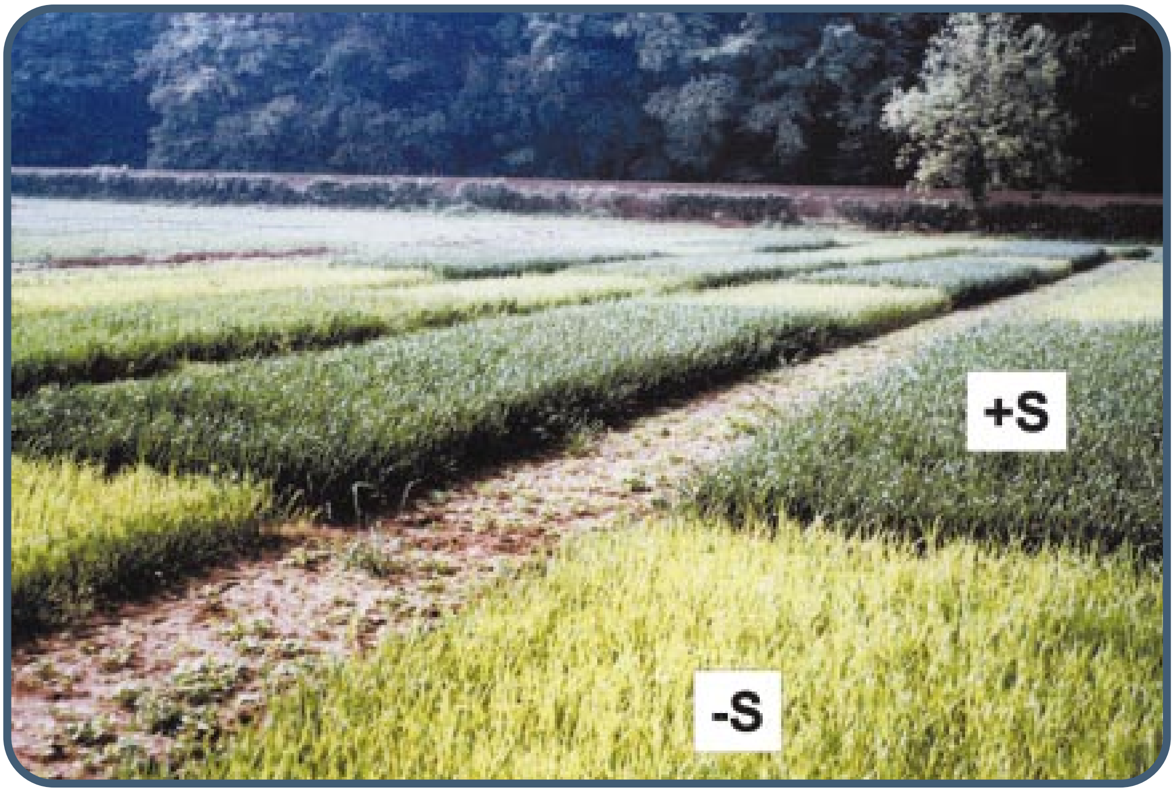

Fig. 27. Sulphur deficiency in wheat

transporter family in the overall sulphur economy of the plant. A next step is to manipulate expression of individual genes, to optimise the delivery of sulphate to those tissues with the greatest requirement, such as the grain of cereal species.

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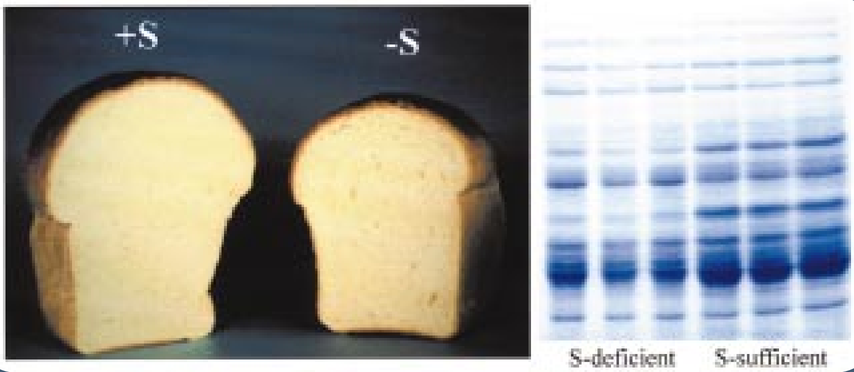

Fig. 28. Sulphur improves bread-making quality of wheat by influencing gluten protein composition (Picture courtesy of the Sulphur Institute)

Regulation of sulphur metabolism

An understanding of the regulation of S uptake, assimilation into cysteine and methionine (two essential amino acids), and the delivery of S to sink tissues is important for improving the nutritive value of crops. New methodology has allowed the measurement of the important precursor and signal molecule, *O*-acetylserine for the first time. Such measurements of metabolites coupled with analysis of gene expression, have shown the existence of a 'highly regulated circuit' controlling sulphate uptake and assimilation. Expression of genes involved in uptake and assimilation are under positive regulation by *O*-acetylserine, which accumulates when insufficient sulphide is available for cysteine synthesis. A negative feedback mechanism, mediated by reduced S-compounds acts antagonistically. As a result, S supply regulates S uptake, with de-repression of sulphate-transporters occurring with S-starvation in both roots and sink tissues such as leaves and seeds.

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Exploitation

Much of our applied research on S is funded by the farming industry through the levy funds of HGCA. We therefore actively participate in technology transfer and dissemination of the information through information leaflets for farmers, meetings of farmers' groups, links with agricultural consultants, roadshows, national events and a large number of direct contacts. This year, our findings were incorporated into the new version of *Fertiliser recommendations for agricultural and horticultural crops* (MAFF Reference Book 209). The efficacy and mode of action of S fertilisers is evaluated collaboratively with various companies, enabling adjustments to be made to products and the identification of specific markets. The plant tissue diagnostic method for S is currently being developed for use by commercial laboratories, so that it will become available to the farming industry. As result of research, it is estimated by HGCA that the proper use of S contributes more than £30M income per year to UK arable farming.

Cloning of genes involved in S-acquisition, notably the transporters, will allow a precise understanding of processes that enable optimum responses to applied fertilisers and facilitate the production of more efficient genotypes. Enhancing nutritional quality of seed by improving the content of essential S-containing amino acids is a specific application. Identification of nutritionally regulated genes will allow the nutrient status of crops to be determined using molecular methods and enable the development of 'smart plants' in which promoter sequences are coupled to readily measurable reporter proteins which signal nutritional status.

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