J Sci Food Agric 1995, **67**, 309–315

The Relation Between Yield and Protein in Cereal Grain

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(Received 28 April 1994; revised version received 8 August 1994; accepted 21 September 1994)

Abstract: An analysis of published data on genetic relations between dry grain yields (y, t ha^{-1}) and protein content [p, protein as a fraction (g g^{-1}) of dry grain] of cereals is presented. In all, 106 usable regressions of y on p across geneotypes were assembled. The long-recognised negative relation between yield and protein concentration was fully substantiated. There is a strong positive relation between grain yield and protein yield. The linear regression coefficient of yield on protein concentration is related to yield, with slope about -15. This relation holds approximately over all cereals. The data can be used to estimate a characteristic parameter described by $C = dy/d(yp) = \sim 15$–25 at the mean of each experiment. The relationship is surprisingly consistent but no simple physiological interpretation is available. In discussion, the high C, the impact of strong negative regressions of y on p for breeding strategies, the fact that protein yield increases with gross grain yield but at falling p and certain socio-economic consequences are emphasized. An acute need for orderly reporting of experimental data is also emphasised; the existing literature is chaotic as to units, moisture contents and conversion factors.

Key words: cereals, grain yield, protein content.

INTRODUCTION

In the late 1960s, there was a considerable stir of interest in the 'protein gap' as a potentially important feature of the ever-worsening shortage of food in the poorer countries of the Third World. The food shortage is still there but the 'protein gap' is hardly heard of nowadays. The concern was connected with the oft-recorded fact (evident since the time of Grant and McCalla, 1938, onwards) that there was a pronounced negative regression of yield on protein concentration in cereal grain. Thus the rising yields characteristic of some cereals (for example, the wheats and rices affected by 'green revolution' technology) were accompanied by falling protein concentrations, though not by declining protein yields. The concern declined in the later 1970s with the downward revision by nutritionists of estimates of human needs for dietary protein (Payne 1978). But the strong negative regressions of yields on protein concentrations remained unexplained, indeed unexplored in quantitative terms. Qualitative accounts tended to centre upon the idea that protein imposed a biological 'cost', but a few authors regarded the regressions as artifacts. At all events, the regressions remained uninterpreted. In this paper the available information is summarised and several orderly relationships identified but theoretical interpretation still eludes us.

MATERIALS AND METHODS

Sources of data

This study is concerned purely with the grass cereals, namely wheats (*Triticum*), barley (*Hordeum*), sorghum (*Sorghum*), oats (*Avena*), rice (*Oryza*) and maize (*Zea*). The data are nearly all from the published literature but a few experiments kindly communicated directly by colleagues are included. A wide range of agricultural research journals, going back to the 1930s was searched. Relatively few experiments were found to be usable and some had to be rejected wherein good data had clearly been available but had not been published in interpretable form. Well-estimated regressions of yield on protein content with $R^2 > 0{\cdot}250$ were used. Examples of lower values of R^2 were few and were usually interpretable either as inaccurate experiments or as trials of

J Sci Food Agric 0022–5142/95/$09.00

TABLE 1
Yields and protein contents of cereals (means, SD given in parentheses)[a]

Crop	*N*	*y*	*p*	*a*	*b*	*C*
Wheat (1)	61 (60)	2·14	0·154	6·84	−31·2	19·2
		(1·07)	(0·029)	(3·48)	(17·5)	(25·0)
Wheat (2)	13	5·35	0·123	13·95	−70·7	27·9
		(1·11)	(0·020)	(3·66)	(22·4)	(11·7)
Wheat, all	74 (73)	2·70	0·149	8·09	−38·1	20·7
		(16·63)	(0·031)	(4·42)	(23·7)	(23·4)
Barley (1)	12	2·05	0·141	6·76	−32·9	15·5
		(1·09	(0·026)	(3·90)	(17·7)	(8·2)
Barley (2)	6	4·71	0·124	11·88	−61·6	103·7
		(0·94)	(0·022)	(4·37)	(37·3)	(129·2)
Barley, all	18	2·93	0·136	8·47	−42·5	44·9
		(1·64)	(0·026)	(4·65)	(28·4)	(82·4)
Sorghum	7 (5)	6·05	0·102	14·19	−84·1	44·8
		(1·30)	(0·015)	(4·42)	(41·4)	(31·9)
Oats	2	3·39	0·164	10·95	−46·5	11·5
Rice	3	4·10	0·093	11·53	−76·1	23·3
Maize	2	6·58	0·095	23·75	−181·1	17·0
Others	14 (12)	5·33	0·109	14·57	−90·0	29·3
		(1·57)	(0·026)	(5·24)	−(47·7)	(24·0)
All	106 (103)	3·09	0·141	9·01	45·8	26·0
		(1·83)	(0·032)	(5·03)	(33·8)	(40·8)

[a] Symbols: *N*, numbers of experiments (in parentheses, numbers for which *C* available); *y*, mean grain yields, dm, t ha^{-1}; *p*, protein contents (g g^{-1}) of grain; *a*, intercepts of regressions of *y* on *p*; *b*, functional regression coefficients (see text) of *y* on *p*; parameter *C* estimated as $b/(a - 2y)$ (see text below). The grouping of wheat and barley data in two categories (1) and (2) relates to data from North America and elsewhere, other than Europe (1) and Europe (2).

materials with genetic ranges too narrow to reveal differences. Many data sets had to be converted from local or arbitrary units to standard metric units and zero moisture contents. Inevitably, some guesswork had to be employed and one can only hope that errors introduced were not too serious. Thus, as nearly as possible, yields are given as grain dry matter in tonnes per hectare (t ha^{-1}), and protein as a fraction of dry grain (g g^{-1}).

In all, 106 usable experiments were assembled from six different cereal species, nearly all grown in North America or Europe, with a few from India and Australia. The experiments were not perfectly independent because some authors presented several similar trials and the data as a whole are heavily weighted towards wheat and barley in Canada around the 1940s, in consequence of the overwhelming contributions of Grant and McCalla (1949) and Neatby and McCalla (1938).

Statistical methods

Statistical calculations were done by use of GENSTAT and MINITAB packages. Ordinary, least-squares, regressions assume that the *x* variate is free of error. That assumption could not be made here and its use would have biassed estimates of *b*. Since regressions were required in 'functional' form, the relation suggested by Ricker (1973), namely $b/|r|$ was used. This ratio of the regression coefficient to the sign-free correlation coefficient, is equivalent to adopting the ratio of the two relevant standard deviations as a measure of slope. Better estimates could have been obtained if errors were fully specified but they were not and Ricker's ratio is the best that can be done with imperfect data. If *r* approaches ± 1, the correction is, of course, small.

RESULTS

Empirical

In all, 106 experiments were used and results are summarised in Table 1. A list of sources follows. It will be

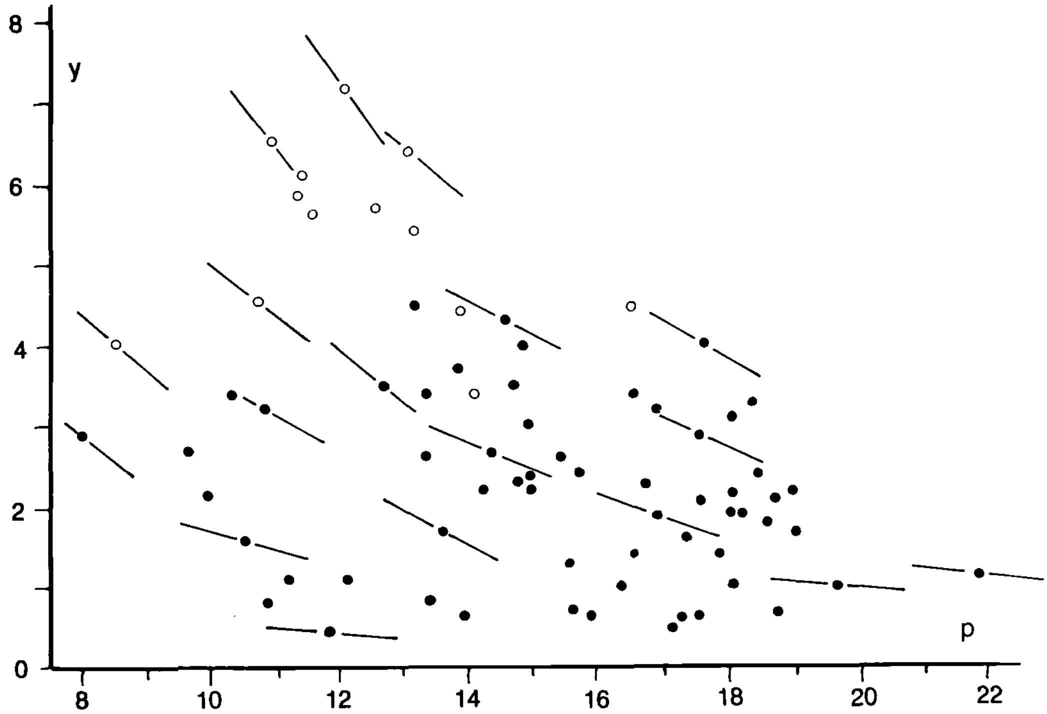

Fig 1. Scatter diagram of yield (y, t ha^{-1}) on protein percent (p) for wheats in ●, North America; and ○, Europe. A sample of linear regressions of y on p within experiments is also plotted.

noted that the wheat and barley data are, for clarity, separated into two groups—(1) and (2); a distinction that is preserved in Figs 1 and 3.

- *Wheat* (*1*): North America, unless otherwise stated: Baker *et al* (1968); Bhatia (1975) (India); Corpuz *et al* (1983); Grant and McCalla (1949); Loffler *et al* (1985); McNeal *et al* (1968, 1972); McNeal and Davies (1954); Nass *et al* (1976); Neatby and McCalla (1938); Noaman *et al* (1990); Noaman and Taylor (1990); Pepe and Heiner (1975a, b); Singhal and Jain (1981) (India); Terman *et al* (1969); Upadhyay *et al* (1984); Waldron (1993); Woodruff (1972) (Australia).
- *Wheat* (*2*): Europe: Austin *et al* (1980); Berg (1941); Dubois and Fossati (1981); Kingston (1981); Lupton (1987); Mann (1987); Paccaud *et al* (1985); Pushman and Bingham (1976).
- *Barley* (*1*): North America: Grant and McCalla (1949); Neatby and McCalla (1938).
- *Barley* (*2*): Europe: Doll *et al* (1974); Kirby (1968); Oram and Doll (1981); Scottish Plant Breeding Station (pers comm); Stolen (1979); Weltzien and Fischbeck (1990).
- *Oats*, North America: Frey (1977).
- *Rice*, Philippine Islands: Beachell *et al* (1972); International Rice Research Institute (pers comm).
- *Sorghum*, North America: Finkner *et al* (1981); Miller *et al* (1964); Ross *et al* (1985); Worker and Ruckmann (1968).
- *Maize*, North America: Duvick (pers comm).

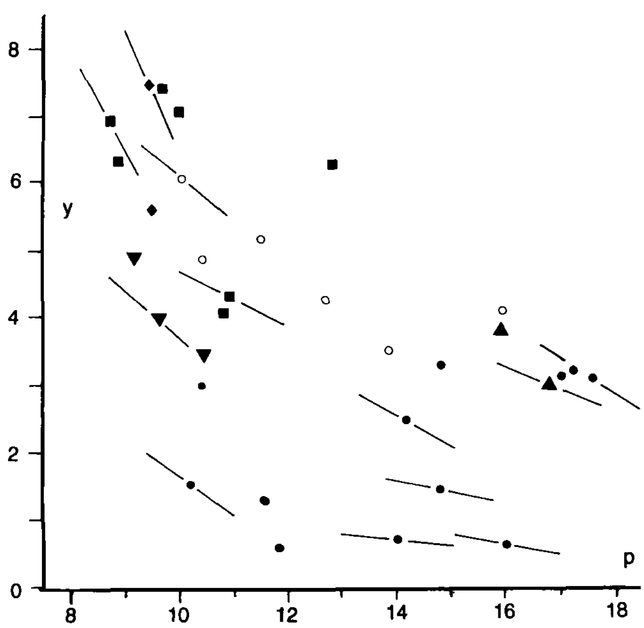

Fig 2. Scatter diagram of yield (y, t ha^{-1}) on protein percent (p) for cereals other than wheats. A sample of linear regressions of y and p within experiments is also plotted. ●, barley in North America; ○, barley in Europe; ■, sorghum; ▲, oats; ▼, rice; ◆, maize.

Relations betwen y and p *within* experiments were good with an average r of $-0{\cdot}705 \pm 0{\cdot}012$. The scatter diagrams in Figs 1 and 2 show that there was no evident environmental relation between mean y and mean p across experiments and the loose scatters closely resemble those of Benzian and Lane referred to later.

Attempts to fit declining curves through the whole 'cloud' of points were fruitless, as would be expected from inspection. Like all other authors, I therefore interpret the regressions within experiments as being essentially genetic, though there must have been some environmental 'noise'.

However, the sample regressions within experiments plotted as short lines in Figs 1 and 2 suggest that yields and slopes between experiments were closely related over varied environments, as indeed becomes plain in Figs 3 and 4. Regressions of b on y over experiments gave the following estimates (means and standard errors of means): wheat, $-14{\cdot}9 \pm 0{\cdot}62$; barley, $-15{\cdot}4 \pm 1{\cdot}45$; other cereals, $-16{\cdot}7 \pm 1{\cdot}70$; all data collectively, $-15{\cdot}2 \pm 0{\cdot}55$. All regressions were highly significant ($t \geqslant 10$) and passed very near the origins so the above slopes are constrained through (0, 0). There is no sign of inhomogeneity, so a general relation $b = -15{\cdot}2y$ may reasonably be adopted.

For a small minority of experiments, data were completely enough reported that regressions of (yp) (ie protein yield, t ha^{-1}) on y were calculable. Such regressions are statistically unsatisfactory because both sides contain y. However, it is reasonable to observe that all were positive and apparently linear in the observed ranges.

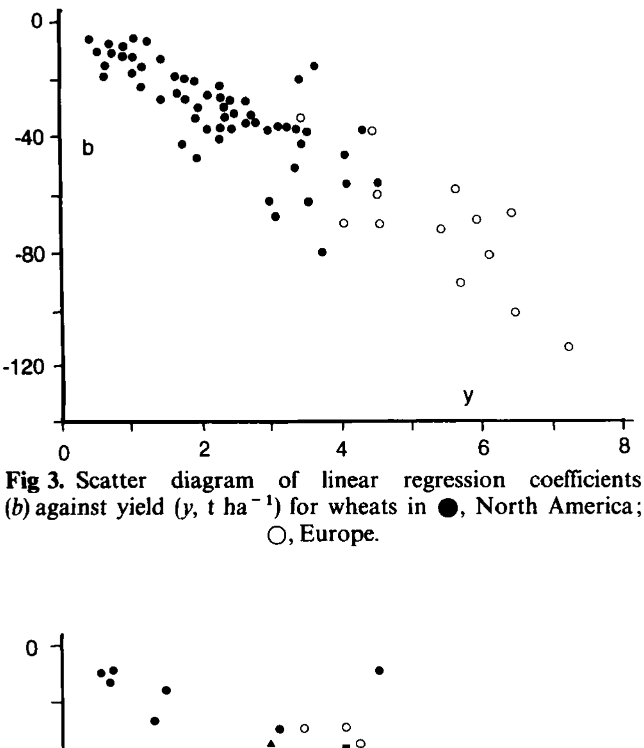

Fig 3. Scatter diagram of linear regression coefficients (b) against yield (y, t ha^{-1}) for wheats in ●, North America; ○, Europe.

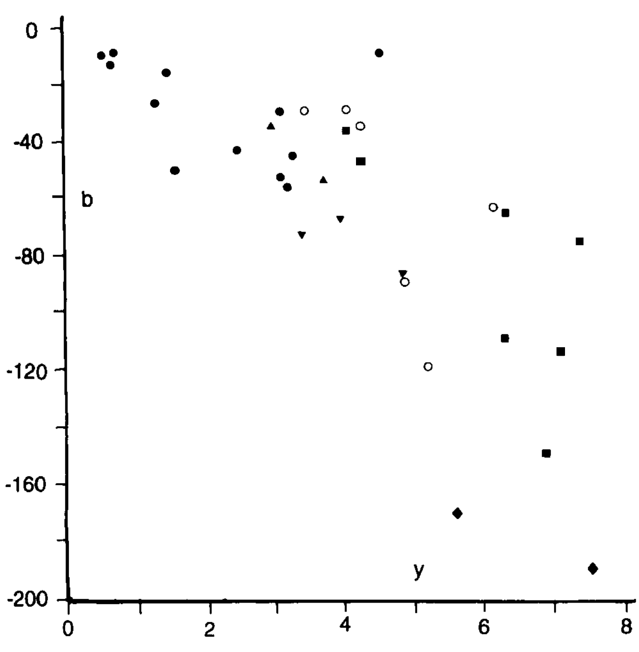

Fig 4. Scatter diagram of linear regression coefficients (b) against yield (y, t ha^{-1}) for cereals other than wheats. Symbols as in Fig 3.

Relationships

The regressions being in 'functional' form, a quantity, C, relating change of grain yield to change of protein yield can be derived thus:

$$y = a - bp \quad (1)$$

$$y^2 = ay - b(yp) \quad (2)$$

$$(yp) = (ay - y^2)/b \quad (3)$$

$$\mathrm{d}y/\mathrm{d}(yp) = b/(a - 2y) = C \quad (4)$$

C is an increment of grain yield per unit increment of protein yield. Mean C at the mean y of each experiment are given in the last column of Table 1. Three negative C (out of 106) in which $2y > a$ were interpreted as 'indefinite' and neglected. Mean C (with standard errors and the related medians given in parentheses) were as follows: wheats 20·7 (2·74, median 13), barleys 44·9 (19·40, median 15), others 29·3 (6·94, median 25), all cereals 26·0 (4·02, median 15). The C tended to skewness, as suggested by differences between means and medians. A substantial and fairly constant quantity of size about 15–25 g g^{-1} is inferred. Thus, a small increment of protein yield is accompanied by and apparently necessitates a very much larger increment of grain yield.

DISCUSSION

There are six topics to be explored. First, the rather large body of material reviewed shows that there is a strong negative relation between y and p viewed across genotypes (Table 1) but (see Figs 1 and 2) no clear environmental relationship across means. This accords well within the results of Benzian and Lane (1979, 1981, 1982) who found very similar scatters and highly erratic regressions of nitrogen concentration on yield across environments. Their scatter diagrams, in fact, closely resembled Figs 1 and 2 herein. On the one occasion they plotted genotypic relationships (Benzian and Lane 1979, Fig 8), they found the expected negative slope of y on p.

I therefore take a negative genetic relation to be the general rule, as virtually all other authors have done. In a review of the matter, Frey (1973) acknowledged the generality of the relation but thought that it reflected some artefact of inadequate soil nitrogen supply. But the examples above contain many cases of very high yields at high inputs and, in general, the higher the yields, the steeper the (negative) regressions (Figs 1 and 2). The relation simply cannot be interpreted as an artefact of nitrogen fertilising accidents.

Secondly, the theoretical biological cost of protein to the plant was calculated by Penning de Vries *et al* (1974) and Penning de Vries (1975) as about 2·5, that is about 2·5 units of carbohydrate would be needed to synthesise one unit of protein. These authors ackowledged that there were considerable uncertainties in the calculation and some other writers even thought that the cost might be zero (eg Miflin 1980). But a cost of about 2·5 was accepted by many writers in the late 1970s and the subject seems to have been ignored since then. The more prominent supporters of the idea of a modest cost included Sinclair and de Wit (1975), Bhatia and Rabson (1976) and Rabson *et al* (1978). All thought that there would be some sacrifice of yield if protein content were to be increased but there was no empirical investigation of the matter. I have been unable to derive any plausible estimate of 'cost' from the experiments reviewed here.

Thirdly, the parameter C is simply an empirical–statistical quantity which yet lacks physiological interpretation. It is evidently not a simple 'cost' of protein of the kind referred to in the preceding paragraph but it gives quantitative substance to the notion that a unit gain in protein yield necessitates a far greater gain in gross grain yield. Nor is the negative slope (b) of y on p a 'cost'. Any substantial 'breaking' of the negative correlation would entail the appearance of points to the north-east of the y–p regressions but of this there is no sign. Some authors have presented examples that seem to offer exceptions to this rule (eg Johnson *et al* 1968, 1969, 1978; Rhodes and Jenkins 1978) but there seem to be no convincing examples still extant. So far, therefore, there does seem to be a price to pay for protein though we do not know how much it is. Fortunately, the matter nowadays seems less important than it did in the 1960s. Meanwhile, any plausible physiological interpretation of the above empirical results, especially if related to biological 'costs', would be valuable. It is noteworthy that pot-trials of small-grain cereals (Spoor and Simmonds 1993) generate negative regression of y on p with C estimated as 8, 10, 11, 14, 25 (mean 13·6) in five experiments in very fair agreement with the $C \approx 15$–25 reported above.

Fourthly, breeding objectives in respect of protein vary with the crop. The breeder of malting barley is free to press yield to the limit, secure in the knowledge that low protein concentration is desired by the maltster. Some wheat breeders may be equally philosophical but the one aiming at bread quality must simply, on present information, accept a yield penalty for the sake of high protein (eg Lupton 1987). Breeders interested in breeding animal feed-grains might prefer grain at high protein concentration but it will usually be more sensible to maximise yields and adjust the protein by other means (eg supplementation). Thus, a proposal to breed high protein barley for feeding monogastic animals was shown to be economically unrealistic by Simmonds (1989); the yield penalty that would have been incurred by meeting the protein concentration requirement would have cost (in money) far more than the protein gained.

The above results bring out a point that is widely but not universally known; that maximal protein yield (yp) is generally, perhaps always, achieved at maximal y and least p. Certainly, to pick high p is very likely to decrease yields by correlated response. On these views, cereals are to be regarded agriculturally as well-packaged and readily stored sources of carbohydrate. Nutritonally, the protein is usually not very well balanced but is excellently complemented by that of legume seeds. Thus, as a matter of plant breeding policy in Third World countries, the sensible strategy would seem to be to seek maximal yields of cereal grain and supplement diets by legumes or other appropriate sources such as spinach or other vegetable proteins. These points were well made by Carpenter (1970), by Payne (1978) and by other authors in Norton (1978). As was remarked at the outset, the 'protein gap' mythology has been abandoned and unreasonable demands need no longer be placed upon the plant breeder. If high protein concentrations are really required, the breeder must simply accept the need for compromises which will be determined by economic factors.

Fifthly, I have not systematically searched the literature for examples of yield–protein relations among the legumes. One's impression is that negative relations again dominate but that, perhaps, regressions are less steep and correlations lower than among the cereals. Further study would be worthwhile but there seem to be very few good experiments published. Sinclair and de Wit (1975) remarked that legume seed yields were generally less than cereal yields and were inclined to attribute the difference to the bioenergetic costs of protein and lipids.

Sixthly and finally, there is a matter of standardisation of data and reporting. There was much difficulty in interpreting non-metric units, uncertain (often unstated) dry-matter conventions, doubtful nitrogen–

protein conversion rates and uncertainties as to whether results referred to husked or unhusked grain. There must have been some mistakes, contributing (I hope not greatly) to statistical noise. Journals and publishers would do us all a great service by insisting upon rigorously orderly reporting of cereal yield data in metric units on a dry matter basis and unambiguously stated nitrogen–protein conversion ratios. Above all, there is a great need for many more really good and well-reported experiments in which yield–protein relations may be critically explored at the level of physiological theory.

ACKNOWLEDGEMENTS

Warm thanks are due to Dr M F Franklin and Mr E A Hunter of the Scottish Agricultural Statistics Service (SASS) for statistical guidance.

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