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THE EFFECTS OF SITE, SEASON AND SULPHUR AND NITROGEN FERTILISER ON YIELD AND SEED GLUCOSINOLATES OF WINTER OILSEED RAPE

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by

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ABSTRACT

The early stages of this project examined the factors causing, and the processes underlying, site and season variation in seed glucosinolate concentrations in winter-sown oilseed rape. The later stages concentrated on the yield responses to applied sulphur and the possibility of predicting these by soil or crop analysis. The project involved a series of experiments conducted between 1990 and 1993 at five sites known to differ in their sulphur status. The experiments tested interactions between site, season and combinations of nitrogen and sulphur treatments, sometimes on a range of cultivars. Measurements were made of crop growth, nitrogen and sulphur uptake, leaf sulphur concentrations, and patterns of growth of seed and their accumulation of nitrogen, sulphur and glucosinolates.

Seed yields ranged from 0.4 to 5.0 t/ha. They were increased by nitrogen at all sites in all three years. There were small responses (<14%) to applied sulphur at Cockle Park in 1991 and 1992, in the Scottish borders in 1992, at ADAS Bridgets in 1992 and 1993, and at Rothamsted in 1993. Applied sulphur doubled the yield of a small crop at Woburn in 1991 and increased yield by 37% in 1992.

Seed glucosinolate concentrations in the cv. Falcon ranged from 8 to 31 μmol/g and varied with site and season. Applied sulphur had no effect on concentrations at Rothamsted and Cockle Park, but greatly increased them in the Scottish borders and at Woburn and ADAS Bridgets. The response to applied nitrogen depended strongly on the sulphur status of the crop. Seed glucosinolate concentrations were increased by applied nitrogen when the sulphur status of the crop was high, and decreased when the sulphur status was low. Leaf sulphur concentrations were not a reliable predictor of the responses of yield and seed glucosinolates to applied sulphur.

The variation in seed glucosinolate concentration between sites was not related to the ratio of crop sulphur to seed number/m^2. Glucosinolate concentrations were related more strongly to seed number alone.

Seed glucosinolate concentrations were measured by both the X-RF and HPLC methods. There was evidence that the X-RF method, even when corrected for seed nitrogen content, could give unreliable values for young seed or seed from sites where the crop nitrogen and sulphur are widely unbalanced.

OBJECTIVES

To examine how site and season factors and nitrogen and sulphur fertiliser practices influence seed glucosinolate concentrations in winter-sown oilseed rape and to establish the physiological basis of the variations in concentration.

INTRODUCTION

Considerable variation occurs between locations and seasons in the glucosinolate concentrations of the seed of double-low cultivars of winter oilseed rape. Earlier work at the Institute of Arable Crops Research Rothamsted and Newcastle University, funded by MAFF Open Contracts CSA 1249 and 1250 showed that variation was not the result of practices used to grow or harvest the crop, implying that other factors associated with the site and season were responsible. Large effects of sulphur and large interactions between nitrogen and sulphur fertiliser on seed glucosinolate concentrations were observed at certain sites. This suggested that natural variations in the atmospheric deposition of sulphur and soil supplies of sulphur and nitrogen, might be major causes of the site and season variation, modified perhaps by the effects of seasonal weather on seed growth.

A physiological understanding is needed of where and when glucosinolates are produced in the oilseed rape plant, what factors influence how much is produced, and what determines how much is stored in the seed. Glucosinolates are synthesised from amino acids and contain sulphur; their formation is therefore closely linked to the nitrogen and sulphur balances of the crop. However, the quantitative relationships between crop sulphur and glucosinolates are not well characterised. French workers have shown good correlations between seed glucosinolate concentrations and the ratio of plant sulphur to seed number/m^2 (Merrien, 1989). German researchers consider glucosinolates to be a recyclable store of sulphur within the plant and believe that double-low varieties of oilseed rape are more prone to sulphur deficiency and their seed glucosinolate concentrations more responsive to applied sulphur (Schnug, 1991).

The research started in October 1990, when a series of experiments were set up at sites of different atmospheric deposition of sulphur, known to produce different levels of glucosinolates in the seed. The experiments tested the effects of differences in the natural supplies of nitrogen and sulphur in the soil, and of varying the amounts supplied in fertilisers in three successive years. Detailed measurements were made during growth to understand the links between the glucosinolates in the plant and those in the seed, their relation to the total sulphur content of the crop, and how all of these factors are affected by site, season and the nitrogen nutrition of the crop and by variations in sulphur supply.

When the research started, the variation in seed glucosinolates was important because the system of subsidy payment for oilseed rape was based on a whole-seed threshold glucosinolate concentration of 25 μmol/g at 9% moisture. Later, the subsidy system was changed to payments based on the area of oilseed rape grown provided certified varieties of low seed glucosinolate concentration were sown, so variation in the harvested crop had fewer implications for the majority of oilseed-rape growers and became less important as a policy issue. The concentration of glucosinolates in the harvested seed now only affects growers using home-saved seed, who have to observe a limit of 18 μmol/g, and feed compounders who used rapeseed meal in livestock rations.

Because of the subsidy changes,the emphasis of the research changed. The decline in atmospheric deposition of sulphur from industrial emissions has led to increased concern about the incidence of sulphur deficiencies in oilseed rape in some regions of the country. HGCA requested that the research concentrate on the yield responses to applied sulphur and the possibility of predicting these by soil or crop analysis. To meet this request, the work was linked to a survey of sulphur deficiency in wheat being done by others. This required extra treatments and extra sampling and analysis of soils and plants. Limited chemical analysis was done on samples taken in the second and third years to interpret site/season changes in glucosinolates.

THE EXPERIMENTS

Experiments were established by Newcastle University and IACR-Rothamsted at five sites in the UK in three seasons (1990/91, 1991/92 and 1992/93) to examine interactive effects of nitrogen and sulphur on the yield and quality of double-low winter, oilseed-rape cultivars. Previous work has shown that crops grown at two of the sites, Cockle Park and Rothamsted, obtain sufficient sulphur from soil and atmospheric sources to sustain good growth and yield. Three other sites, one at Woburn, one at ADAS Bridgets and one in the Scottish borders, were chosen as being in areas of low sulphur deposition and hence potentially sulphur deficient.

The experiments at Cockle Park and at Rothamsted tested the effects of three rates of nitrogen (0, 150 and 250 kg/ha) and three rates of sulphur (0, 50 and 100 kg/ha) in factorial combination on three cultivars, Ariana, Libravo (Tapidor in 1992) and Falcon. The same three rates of sulphur were tested in the Scottish borders with 50, 150 and 250 kg/ha of nitrogen on the cv. Falcon. The experiments at Woburn tested lower rates of sulphur (0, 10, 20 and 40 kg/ha) in combination with 0, 180 and 230 kg/ha of nitrogen on the cv. Libravo, and those at ADAS Bridgets tested only extreme rates of sulphur (0 and 100 kg/ha) with extreme rates of nitrogen (0 and 250 kg/ha) on the cv. Falcon. In each case, a randomised block design was used with three or four replications. Nitrogen was applied as ammonium nitrate at all sites. The sulphur was applied as potassium sulphate at Cockle Park and in the Scottish borders, and as calcium sulphate at Rothamsted, Woburn and ADAS Bridgets. The times of application of nitrogen and sulphur are given in Table 12 in the Appendix .

Leaf sulphur concentrations were measured at flowering, and yield and the glucosinolate concentration of the seed measured at harvest. In the 1990/91 and 1991/92 experiments, plants from representative treatments were sampled at frequent intervals during growth and the glucosinolate, nitrogen and sulphur contents of plant parts and seed measured. In all experiments, glucosinolate concentrations in mature seed were measured by the XRF method with correction for seed nitrogen (Zhao *et al.*, 1992) with some comparative measurements being made by the FRI glucose-release method and HPLC in experiments done by IACR-Rothamsted. Nitrogen concentrations were either measured with a Carlo-Erba elemental analyser or by Kjeldahl analysis, and sulphur by XRF or inductively-coupled plasma emission spectrometry. Except where stated, good agreement was obtained between the various methods of measurement throughout the whole series of experiments,.

SITE AND SEASON VARIATION IN YIELD AND SEED GLUCOSINOLATES

The effects of the nitrogen and sulphur treatments on leaf sulphur concentration, and the yield and glucosinolate concentration of the seed are shown for each experiment at each site in each year in Tables 13-51 in the Appendix. In these, statistically significant responses to treatments and interactions between treatments are highlighted by blocked print.

The experiments fall into two categories. Those at Rothamsted and Cockle Park tested a full factorial combination of three rates of nitrogen and three rates of sulphur on three varieties. Complete data sets are available only for 1991 and 1992 because the experiment at Cockle Park in 1993 failed (being replaced by an experiment comparing the treatments only on the cv. Falcon). Glucosinolate concentrations were measured in one cultivar (Falcon) at Rothamsted in 1993.

The second category contains experiments which tested extreme rates of both nitrogen (usually 0 and 250 kg/ha) and sulphur (0 and 100 kg/ha, except at Woburn where the highest rate was 40 kg/ha) on a single cultivar at all five sites. Again, complete data are available for two years.

For each category, the data for 1991 and 1992 were analysed using a split-plot design with season, season x site, season x site x cultivar, and season x site x cultivar x fertiliser treatment as stratum levels where appropriate. Data for 1993 were incomplete and were not analysed. Treatment means, where available, are included in the Tables for comparison.

Variation in yield

Comparison of cultivars at Rothamsted and Cockle Park. There were no yield responses to sulphur at either site in either year, but there were significant site x cultivar and site x season x rate of nitrogen interactions. Yields averaged over all treatments were slightly greater at Cockle Park than Rothamsted, slightly greater in 1991 than 1992, and Falcon outyielded the other two cultivars at Cockle Park but not at Rothamsted (Table 1).

Crops grown without nitrogen fertiliser (N_0) produced greater yields in 1991 than 1992 at Rothamsted, and greater yields in 1992 than 1991 at Cockle Park. The yields of N_0 plots were greater at Rothamsted than Cockle Park in 1991, and greater at Cockle Park than Rothamsted in 1992 (Table 2). An application of 150 kg/ha of nitrogen was sufficient to achieve near maximum yield in situations where the N_0 crops yielded well, but 250 kg/ha was required to achieve maximum yield where they did not. The yields of the N_0 crops and the responses to applied nitrogen suggest there were probably large nitrogen residues from the preceding cereal crops at Rothamsted in 1991 and at Cockle Park in 1992.

Comparisons across five sites. These experiments tested only extreme rates of nitrogen (0 and 250 kg/ha) and sulphur (0 and 100 kg/ha). Significant interactions between the effects of the rate of applied nitrogen, site and season occurred on yield. Woburn was the lowest yielding of the five sites in both years. Yields of the N_0 plots ranged from 0.42 t/ha at Woburn to 4.01 t/ha at Cockle Park, both in 1991. Yields were lower in the Scottish borders and at ADAS Bridgets than at Rothamsted and Cockle Park in 1991, and lower at Rothamsted than the other three sites in 1992 (Table 3). Large yield responses to the application of 250 kg/ha of nitrogen were obtained on all occasions except in the Scottish borders in 1992. When expressed as a percentage of the N_0 crop, the yield response to applied nitrogen was particularly large at Woburn in both years.

An application of 100 kg/ha of sulphur produced small increases in yield (*ca* 10-14%) at Cockle Park in 1991, in the Scottish borders and at ADAS Bridgets in 1992, and at Rothamsted and ADAS Bridgets in 1993 (Table 4). There were proportionately greater responses at Woburn where an application of 40 kg /ha of sulphur to low-yielding crops doubled yield in 1991 and increased it by 37% in 1992. However, the responses to applied sulphur at Woburn occurred only in crops also given 250 kg/ha of nitrogen (Table 5).

Variation in seed glucosinolate concentrations

Glucosinolate concentrations in seed harvested from the cv. Falcon ranged from 8.9 μmol/g at ADAS Bridgets in 1991 (Table 15 in the Appendix) to 31.1 μmol/g in the Scottish borders in 1992 (Table 28 in the Appendix).

Comparison of cultivars at Rothamsted and Cockle Park. The cultivars were selected for their different certified seed glucosinolate concentration. That of the sown seed of Ariana was close to 25 μmol/g, and those of Falcon, Libravo (grown in 1991) and Tapidor (grown in 1992) were below 15 μmol/g. Therefore, a strong cultivar effect on glucosinolate concentrations in the harvested seed was expected. However, cultivar differences were further modified by interactions between the effects of site and season and site and rate of nitrogen.

Seed glucosinolate concentrations of Ariana and Falcon were lower at Rothamsted than Cockle Park in both years. They were also lower at Rothamsted in 1991 than 1992 but similar in the two years at Cockle Park. Concentrations in Libravo were similar at the two sites in 1991, but lower in Tapidor at Rothamsted than Cockle Park when this cultivar replaced Libravo in 1992 (Table 6).

Nitrogen fertiliser increased the seed glucosinolate concentrations of all cultivars at both sites. There was a small response to 150 kg/ha of nitrogen in Ariana and Libravo but none in Falcon, and large responses to 250 kg/ha of nitrogen in all three cultivars (Table 7).

The sulphur fertiliser treatments had no effect on seed glucosinolate concentrations at Rothamsted or Cockle Park in either season.

Comparisons across five sites. Applied sulphur significantly increased seed glucosinolate concentrations at Woburn and ADAS Bridgets in 1991 and at Woburn, ADAS Bridgets and in the Scottish borders in 1992 (Table 8). In the latter case, the response was particularly large (*ie* from 8.9 to 30.1 μmol/g).

There were also different interactions between nitrogen and sulphur at particular sites. Seed glucosinolate concentrations were significantly increased by applied sulphur in the Scottish borders irrespective of whether nitrogen was also given, but at Woburn and ADAS Bridgets concentrations were increased by sulphur only when 250 kg/ha of nitrogen was also applied (Table 9).

DRY MATTER PRODUCTION AND NITROGEN AND SULPHUR UPTAKE

The five sites were selected to provide a suitable range in plant sulphur status for oilseed rape. Plant sulphur status depends on the amount of sulphur made available from sources within the soil and from atmospheric deposition, and the proportions of these that are taken up by the plant. The soils at each of the five sites were extensively sampled in the autumn of 1991, in the spring of 1992 before the sulphur was applied, and again in the summer. The concentrations of soil sulphate present within the 0-30, 30-60 and 60-90 cm horizons are given in Table 10.

High concentrations of sulphate were available in the soil at Cockle Park and Rothamsted in the autumn and spring, especially at depth. Intermediate concentrations were available in the soil in the Scottish borders and at ADAS Bridgets, and very low concentrations at Woburn. Soil sulphate concentrations in the summer remained low at Woburn even after an application of 40 kg/ha of sulphur, but at the other four sites they were increased by the applied sulphur. The applied sulphur appeared to remain in the topsoil at all sites except in the Scottish borders where some was leached to depth. Wet deposition of sulphur from the atmosphere ranged from 8 to 12 kg/ha in 1992 and dry deposition (estimated from measurements made in 1993) ranged from 4 to 9 kg/ha. Based on these figures, the total atmospheric deposition of sulphur ranged from 12 kg/ha in the Scottish borders to 17 kg/ha at Rothamsted. These small differences in atmospheric deposition are unlikely to be a major cause of the between-site variation in the responses of oilseed rape to applied sulphur.

Additional measurements of dry matter production and nutrient uptake were made at key stages in crop growth to help interpret the yield responses in the core treatments that compared the extreme rates of nitrogen and sulphur on the cv. Falcon at five sites in 1991 and 1992. The sites were classified as responsive, marginally responsive and unresponsive on the basis of their yield response and examples of the dry matter production and uptakes of nitrogen and sulphur from each category are presented in Figs 1-3. The full data for all sites are given in Tables 52-59 in the Appendix.

Responsive sites - Woburn in 1991 and 1992. Changes in dry matter and nitrogen and sulphur uptake at Woburn in 1991 are shown in Fig. 1. Even though the highest rate of sulphur tested was only 40 kg/ha, it increased yield by 143% in 1991 and by 65% in 1992. The size of the crops at Woburn was relatively small, especially in 1992. Crops given 250 kg/ha of nitrogen produced only 623 and 231 g/m^2 of dry matter, respectively, in 1991 and 1992 and had particularly low nitrogen (83 and 30 kg/ha) and sulphur (22 and 5 kg/ha) uptakes. The application of 40 kg/ha of sulphur increased crop dry matter production (to 955 and 611 g/m^2 respectively in the two years), and both nitrogen (to 116 and 91 g/m^2), and sulphur (to 51 and 28 g/m^2) uptake. The 1993 crop established well but grew poorly overwinter, and eventually failed.

Marginally responsive sites - ADAS Bridgets in 1991 and the Scottish borders in 1992. Changes in dry matter and nitrogen and sulphur uptakes at ADAS Bridgets in 1991 are shown in Fig. 2. The application of 100 kg/ha of sulphur greatly increased dry matter production and the uptakes of sulphur and nitrogen but did not increase yield. Applied sulphur increased dry matter production in a crop grown with no nitrogen from 364 to 511 g/m^2, its nitrogen uptake from 106 to 139 kg/ha, and its sulphur uptake from 22 to 28 kg/ha. In a crop grown with 250 kg/ha of nitrogen, applied sulphur increased dry matter production from 743 to 959 g/m^2, nitrogen uptake from 183 to 258 kg/ha, and sulphur uptake from 20 to 47 kg/ha.

The trial in Scotland in 1992 did not test crops grown without nitrogen fertiliser, instead it compared crops given 150 and 250 kg/ha of nitrogen. In these, 100 kg/ha of sulphur did not affect dry matter production but increased yield by 11%. When given with 150 kg N/ha, the applied sulphur increased sulphur uptake from 80 to 118 kg/ha; with 250 kg/ha of nitrogen, it increased sulphur uptake from 63 to 124 kg/ha and nitrogen uptake from 204 to 230 kg/ha.

Non-responsive sites - Cockle Park and Rothamsted in 1991, and Cockle Park and the Scottish borders in 1992. Changes in dry matter production and the nitrogen and sulphur uptakes are shown for the crops grown at Rothamsted in 1991in Fig. 3. At the non-responsive sites, the applied sulphur had no effect on yield, dry matter production, or the nitrogen and sulphur uptakes. The amounts of dry matter produced ranged from 1260 to 1700 g/m^2, nitrogen uptake was usually in excess of 200 kg/ha, and sulphur uptakes ranged from 79 to 133 kg/ha. The highest values were usually obtained with the higher rates of applied nitrogen.

SEED DEVELOPMENT

The basal pods on the terminal racemes were sampled at regular intervals after flowering from 20 plants in the extreme nitrogen and sulphur core treatments at each site to study the patterns of seed growth and nitrogen, sulphur and glucosinolate accumulation. The core treatments comprised combinations of none or 250 kg/ha of nitrogen with none or 100 kg/ha of sulphur (denoted N_0S_0, N_0S_{100}, $N_{250}S_0$ and $N_{250}S_{100}$) except at Woburn where the highest rate of sulphur was 40 kg/ha. The basal 20 pods on each raceme were sampled at Rothamsted, Woburn and ADAS Bridgets and the basal 10 pods in the Scottish borders and at Cockle Park. Pods were separated into the component seed and hull fractions and the number, dry weight and nitrogen, sulphur and glucosinolate concentrations of the seed measured. Seed glucosinolate concentrations at all sites were calculated from the seed concentrations of nitrogen and sulphur as described byf Zhao *et al.* (1992). They were also measured by the FRI glucose-release and HPLC methods on some samples from Rothamsted, Woburn and ADAS Bridgets. These measurements were made only in the 1991 season. The full data are given in Tables 60-64 in the Appendix .

The patterns of seed development at the five sites are compared using data for crops grown with adequate nitrogen but no sulphur (*ie* the $N_{250}S_0$ treatment). Only three samples were taken during the later stages of seed development at Woburn, so the analysis concentrates on the other four sites. Limited data from Cockle Park and the Scottish borders allow some comparisons to be made between the 1991 and 1992 seasons.

Seed growth. The patterns of seed growth and accumulation of nitrogen and sulphur in the seed at the five sites are shown in Fig. 4. Seed growth ceased between 70 and 75 days after the start of flowering at all sites. Mean seed weight increased from 1.1-1.7 mg at 30 days after the start of flowering, to 4.2-4.8 mg at maturity. Seed tended to be larger in the Scottish borders and at Woburn (where seed numbers were small) and smaller at Cockle Park (where seed numbers were large).

The effects of the nitrogen and sulphur fertiliser treatments are given in Appendix Tables 41-45. Applications of nitrogen and sulphur did not consistently affect seed growth. At Cockle Park, mean seed weight was smaller with nitrogen than without; at Woburn mean seed weight was increased only when high rates of nitrogen and sulphur were applied ($N_{250}S_{100}$). Mean seed weight at Rothamsted, Cockle Park and ADAS Bridgets tended to decrease at the later samplings in crops given a high rate of nitrogen.

Seed sulphur. Seed sulphur concentrations increased up to day 55 from flowering and then gradually decreased in the Scottish borders and at Cockle Park and Rothamsted. The concentrations were increased by both applied nitrogen and applied sulphur. The patterns and responses were similar in both 1991 and 1992 in the Scottish borders and at Cockle Park. In contrast, at ADAS Bridgets, seed sulphur concentrations in 1991 declined continuously from day 34 after flowering to maturity. They were not affected by the applied sulphur but were decreased by the applied nitrogen.

The amount of sulphur per seed increased from 5μg at 35-45 days after flowering to between 10 and 20 μg at maturity. Seed accumulated much less sulphur at ADAS Bridgets than at other sites and, although the sulphur content of the seed was initially small at Cockle Park, it did not differ greatly from those at the other sites at maturity. The amount of sulphur in the seed was increased by the applied nitrogen but not by the sulphur in the Scottish borders and at Cockle Park and Rothamsted. It was increased by the applied sulphur at both Woburn and ADAS Bridgets, but only when a high rate of nitrogen was also given.

In Fig. 4, the changes in the seed sulphur contents during seed development are plotted against mean seed weight for crops at each of the five sites that were given a large amount of nitrogen but no sulphur ($N_{250}S_0$). Seed sulphur increased linearly with seed weight with virtually no difference between most of the sites. The exception was ADAS Bridgets where seeds contained much less sulphur relative to their weight throughout their growth.

Seed nitrogen. Seed concentrations of nitrogen increased slightly during seed development (on average, from 28 to 36 mg/g), and were increased by the applied nitrogen in the Scottish borders and at Cockle Park and Rothamsted. Concentrations were not affected by the applied sulphur at Cockle Park and ADAS Bridgets but were increased in the Scottish borders and at Rothamsted when sulphur was applied with no nitrogen. They were decreased In the Scottish borders when both were applied.

In Fig. 4, the amount of nitrogen per seed is plotted against mean seed weight for crops given a large amount of nitrogen but no sulphur ($N_{250}S_0$). The amount of nitrogen per seed increased linearly with seed size and with virtually no difference between sites. In the other treaments, the applied nitrogen increased the amount of nitrogen in the seed in the Scottish borders and at Cockle Park and Rothamsted, but the applied sulphur did not. Neither treatment affected seed nitrogen content at ADAS Bridgets.

Seed glucosinolates. Seed glucosinolate concentrations, calculated from seed nitrogen and sulphur concentrations by the method of Zhao *et al.* (1992) are shown in Fig. 5*a*. In experiments in the Scottish borders and at Cockle Park and Rothamsted, glucosinolate concentrations increased during early seed development (30-55 days from flowering) and then subsequently declined gradually till maturity. They also appeared to do so at Woburn but concentrations at ADAS Bridgets initially declined, and then stabilised during the later stages of seed development.

In the experiments at Rothamsted and ADAS Bridgets, seed glucosinolate concentrations were also measured directly by HPLC and the FRI glucose-release methods. The seasonal trends in these were very different from those of the calculated concentrations in that they increased to a maximum, at about 60 days after flowering, and thereafter remained more or less constant (Fig. 5*b*). However, irrespective of the trend during seed development, both methods gave generally similar final concentrations in the mature seed.

In the wide range of agronomic experiments done up till now, measurements of glucosinolate concentrations in mature seed made using the different methods have agreed well. The current experiments are the first in which the methods have been used to compare changes in immature seed. The different patterns obtainedwith the different methods of analysis could have arisen as the result of the presence of sulphur-containing compounds other than proteins and glucosinolates whose presence would be detected by the indirect determination but not measured by HPLC.

The current experiments were also the first time that the two methods had been compared to measure glucosinolate concentrations of seed grown under conditions of severe sulphur deficiency and unbalanced sulphur:nitrogen ratios. These, also, may have contributed to the discrepancies. To examine this further, a wider comparison is presented in Fig. 6 of the glucosinolate concentrations in mature seed measured by the two methods. The seed was harvested from plots given extreme combinations of nitrogen and sulphur in the series of experiments done at Rothamsted, Woburn and ADAS Bridgets between 1991 and 1993. Overall, there was reasonable agreement between the two methods, especially at Rothamsted with the indirect method of Zhao *et al.* (1992) tending to produce slightly higher values than HPLC. The same was true for four or five treatments at the sulphur-deficient site at Woburn in 1992 where the amounts of nitrogen and sulphur in the crop were reasonably balanced. But there were large discrepancies between the two methods in treatments at both Woburn and ADAS Bridgets where large amounts of sulphur were applied to a crop given little nitrogen (N_0S_{40}) or much nitrogen was given wihout additional sulphur ($N_{250}S_0$). For the indirect method of estimating glucosinolate concentration, the discrepancy was associated more with variation in the nitrogen and protein concentrations in the seed than in the sulphur content.

Because of the discrepancies introduced by the method of measurement, changes in seed glucosinolate concentration during seed development cannot easily or confidently be compared across sites. The calculated concentrations appeared to be increased by applied nitrogen but not by applied sulphur in the Scottish borders and at Cockle Park and Rothamsted. There were strong interactions between the nitrogen and sulphur treatments at some sites. At ADAS Bridgets, seed glucosinolate concentrations were *decreased* from 12.8 to 9.1 μmol/g when sulphur was applied without nitrogen, and were *increased* from 4.3 to 7.0 μmol/g when sulphur was applied with nitrogen. Concentrations at Woburn were also increased when nitrogen was applied with sulphur but were decreased when nitrogen was applied by itself.

INTERPRETATION OF SITE/SEASON EFFECTS ON GLUCOSINOLATE CONCENTRATION

The relative importance of individual factors and their interactions. In the experiments that compared the effects of extreme nitrogen and sulphur applications at five sites, the seed glucosinolate concentrations in the cv. Falcon ranged from 8.9 μmol/g at ADAS Bridgets in 1991 (Table 27 in the Appendix) to 31.1 μmol/g in the Scottish borders in 1992 (Table 40 in the Appendix). Almost a quarter of the 96 site x season x treatment combinations produced concentrations above 20 μmol/g.

The relative contributions of the various factors to the overall variation in seed glucosinolate concentration were assessed from the proportion of the total sum of squares that each accounted for in the analysis of variance. Site factors and the sulphur fertiliser treatment each accounted for about 10% of the variance, and the site x sulphur and the site x season x sulphur interactions a further 15% each. Together, the site, season and sulphur factors and their interactions accounted for about half the observed variation in seed glucosinolate concentration.

This strongly contrasts with the effects of the nitrogen treatments and of season; these individually accounted for only 4% and 2% of the variance in seed glucosinolate concentration. However, the nitrogen supply did greatly modify the effects of applied sulphur. Our current concept of the nitrogen/sulphur interaction is illustrated in Fig. 7. When sulphur was abundant, as at Rothamsted and Cockle Park, applied nitrogen *increased* seed glucosinolates. When sulphur was deficient, as in the Scottish borders and at Woburn and ADAS Bridgets, applied nitrogen *decreased* seed glucosinolate concentrations. When sulphur was marginal, as at some sites in one or the other of the two years, applied nitrogen had no effect.

These interactive effects can be explained in terms of the effects of the plant's nitrogen:sulphur balance on secondary metabolism. When sufficient sulphur is available, an increased supply of nitrogen enhances the synthesis of amino acids for growth, and of sulphur-containing amino acids for the biosynthesis of glucosinolates. Seed yields and seed glucosinolate concentrations are both increased. When less sulphur is available, an increased supply of nitrogen diverts amino acids into primary metabolism and away from glucosinolate synthesis. There may be no effect on seed glucosinolates if sulphur availability is borderline, and concentrations will decrease if sulphur is deficient.

Differences due to seed development. The previous MAFF Open Contract study (CSA 1249 and CSA 1250) suggested that differences in the patterns of seed growth might help explain the observed site and season variation in seed glucosinolate concentrations. A further year's data (for 1991) is available to extend the analysis. In the current study, the curves of seed growth were similar at all sites; growth ceased between 70 and 75 days after flowering, and the differences in seed weight at maturity were relatively small (Fig. 4).The only major difference between sites was in the amount of sulphur per seed, which remained lower throughout seed development at ADAS Bridgets than the other four sites (Fig. 4). The small seed sulphur content in the crop given plenty of nitrogen but no sulphur ($N_{250}S_0$) at ADAS Bridgets was probably a consequence of its lack of sulphur uptake (Fig. 2), since neither the low concentrations nor the small amounts of sulphur in the seed were fully accounted for by differences in seed size.

Differences in seed number. Merrien (1989) suggested that much of the variation in seed glucosinolate concentration between sites in France could be accounted for by the ratio of sulphur in the crop to the number of seeds/m^2. This is an approximate measure of the amount of sulphur available to each seed and a large ratio tends to be associated with high seed glucosinolate concentrations. Factors that decrease crop sulphur or increase seed number/m^2 will tend to decrease seed glucosinolate concentration. Seed glucosinolate concentrations are plotted against this ratio in Fig. 8*a* and against the number of seed/m^2 in Fig. 8*b* using data from the current series of experiments. In contrast to the situation in France, there was little correlation between seed glucosinolate concentration and the ratio of crop sulphur to seed number in the UK. One reason for this might be that the correlation could have been accentuated in the French study by the inclusion of a number of sites in which drought would have independently decreased seed number and increased seed glucosinolate concentration. There were no such sites in the present study, and the ranges in seed numbers and glucosinolate concentration were small. There was, however, a strong relationship between seed glucosinolate concentration and the number of seed/m^2 (Fig. 8*b*). When all sites are considered, the relation appeared to be curvilinear with seed glucosinolate concentration being high when there were very few (*ca* 20/m^2) or very many (> 90/m^2) seeds, and they were lowest at seed numbers between 50-80 seeds/m^2. An explanation for this could be that at low seed number, a given total amount of glucosinolate is distributed between few seeds so the concentration per seed is high, whereas when many seeds are present seeds tend to be small and there is less tendency for seed glucosinolates to be diluted by seed dry matter. With this relationship, the lowest seed glucosinolate concentrations were obtained with intermediate seed populations, but whether such good quality can consistently be achieved in farming practice without penalty to yield requires further study.

Alternatively, if the data for Woburn is excluded from the relationship in Fig, 8*b* as being exceptional, the relationship between seed glucosinolate concentration and seed number becomes more obviously linear. However, in these experiments the greatest glucosinolate concentrations were obtained when many seeds were present, which is the opposite of that found in France by Merrien (1989). The underlying causes of the relationships between seed number, seed size and seed glucosinolate concentration and the reasons why they should differ from one country to another and should be so exceptional under the conditions of severe sulphur deficiency at Woburn have not yet been ascertained.

PREDICTION OF YIELD AND SEED GLUCOSINOLATE RESPONSES TO APPLIED SULPHUR

Leaf sulphur concentrations. The symptoms of crop sulphur deficiency usually appear in spring when growth is rapid and the daily demand for sulphur is greatest. At this time, the sulphur concentrations in the youngest, fully-expanded leaves provide a useful indication of the crop's sulphur status and it has been proposed that they might offer a means of predicting responses to applied sulphur. Leaf sulphur concentrations were measured in most of the experimental crops to test whether this might be so. Full details of the leaf sulphur concentrations are given in Tables 18-21 in the Appendix for 1991, Tables 33-37 in the Appendix for 1992, and Tables 50 and 51 in the Appendix for 1993.

The summary in Table 11 shows leaf sulphur concentrations in crops grown with adequate nitrogen (usually 250 kg/ha) and no applied sulphur, and the changes in concentration induced by a large application of sulphur. Leaf sulphur concentrations in crops grown without applied sulphur ranged from 2.46 mg/g at Woburn to 8.07 mg/g at Cockle Park, both in 1992. The range in concentration from one site to another was small in 1991, and small for most sites in 1992 (ie 2.5-5.5 mg/g). The exception in 1992 was Cockle Park where leaf sulphur concentrations were high (8.1 mg/g). High leaf sulphur concentrations were also measured in the Scottish borders and at Cockle Park in 1993. In all situations, the applied sulphur increased concentrations in the leaf, the increase being particularly large in 1992.

Leaf sulphur concentrations and yield responses to applied sulphur. There was no consistent relationship between leaf sulphur concentrations in crops grown without applied sulphur at a particular site and the responses of yield and seed glucosinolates to applied sulphur. There was a reasonable relationship across sites between the yield resonse to applied sulphur and leaf sulphur concentration in 1992 with increasingly greater yield responses being obtained when leaf sulphur concentrations were below 4 mg/g. However, there was no yield response to applied sulphur in 1991 (except at the sulphur-deficient site at Woburn) even though leaf sulphur concentrations were comparably low.

Leaf sulphur concentrations and seed glucosinolate responses to applied sulphur. There was even less correlation between leaf sulphur concentration and the response of seed glucosinolate concentrations to applied sulphur. Equally large increases in glucosinolate concentration were obtained with applied sulphur in crops of high and low leaf sulphur concentration. For instance, at Woburn in 1992 (where the leaf sulphur concentration was 2.46 mg/g) an application of 40 kg/ha of sulphur increased the seed glucosinolate concentration from 13.4 to 21.1 μmol/g, and in the Scottish borders in 1993 (where the leaf sulphur concentration was 7.50 mg/g) an application of 100 kg/ha of sulphur increased the seed glucosinolate concentration from 5.3 to 17.5 μmol/g.

In 1992 and 1993, soil sulphur and atmospheric deposition were measured at the five sites, together with the sulphur uptake and responses of yield and seed glucosinolates to applied sulphur. The report on this ancillary study (HGCA OS20/1/91A) will be made by PJA Withers of ADAS Bridgets.

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Table 1. **Site, season and cultivar interactions on the yield (t/ha) of winter oilseed rape. Comparison of Rothamsted (RES) and Cockle Park.**

	1990/91		**1991/92**		**1992/93**	
	RES	**Cockle Park**	**RES**	**Cockle Park**	**RES**	**Cockle Park**
Ariana	3.47	3.45	2.59	4.00	3.14	-
Falcon	3.40	3.99	2.67	4.67	3.62	4.20
Libravo*	3.17	3.44	2.57	3.79	3.34	-
Site/season	3.34	3.63	2.61	4.15		
Season	3.49		3.38			

* Tapidor in 1991/92 and 1992/93

SEDs (DF)

Season	0.068	(3)
Season x Site	0.087	(6)
except within same season	0.078	
Site x Season x cultivar	0.125	(24)
except within same season	0.119	
same cv. within same season	0.119	

Table 2. ***Site, season and N interactions on the yield (t/ha) of winter oilseed rape. Comparison of Rothamsted (RES) and Cockle Park.***

	1990/91		**1991/92**		**1992/93**	
	RES	**Cockle Park**	**RES**	**Cockle Park**	**RES**	**Cockle Park**
N_0	2.90	2.45	1.29	3.89	3.23	3.02
N_{150}	3.60	3.97	3.47	4.25	3.46	4.75
N_{250}	3.54	4.46	3.48	4.32	3.42	4.83
Site/season	3.34	3.63	2.61	4.15		
Season	3.49		3.38			

SEDs (DF)

Season	0.068	(3)
Season x Site	0.087	(6)
except sites in same season	0.078	
Site x Season x N rate	0.102	(324)
except within same season	0.094	
same N rates in same season	0.094	

Table 3. *Site, season and N interactions on the yield (t/ha) of winter oilseed rape. Comparison of five sites.*

	1990/91		1991/92		1992/93	
	N_0	N_{250}	N_0	N_{250}	N_0	N_{250}
S Scotland	1.28	4.04	2.92	2.87	3.97	4.36
Cockle Park	2.54	4.96	4.01	5.11	3.03	4.83
Rothamsted	2.89	3.83	1.31	3.55	3.23	3.42
Woburn	0.42	1.92	0.55	1.39	3.78	4.18
Bridgets	1.30	3.43	2.55	3.28	1.69	4.06
Season/N rate	1.69	3.64	2.27	3.24		
Season	2.66		2.75			

SEDs (DF)

Season	0.061	(3)
Season x N rate	0.078	(94)
except N rates within same season	0.070	
Site x Season x N rate	0.211	(94)
except within same season	0.220	
same N rate and same season	0.220	

Table 4. *Site, season and S interactions on the yield (t/ha) of winter oilseed rape. Comparison of five sites.*

	1990/91		1991/92		1992/93	
	S_0	S_{100}	S_0	S_{100}	S_0	S_{100}
S Scotland	2.61	2.71	2.71	3.07	4.14	4.25
Cockle Park	3.57	3.93	4.53	4.59	4.11	4.28
Rothamsted	3.46	3.27	2.37	2.49	3.30	3.42
Woburn*	0.78	1.56	0.82	1.12	4.16	4.07
Bridgets	2.34	2.39	2.77	3.06	2.71	3.04
Season/S rate	2.55	2.77	2.64	2.87		
Season	2.66		2.75			

* 40 kg S/ha in all years and spring rape in 1992/93

SEDs (DF)

Season	0.061	(3)
Season x S rate	0.078	(94)
except S rates in same season	0.070	
Site x Season x S rate	0.211	(94)
except within same season	0.220	
same S rate and same season	0.220	

Table 5. *Site, N and S interactions on the yield (t/ha) of winter oilseed rape. Comparison of five sites in 1990/91 and 1991/92.*

	N_0		N_{250}	
	S_0	S_{100}	S_0	S_{100}
S Scotland	1.96	2.23	3.36	3.55
Cockle Park	3.19	3.37	4.92	5.16
Rothamsted	2.08	2.12	3.75	3.63
Woburn	0.50	0.47	1.10	2.21
Bridgets	1.82	2.03	3.30	3.42
S rate/N rate	1.69	3.64	2.27	3.24
N rate	2.66		2.75	

SEDs (DF)

N rate	0.049	(24)
S rate x N rate	0.070	(94)
Site x N x S rate	0.191	(94)
except within same site	0.156	
same N rate at same site	0.156	
same S rate at same site	0.156	

Table 6. *Site, season and cultivar interactions on seed glucosinolate concentrations (µmol/g) of winter oilseed rape. Comparison of Rothamsted (RES) and Cockle Park.*

	1990/91		1991/92		1992/93	
	RES	Cockle Park	RES	Cockle Park	RES	Cockle Park
Ariana	19.4	31.8	24.6	29.4	-	-
Falcon	11.8	13.4	15.4	14.6	16.3	-
Libravo*	18.4	19.5	11.1	14.2	-	
Site/season	16.6	21.6	17.0	19.4		
Season	19.1		18.2			

* Tapidor in 1991/92 and 1992/93

SEDs (DF)

Season	0.76	(3)
Season x Site	1.19	(6)
except within same season	1.29	
Site x Season x Cultivar	1.44	(24)
except within same season	1.53	
same cv. within same season	1.53	

Table 7. ***Site, season and cultivar interactions on seed glucosinolate concentrations (μmol/g) of winter oilseed rape. Comparison of Rothamsted (RES) and Cockle Park.***

	Rothamsted			Cockle Park			
	N_0	N_{150}	N_{250}	N_0	N_{100}	N_{250}	Cv.
Ariana	18.3	21.4	26.3	28.2	30.2	33.4	26.3
Falcon	13.2	12.6	15.0	12.1	13.6	16.3	13.8
Libravo*	12.4	15.4	16.5	15.0	17.4	18.0	15.8
Site/N rate	14.6	16.5	19.3	18.4	20.4	22.6	
Site		16.8			20.5		

* Tapidor in 1991/92

SEDs (DF)		
Site	0.91	(6)
Cultivar	0.50	(24)
Site x N rate	1.00	(324)
except within same site	0.51	
Site x N rate x cultivar	1.30	(324)
except same cv. at same site	1.01	

Table 8. *Site, season and S interactions on seed glucosinolates (μmol/g) of winter oilseed rape. Comparison of five sites*

	1990/91		1991/92		1992/93	
	S_0	S_{100}	S_0	S_{100}	S_0	S_{100}
S Scotland	11.8	12.5	8.9	30.1	8.4	16.4
Cockle Park	14.0	14.3	13.4	15.2	-	-
Rothamsted	12.0	12.4	13.4	12.8	16.3	16.0
Woburn	15.6	17.0	14.3	17.0	-	-
Bridgets	9.4	11.4	11.0	14.8	12.5	21.2
Season/S rate	12.6	13.5	12.2	18.0		
Season	13.0		15.1			

SEDs (DF)

Season	0.53	(3)
Season x S rate	0.66	(94)
except S rates in same season	0.55	
Site x Season x S rate	1.63	(94)
except within same season	1.66	
same S rate and same season	1.66	

Table 9. *Site, N and S interactions on seed glucosinolate concentrations (μmol/g) of winter oilseed rape. Comparison of five sites in 1990/91 and 1991/92.*

	N_0		N_{250}	
	S_0	S_{100}	S_0	S_{100}
S Scotland	10.4	20.2	10.4	22.4
Cockle Park	11.2	13.0	16.2	16.6
Rothamsted	11.8	11.0	13.6	14.1
Woburn	15.6	16.6	14.4	17.4
Bridgets	11.5	12.1	9.0	14.1
S rate/N rate	12.1	14.6	12.7	16.9
N rate	13.3		14.8	

SEDs (DF)

N rate	0.39	(94)
S rate x N rate	0.55	(94)
Site x N x S rate	1.47	(94)
except within same site	1.24	
same N rate at same site	1.24	
same S rate at same site	1.24	

Table 10. *Soil sulphate concentrations (mg/kg) at the five sites in the autumn and spring prior to the application of the sulphur treatments, and afterwards in the summer of 1991/92.*

Depth (cm)	Autumn Without S	Spring Without S	Summer Without S	Summer With S
		Scottish borders		
0-30	2.7	2.7	5.0	11.9
30-60	4.0	3.9	5.1	4.4
60-90	4.1	4.7	3.5	7.2
		Cockle Park		
0-30	4.6	4.4	2.7	8.8
30-60	11.4	13.2	13.3	8.4
60-90	16.4	17.3	19.8	20.6
		Rothamsted		
0-30	5.7	6.8	2.6	6.6
30-60	7.6	8.6	7.7	7.1
60-90	11.5	10.3	9.2	10.4
		Woburn		
0-30	2.0	5.5	1.8	2.0
30-60	2.4	2.6	1.4	2.5
60-90	2.6	2.4	2.1	2.8
		ADAS Bridgets		
0-30	4.8	4.1	4.4	11.0
30-60	3.9	5.3	4.9	6.1
60-90		Not sampled		

Table 11. *Dry matter and seed yields and seed glucosinolate and leaf sulphur concentrations of $N_{250}S_0$ crops (adequate N but no S) and responses of leaf sulphur, yield and seed glucosinolates to 100 kg S/ha at the five sites in different years.*

		Crop DM	Yield	Seed GLS	Leaf S	Soil SO_4	N uptake	S uptake	Response to applied S		
		t/ha	t/ha	μmol/g	mg/g	mg/kg	kg/ha	kg/ha	Yield*	Seed GLS*	Leaf S
1990/91	S Scotland	12.6	4.01	13.2	3.21	11.2	-	90	102	104	4.27
	Cockle Park	17.0	4.77	18.1	3.65	39.7	-	133	108	92	4.52
	Rothamsted	16.4	3.97	13.5	5.47	28.2	243	108	93	96	5.66
	Woburn**	2.3	1.12	15.3	4.02	7.5	83	22	243	120	4.79
	Bridgets	7.4	3.41	8.9	3.13	9.4	183	20	101	131	4.12
1991/92	S Scotland	15.5	2.72	7.5	3.23		230	124	111	415	8.61
	Cockle Park	13.4	4.63	14.8	8.07		223	129	102	101	9.10
	Rothamsted	-	3.61	12.2	4.68		-	-	103	143	9.64
	Woburn**	2.3	1.03	13.4	2.46		30	5	165	158	5.42
	Bridgets	-	3.17	10.3	4.03		-	-	107	275	9.06
1992/93	S Scotland	-	4.33	5.3	7.50		-	-	101	330	9.87
	Cockle Park	-	4.79	-	6.71		-	-	105	-	9.93
	Rothamsted	-	3.69	18.8	-		-	-	104	101	-
	Bridgets	-	3.69	10.0	-		-	-	120	244	-

* As percentage of corresponding S_0 treatment. **Sulphur responses to 40 kg S/ha

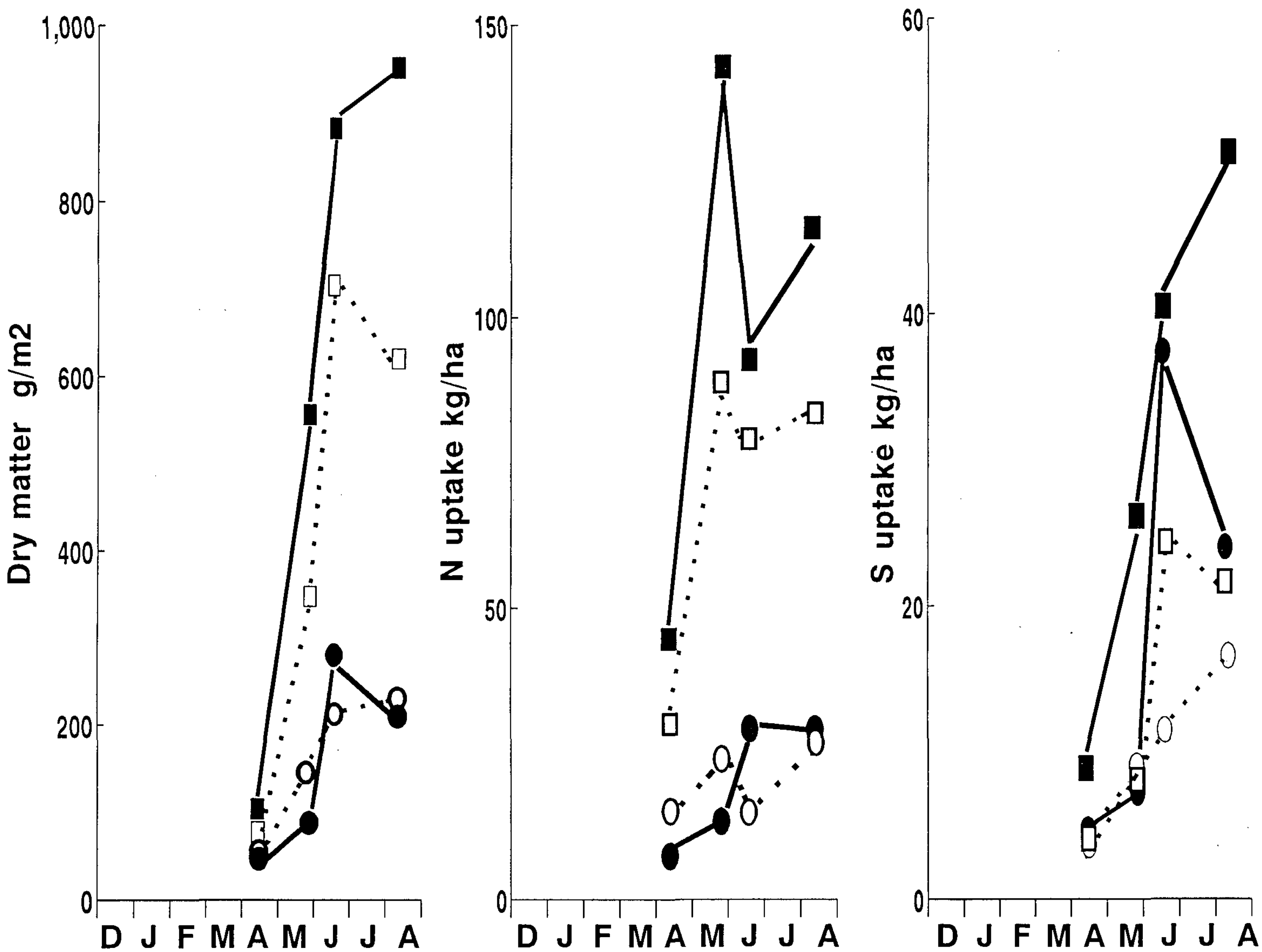

Fig. 1. Changes in dry matter and the nitrogen and sulphur contents of crops grown with extreme rates of N and S at Woburn in 1991.
O, N_0S_0; ●, N_0S_{40}; □, $N_{250}S_0$; ■, $N_{250}S_{40}$.

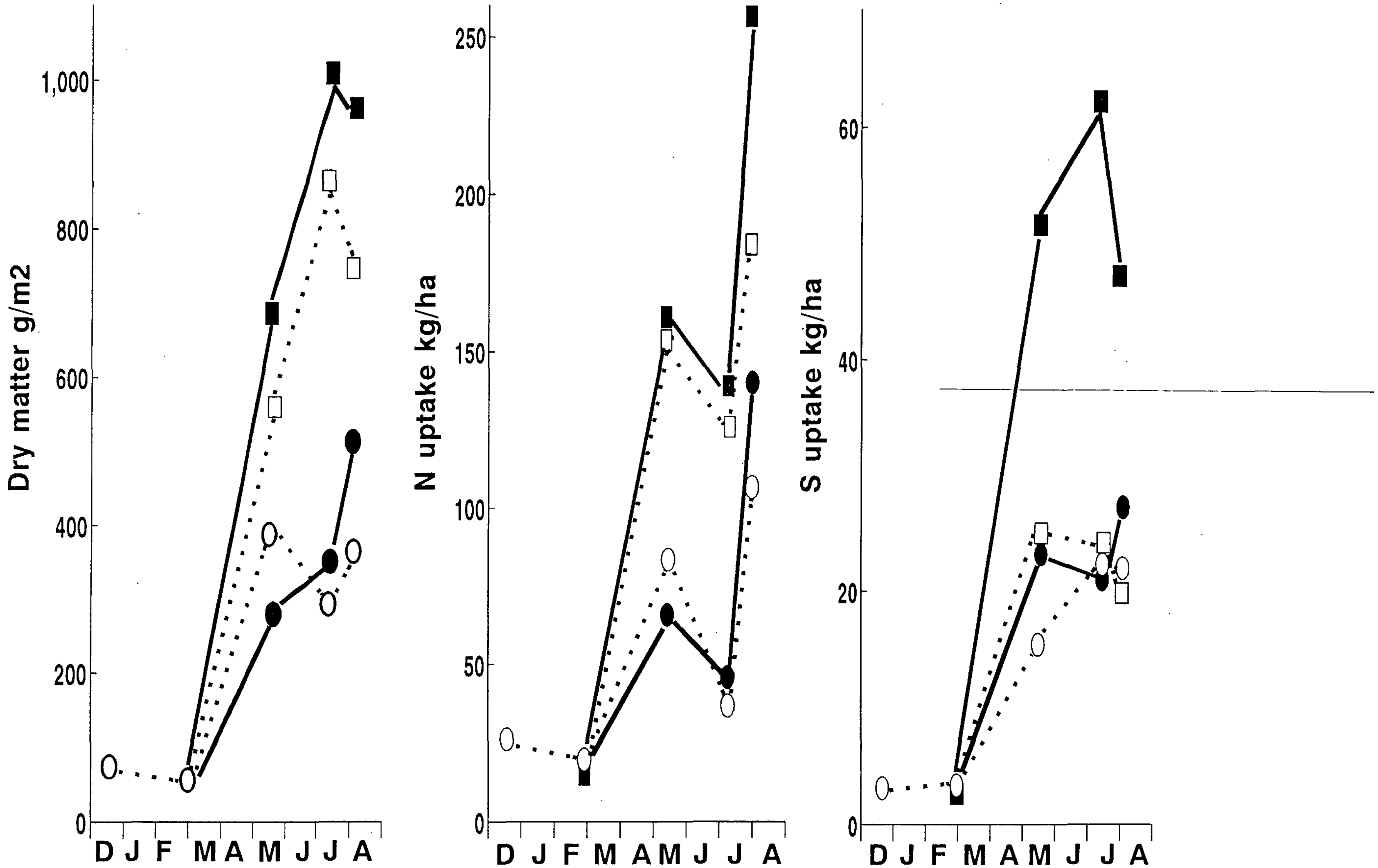

Fig. 2. Changes in dry matter and the nitrogen and sulphur contents of crops grown with extreme rates of N and S at ADAS Bridgets in 1991. O, N_0S_0; ●, N_0S_{100}; □, $N_{250}S_0$; ■, $N_{250}S_{100}$.

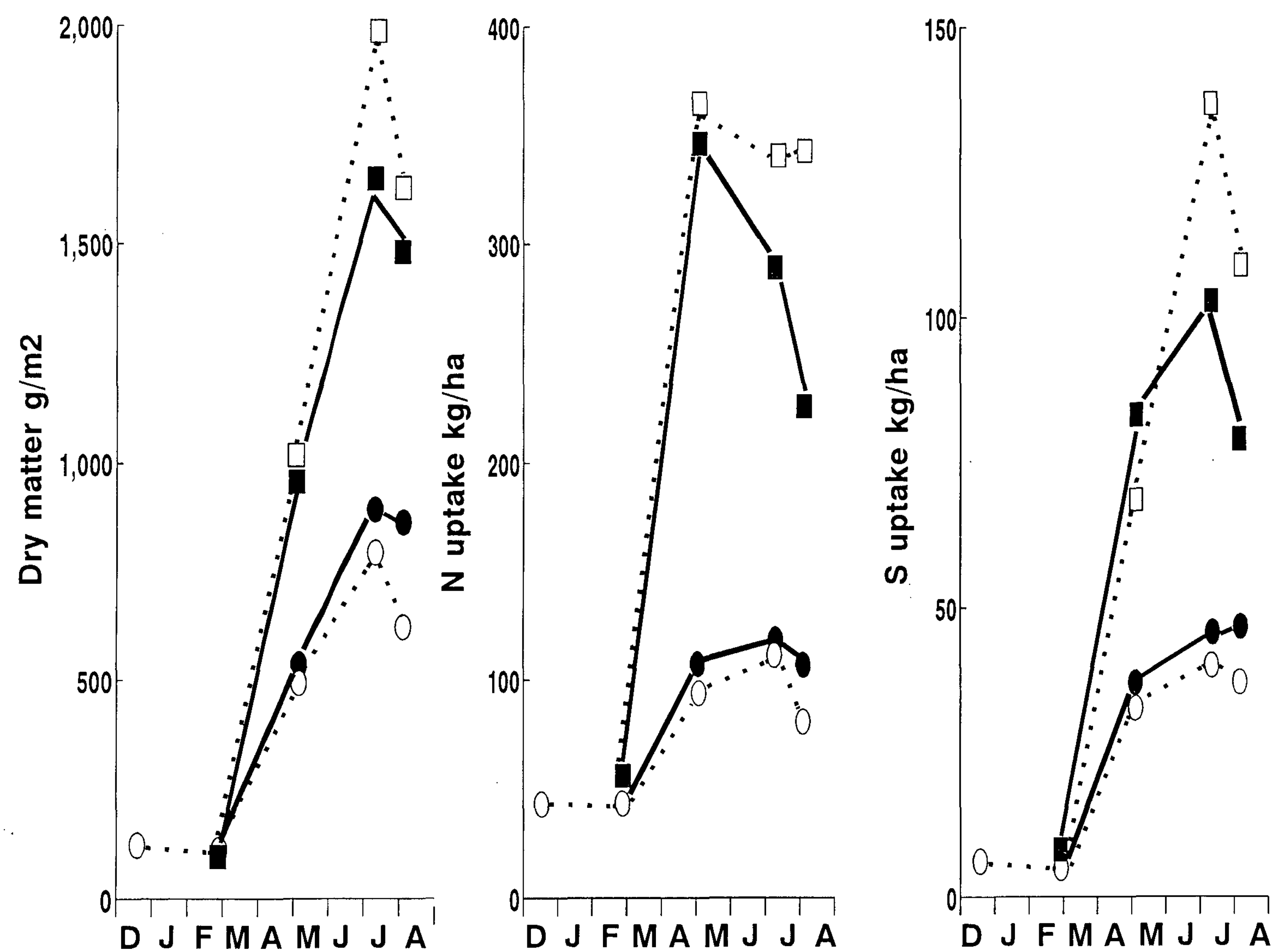

Fig. 3. Changes in dry matter and the nitrogen and sulphur contents of crops grown with extreme rates of N and S at Rothamsted in 1991. O, N_0S_0; ●, N_0S_{100}; □, $N_{250}S_0$; ■, $N_{250}S_{100}$.

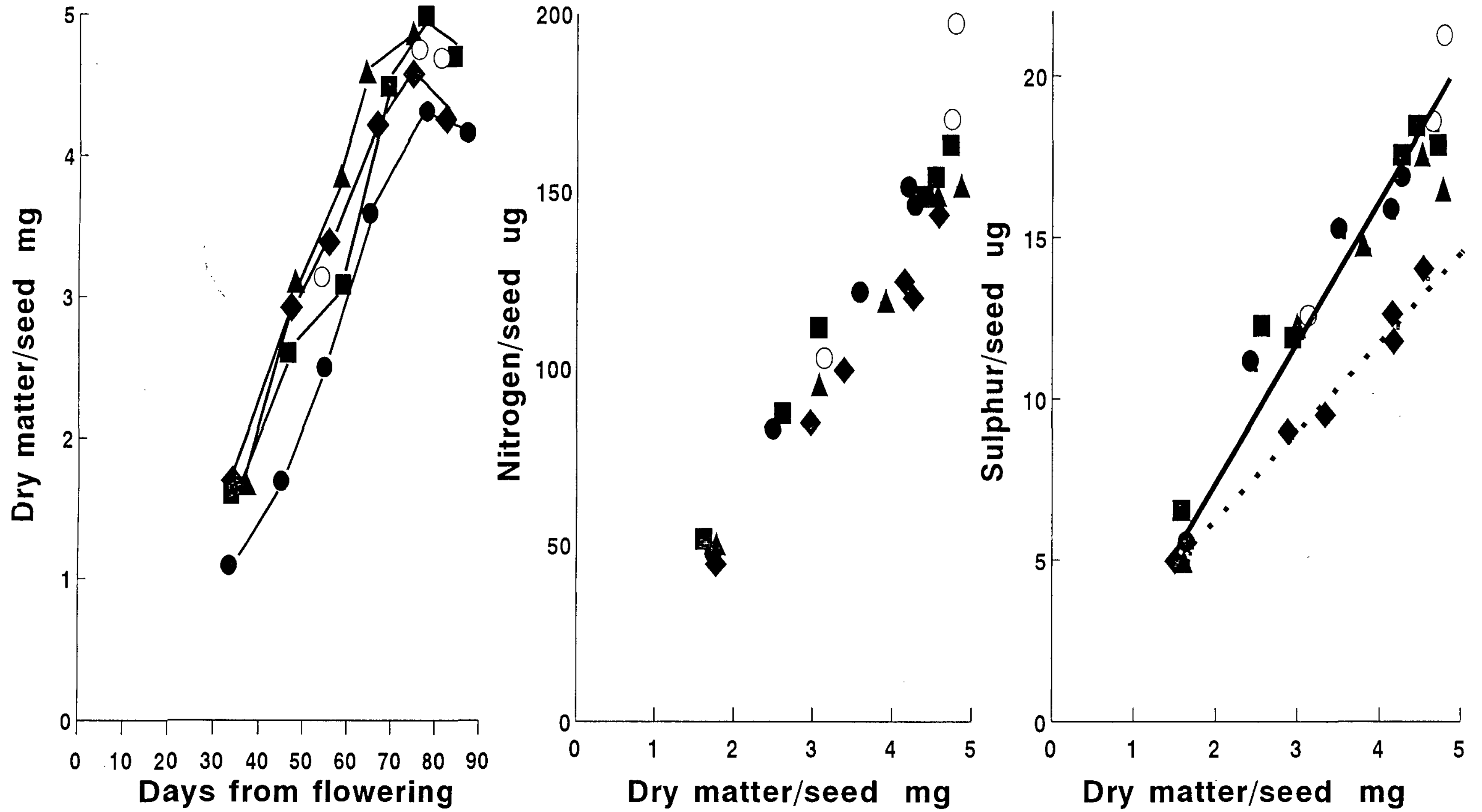

Fig. 4. Changes in mean seed weight and seed nitrogen and sulphur contents during seed development at different sites in 1991. ●, Cockle Park; ▲, Scottish borders; ■, Rothamsted; O, Woburn; ◆, ADAS Bridgets.

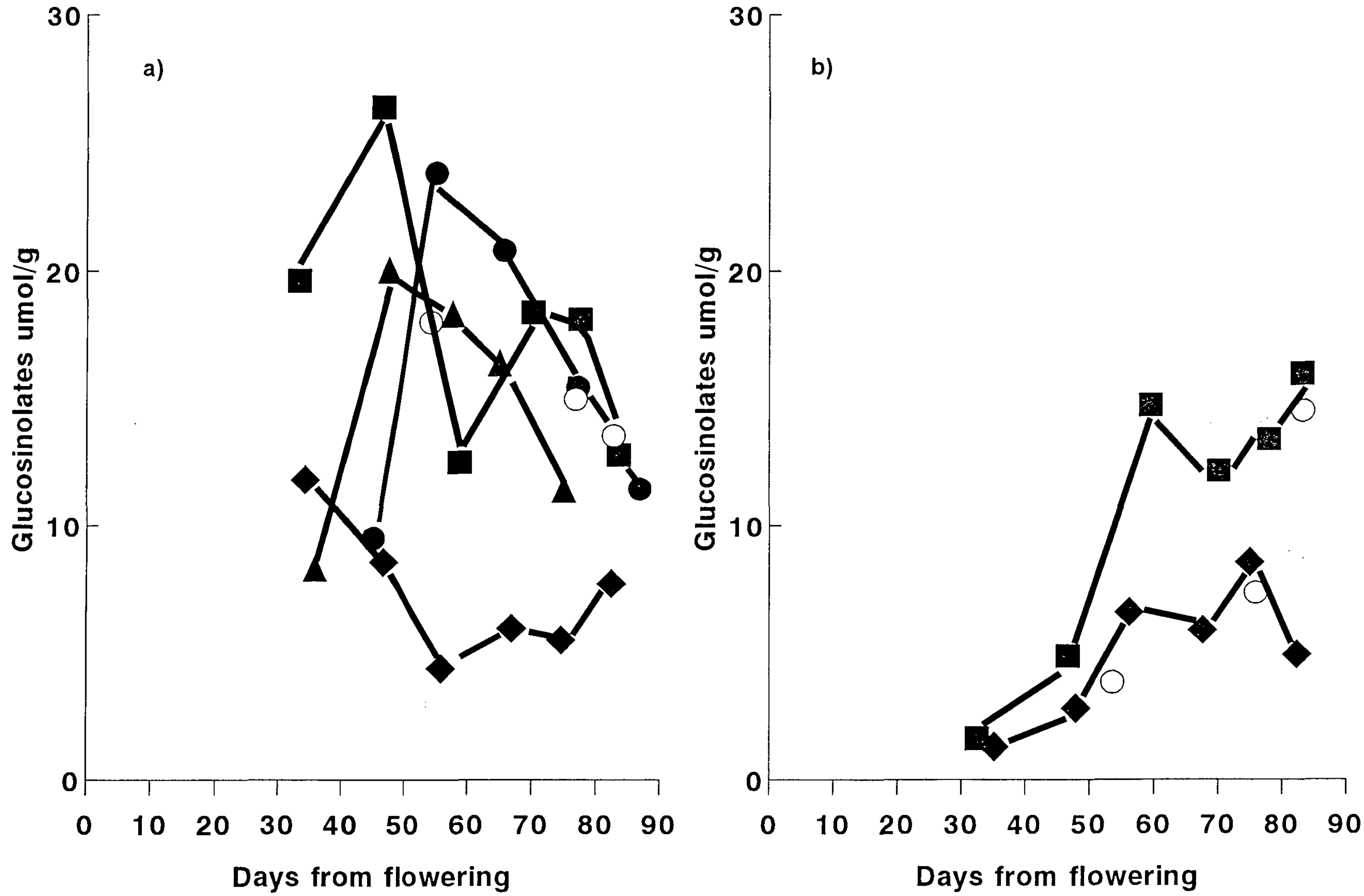

Fig. 5. Seed glucosinolate concentrations during seed development in 1991, a) calculated from N and S concentrations and b) measured by HPLC. ●, Cockle Park; ▲, Scottish borders; ■, Rothamsted; O, Woburn; ◆, ADAS Bridgets.

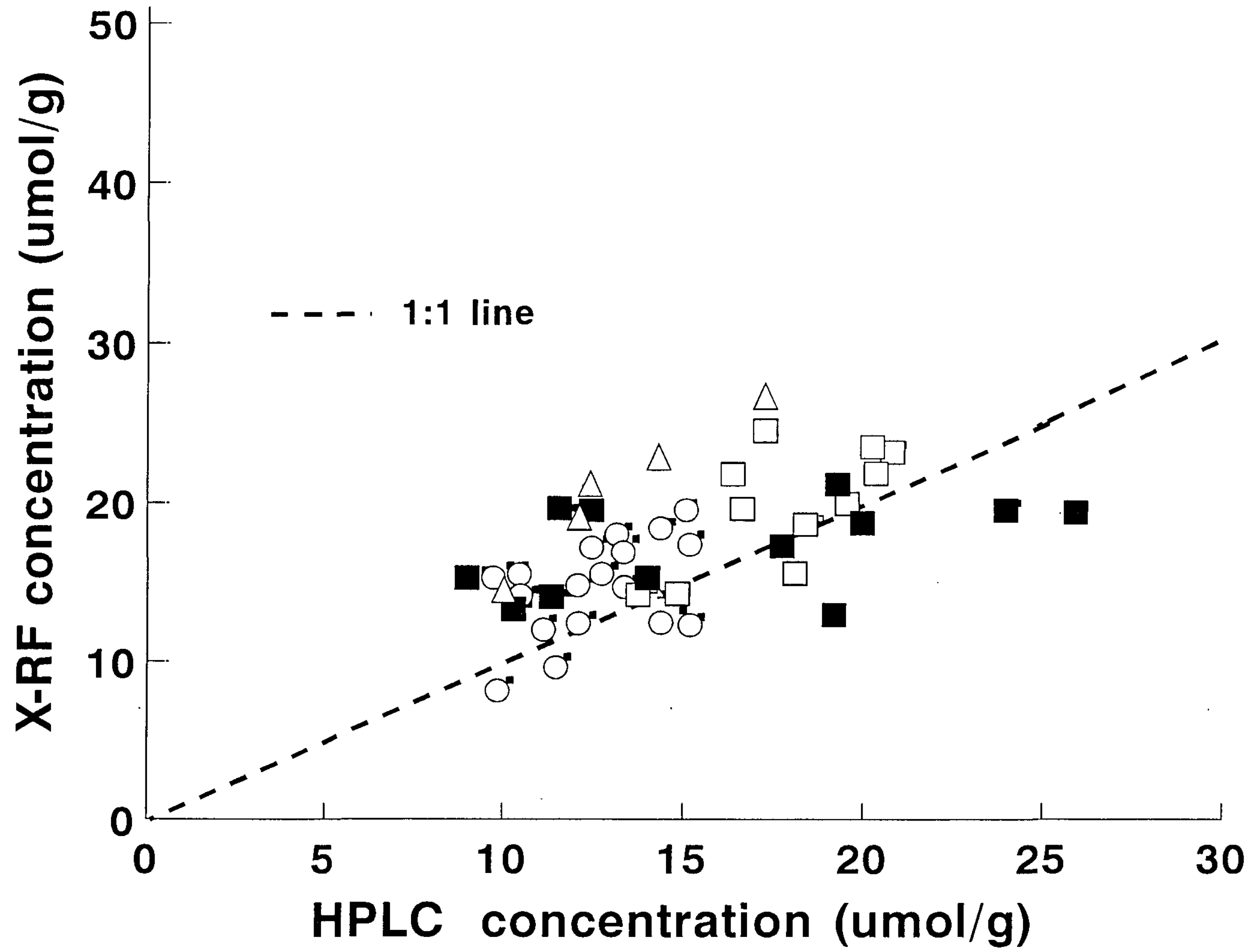

Fig. 6. Comparison of glucosinolate concentrations of seed harvested from different sites calculated from N and S contents or measured by HPLC. O, Rothamsted, 1991, 1992. 1993; □, Woburn 1991; ■, Woburn 1992; △, ADAS Bridgets 1992.

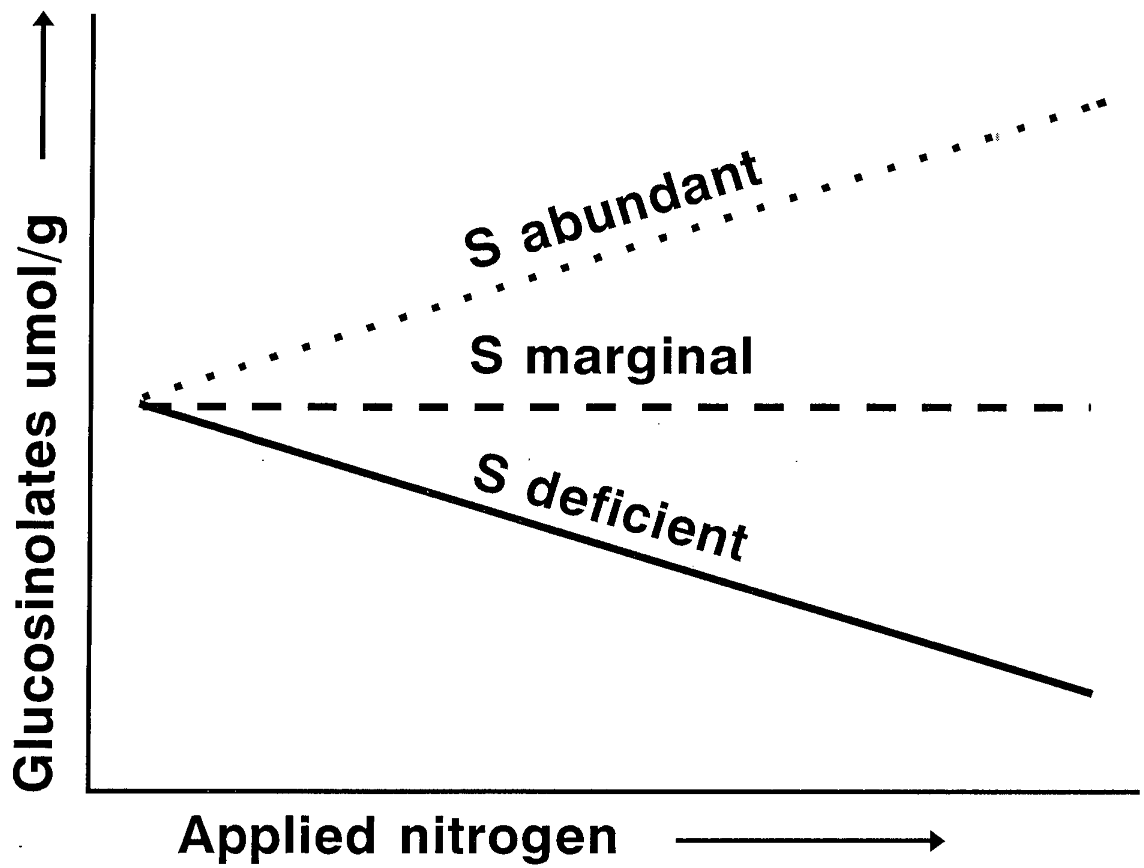

Fig. 7. Conceptual diagram of the responses of Seed glucosinolate concentrations to applied nitrogen at sites of different sulphur status.

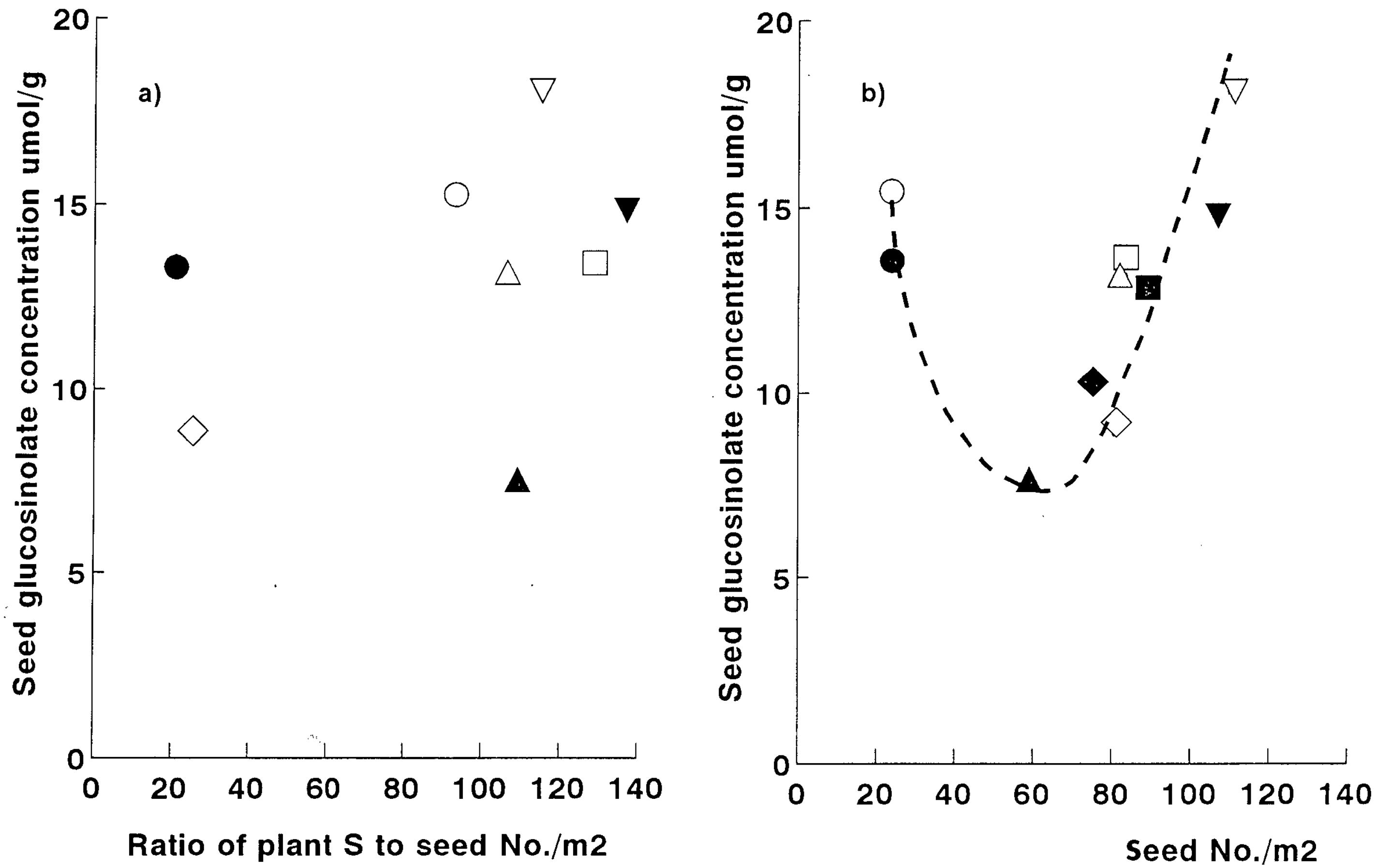

Fig. 8. Seed glucosinolate concentrations and a) crop S to seed number ratio, b) seed number/m^2 ▽,▼, Cockle Park 1991, 1992; △,▲, Scottish borders 1991,1992; □,■, Rothamsted 1991, 1992; O,●, Woburn 1991, 1992: ◇,◆, ADAS Bridgets 1991, 1992.

APPENDIX TABLES

Table 12. *Times of application of nitrogen and sulphur treatments.*

		Nitrogen		Sulphur
Scottish borders	**1990/91**	50 kg/ha	13 March	25 March
		Remainder	8 April	
	1991/92	150 kg/ha	20 February	7 April
		Remainder	4 May	
	1992/93	50 kg/ha	4 March	25 March
		Remainder	7 April	
Cockle Park	**1990/91**	50 kg/ha	4 March	22 March
		Remainder	26 March	
	1991/92	50 kg/ha	26 February	19 March
		Remainder	26 March	
	1992/93	50 kg/ha	8 March	
Rothamsted	**1990/91**	All of the N applied 12 March		13 March
	1991/92	50 kg/ha	20 February	5 March
		Remainder	5 March	
	1992/93	50 kg/ha	22 February	15 March
Woburn	**1990/91**	50 kg/ha	26 February	26 February
		Remainder	5 April	
	1991/92	50 kg/ha	13 February	13 February
		Remainder	1 April	
		50 kg/ha to nil plots	23 April	
	1992/93	Crop failed		
Bridgets	**1990/91**	50 kg/ha	18 March	27 March
		Remainder	27 March	
	1991/92	50 kg/ha	6 March	17 March
		Remainder	10 April	
	1992/93	50 kg/ha	25 February	25 February
		Remainder	17 March	

Table 13. **Yield response (t/ha) of winter oilseed rape to applied N and S at Cockle Park in 1990-91.**

	S kg/ha	N kg/ha 0	150	250	S mean
Ariana	0	2.46	3.82	3.97	3.42
	50	2.54	3.56	4.16	3.42
	100	2.56	3.78	4.11	3.48
	N mean	2.52	3.72	4.08	3.44
Libravo	0	2.21	3.81	4.29	3.44
	50	2.15	3.64	4.38	3.39
	100	2.34	3.82	4.09	3.42
	N mean	2.23	3.76	4.25	3.41
Falcon	0	2.36	4.28	4.77	3.80
	50	2.63	4.69	5.04	4.12
	100	2.72	4.26	5.14	4.04
	N mean	2.57	4.41	4.98	3.99

SED (78 DF)	
Variety, N, S	0.054
Variety x N, Variety x S, N x S	0.094
Variety x N x S	0.162

Table 14. **Yield responses (t/ha) of winter oilseed rape to applied N and S at Rothamsted in 1990/1991.**

	kg S/ha	kg N/ha 0	150	250	S mean
	0	3.11	3.73	3.73	3.53
Ariana	50	2.81	3.71	3.66	3.39
	100	2.90	3.94	3.61	3.49
	N mean	2.94	3.80	3.67	3.47
	0	2.86	3.63	2.63	3.04
Libravo	50	2.91	3.58	3.31	3.27
	100	2.85	3.35	3.25	3.15
	N mean	2.88	3.52	3.06	3.15
	0	3.00	3.06	3.97	3.34
Falcon	50	2.74	3.76	3.94	3.48
	100	2.88	3.76	3.63	3.43
	N mean	2.87	3.53	3.85	3.42
	Overall N mean	2.90	3.61	3.53	

SED (78 DF)

Variety, N	0.067
N x Variety	0.116
N x S x Variety	0.211

Table 15. Yield response (t/ha) of winter oilseed rape (cv. Falcon) to applied N and S in the Scottish borders in 1990-91.

S kg/ha	N kg/ha 50	150	250	S mean
0	1.22	2.41	4.01	2.55
150	1.18	2.37	4.05	2.53
250	1.33	2.71	4.07	2.70
N mean	1.24	2.50	4.04	2.59

SED (27 DF)	
N, S	0.114
N x S	0.198

Table 16. Yield responses (t/ha) of winter oilseed rape (cv. Libravo) to applied N and S at Woburn in 1990/91.

kg S/ha	kg N/ha 0	180	230	S mean
0	0.44	1.90	1.12	1.15
10	0.44	2.69	1.74	1.62
20	0.30	2.14	2.73	1.72
40	0.40	2.31	2.72	1.81
N mean	0.39	2.26	2.08	

SED (22 DF)	
N	0.207
S	0.239
N x S	0.413

Table 17. **Yield responses (t/ha) of winter oilseed rape (cv. Falcon) to applied N and S at Bridgets in 1990/91.**

kg S/ha	**kg N/ha** 0	250	**S mean**
0	1.27	3.41	2.34
100	1.33	3.44	2.39
N mean	1.30	3.43	

SED (9 DF)

N,S	0.183

Table 18. **The effects of applied N and S on leaf sulphur concentrations (mg/g) of winter oilseed rape at Cockle Park in 1990-91.**

	S kg/ha	**N kg/ha** 0	150	250	**S mean**
	0	4.60	3.67	3.83	4.03
Ariana	50	4.97	4.90	4.80	4.89
	100	4.98	4.99	4.70	4.89
	N mean	4.85	4.52	4.44	4.60
	0	4.55	3.62	3.79	3.99
Libravo	50	4.93	4.68	4.53	4.71
	100	5.02	5.18	4.70	4.97
	N mean	4.83	4.49	4.34	4.56
	0	4.19	3.74	3.65	3.86
Falcon	50	4.33	4.58	4.28	4.40
	100	4.43	4.81	4.52	4.59
	N mean	4.32	4.38	4.15	4.28

SED (78 DF)

Variety, N, S	0.073
Variety x N, Variety x S, N x S	0.127
Variety x N x S	0.220

Table 19. The effects of applied N and S on leaf sulphur concentrations (mg/g) of winter oilseed rape at Rothamsted in 1990/91.

	kg S/ha	kg N/ha 0	250	S mean
Ariana	0	4.44	5.17	4.68
	100	4.92	6.72	5.95
	N mean	4.80	5.82	5.31
Libravo	0	4.83	6.08	5.45
	100	4.73	6.18	5.45
	N mean	4.78	6.13	5.45
Falcon	0	4.47	5.47	4.97
	100	4.62	5.66	5.14
	N mean	4.55	5.56	5.05

SED (10 DF)	
N, S	0.152
Variety x S, Variety X N	0.263

Table 20. The effects of applied N and S on leaf S concentrations (mg/g) of winter oilseed rape (cv. Falcon) in the Scottish borders in 1990-91.

S kg/ha	N kg/ha 50	150	250	S mean
0	4.42	3.60	3.21	3.74
50	4.49	4.42	4.07	4.33
100	4.57	4.56	4.27	4.47
N mean	4.49	4.19	3.85	4.18

SED (27 DF)	
N, S	0.071
N x S	0.123

Table 21. **The effects of applied N and S on leaf sulphur concentrations (mg/g) of winter oilseed rape (cv. Libravo) at Woburn in 1990/91.**

kg S/ha	N kg/ha 0	180	230	S mean
0	-	3.82	4.02	3.92
10	-	4.17	4.43	4.30
20	-	4.87	4.51	4.69
40	-	5.16	4.79	4.98
N mean	-	4.51	4.44	4.47

SED (14 DF)	
N, S	0.300
N x S	0.600

- , insufficient crop sample for accurate measurement

Table 22. **The effects of applied N and S on leaf sulphur concentrations (mg/g) of winter oilseed rape (cv. Falcon) at Bridgets in 1990/91.**

kg S/ha	kg N/ha 0	250	S mean
0	3.84	3.13	3.48
100	4.08	4.12	4.10
N mean	3.96	3.62	3.79

SED (9 DF)	
N, S	0.197
S x N	0.279

Table 23. Responses of seed glucosinolates (μmol/g) of winter oilseed rape to applied N and S at Cockle Park in 1990/91.

	kg S/ha	kg N/ha 0	150	250	S mean
Ariana	0	29.3	29.2	36.9	31.8
	50	31.2	30.4	35.3	32.3
	100	28.3	31.9	33.5	31.2
	N mean	29.6	30.5	35.2	31.8
Libravo	0	17.7	19.3	21.5	19.5
	50	16.5	21.3	19.6	19.1
	100	17.6	20.0	21.7	19.8
	N mean	17.3	20.2	20.4	19.5
Falcon	0	9.9	14.6	18.1	14.2
	50	11.2	10.3	15.8	12.4
	100	11.9	12.5	16.7	13.7
	N mean	11.0	12.5	16.9	13.4

SED (78 DF)	
Variety	0.26
N	0.45
N x Variety	0.77

Table 24. **Responses of seed glucosinolates (μmol/g) of winter oilseed rape to applied N and S at Rothamsted in 1990/91.**

		kg N/ha			
	S kg/ha	**0**	**150**	**250**	**S mean**
	0	13.2	16.8	25.6	18.5
Ariana	**50**	18.1	20.3	14.1	20.9
	100	13.9	18.7	24.5	19.1
	N mean	15.1	18.6	24.7	14.5
	0	11.1	23.0	21.1	18.4
Libravo	**50**	14.0	17.9	21.6	17.9
	100	14.4	21.7	22.3	19.4
	N mean	13.3	16.8	19.8	18.6
	0	10.6	10.2	13.5	11.4
Falcon	**50**	12.5	11.4	12.5	12.1
	100	11.8	10.9	12.9	11.9
	N mean	11.6	10.8	13.0	11.8

SED (78 DF)	
N, Variety	0.62
N x Variety	1.07

Table 25. **Responses of seed glucosinolates (μmol/g) of winter oilseed rape (cv. Falcon) to applied N and S in the Scottish borders in 1990/91.**

	kg N/ha			
kg S/ha	**0**	**150**	**250**	**S mean**
0	10.4	11.0	13.2	11.5
50	11.1	11.5	13.2	11.9
100	11.3	11.8	13.7	12.3
N mean	10.9	11.4	13.4	11.9

SED (27 DF)	
N,S	0.58
N x S	1.01

Table 26. **Responses of seed glucosinolates (μmol/g) of winter oilseed rape (cv. Libravo) to applied N and S at Woburn in 1990/91.**

	kg N/ha			
kg S/ha	**0**	**180**	**230**	**S mean**
0	17.9	15.6	15.3	16.3
10	21.9	20.0	15.1	19.0
20	19.4	21.0	22.2	20.9
40	19.5	22.1	18.4	20.0
N mean	19.7	19.7	17.8	

SED (22 DF)	
N	1.04
S	1.20
N x S	2.07

Table 27. Responses of seed glucosinolates (µmol/g) of winter oilseed rape (cv. Falcon) to applied N and S at Bridgets in 1990/91.

	kg N/ha		
kg S/ha	**0**	**250**	**S mean**
0	11.4	8.9	10.1
100	12.7	11.7	12.2
	12.1	10.3	

SED (9 DF)	
N,S	0.62
S x N	0.88

Table 28. Yield response (t/ha) of winter oilseed rape (cv. Falcon) to applied N and S in the Scottish borders in 1991-92.

	N kg/ha		
S kg/ha	**150**	**250**	**S mean**
0	2.71	2.72	2.72
50	2.90	3.12	3.01
100	3.14	3.02	3.07
N mean	2.91	2.95	2.93

SED (18 DF)	
N	0.094
S	0.116
N x S	0.164

Table 29. **Yield response (t/ha) of autumn-sown oilseed rape to applied N and S at Cockle Park in 1991-92.**

		N kg/ha			
	S kg/ha	**0**	**150**	**250**	**S mean**
	0	3.95	4.08	4.17	4.07
Ariana	**50**	3.84	4.22	4.08	4.05
	100	3.96	3.87	3.81	3.8
	N mean	3.92	4.06	4.02	4.00
	0	4.02	4.44	4.63	4.36
Falcon	**50**	4.04	4.21	4.84	4.36
	100	3.99	4.54	4.67	4.40
	N mean	4.02	4.40	4.71	4.37
	0	3.64	3.79	3.94	3.79
Tapidor	**50**	3.82	3.67	3.75	3.75
	100	3.68	3.87	3.89	3.81
	N mean	3.71	3.78	3.86	3.78

SED (78 DF)	
Variety, N, S	0.058
Variety x N, Variety x S, N x S	0.100
Variety x N x S	0.174

Table 30. **Yield responses (t/ha) of winter oilseed rape to applied N and S at Rothamsted in 1991/1992.**

		kg N/ha			
	kg S/ha	**0**	**150**	**250**	**S mean**
	0	1.21	3.27	3.27	2.58
Ariana	**50**	1.41	3.06	3.38	2.62
	100	1.25	2.94	3.52	2.57
	N mean	1.29	3.09	3.39	2.59
	0	1.21	3.12	3.50	2.62
Falcon	**50**	1.37	3.15	3.62	2.71
	100	1.37	3.04	3.61	2.67
	N mean	1.33	3.10	3.57	2.67
	0	1.18	3.22	3.41	2.60
Tapidor	**50**	1.13	2.97	3.36	3.06
	100	1.41	2.86	3.62	2.95
	N mean	1.24	3.02	3.46	2.57
	0	1.21	3.20	3.39	2.60
All varieties	**50**	1.30	3.06	3.45	2.61
	100	1.34	2.95	3.58	2.62
	N mean	1.29	3.07	3.48	2.61

SED (78 DF)	
Variety,N,S	0.058
NxS	0.100
NxSxVariety	0.174

Table 31. Yield responses (t/ha) of winter oilseed rape (cv. Falcon) to applied N and S at Woburn in 1991/92.

	kg N/ha			
kg S/ha	**0**	**180**	**230**	**S mean**
0	0.56	0.89	1.03	0.83
10	0.77	1.29	1.04	1.15
20	0.52	1.52	1.45	1.17
40	0.55	1.55	1.70	1.27
N mean	0.60	1.31	1.40	

SED (22 DF)	
N	0.098
S	0.113
N x S	0.195

Table 32. Yield responses (t/ha) of winter oilseed rape (cv. Falcon) to applied N and S at ADAS Bridgets in 1991/92.

	kg N/ha		
kg S/ha	**0**	**250**	**S mean**
0	2.37	3.17	2.77
100	2.73	3.39	3.06
N mean	2.55	3.28	

SED (9 DF)	
N,S	0.210
NxS	0.297

Table 33. **The effects of applied N and S on leaf sulphur concentrations (mg/g) of winter oilseed rape at Cockle Park in 1991/92.**

	S kg/ha	N kg/ha 0	150	250	S mean
Ariana	0	8.20	8.65	7.58	8.14
	50	9.50	8.94	9.53	9.32
	100	9.51	9.70	9.86	9.69
	N mean	9.07	9.10	8.99	9.05
Falcon	0	8.17	7.49	8.07	7.91
	50	8.32	8.46	8.31	8.36
	100	8.71	8.42	9.10	8.74
	N mean	8.40	8.12	8.39	8.34
Tapidor	0	7.99	8.10	7.60	7.90
	50	9.93	9.34	9.27	9.51
	100	9.74	9.15	9.32	9.40
	N mean	9.22	8.86	8.73	8.94

SED (78 DF)	
Variety, N, S	0.201
Variety x N, Variety x S, N x S	0.348
Variety x N x S	0.603

Table 34. The effects of applied N and S on leaf S concentrations (mg/g) of winter oilseed rape (cv. Falcon) in the Scottish borders in 1991/92.

S kg/ha	N kg/ha 150	N kg/ha 250	S mean
0	3.08	3.23	3.15
50	8.17	7.59	7.88
100	9.81	8.61	9.21
N mean	7.02	6.48	6.75

SED (18 DF)	
N	0.240
S	0.294
N x S	0.415

Table 35. The effects of applied N and S on leaf sulphur concentrations (mg/g) of winter oilseed rape at Rothamsted in 1991/92.

	kg S/ha	kg N/ha 0	kg N/ha 150	kg N/ha 250	S mean
Ariana	0	8.65	7.94	6.92	7.83
	50	8.97	14.25	11.90	11.70
	100	8.93	15.59	13.82	12.78
	N mean	8.95	12.59	10.88	10.77
Falcon	0	7.06	6.26	4.68	6.00
	50	7.25	9.85	9.85	8.98
	100	7.25	12.48	9.64	9.79
	N mean	7.18	9.53	8.05	8.26
Tapidor	0				
	50		Not measured		
	100				

SED (53 DF)	
Variety	0.332
N, S	0.263
N x S	0.704

Table 36. **The effects of applied N and S on leaf sulphur concentrations (mg/g) of winter oilseed rape at Woburn in 1991/92.**

kg S/ha	N kg/ha 0	180	230	S mean
0	4.26	2.79	2.46	3.17
10	5.33	3.11	3.05	3.83
20	6.40	4.49	3.23	4.71
40	6.11	4.57	5.42	5.37
N mean	5.53	3.74	3.54	4.47

SED (14 DF)	
N	0.373
S	0.431
N x S	0.747

Table 37. **The effects of applied N and S on leaf sulphur concentrations (mg/g) of winter oilseed rape at ADAS Bridgets in 1991/92.**

kg S/ha	kg N/ha 0	250	S mean
0	4.93	4.03	4.48
100	8.86	9.06	8.96
N mean	6.90	6.54	6.72

SED (9 DF)	
N, S	0.421
S x N	0.596

Table 38. **Responses of seed glucosinolates (μmol/g) of winter oilseed rape to applied N and S at Cockle Park in 1991/92.**

	kg S/ha	kg N/ha 0	150	250	S mean
	0	26.7	27.2	31.1	28.3
Ariana	50	24.7	32.0	32.4	29.7
	100	28.6	30.6	31.2	30.1
	N mean	26.7	29.9	31.6	29.4
	0	12.5	14.6	14.8	13.9
Falcon	50	12.5	14.4	15.5	14.1
	100	12.5	14.1	15.0	13.8
	N mean	12.5	14.3	15.1	13.9
	0	13.4	14.2	15.7	14.4
Tapidor	50	12.8	14.9	13.4	13.7
	100	12.2	14.9	16.2	14.5
	N mean	12.8	14.7	15.1	14.2

SED (78 DF)	
Variety, N, S	0.494
NxVar; SxVar; NxS	0.856
Var x N x S	1.483

Table 39. Responses of seed glucosinolates (μmol/g) of winter oilseed rape to applied N and S at Rothamsted in 1991/92.

		kg N/ha			
	S kg/ha	0	150	250	S mean
Ariana	0	23.6	27.3	29.2	26.7
	50	21.1	23.6	27.4	24.0
	100	20.7	28.1	29.8	26.2
	N mean	21.8	26.3	28.8	25.6
Falcon	0	16.8	14.3	12.2	14.4
	50	13.8	13.1	13.9	13.6
	100	9.9	18.0	17.5	15.4
	N mean	13.5	15.4	14.5	14.5
Tapidor	0	10.0	8.9	5.7	8.2
	50	9.9	10.9	11.7	10.8
	100	8.0	10.3	8.6	9.0
	N mean	9.3	10.0	8.6	11.8

SED (78 DF)	
N, Variety	0.64
N x Variety	1.12
N x S x Variety	1.93

Table 40. Responses of seed glucosinolates (μmol/g) of winter oilseed rape (cv. Falcon) to applied N and S in the Scottish borders in 1991/92.

kg S/ha	kg N/ha 150	250	S mean
0	10.3	7.5	8.9
50	28.9	28.3	28.6
100	29.1	31.1	30.1
N mean	22.8	22.3	13.4

SED (18 DF)	
N	1.84
S	2.25
N x S	3.18

Table 41. Responses of seed glucosinolates (μmol/g) of winter oilseed rape (cv. Falcon) to applied N and S at Woburn in 1991/92.

kg S/ha	kg N/ha 0	180	230	S mean
0	17.4	17.7	13.4	16.2
10	22.0	14.3	10.2	15.5
20	18.6	17.6	15.9	17.4
40	16.6	21.8	21.1	19.9
N mean	18.7	17.9	15.2	17.2

SED (22 DF)	
N	1.10
S	1.28
N x S	2.22

Table 42. Responses of seed glucosinolates (μmol/g) of winter oilseed rape (cv. Falcon) to applied N and S at ADAS Bridgets in 1991/92.

	kg N/ha		
kg S/ha	0	250	S mean
0	19.2	10.3	14.7
100	21.0	28.3	24.5
N mean	20.1	19.3	

SED (9 DF)	
N,S	1.07
S x N	1.52

Table 43. Yield responses (t/ha) of winter oilseed rape (cv. Falcon) to applied N and S at Cockle Park in 1992/93.

	kg N/ha			
kg S/ha	0	150	250	S mean
0	2.76	4.79	4.79	4.11
50	3.19	4.74	4.70	4.21
100	3.14	4.71	5.01	4.28
N mean	3.03	4.75	4.83	4.20

SED (24 DF)	
N,S	0.173
N x S	0.300

Table 44. Yield responses (t/ha) of winter oilseed rape (cv. Envol to applied N and S in the Scottish Borders in 1992/93.

	kg N/ha			
kg S/ha	0	150	250	S mean
0	3.82	4.23	4.33	4.14
50	3.90	4.34	4.41	4.22
100	4.14	4.25	4.35	4.25
N mean	3.97	4.27	4.36	4.20

SEDs (24 DF)	
N,S	0.076
N x S	0.131

Table 45. Yield responses (t/ha) of winter oilseed rape (cv. Falcon) to applied N and S at ADAS Bridgets in 1992/93.

	kg N/ha		
kg S/ha	0	250	S mean
0	1.72	3.69	2.71
100	1.65	4.43	3.04
N mean	1.69	4.06	2.87

SED (9 DF)	
N,S	0.195
NxS	0.271

Table 46. Yield responses (t/ha) of winter oilseed rape to applied N and S at Rothamsted in 1992/1993.

	kg S/ha	kg N/ha 0	150	250	S mean
Ariana	0	3.19	3.17	3.02	3.13
	50	2.89	3.34	3.00	3.08
	100	3.23	3.19	3.24	3.22
	N mean	3.10	3.23	3.09	3.23
Falcon	0	3.34	3.52	3.69	3.52
	50	3.42	3.80	3.79	3.67
	100	3.52	3.67	3.85	3.68
	N mean	3.43	3.66	3.78	3.62
Tapidor	0	3.11	3.39	3.23	3.24
	50	3.37	3.43	3.48	3.43
	100	2.97	3.62	3.50	3.37
	N mean	3.15	3.48	3.40	3.42
All varieties	0	3.21	3.36	3.31	3.30
	50	3.23	3.52	3.43	3.39
	100	3.24	3.43	3.53	3.42
	N mean	3.23	3.46	3.42	3.37

SED (78 DF)	
Variety,N,S	0.065
NxS	0.113
NxSxVariety	0.196

Table 47. Responses of seed glucosinolates (μmol/g) of winter oilseed rape (cv. Envol) to applied N and S in the Scottish Borders in 1992/93.

	kg N/ha			
kg S/ha	0	150	250	S mean
0	10.7	9.1	5.3	8.4
50	11.9	16.3	18.3	15.5
100	15.6	16.2	17.5	16.4
N mean	12.7	13.8	13.7	13.4

SED (24 DF)	
N,S	0.91
N x S	1.58

Table 48. Responses of seed glucosinolates (μmol/g) of winter oilseed rape (cv. Falcon) to applied N and S at Rothamsted in 1992/93.

	kg N/ha			
kg S/ha	0	150	250	S mean
0	12.4	17.7	18.8	16.3
50	13.8	18.0	18.3	16.7
100	12.8	16.6	18.6	16.0
N mean	13.0	17.4	18.5	16.3

SED (24 DF)	
N,S	0.59
N x S	1.03

Table 49. **Responses of seed glucosinolates (μmol/g) of winter oilseed rape (cv. Falcon) to applied N and S at ADAS Bridgets in 1992/93.**

	kg N/ha		
kg S/ha	**0**	**250**	**S mean**
0	14.9	10.0	12.5
100	18.1	24.4	21.2
N mean	16.5	17.2	

SED (9 DF)	
N,S	1.60
S x N	2.26

Table 50. **Responses of leaf sulphur concentrations (mg/g) of winter oilseed rape (cv. Falcon) to applied N and S at Cockle Park in 1992/93.**

	kg N/ha			
kg S/ha	**0**	**150**	**250**	**S mean**
0	8.14	6.28	6.71	7.04
50	9.20	10.50	9.53	9.74
100	8.82	11.84	9.93	10.20
N mean	8.72	9.54	8.72	8.99

SED (24 DF)	
N,S	0.345
N x S	0.598

Table 51. **Responses of leaf sulphur concentrations (mg/g) of winter oilseed rape (cv. Envol) to applied N and S in the Scottish Borders in 1992/93.**

	kg N/ha			
kg S/ha	**0**	**150**	**250**	**S mean**
0	9.05	9.12	7.50	8.56
50	9.76	10.19	10.07	10.00
100	9.37	10.11	9.87	9.78
N mean	9.39	9.80	9.15	9.45

SED (24 DF)	
N,S	0.467
N x S	0.809

Table 52. **Changes in crop dry matter and N and S contents at Cockle Park in 1991.**

	Days from 1 December					
	5	91	117	130	223	244
	Dry matter (g/m^2)					
N_0S_0	81	84	174	172	1033	1079
N_0S_{100}	-	-	-	215	972	1060
$N_{250}S_0$	-	-	168	388	1829	1559
$N_{250}S_{100}$	-	-	-	423	1416	1699
	N uptake (kg/ha)					
N_0S_0						
N_0S_{100}				Not		
$N_{250}S_0$				measured		
$N_{250}S_{100}$						
	S uptake (kg/ha)					
N_0S_0	5.2	8.4	14.1	9.6	58.3	67.1
N_0S_{100}	-	-	-	11.8	58.4	67.7
$N_{250}S_0$	-	-	11.7	20.3	126.3	126.4
$N_{250}S_{100}$	-	-	-	23.4	82.3	132.7

Table 53. Changes in crop dry matter and N and S contents in the Scottish borders in 1991.

	Days from 1 December					
	5	91	117	130	223	244
	Dry matter (g/m^2)					
N_0S_0	21	22	34	105	343	440
N_0S_{100}	-	-	-	109	360	434
$N_{250}S_0$	-	-	-	207	790	1404
$N_{250}S_{100}$	-	-	-	292	868	1265
	N uptake (kg/ha)					
N_0S_0						
N_0S_{100}				Not		
$N_{250}S_0$				measured		
$N_{250}S_{100}$						
	S uptake (kg/ha)					
N_0S_0	1.4	1.9	2.1	5.8	17.8	20.5
N_0S_{100}	-	-	-	6.4	20.3	20.2
$N_{250}S_0$	-	-	2.0	10.4	47.6	88.2
$N_{250}S_{100}$	-	-	-	18.4	46.9	90.3

Table 54. **Changes in crop dry matter and N and S contents at Rothamsted in 1991.**

	Days from 1 December				
	17	87	154	220	244
			Dry matter (g/m^2)		
N_0S_0	127	120	490	795	630
N_0S_{100}	-	-	533	896	859
$N_{250}S_0$	-	-	1020	1977	1638
$N_{250}S_{100}$	-	132	964	1647	1482
			N uptake (kg/ha)		
N_0S_0	44.2	42.4	98.2	112.9	81.4
N_0S_{100}	-	-	106.9	117.7	108.0
$N_{250}S_0$	-	-	365.1	340.3	289.0
$N_{250}S_{100}$	-	56.6	345.8	289.0	224.6
			S uptake (kg/ha)		
N_0S_0	6.7	5.5	33.0	39.8	37.9
N_0S_{100}	-	-	37.2	45.8	47.3
$N_{250}S_0$	-	-	68.6	137.2	108.0
$N_{250}S_{100}$	-	7.2	82.5	103.6	79.2

Table 55. Changes in crop dry matter and N and S contents at Woburn in 1991.

	Days from 1 December			
	133	174	197	250
	Dry matter (g/m^2)			
N_0S_0	68	146	214	230
N_0S_{100}	49	83	282	216
$N_{250}S_0$	76	347	709	623
$N_{250}S_{100}$	106	557	885	955
	N uptake (kg/ha)			
N_0S_0	15.6	23.8	15.5	27.2
N_0S_{100}	7.6	12.8	29.3	25.0
$N_{250}S_0$	30.1	89.2	79.1	83.4
$N_{250}S_{100}$	45.1	143.0	92.9	115.7
	S uptake (kg/ha)			
N_0S_0	3.8	8.7	11.4	16.6
N_0S_{100}	4.5	8.8	37.4	24.0
$N_{250}S_0$	2.9	7.5	24.5	21.9
$N_{250}S_{100}$	9.0	26.2	40.8	51.2

Table 56. Changes in crop dry matter and N and S contents at ADAS Bridgets in 1991.

	Days from 1 December				
	20	90	167	223	242
			Dry matter (g/m^2)		
N_0S_0	80	53	389	290	364
N_0S_{100}	-	-	279	350	511
$N_{250}S_0$	-	-	559	857	743
$N_{250}S_{100}$	-	48	680	1012	959
			N uptake (kg/ha)		
N_0S_0	26.1	19.4	82.2	35.9	106.1
N_0S_{100}	-	-	66.8	46.2	139.4
$N_{250}S_0$	-	-	154.4	126.3	183.1
$N_{250}S_{100}$	-	14.8	159.4	137.4	258.0
			S uptake (kg/ha)		
N_0S_0	3.1	2.8	15.3	21.8	21.5
N_0S_{100}	-	-	23.8	21.2	27.5
$N_{250}S_0$	-	-	24.5	24.2	19.9
$N_{250}S_{100}$	-	2.7	51.6	62.3	47.3

Table 57. Changes in crop dry matter and N and S contents at Cockle Park in 1992.

	Days from 1 December				
	4	107	159	205	243
	Dry matter (g/m^2)				
N_0S_0	12	41	614	1215	1163
N_0S_{100}	-	-	691	1168	1374
$N_{250}S_0$	-	-	686	1126	1409
$N_{250}S_{100}$	-	-	821	1412	1340
	N uptake (kg/ha)				
N_0S_0	-	-	-	-	-
N_0S_{100}	-	-	-	-	-
$N_{250}S_0$	4.7	17.6	192.2	161.4	225.1
$N_{250}S_{100}$	-	-	227.6	206.5	222.6
	S uptake (kg/ha)				
N_0S_0	1.1	4.2	46.6	86.3	102.6
N_0S_{100}	-	-	52.4	88.4	128.6
$N_{250}S_0$	-	-	41.8	84.8	145.2
$N_{250}S_{100}$	-	-	67.9	106.0	129.2

Table 58. Changes in crop dry matter and N and S contents in the Scottish borders in 1992.

	Days from 1 December			
	4	164	204	222
	Dry matter (g/m^2)			
N_0S_0	48	567	956	1519
N_0S_{100}	-	586	1335	1466
$N_{250}S_0$	-	583	1034	1416
$N_{250}S_{100}$	-	614	1345	1551
	N uptake (kg/ha)			
N_0S_0	-	-	-	-
N_0S_{100}	-	-	-	-
$N_{250}S_0$	16.7	123.8	132.8	203.8
$N_{250}S_{100}$	-	146.2	221.6	229.6
	S uptake (kg/ha)			
N_0S_0	4.2	22.0	36.2	79.8
N_0S_{100}	-	52.5	96.8	117.8
$N_{250}S_0$	-	22.7	39.3	63.2
$N_{250}S_{100}$	-	56.9	99.2	124.1

Table 59. Changes in crop dry matter and N and S contents at Woburn in 1992.

	Days from 1 December					
	13	82	142	159	207	227
			Dry matter (g/m^2)			
N_0S_0	18	13	35	83	103	115
N_0S_{100}	-	-	23	86	194	171
$N_{250}S_0$	-	-	77	236	231	231
$N_{250}S_{100}$	-	-	108	283	581	611
			N uptake (kg/ha)			
N_0S_0	3.6	3.4	6.6	26.0	10.4	13.9
N_0S_{100}	-	-	4.8	26.1	23.6	22.9
$N_{250}S_0$	-	-	26.6	68.7	30.8	29.8
$N_{250}S_{100}$	-	-	41.5	76.8	79.3	90.7
			S uptake (kg/ha)			
N_0S_0	0.6	0.7	2.1	3.6	3.1	4.5
N_0S_{100}	-	-	1.6	5.0	8.0	8.1
$N_{250}S_0$	-	-	2.1	3.4	6.7	4.6
$N_{250}S_{100}$	-	-	6.8	13.1	17.2	28.3

Table 60. **Changes in seed dry matter and N, S and glucosinolate contents during seed development (DAF, days after flowering) at Cockle Park in 1991.**

DAF	33	45	55	66	77	87
			Dry matter per seed (mg)			
N_0S_0	1.10	1.93	2.99	3.98	4.26	4.34
N_0S_{100}	1.03	1.83	2.93	4.09	4.21	4.37
$N_{250}S_0$	1.10	1.69	2.49	3.57	4.32	4.18
$N_{250}S_{100}$	1.07	1.60	2.50	3.66	4.08	4.04
			Seed N concentration (mg/g)			
N_0S_0	26.6	25.3	27.5	25.3	24.4	28.0
N_0S_{100}	26.4	25.1	28.0	24.3	24.9	26.5
$N_{250}S_0$	29.1	29.1	33.0	33.8	33.9	35.7
$N_{250}S_{100}$	29.2	28.4	33.8	32.2	35.4	34.0
			Seed N content (μg per seed)			
N_0S_0	-	49	82	101	104	122
N_0S_{100}	-	46	82	99	105	122
$N_{250}S_0$	-	49	83	121	147	149
$N_{250}S_{100}$	-	45	85	118	145	137
			Seed S concentration (mg/g)			
N_0S_0	-	3.03	3.26	2.88	2.74	2.93
N_0S_{100}	-	2.97	3.38	2.84	2.61	2.70
$N_{250}S_0$	-	3.06	4.34	4.20	3.85	3.73
$N_{250}S_{100}$	-	3.46	4.44	4.14	3.93	3.80
			Seed S content (μg per seed)			
N_0S_0	-	5.9	9.8	11.5	11.7	12.7
N_0S_{100}	-	5.5	9.9	11.6	11.0	11.8
$N_{250}S_0$	-	5.2	10.9	15.0	16.7	15.6
$N_{250}S_{100}$	-	5.5	11.1	15.1	16.1	15.3
			Seed glucosinolate content (nmol per seed)			
N_0S_0	-	27.1	44.0	45.9	45.0	38.6
N_0S_{100}	-	24.5	46.0	50.1	33.5	32.0
$N_{250}S_0$	-	16.3	60.1	73.8	67.2	47.2
$N_{250}S_{100}$	-	26.5	61.6	79.8	60.4	58.6

Table 61. Changes in seed dry matter and N, S and glucosinolate contents during seed development at Rothamsted in 1991.

DAF	33	46	59	70	77	83
			Dry matter per seed (mg)			
N_0S_0	1.37	2.48	2.83	4.28	5.22	5.28
N_0S_{100}	1.62	2.66	2.27	4.70	5.41	5.01
$N_{250}S_0$	1.61	2.62	3.06	4.51	4.33	4.72
$N_{250}S_{100}$	1.52	2.30	3.11	4.57	4.27	4.54
			Seed N concentration (mg/g)			
N_0S_0	32.4	28.9	35.5	33.6	29.4	35.4
N_0S_{100}	29.1	28.4	34.1	28.0	27.4	31.2
$N_{250}S_0$	31.7	33.3	36.7	34.0	33.9	36.2
$N_{250}S_{100}$	31.9	34.8	37.1	36.6	36.2	35.7
			Seed N content (µg per seed)			
N_0S_0	45	72	101	141	153	182
N_0S_{100}	47	75	78	131	148	155
$N_{250}S_0$	51	88	112	153	147	163
$N_{250}S_{100}$	48	80	116	167	154	146
			Seed S concentration (mg/g)			
N_0S_0	3.89	4.02	3.58	3.92	3.32	3.39
N_0S_{100}	3.60	4.02	3.61	4.00	3.42	3.14
$N_{250}S_0$	3.96	4.56	3.88	4.06	4.02	3.76
$N_{250}S_{100}$	4.10	4.83	4.22	4.33	4.32	3.32
			Seed S content (µg per seed)			
N_0S_0	5.4	10.0	10.1	16.2	17.4	17.9
N_0S_{100}	5.9	10.7	8.2	18.5	18.6	15.7
$N_{250}S_0$	6.4	12.0	11.9	18.3	17.4	17.7
$N_{250}S_{100}$	6.2	11.1	13.1	19.8	18.5	15.1
			Seed glucosinolate content (nmol per seed)			
N_0S_0	2.3	3.7	21.2	40.6	58.8	51.8
N_0S_{100}	2.9	12.5	45.5	54.5	69.7	57.5
$N_{250}S_0$	2.9	12.5	45.5	54.5	58.4	76.8
$N_{250}S_{100}$	6.1	9.6	40.2	55.7	44.9	61.8

Table 62. **Changes in seed dry matter and N, S and glucosinolate contents during seed development in the Scottish borders in 1991.**

DAF	36	48	58	65	75
		Dry matter per seed (mg)			
N_0S_0	1.79	3.01	4.08	4.58	4.70
N_0S_{100}	1.75	3.22	4.13	4.70	4.69
$N_{250}S_0$	1.67	3.08	3.87	4.58	4.82
$N_{250}S_{100}$	1.66	3.06	4.04	4.30	4.83
		Seed N concentration (mg/g)			
N_0S_0	23.3	21.6	20.9	23.4	24.6
N_0S_{100}	25.3	23.3	22.3	22.7	22.9
$N_{250}S_0$	28.9	30.8	30.6	32.5	31.2
$N_{250}S_{100}$	27.5	29.5	30.6	30.2	28.2
		Seed N content (μg per seed)			
N_0S_0	42	65	85	107	116
N_0S_{100}	44	74	95	107	107
$N_{250}S_0$	48	95	118	149	151
$N_{250}S_{100}$	46	90	124	130	137
		Seed S concentration (mg/g)			
N_0S_0	2.58	2.72	2.62	2.55	2.76
N_0S_{100}	2.65	3.09	2.72	2.53	2.69
$N_{250}S_0$	2.97	3.91	3.77	3.80	3.36
$N_{250}S_{100}$	2.90	3.93	3.87	3.49	3.26
		Seed S content (μg per seed)			
N_0S_0	4.6	8.2	10.7	11.7	13.0
N_0S_{100}	4.6	9.9	11.6	11.9	12.7
$N_{250}S_0$	5.0	12.0	14.6	17.4	16.2
$N_{250}S_{100}$	4.8	12.0	15.7	15.0	15.8
		Seed glucosinolate content (nmol per seed)			
N_0S_0	17.1	41.3	53.8	41.5	51.0
N_0S_{100}	14.2	56.0	55.1	45.4	55.6
$N_{250}S_0$	14.2	61.8	71.2	75.0	54.9
$N_{250}S_{100}$	14.8	67.5	80.1	62.6	65.8

Table 63. **Changes in seed dry matter and N, S and glucosinolate contents during seed development at Bridgets in 1991.**

DAF	34	47	56	67	75	82
			Dry matter per seed (mg)			
N_0S_0	1.47	2.45	3.31	4.53	4.29	4.92
N_0S_{100}	1.17	2.62	3.26	4.31	4.38	4.83
$N_{250}S_0$	1.71	2.94	3.38	4.20	4.60	4.23
$N_{250}S_{100}$	1.82	2.71	4.05	4.17	4.41	4.05
			Seed N concentration (mg/g)			
N_0S_0	25.7	27.2	30.9	28.2	-	30.3
N_0S_{100}	24.5	28.3	28.8	28.5	-	30.1
$N_{250}S_0$	28.5	29.1	29.6	28.8	-	28.3
$N_{250}S_{100}$	25.5	28.4	28.1	28.4	-	22.9
			Seed N content (μg per seed)			
N_0S_0	38	67	102	128	-	149
N_0S_{100}	29	85	100	121	-	146
$N_{250}S_0$	49	85	100	121	-	119
$N_{250}S_{100}$	46	77	114	117	-	123
			Seed S concentration (mg/g)			
N_0S_0	3.38	4.22	3.48	2.96	-	3.81
N_0S_{100}	4.15	3.74	3.22	3.31	3.67	3.50
$N_{250}S_0$	3.17	3.00	2.76	2.80	2.97	2.88
$N_{250}S_{100}$	3.64	3.64	3.18	3.76	3.63	3.71
			Seed S content (μg per seed)			
N_0S_0	5.0	10.6	11.5	13.4	-	18.7
N_0S_{100}	4.8	9.9	10.5	14.2	16.1	16.9
$N_{250}S_0$	5.4	8.8	9.3	11.7	13.7	12.2
$N_{250}S_{100}$	6.6	9.9	12.9	15.6	16.0	15.0
			Seed glucosinolate content (nmol per seed)			
N_0S_0	4.0	43.4	58.6	106.8	-	62.6
N_0S_{100}	4.7	21.2	41.4	70.3	57.9	103.8
$N_{250}S_0$	3.1	7.9	21.9	24.4	38.2	33.6
$N_{250}S_{100}$	3.8	11.1	27.1	39.2	78.4	82.4

Table 64. **Changes in seed dry matter and N, S and glucosinolate contents during seed development at Woburn in 1991.**

DAF	54	76	82
	Dry matter per seed (mg)		
N_0S_0	2.92	4.98	4.93
N_0S_{100}	3.63	4.76	4.84
$N_{250}S_0$	3.14	4.76	4.71
$N_{250}S_{100}$	3.76	5.25	5.41
	Seed N concentration (mg/g)		
N_0S_0	34.6	37.5	35.8
N_0S_{100}	34.6	38.4	33.7
$N_{250}S_0$	33.1	41.0	35.9
$N_{250}S_{100}$	34.0	36.8	35.9
	Seed N content (μg per seed)		
N_0S_0	100	188	176
N_0S_{100}	127	182	163
$N_{250}S_0$	104	196	169
$N_{250}S_{100}$	128	193	194
	Seed S concentration (mg/g)		
N_0S_0	4.37	4.22	3.58
N_0S_{100}	4.32	4.51	3.61
$N_{250}S_0$	3.95	4.47	3.88
$N_{250}S_{100}$	3.92	4.35	4.22
	Seed S content (μg per seed)		
N_0S_0	12.7	21.2	17.6
N_0S_{100}	15.8	21.3	17.4
$N_{250}S_0$	12.4	21.3	18.3
$N_{250}S_{100}$	14.8	22.8	22.8
	Seed glucosinolate content (nmol per seed)		
N_0S_0	39.7	73.1	82.7
N_0S_{100}	56.7	72.8	80.2
$N_{250}S_0$	11.9	35.2	67.9
$N_{250}S_{100}$	47.0	106.8	94.0