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The influence of foliar diseases, and their control by fungicides, on the protein concentration in wheat grain: a review

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SUMMARY

Experiments investigating effects of foliar disease control on wheat grain protein concentration (GPC) are reviewed. Fungicidal control of rusts (*Puccinia* spp.) and powdery mildew (*Erysiphe graminis*) increased or had no significant effect on GPC in almost all cases, whilst control of the *Septoria* spp. often resulted in reduced GPC, but with exceptions. Reasons for these differences are discussed with reference to host pathogen interactions. Irrespective of infection strategy (biotrophic or necrotrophic), controlling severe infection increased nitrogen yield and the proportion of above-ground crop nitrogen that was partitioned to the grain. Similar effects are recorded for above-ground biomass and dry matter harvest index. The relationships between fungicide effects on green flag leaf area duration (GFLAD) and GPC were examined and shown to be unaffected by mode of action of the fungicide. Interactions between fungicide use and cultivar, nitrogen and growing season are related to the amount and type of pathogen present, and environment. An economic analysis demonstrated that fungicide effects on GPC should not affect the choice of fungicide or application programme, but that applications of foliar urea at the start of grain filling can deliver a cost-effective method of eliminating GPC reductions that may occasionally result from fungicide use.

INTRODUCTION

Doughs prepared from wheat (*T. aestivum*) flour have unique rheological properties which have contributed to the importance of the crop in world agriculture, human nutrition and commerce (Faridi & Faubion 1995). The behaviour of doughs is strongly linked to the type and amount of protein present in the flour, and hence the concentration of protein in the wheat grain at harvest (Gooding & Davies 1997). Grain protein concentration (GPC), usually expressed crudely as a multiple (often 5·7) of nitrogen concentration is, therefore, listed in grain specifications (Table 1) for numerous types of wheat-based products including bread, noodles, pasta, steamed breads, flat breads, biscuits and cakes (Blackman & Payne 1987; Lin *et al.* 1990; Morris & Rose 1996; Gooding & Davies 1997). Low GPC levels are desired in wheat for alcohol production (Taylor *et al.* 1993). Measurement of GPC is also important for grading wheat from major exporting countries such as Canada, USA, Australia and also from the EU. In areas where production has increased rapidly, but population levels have remained static such as in western Europe, farmers are increasingly pressured to find outlets for their wheat and meet ever more stringent quality requirements for a range of markets (Askew 2001; Jellis 2001). The UK wheat market, in common with many others, provides price premiums for wheat particularly suited for bread production. Premiums averaging 16% (S.D. = 9·7) over prices given for wheat destined for livestock feed were available to UK farmers between 1986 and 2001 for wheat meeting threshold values for a number of quality criteria, including GPC. It is important, therefore, that farmers and their advisors are aware of how agronomic inputs and their management influence quality.

Fungicides are important inputs to temperate cereal production, particularly to winter wheat. Europe is the primary market accounting for over 60% of worldwide fungicide sales for temperate cereals (Hewitt 1998). Germany, France and the UK are the most important countries because use is often justified economically by a combination of high potential yields and high infection pressures; both deriving

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Table 1. *Grain protein concentrations (% at 86% DM) for a series of end uses and national standards*

Product	Blackman & Payne (1987)	UK Home Grown Cereals Authority	Canadian Grain Commission (typical, Depauw & Hunt 2001)*	Australian wheat grades (O'Brien *et al.* 2001)*	Japan (Morris & Rose 1996)
Crusty bread, wholemeals	14%	–	CWRS 14·5%	Prime Hard > 13%	Strong 11·7–12·7%
General-purpose bread/Pan bread	13%	> 12%	CWES 13% CWRW 12%	Hard > 11·5%	Semi-strong 11·2–12·2%
Chorleywood Process bread	11·5–12·5%	> 10%			
UK Intervention		11·5% (*deductions if lower*)			
Puff/flaky pastry	12–13%	–			
Crackers (fermented)	10·3–11·3%	–	CWSWS < 11%		
Household (inc. self-raising)	10–11%	–		Premium White > 10%	9·5–10·5%
Short pastry	9–11·5%	–	CWSWS < 11%	Soft < 9·5%	
Cake	8–10%	–		Soft < 9·5%	6·5–8·0%
Wafers/ice cream cones	up to 10·5%	–		Soft < 9·5%	
Biscuits	8–10·5%	10%		Soft < 9·5%	7·8–8·5%
Chapatis	10–11%	–		ASW > 9%	
Japanese noodles	8–10%			Noodle 9–11·5%	8·5–9·5%
Chinese noodles		–		Noodle 9–11·5%	10·5–11·5%
Pasta (durum wheat)	13–14%	–		ADR1 > 13%	

* CWRS, Canadian Western Red Spring; CWES, Canadian Western Extra Strong; CWSWS, Canadian Western Soft White Spring; CWRW, Canadian Western Red Winter; ASW, Australian Standard White; ADR1, Australian Durum No. 1.

from temperate conditions with adequate moisture, large applications of nitrogenous fertilizers and rotations dominated by cereals (Christen 2001). In north-west Europe the foliar diseases that most commonly justify fungicide use are *Septoria tritici* Rob. in Desm. (perfect stage *Mycosphaerella graminicola*) and *Septoria nodorum* Berk. (perfect stage *Phaeosphaeria* (syn. *Leptosphaera*) *nodorum*) (Royle *et al.* 1995), powdery mildew (*Erysiphe graminis* DC f. sp. *tritici* E. Marchel) (Engels 1995) and rusts (*Puccinia* spp.) (Orson 1995). Wheat in North America also suffers from these pathogens, but production is often limited more by water shortage than by disease, and common fungicide use is mostly localized to Washington, Oregon, Idaho and N. Carolina. Nonetheless, North America still accounts for 22% of fungicide sales for use on temperate cereals (Hewitt 1998).

From the earliest days of fungicide use on wheat there has been an interest in the effects of disease control on grain quality (Broadfoot 1931; Caldwell *et al.* 1934). One of the most commonly reported benefits is that controlling foliar diseases helps maintain grain filling and thereby reduces the occurrence and severity of grain shrivelling. Shrivelled grains are undesirable because they are associated with low flour extraction rates in milling and low energy contents for livestock feed (Gooding & Davies 1997; Rose *et al.* 2001). Poorly filled grains also contribute to low grain specific (test, hectolitre or bushel) weights (Dimmock & Gooding 2002), probably the most widely used assessment of grain quality (Clark 1993). In the maritime and temperate conditions of the UK, and in other areas with climates conducive to long potential grain filling periods, fungicides applied at and shortly after flag leaf emergence have the greatest effect on yield, mean grain weight and specific weight (Cook & King 1984; Cook & Thomas 1990), commensurate with their effects on delaying senescence (Bryson *et al.* 1995; Gooding *et al.* 2000; Dimmock & Gooding 2002). Despite these positive influences on quality there are concerns that substantial yield gains may compromise GPCs, with the suggestion that protein levels might be diluted by additional carbohydrate production. Increasing yields through genetic means, for example, is often associated with reductions in protein concentrations (Simmonds 1995; Feil 1997; Smith & Gooding 1999). Concerns are heightened by the recent introduction and widespread use of new fungicide chemistries such as strobilurins which offer unprecedented levels of disease control, delays in senescence and yield responses (Bayles & Hilton 2000; Dimmock & Gooding 2002).

This paper reviews the reported effects of disease control on GPC. Interactions with pathogen, climate and agronomic factors are analysed to help identify how and when fungicides might affect protein concen-

trations. Effects of fungicides on the time to senescence are related to effects on GPCs. Finally, an analysis is performed to determine whether fungicide effects on GPCs should alter fungicide and nitrogen use on bread-making quality wheat.

THE EFFECTS OF FOLIAR FUNGICIDES AND DISEASES ON PROTEIN CONCENTRATION

Rusts (Puccinia *spp*.)

Tables 2 to 4 summarize reports of the effects of fungicides on the GPCs together with the predominant diseases controlled on wheat in N. America, Australia plus Africa, and Europe respectively. The earliest work, from the 1920s to 1940s, was principally concerned with the control of leaf or brown rust (*P. recondita* Rob. ex Desm. f. sp. *tritici*) and, less frequently, stem rust (*P. graminis* Pers. f. sp. *tritici* Eriks & Henn.), in North America and Australia with repeated applications of sulphur. Over all these studies, yields in the sulphur-treated plots averaged 2·7 t/ha compared with only 1·9 t/ha in the untreated controls. Despite the yield increases, applying sulphur in these systems almost invariably increased protein concentration at the same time, i.e. there was no

Table 2. *Reports of protein concentrations following control of wheat pathogens with either sulphur* (*S*) *or ergosterol biosynthesis inhibitor* (*E*) *fungicides in North America*

Year(s) of expt	Location	Disease(s) present	Effect of disease control on grain protein concentration	Fungicide group(s)	Reference
1927	Minnesota, USA	*P. graminis* and *P. recondita*	↓	S	Broadfoot (1931)
1931	Indiana, USA	*P. recondita*	↑	S	Caldwell *et al.* (1934)
1934, 35 and 37	Ontario, Canada	*P. graminis* and *P. recondita*	↑	S	Greaney *et al.* (1941)
1938	Manitoba, Canada	*P. recondita*	↑	S	Peturson & Newton (1939)
1940, 41 and 43	Manitoba, Canada	*P. recondita*	↑ and ↓	S	Peturson *et al.* (1945)
1944–46	Manitoba, Canada	*P. recondita*	↑ and =	S	Peturson *et al.* (1948)
1985	Kansas, USA	*S. tritici* and *P. recondita*	↑ and =	E	Morris *et al.* (1989)
1987–90	Kansas, USA	*P. recondita*	=	E	Kelley (1993)
1990–95	Kansas, USA	?	=	E	Kelley (2001)
1992–93	Kansas, USA	*P. recondita*	↑	E	Herrman *et al.* (1996)
1995	Kansas, USA	*S. tritici* and *P. recondita*	↑, = and ↓	E	Puppala *et al.* (1998)

↑, ↓, = , fungicide increased, decreased or had no effect on grain protein concentration, respectively.

Table 3. *Reports of protein concentrations following control of wheat pathogens with either sulphur* (*S*), *other protectant* (*P*) *or ergosterol biosynthesis inhibitor* (*E*) *fungicides in Australia and Africa*

Years(s) of expt	Location	Disease(s) present	Effect of disease control on grain protein concentration	Fungicide group(s)	Reference
1937	Australia	*P. recondita*	↑	S	Phipps (1938)
1965–67	NS Wales, Australia	*P. graminis* and *P. recondita*	↑	P	Keed & White (1970)
1979	Queensland, Australia	*P. graminis*	↓ and ↑	E	Rees & Syme (1981)
1980	Queensland, Australia	*Pyrenophora tritici-repentis*	↓	E	Rees *et al.* (1982)
1983	Egypt	*P. striiformis*	↑	E	Abdel-Hak *et al.* (1987)
1984–85	Queensland, Australia	*P. striiformis*	↑	E	Park *et al.* (1988)
1986	NS Wales, Australia	*P. striiformis*	=	E	Ash & Brown (1990)

↑, ↓, = , fungicide increased, decreased or had no effect on grain protein concentration, respectively.

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Table 4. *Reports of protein concentrations following control of wheat pathogens with either protectant (P), benzimidazole (B), ergosterol biosynthesis inhibitor (E), or mitochondrial respiration inhibitor (M) fungicides in Europe*

Year(s) of expt	Location	Disease(s) present	Effect of disease control on grain protein concentration	Fungicide group(s)	Reference
1974–76	UK	*E. graminis* and *Septoria* spp.	=	P+B	Penny *et al.* (1978)
1977–79	UK	*P. recondita*, *E. graminis* and *S. tritici*	↓	P+B	Penny *et al.* (1983)
1979		*E. graminis*	=		
1980	UK	*S. nodorum*	↓	P+B+E	Myram & Kelly (1981)
1981		*P. recondita*	↓		
1983–85	UK	*S. tritici*	↓	E	Kettlewell *et al.* (1987)
1985–86	UK	*S. tritici*	↓	P+B+E	Salmon & Cook (1987)
1986–87	Finland	*S. nodorum*	=	E	Peltonen & Karjalainen (1992)
1986	UK	*E. graminis*	↑	E	Gooding (1988)
1985, 87–90	UK	*S. tritici*	↓ and =	E	Gooding *et al.* (1994)
1986		*E. graminis*	=		
1986		?	=		
1988	UK	*S. tritici*	↓	E	West (1990)
1989		?	↑		
1988–89	UK	*S. tritici* and *E. graminis*	=	E	Gooding *et al.* (1993)
1988	UK	*S. tritici*	↓	E	Clare *et al.* (1990)
1989		*P. recondita*	↑	E	
1988–89	UK	?	↓	P+E	Clark (1993)
1989–91	UK	*S. tritici*	=	P+E	Clare *et al.* (1993)
1991	Ireland	*S. tritici* and *E. graminis*	=	P+E	McCabe & Gallagher (1993)
1992			↓		
1994–95	Germany	*Septoria* spp. and *E. graminis*	↑	E and M	Hedke and Verreet (1999)
1998, 99	UK	*S. tritici*	↓ and ↑	E and M	Dimmock & Gooding (2000)
2000	UK	*S. tritici*	↓	M	Ruske *et al.* (2001)
2000	UK	*S. tritici*	↓ and =	E+M and E	Ishikawa *et al.* (2001)

↑, ↓, =, fungicide increased, decreased or had no effect on grain protein concentration, respectively.

evidence that protein was diluted, much the reverse. This may partly be attributable to nutritional effects of the sulphur because GPC can be increased by sulphur application in the absence of disease (Byers *et al.* 1987; Dampney & Salmon 1990) particularly, it appears, when little nitrogen fertilizer has been applied (Camblin & Gall 1987). However, comparison of genotypes in the 1930s strongly implicated rust control as the main reason for increases in protein concentration (Caldwell *et al.* 1934; Waldron 1936). More latterly this has been confirmed in diverse systems of production with other fungicides including other protectants in Australia (nickel sulphate plus maneb; Keed & White 1970), morpholines in the UK (fenpropimorph; Clare *et al.* 1990) and triazoles in the USA (tebuconazole and propiconazole; Herrman *et al.* 1996). The wheat production system that perhaps contrasts most with the early American work is that reported by Clare *et al.* (1990) in the UK. They applied fenpropimorph at flag leaf emergence (growth stage (GS) 37; Zadoks *et al.* 1974) and ear emergence (GS 59) and thus reduced leaf-rust infection on the flag leaves at GS 75 from 25% to 14%, increased grain yields from 5·6 to 6·7 t DM/ha, and increased protein concentration from 12·9% DM to 13·5% DM (S.E. 0·08). Work in Australia and Egypt report yellow (or stripe) rust (*P. striiformis* West.) to have similar effects on GPC; i.e. infected plants have reduced levels and controlling the disease with fungicides (triadimefon, propiconazole and dichlobutrazol; Abdel-Hak *et al.* 1987; Park *et al.* 1988) increases GPC.

There is much evidence, therefore, that infection by *Puccinia* spp. can be more detrimental to nitrogen accumulation in the grain than to dry matter accumulation. GPC is often reduced with infection by rust and, therefore, increased by methods adopted to

control rusts. There are some reports to the contrary, discussed later, but clearly rusts must be deleterious to the nitrogen accumulation and/or partitioning within plants. Shutt (1905) reported that protein in straw from rusted wheat was over three times more concentrated than rust-free straw. Caldwell *et al.* (1934) and Greaney *et al.* (1941) clearly showed that *P. recondita* infection on more susceptible cultivars could increase protein concentration in leaves and stems at the same time as reducing protein concentration in the grain. The data presented by Caldwell *et al.* (1934) suggest that controlling the disease on a susceptible cultivar increased nitrogen harvest index from 73% on the rusted plants to 81% on the sulphur-treated plants at the hard dough stage. Total above-ground nitrogen per stem was also increased by 38%. These effects were greater than the effects on dry matter accumulation and partitioning to the grain such that protein yield from one cultivar was reduced by 14% by rust infection in the absence of a significant effect on grain DM yield.

Walters (1989) reported substantial accumulation of N within pustules of *P. graminis* on wheat leaves while the concentration of N in the surrounding areas was unaltered. This implied net import of N into the infected region and leaf. Similarly others (Ahmad *et al.* 1982) found more import of N into, and less export from, barley leaves infected with *P. hordei*. The situation is significantly different from effects on carbon as there has been no evidence of any biotroph causing a net import of sugars into an infected cereal leaf nor transport against the normal direction of phloem flow within the leaf, i.e. carbon requirements can be met by local diffusion and photosynthesis (Walters 1989). This is not to say that carbon accumulation and translocation is not also severely affected by rust infection. The uredia of rusts occur in small pustules on the leaves, reducing the amount of green area available for radiation interception. Penetration is usually via stomata (*P. striiformis*) or via an appresorial peg, and disruption to the balance between water uptake and transpiration is further exacerbated when the uredia erupt through the cuticle. Resistance to water loss is lowered and, therefore, rate of expansion of new leaves is reduced, and mature leaves senesce prematurely, thus reducing radiation interception and photosynthesis (Bryson *et al.* 1995). Radiation use efficiency is also lowered as respiration increases and carbon is utilized in fungal structures.

The retention of assimilate in plant organs infected by biotrophic pathogens such as rusts has been frequently reported (Crowdy & Manners 1971) and contrasts with the situation with necrotrophs where there is little or no accumulation. Lucas (1998) reports that rusts cause a disturbance in the nutrient balance of the plant through physical damage to leaves causing both reduced photosynthesis and reduced translocation. Damage to cuticles also substantially increases transpiration and causes leaves to senesce prematurely through desiccation. This greatly increases retention of sugars and amino acids in diseased leaves, and restricts the remobilization to developing grains. If disease disrupts the control of water loss, effects on yield and quality are likely to be exacerbated when severe infection is followed by hot dry conditions during grain filling and maturation, as found by Hartill (1961) with *P. striiformis*. Nitrogen concentration commonly increases during the latter stages of grain filling so premature and disrupted ripening may affect a reduction in protein concentration, particularly in dry conditions.

It is not surprising, therefore, that *Puccinia* spp. can reduce both nitrogen and carbon accumulation by the grain, and often the nitrogen accretion is more severely affected compared to carbon. There are, however, some instances when the reverse has been true. Broadfoot (1931) reported some large reductions in protein concentration in one series of comparisons, following control of *P. graminis* and *P. recondita* but statistical significance of this early work is unclear. Similarly, over a period of seven years of successive experiments in Canada (Peturson & Newton 1939; Peturson *et al.* 1945, 1948) in one year it appeared that controlling *P. recondita* reduced protein concentration, compared with five years when the opposite occurred. Again, the statistical significance of the reduction is not quantified, although some of the results when increases in GPC occurred are quoted with errors and do indicate significant enhancements. Rees & Syme (1981) found the concentration of nitrogen in the grain to be significantly ($P < 0{\cdot}05$) reduced following control of severe *P. graminis* infections with triadimefon on two highly susceptible cultivars, but when the same pathogen was controlled on a moderately susceptible cultivar grain, nitrogen concentration was significantly increased. Penny *et al.* (1983) report that application of a fungicide with some specificity for rust (benodanil) reduced grain nitrogen concentration, but only in years when slight infection with *P. recondita* occurred alongside much higher levels of *Septoria* spp. In a previous year, nitrogen concentrations appeared to be reduced from 1·86 to 1·80% DM (S.E. 0·026) by a broad-spectrum fungicide (benomyl and maneb plus mancozeb) when *P. recondita* was the most important disease. Myram & Kelly (1981) found that in one year when 'late season diseases such as brown rust (*P. recondita*)' were prevalent a 'crop protection programme' including application of triadimefon, carbendazim and captafol fungicides, but also including aphicide and a growth regulator, significantly ($P < 0{\cdot}01$) reduced GPC. From the above it does appear that there are situations when control of *Puccinia* spp. can reduce GPCs but examples are more tenuous and less consistent than for when the reverse is true.

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Powdery mildew (Erysiphe graminis)

There are few conclusive reports of the effects of controlling *E. graminis* on GPC of wheat, not least because it is often complexed with infections by rusts and/or *Septoria* spp. Penny *et al.* (1978) found fungicide to have no effect on GPC in the one year in three when *E. graminis* was the most important disease. Myram & Kelly (1981) did not find their crop protection programme, that increased yield by 2 t/ha, to affect GPC at a site where *E. graminis* was the major disease present on the untreated plots. Similarly Gooding *et al.* (1993) report one experiment where fenpropimorph reduced *E. graminis* from 20% to 2·5% on the penultimate leaves during grain filling, increased grain yield by 0·8 t/ha, yet had no effect on GPC. Gooding *et al.* (1994) only found *E. graminis* to predominate in one year in six, and in that year propiconazole plus tridemorph fungicide reduced the area of *E. graminis* on the flag leaves of the most susceptible cultivar from 7·5% to 0·2%, increased yield from 6·5 to 7·4 t/ha (S.E. 0·17) and appeared to increase protein concentration from 13·0 to 13·4% DM (S.E. 0·08). In a neighbouring experiment in the same year, significant ($P < 0·05$) increases in both grain yield and protein concentration were obtained from the same fungicide treatment (Gooding 1988).

The effect of *E. graminis* has been isolated from the effect of associated pathogens in two ways. Firstly, Johnson *et al.* (1979) compared 13 near-isogenic lines differing in at least seven single independent genes for resistance to *E. graminis* in field plots in Maryland, USA. Mildew severity on the upper two leaves was closely and negatively correlated with protein concentration in the flour. Secondly, in controlled environments, infections of *E. graminis* can be readily encouraged in the absence of other pathogens. Under glass, Gooding *et al.* (1994) found that propiconazole applied at GS 39 and GS 59 reduced severity of powdery mildew pustules from 27% to 6% on the flag leaf, increased grain yield by 12% (S.E. 3·2) and increased GPC from 10·8% to 11·6% (S.E. 0·26). Similarly, Smedegaard-Petersen & Stølen (1981) found that inoculating barley in growth chambers with *E. graminis* reduced GPC.

The weight of evidence indicates that control of *E. graminis* will increase GPC rather than reducing it, even when severe infection is well controlled in high-yielding conditions. As with the *Puccinia* spp., therefore, infection causes severe disruption to nitrogen accumulation and partitioning. Most of the relevant work on nitrogen metabolism has been in barley, where infection by *E. graminis* has lowered the rate of nitrate uptake and reduction in the roots (Murray & Ayres 1986; Schmidt *et al.* 1994), but may yet increase the amount (Schmidt *et al.* 1994) or concentration (Murray & Ayres 1986) of nitrogen in infected leaves. Furthermore, the results of Finney (1979) suggest that *E. graminis* infection restricts the movement of N out of senescing leaves. This may be, at least partly, due to the formation of 'green islands' and localized enhancement of cytokinin-like activity. Mildewed leaves appear to lose nitrogen as ammonia gas (Sadler & Scott 1974) and additional N loss from the plant may be in the production and dispersal of conidia. Murray & Ayres (1986) found that conidia from infected barley plants grown in controlled environments accounted for 150 μg N/plant/day. There are large errors in extrapolating to the field but multiplying up for a 28-day infection and 200 plants/m², suggests a possible loss of about 10 kg N/ha.

As with *Puccinia* spp., infection with *E. graminis* is also very detrimental to carbon accumulation by the grain due to disrupted photosynthesis, increased respiration, reduced translocation and premature senescence but, on balance, nitrogen accumulation appears more severely affected. In contrast to the effects of *Puccinia* spp., *E. graminis* is restricted to the epidermal cells and effects on the water relations of the plant appear to be relatively minor, even under drought (Ayres & Zadoks 1979).

Septoria *spp.*

The effect of *Septoria* spp. on GPC has long been suggested to be different from the effect of the biotrophs mentioned above (Shipton *et al.* 1971). The earliest reports of effects of *S. nodorum* were that infection increased protein concentration (Bockmann 1964); an effect confirmed in inoculation studies in Finland (Karjalainen & Salovaara 1988). This is consistent with much of the subsequent work where a range of fungicides controlling *S. nodorum* or *S. tritici* have usually either had no effect, or have reduced GPC. Significant ($P < 0·05$) reductions have arisen following the use of triazoles and/or morpholines (Clare *et al.* 1990; Gooding *et al.* 1994; Puppala *et al.* 1998), strobilurins (Dimmock & Gooding 2000; Ruske *et al.* 2001), and an oxazolidinedione (Dimmock & Gooding 2000). There appears to be evidence to suggest that this difference to the general response of controlling the biotrophic pathogens is due to the largely necrotrophic infection strategy of the *Septoria* spp. The latter does not, for instance, interfere significantly with translocation (Scharen *et al.* 1975; Wafford & Whitbread 1976), but affects the overall supply of assimilates through reducing the photosynthetic capacity of the plant via destruction of leaf tissue. The ability of biotrophic pathogens to redirect and retain nitrogen to and in infected tissues, rather than the grain, contrasts with the effects of the main necrotroph strategy of destroying photosynthetic capacity and, therefore, having a much larger effect on carbon accumulation than nitrogen. This is an over simplification, and could also be the result of

confounding influences. It is unfortunate but probably inevitable, for example, that virtually all the work on *Septoria* spp. and GPC has been done in high-yielding maritime and/or temperate conditions in Europe. In contrast, most work on *Puccinia* spp. has been done in very different conditions and production systems in North America and Australia. The oversimplification arises because epidemics of *Septoria* spp., like those of the biotrophs, regularly reduce the yield of grain protein per unit area by reducing both nitrogen uptake and partitioning of nitrogen to the grain (McCabe *et al.* 2001; Ruske *et al.* 2001). Ruske *et al.* (2001) obtained a greater control of a *S. tritici* infection by adding a strobilurin (azoxystrobin) to a triazole programme. This increased nitrogen grain yield from 145 to 155 kg N/ha (S.E. 1·87) and nitrogen harvest index from 70·3 to 72·0% (S.E. 0·0052). In exceptional cases these effects on N accumulation do occur to a greater extent than effects on dry-matter grain yield such that GPC rises when *Septoria* spp. are controlled (Hedke & Verreet 1999; Dimmock & Gooding 2000). Even allowing for the confounding effects of climate and production system, therefore, the distinction between effects of *Septoria* spp., and those of *Puccinia* spp. and *E. graminis* on GPC is not absolute. Indeed, *S. tritici* has been regarded to exhibit some characteristics of biotrophy in the early stages of infection (Royle *et al.* 1995). The fact remains, however, that controlling *Septoria* spp. often reduces GPC and it is unfortunate that this occurs in the production area most reliant on fungicide use to protect yields, and also in an area where high GPCs are difficult to achieve because the climate is often conducive to long grain-filling periods. The practical and economic consequences of this are dealt with later.

Relationships with green leaf area duration

Whilst it is useful to differentiate between the effects of particular pathogens on GPC, usually diseases will not infect a crop alone but will occur as a complex of different species, competing for nutrients and proliferating as environmental conditions and host-responses permit. Furthermore, there are possibilities that fungicides may have effects on a range of largely saprophytic, phylloplane fungi that may act as minor pathogens and whose control may extend leaf life and increase yields (Dickinson 1973; Bertelsen *et al.* 2001). There may be additional direct beneficial 'physiological effects' following fungicide use, not mediated through pathogen control. Such effects have been claimed for many fungicide groups including benzimidazoles (Bruck *et al.* 1984), triazoles (Kettlewell *et al.* 1982; Fletcher & Nath 1984), and, more recently, strobilurins (Konradt *et al.* 1996; Grossmann & Retzlaff 1997; Habermeyer *et al.* 1998; Gerhard *et al.* 1999).

Pathogen effects on canopy size, green area duration and light interception are often adequate to explain their effects on grain yield (Gaunt 1995; Bryson *et al.* 1997). This approach characterizes the benefits of fungicides on grain yield without the need to understand the precise mechanism(s) by which fungicides increase green leaf area and its duration. We have recently shown that fungicide effects on green flag leaf area duration can be closely related to effects on grain yield for contrasting seasons, genotypes, active ingredients and foliar pathogens (Gooding *et al.* 2000). We propose that a similar analysis can help to investigate fungicide effects on GPC (Gooding & Davies 1997; Dimmock & Gooding 2000). In Fig. 1, GPCs, grain dry-matter yields and grain nitrogen yields are related to the time taken for flag leaf green area to decline to 37%. This parameter is estimated by fitting a modified Gompertz model to the % green area × day curve (Gooding *et al.* 2000) and is described as green flag leaf area duration (GFLAD). Data presented are for one cultivar with potential for biscuit making, growing on a sandy loam where the main disease present was *S. tritici*. Full experimental details are available in Dimmock & Gooding (2002). It is clear that for every incremental delay in the time to flag leaf senescence there are incremental increases in yield of grain dry matter and grain nitrogen, but also incremental decreases in GPC. Over the durations of flag leaf life achieved there is no evidence that relationships with the three response variables are anything other than linear. Neither is there any evidence that the active ingredients used change the relationship between delay in senescence and GPC, i.e. common relationships are appropriate whether a triazole, a strobilurin, or their mixtures with each other, or with an oxazolidinedione is used.

Interactions between cultivar and foliar fungicides on protein concentration

The literature reveals three types of interaction between the effects of cultivar and fungicide on GPC. Interactions can be explained on the basis of: (a) susceptibility to one disease; (b) susceptibility to different diseases; or (c) they cannot be explained on the basis of disease severity or species.

In the first case the fungicide has the greatest effect on GPC when it controls the greatest levels of a particular pathogen on the most susceptible genotypes. This type of interaction is observed for reductions in GPC following control of *S. tritici* (Salmon & Cook 1987), increases in GPC following inoculation with *S. nodorum* (Karjalainen & Salovaara 1988) and increases in GPC following control of *P. striiformis* (Park *et al.* 1988).

The second type of fungicide × cultivar interaction occurs when the same fungicide controls different disease species on different cultivars within the same

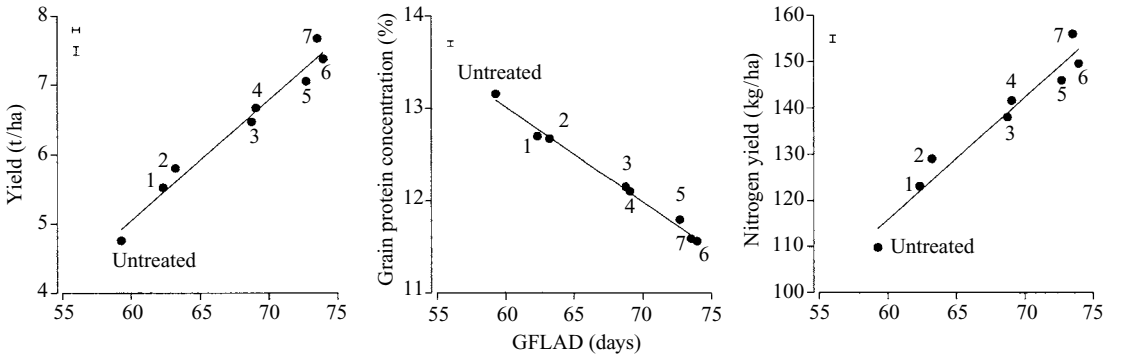

Fig. 1. Relationships between fungicide treatment means of the duration from flag leaf emergence to 37% flag leaf green area (GFLAD), and grain yield, grain protein concentration and nitrogen yield for winter wheat cv. Consort in 2000. 1–7 denote fungicide treatments applied at flag leaf emergence and again at ear emergence. 1. flusilazole (107 g a.i./ha); 2. flusilazole (160 g a.i./ha); 3. famoxadone + flusilazole (100 + 107 g a.i./ha); 4. famoxadone + flusilazole (150 + 160 g a.i./ha); 5. azoxystrobin (125 g a.i./ha); 6. azoxystrobin + flusilazole (125 g + 107 g a.i./ha); 7. azoxystrobin + famoxadone + flusilazole (125 g + 100 g + 107 g a.i./ha). The principal disease controlled was *Septoria tritici*. Bars represent S.E.

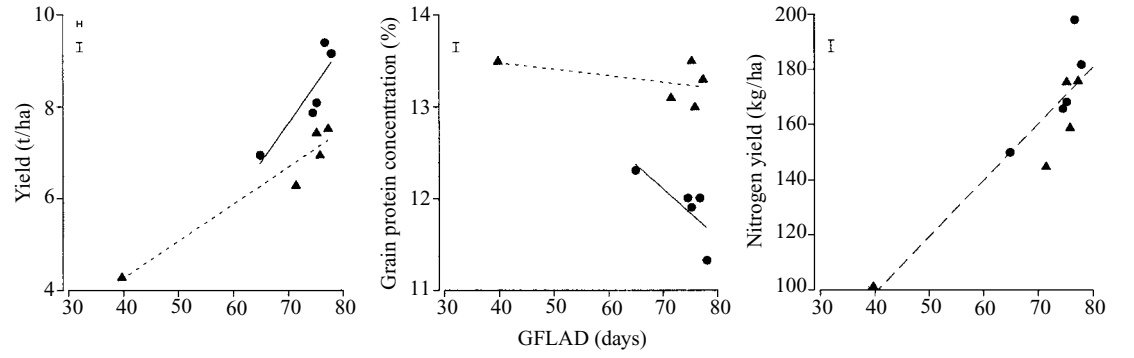

Fig. 2. Relationships between fungicide treatment means of the duration from flag leaf emergence to 37% flag leaf green area (GFLAD), and grain yield, grain protein concentration and nitrogen yield for winter wheat cv. Consort (●, solid line) where *Septoria tritici* was the principal disease controlled, and cv. Cockpit (▲, dashed line) where *Puccinia striiformis* was the principal disease controlled. The lowest GFLAD within each cultivar corresponds to the untreated while all other results were achieved with different fungicide treatments applied at flag leaf emergence and again at ear emergence. Bars represent S.E.

experiment. Puppala *et al.* (1998) suggest that the reason why fungicide treatment both increased and decreased GPC on different cultivars was possibly due to the control of rust in the former and *S. tritici* in the latter case. In Fig. 2 we relate the effects of fungicides on the life of the flag leaf to GPC when severe *P. striiformis* (99% of flag leaf area on untreated plants) is controlled (5% of flag leaf area following application of azoxystrobin) on the hybrid cultivar Cockpit compared to when severe *S. tritici* (77% of flag leaf area on untreated plants) is controlled (5% of flag leaf area following application of azoxystrobin) on cv. Consort in the same field experiment in 1999. Grain yield responses to GFLAD differed significantly, with Consort returning 0·17 t/ha/day GFLAD (S.E. 0·047) and Cockpit a significantly lower 0·08 t/ha/day GFLAD (S.E. 0·049). A significant difference existed between the GPC responses of the two cultivars, with the necrotroph-infected Consort having a negative trend of −0·05% GPC/day GFLAD (S.E. 0·025), and the biotroph-infected cv. Cockpit (−0·01; S.E. 0·026) showing no appreciable response. A similar experiment in 2000 produced comparable results, with Consort showing a strongly negative response of −0·10% GPC/day GFLAD (S.E. 0·010), whilst Cockpit had a significant but markedly shallower response of −0·04 (S.E. 0·012). It is not possible to be certain that the differences between GPC responses of Consort and Cockpit to GFLAD are due solely to the different pathogens present rather than additional, confounding genotypic interactions, but the results do add to the existing evidence that control of biotrophs with fungicides is usually less damaging to GPC than when controlling *Septoria*

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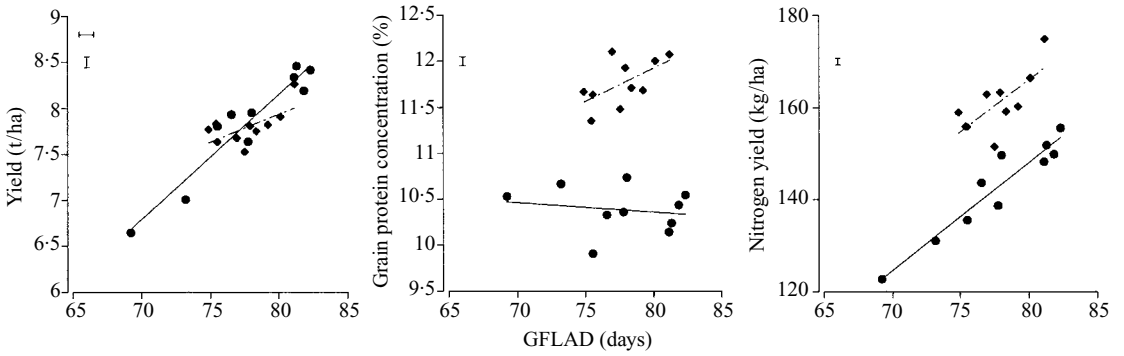

Fig. 3. Relationships between fungicide treatment means of the duration from flag leaf emergence to 37% flag leaf green area (GFLAD), and grain yield, grain protein concentration and nitrogen yield for winter wheat cvs. Consort (●, solid line) and Hereward (◆, dashed/dotted line). The lowest GFLAD within each cultivar corresponds to the untreated while all other results were achieved with different fungicide treatments applied at flag leaf emergence and again at ear emergence. The principal disease controlled was *Septoria tritici*. Bars represent S.E.

spp. It is also notable that GFLAD gains for cv. Cockpit in excess of one month in 1999 were not associated with any dilution of GPC.

The third type of cultivar × fungicide interaction appears when fungicide controls the same disease but the direction of the protein concentration response is different for different cultivars, or the same level of disease control gives rise to different effects on GPC. In these circumstances neither the amount nor the type of the pathogen present can explain the differential response of GPC in different cultivars. This type of interaction, for instance, is recorded for the control of *P. graminis* with triadimefon (Rees & Syme 1981) where, as previously mentioned, the GPC is both increased and decreased in different cultivars. Figure 3 shows a cultivar × fungicide interaction on GPC related to GFLAD where *S. tritici* is the disease controlled in both cv. Hereward, a bread-making cultivar, and cv. Consort, a biscuit-making cultivar, in 1998. In cv. Hereward GPC increased as greater reductions in *S. tritici* and greater increases in GFLAD were achieved whilst there was no response of GPC in Consort despite control of severe infection pressures. This interaction is demonstrated with differences in response of grain yield and nitrogen yield to additional GFLAD. The response of grain nitrogen yield was similar for the two cultivars (2·42 kg N/ha/day GFLAD; S.E. 0·29). The grain yield responses for the two cultivars, however, interacted significantly ($P < 0{\cdot}05$), with Consort having a greater coefficient (0·14 t/ha/day GFLAD; S.E. 0·014) than Hereward (0·061 t/ha/day GFLAD; S.E. 0·031). It therefore follows that whilst grain nitrogen is accumulated at the same rate by both cultivars for each fungicide-mediated day of GFLAD gained, the GPC interaction exists through Hereward's lower grain-yield response, allowing this nitrogen to be deposited at greater concentrations than in Consort.

Ruske *et al.* (2001) also record no significant effects of azoxystrobin on GPC of cv. Hereward, despite the fungicide delaying flag leaf senescence by the same amount as on other cultivars where the fungicide significantly reduced GPC. In this experiment it appeared that the cultivar was becoming sink limited for grain yield as indicated in a neighbouring study (Dimmock & Gooding 2002). Clearly, the balance between nitrogen and dry-matter accumulation is affected by a series of variables, not just type and amount of pathogen controlled. Van Sanford & MacKown (1987) showed that the percentage of plant nitrogen accumulated in the spike following remobilization can vary between wheat cultivars from 51 to 91%. Differences of such a magnitude could easily account for the cultivar × fungicide interactions seen in our experiments. It is speculative, but not unreasonable to suppose that cultivars specifically bred for bread-making, where high protein concentration is a selection criterion together with high grain yield, may be able to maintain grain nitrogen accumulation more effectively as senescence is delayed and yields increase, compared with cultivars suited to biscuit and livestock feed markets where protein concentration is much less important. Puppala *et al.* (1998) report large increases in protein concentration following fungicide use on a cultivar specifically bred for high protein concentration. Clark (1993) mentions that protein concentration reductions following fungicide use were less in bread-making cultivars, but this interaction also reflected varietal differences in disease susceptibility and yield responses.

Interactions between nitrogen fertilizer and foliar fungicides on protein concentration

Nitrogen fertilizer is the most important fertilizer element determining the productivity and quality of

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wheat in most major areas of production. Grain yields are increased most effectively by applications to the soil before or during stem extension. Protein concentrations in the grain can be increased by these applications but greater responses are achieved by foliar spray applications of urea solution at, and shortly after, anthesis (Gooding & Davies 1992). Nitrogen × fungicide interactions are frequently reported for grain yield (Penny *et al*. 1978; Kelley 1993) as, with adequate rainfall, increasing nitrogen often increases yield potential yet encourages the development of several foliar diseases, particularly *Puccinia* spp. and *E. graminis*. There have also been some suggestions that nitrogen and fungicide applications interact with respect to protein concentrations. In barley, Jenkyn & Finney (1981) report tridemorph to decrease grain nitrogen concentrations at low N application rates (25 kg N/ha) yet have the opposite effect at high N application rates (135 kg N/ha). Penny *et al*. (1978) found positive interactions between fungicide and liquid N (solution of ammonium nitrate and urea) applications at ear emergence on grain protein concentration of wheat. A similar interaction has been reported less formally for late-season foliar urea (Anon. 1997). However, despite numerous studies, no other N fertilizer × fungicide interactions on GPC have been found, whether nitrogen has been applied to the soil or to the leaves as a late-season, foliar spray of urea (Morris *et al*. 1989; Clare *et al*. 1990; Gooding *et al*. 1991; Kelley 1993; Dimmock 2001; Ishikawa *et al*. 2001; Ruske *et al*. 2001).

Interactions between seasons and foliar fungicides on protein concentration

Examples of difference in effects on GPC from controlling diseases in different years occur frequently in Table 2, especially where different pathogens have been controlled (Myram & Kelly 1981; Gooding *et al*. 1994). However, where the same pathogen has been controlled in different years, variation in direction and size of GPC response is more difficult to explain, even accounting for differences in disease severity and yield improvements following fungicide use. Peturson *et al*. (1948) provides an example, where *P. recondita* control in 1944 resulted in a 52% increase in grain yield from 2·35 to 3·58 t/ha and increase in GPC from 14·0 to 15·2%, whilst in 1946, a similar increase (8·9%) in GPC was obtained with only a 9·3% increase in grain yield.

Further interactions between year and fungicide on GPC are demonstrated in Fig. 4, where the effects of different fungicide treatments (fungicide treatment mean minus untreated mean) applied at flag leaf and ear emergence on GPC, grain yield and grain nitrogen yield are related to effects on GFLAD in 1998, 1999 and 2000. In each year the site and soil (sandy loam), cultivar (cv. Consort), agronomy and rotational position (after 2 years of unfertilized grass) is similar. In each year, the untreated plots suffered from *S. tritici* infection, and its control by the most effective fungicides delayed senescence of the flag leaf by about 2 weeks. Other diseases (*E. graminis* and *Puccinia* spp.) remained at trace levels (< 1% flag leaf area) throughout. There is no evidence that relationships were anything other than linear and neither was there any evidence that fungicides had an effect on the grain yield and composition when they had no effect on flag leaf senescence, hence the constant term is omitted.

Despite these similarities, fungicides produced markedly different effects on GPC in the three years. In 1998 there was little or no effect of fungicide on GPC with only a very shallow and tenuous relationship between GPC and GFLAD (regression coefficient (b) = −0·016% GPC/day GFLAD, S.E. 0·008, P = 0·055). This was despite the best fungicides increasing grain yield by more than 1·5 t/ha and reflects that the commensurate increase in grain nitrogen yield of 30 kg/ha was sufficient to maintain GPC. In 1999, the most effective fungicides significantly (P < 0·05) decreased GPC, reflecting a moderate, negative response to GFLAD (b = −0·042% GPC/day GFLAD, S.E. 0·012). The situation deteriorated markedly in 2000 when fungicides returned the greatest GPC reductions of any seen in 14 experiments where similar analyses have been possible (Fig. 6). In 2000, the most effective fungicide treatments reduced GPC by 1·5% resulting from a decline of −0·11% GPC/day GFLAD (S.E. 0·011). This rate of decline is, perhaps, particularly surprising given that the 2000 experiment saw the greatest response of grain nitrogen yield to incremental delays in flag leaf senescence (Fig. 4). The reduction occurred because increases in grain yield were yet more impressive compared with the two previous years. Clearly, large differences in GPC can occur following apparently small differences in the relative responses of grain dry matter and grain nitrogen yields to delays in senescence. Given this observation, predicting when control of severe *S. tritici* might lead to a significant reduction in GPC presents a challenge. It is well known that temperature, rainfall and radiation all affect GPC and hence the balance between nitrogen and dry-matter accumulation (Farrand 1972; Benzian & Lane 1986; Smith & Gooding 1999). It would not be surprising if these factors also influenced the effect of delaying senescence on GPC. To investigate this further we have calculated the regression coefficient (b) between fungicide effects on GPC and GFLAD for five years where *S. tritici* was the major disease controlled on bread-making cultivars of wheat grown with commercially relevant agronomy on sandy loam in the UK. Analyses to explain the yearly variation in b, weighted for the inverse of the variance of yearly estimates, demonstrate that the negative effects seen in 2000 were

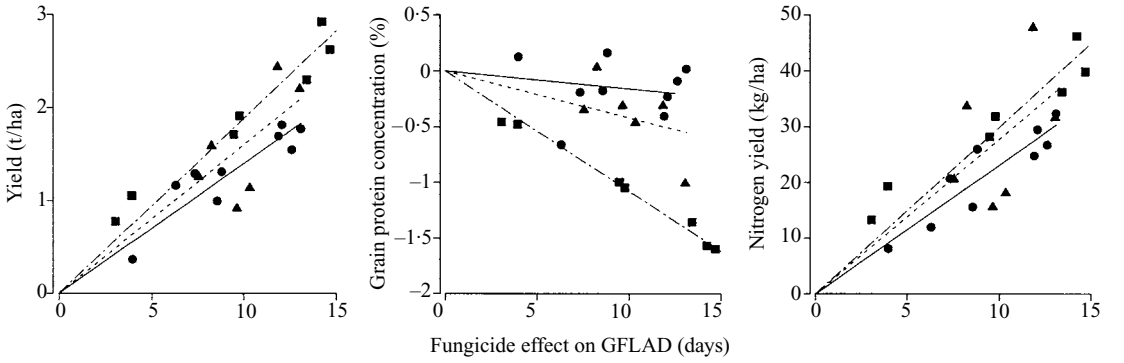

Fig. 4. Relationships between fungicide effects (fungicide treatment mean minus untreated mean) on the duration from flag leaf emergence to 37% flag leaf green area (GFLAD), and grain yield, grain protein concentration and nitrogen yield in 1998 (●, solid line), 1999 (▲, dashed line) and 2000 (■, dashed/dotted line) for winter wheat cv. Consort. The principal disease controlled was *Septoria tritici*.

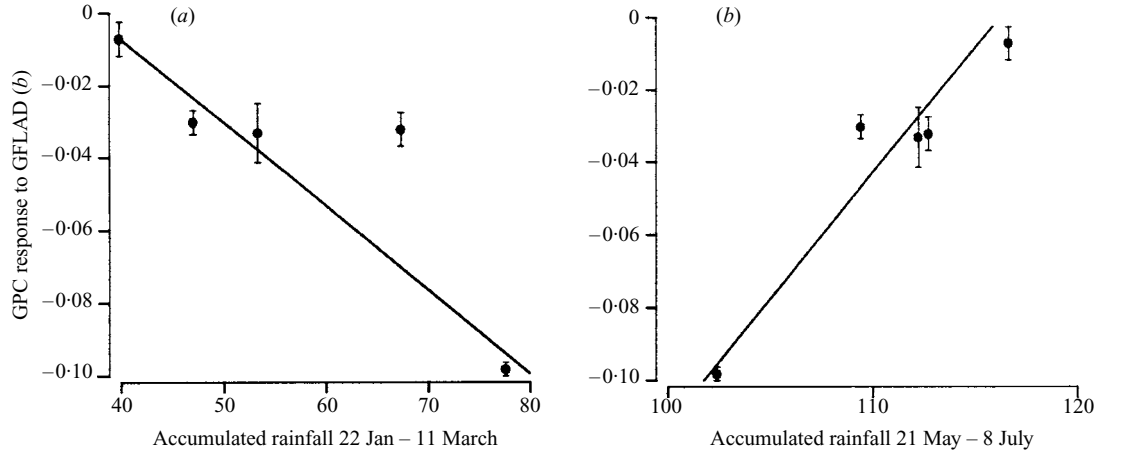

Fig. 5. Relationships between the regression coefficient (*b*) for grain protein concentration against flag leaf green area duration (GFLAD), and rainfall during 7-week periods. Points represent coefficients for different years and are estimated when fungicides are used to modify GFLAD e.g. as in Fig. 4. Bars represent S.E.

associated with increased rainfall in February and March. Rainfall in this period was negatively associated with *b* (Fig. 5*a*). Conversely, rainfall during grain filling was positively associated with *b* (Fig. 5*b*). Clearly data from more years are needed to reach firmer conclusions but it is notable that these associations with rainfall are broadly coincident with the main effects of rainfall on GPC. For example, spring and winter rainfall in the UK has been negatively related to GPC (Smith & Gooding 1999). It is thought that rainfall prior to grain filling reduces CP because it encourages dilution of early nitrogen reserves by vegetative proliferation; it increases leaching and other forms of soil nitrogen loss; and it may augment soil moisture reserves so that leaf life is extended during grain growth favouring carbohydrate assimilation and translocation more than that of nitrogen (Schlehuber & Tucker 1959; Hopkins 1968; Taylor & Gilmour 1971). Conversely, summer rainfall, during grain filling, has been positively associated with GPC in the UK (Farrand 1972; Smith & Gooding 1996), possibly because it encourages mineralization of nitrogen at a time when availability of the nutrient has a large impact on GPC (Gooding & Davies 1997).

Average effects on GPC and nitrogen capture

Given that we are not yet in a position to predict the effect of fungicides on GPC before they are applied at flag leaf emergence, one approach is to look at responses over an extended period of time and determine whether, on average, accounting for fungicide

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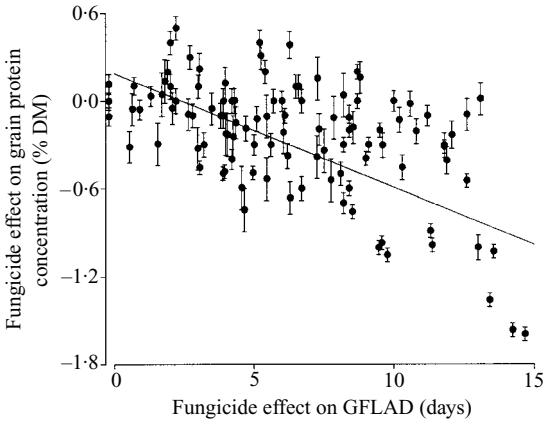

Fig. 6. Relationship between fungicide effects (fungicide treatment mean minus untreated mean) on the duration from flag leaf emergence to 37% flag leaf green area (GFLAD), and grain protein concentration (GPC) from 14 separate experiments. Error bars represent one S.E. of the treatment mean (minimum D.F. 9). Solid line is the regression where the constant is 0·13 (S.E. 0·065) and the regression coefficient is −0·058 (S.E. 0·0088, D.F. 105).

effects on GPC is likely to alter advice given on their use. To this end, Fig. 6 shows the relationship between effects of fungicides applied at flag leaf and ear emergence on GFLAD and fungicide effects on GPC. These results are from 14 separate experiments conducted at three sites in England between 1983 and 2000, mostly on sandy loam soil using commercially recommended cultivars and rates of nitrogen fertilizer during and before stem extension (between 160 and 240 kg N/ha). In all but two experiments the principal foliar disease controlled on the flag leaf was *S. tritici*, otherwise it was *E. graminis*. Full husbandry and climatic details are available in Gooding (1988), Lawson (1989) and Dimmock (2001) while more summary information is given in Kettlewell (1997), Gooding *et al.* (2000) and Dimmock & Gooding (2002). The fungicides used included triazoles, morpholines, strobilurins and an oxazolidinedione. This analysis reveals an average decline in GPC as fungicides delay senescence of the flag leaf (GFLAD), commensurate with the usual effect of controlling *S. tritici* in the UK. The regression coefficient suggests that in commercially relevant situations within England, grain protein concentration is reduced by 0·4% DM for every 7 days the flag leaf is kept alive by the use of fungicides. There is, however, a large degree of variation around this average response and the variance accounted for (r^2 adj., Genstat Committee 1993) is only 29%. Curiously, the constant is positive and significant ($P = 0{\cdot}049$). This is partly because several of the fungicide treatments giving small increases in flag leaf life also significantly increased CP. We do not suggest, despite the statistical inference, that fungicides increase CP when they have no effect on flag leaf life. There is no evidence for this from within-year analyses, nor do such analyses suggest that the relationship between effects on GFLAD and CP is anything other than linear (see Fig. 1). As well as reducing grain protein concentration, delay in flag leaf senescence following fungicide use was associated with increased grain yield, mostly accounted for by increases in mean grain weight (Fig. 7). However, again, the effects of fungicide on GPC cannot simply be ascribed to a general dilution effect caused by increased carbohydrate accumulation because they also increased the yield of nitrogen, whether expressed on a per hectare or on a per grain basis (Fig. 7). Indeed, fungicide effects on mean grain weight and grain yield only accounted for 39 and 29% of the variation in protein concentration respectively.

The average response of grain nitrogen yield to delayed senescence appears to be well within what would be predicted from nitrogen capture experiments in the UK (Sylvester-Bradley *et al.* 2001). When nitrogen fertilizer has been applied at the start of stem extension, nitrogen capture during grain growth proceeds at about 1 kg N ha/day (Sylvester-Bradley & Stokes 2001; Sylvester-Bradley *et al.* 2001). If we assume a green area index of 6 at anthesis, and therefore, 180 kg N/ha in the canopy (Sylvester-Bradley *et al.* 1997), the amount of nitrogen in the crop at the end of grain growth, approximately 35 days later, would be 215 kg N/ha (Ruske *et al.* 2001). Assuming a nitrogen harvest index of about 70% (Ruske *et al.* 2001) the amount of nitrogen in the grain would have increased from 0 at anthesis to 150 kg N/ha 35 days later, i.e. an increase of 4·3 kg grain N/day. This is markedly more than the regression coefficient of 2·2 illustrated in Fig. 7*b* relating grain N yield to delays in flag leaf senescence. There are several reasons for this discrepancy. First, there is no equivalence between the time taken for the flag leaf to senescence and the time to the end of grain filling. Dimmock & Gooding (2002), for example, report that for every 1 day that the senescence of the flag leaf was delayed, the end of grain growth was only delayed by 0·7 days in the most responsive cultivar. Second, it is unlikely that hastening senescence has no effect on the rate of increase in harvest index, and nitrogen harvest index (NHI) is likely to be better conserved than nitrogen capture. For example, if the above example is used, and we assume a linear increase in NHI during grain growth, a 7-day delay in senescence might be expected to reduce NHI by $7 \times 0{\cdot}7 \times 70/35 = 9{\cdot}8$%. In reality, Ruske *et al.* (2001) found no significant effect of a fungicide treatment giving a 7-day delay in senescence on NHI. Conversely, the same treatment increased nitrogen capture in the above-ground crop by 7·6 kg N/ha, i.e. in almost exact agreement with Sylvester-Bradley *et al.* (2001).

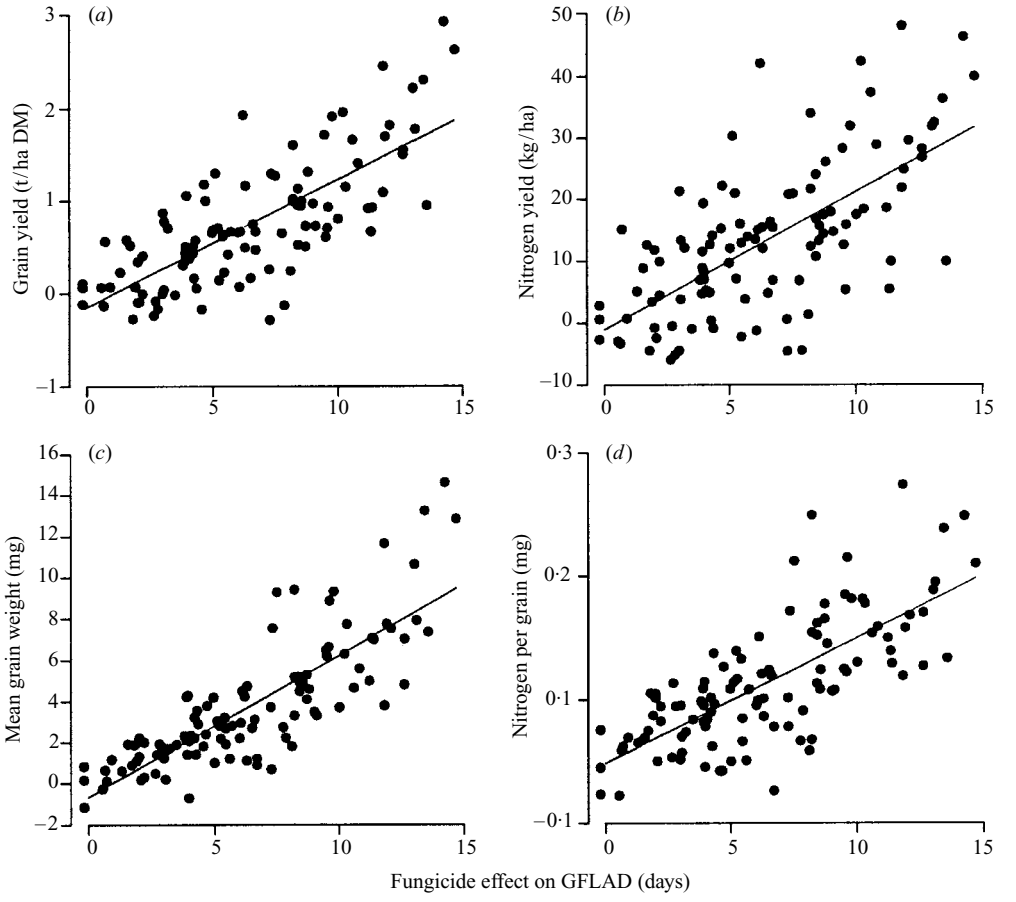

Fig. 7. Relationship between fungicide effects (fungicide treatment mean minus untreated mean) on the duration from flag leaf emergence to 37% flag leaf green area (GFLAD) in 14 separate experiments, and (*a*) fungicide effects on grain yield (regression coefficient (b) = 0·137, S.E. 0·0117), (*b*) fungicide effects on grain nitrogen yield (b = 2·24, S.E. 0·249), (*c*) fungicide effects on mean grain weight (b = 0·689, S.E. 0·0468), and (*d*) fungicide effects on nitrogen per grain (b = 0·0102, S.E. 0·00093).

Implications of reductions in protein concentration following fungicide use

Using the linear relationship in Fig. 7*a* we can calculate, based purely on yield responses, the number of days (D) that a fungicide programme needs to keep the flag leaf alive to justify the cost of the chemical application, i.e.

$$D = \frac{F - c_y}{b_y} \quad (1)$$

where F is the cost of the fungicide programme expressed as a proportion of the value of 1 t of grain, and b_y and c_y are the regression coefficient and constant relating fungicide effects on GFLAD to yield (i.e. 0·137 t/day and −0·144 t respectively). Figure 8 shows how the number of days extra GFLAD that are needed to 'break even' increases as the relative cost of the fungicide programme increases. Nix (1999) suggests that typical fungicide programmes in the UK cost £53/ha and feed wheat is sold at £82·4/t DM, i.e. a relative fungicide cost of 0·64 t of grain. To justify application, Fig. 8 suggests that a typical programme would need to extend flag leaf life by 5·7 days.

The effect of accounting for reductions in protein concentration is more complex. Reductions may have a large impact if they cause premium prices to be forfeited due to failure to make threshold values. Alternatively, sliding-scale reductions in price may be more applicable if grain is blended or sliding scales are imposed directly by purchasers of grain. To simplify this complex situation, we propose that the cost of the reduction in grain protein concentration should never exceed the cost of the amount of late-season foliar urea needed to correct the reduction. Responses to late-season foliar urea are relatively

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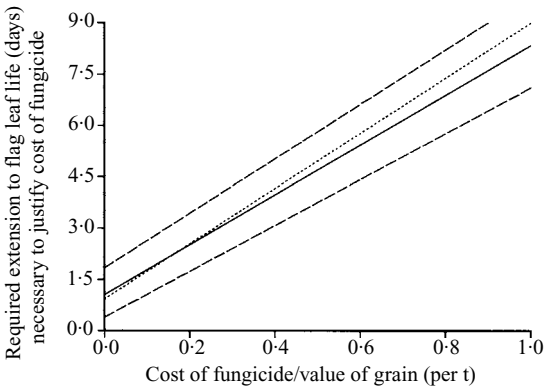

Fig. 8. Effect of relative cost of fungicide on the number of days the fungicide programme needs to extend flag leaf life in order to justify the cost. The solid line accounts for effects on yield, using the relationship illustrated in Fig. 7*a*. The dashed lines show plus and minus S.E. for the constant and the regression coefficient. The dotted line is an attempt to account for the cost of reductions in protein concentration using the relationship illustrated in Fig. 6.

consistent and, as already discussed, do not interact negatively with fungicide treatments. In typical wheat production on sandy loams in the UK, 40 kg N/ha has increased protein concentration from 11·9 to 12·8% (Ruske *et al.* 2001). Assuming a near linear response of protein concentration to rate of late-season urea a 1% increase in protein would need 57 kg N, and assuming a price of nitrogen of £0·33/kg would cost £18/ha or 0·20 t of grain receiving a 10% milling premium (i.e. total value of £90·6/t DM). More generally, costs of protein reduction can be incorporated into Eqn 1:

$$D = \frac{F - c_{cp}N - c_y}{b_y + b_{cp}N} \qquad (2)$$

where N is the relative cost of nitrogen for increasing GPC by 1% (i.e. 0·20 in the example above) and b_{cp} and c_{cp} are the regression coefficient and constant relating fungicide effects on GPC to GFLAD (i.e. the relationship illustrated in Fig. 6).

Using these values results in the dotted line in Fig. 8. This illustrates that the cost of the reduction in protein concentration makes no appreciable difference to the performance required of the fungicide (in terms of extending green leaf life) to 'break even'. In this latter scenario the relative cost of the typical fungicide programme is less because the value of the grain is more. If we again use the figures of Nix (1999) the typical cost of the fungicide programme is still £53 ha/t but milling wheat is sold at £90·6/t DM, i.e. a relative fungicide cost of 0·58 t of grain. The response in Fig. 8 suggests that this could be justified if the fungicide delayed senescence by 5·6 days; i.e. almost exactly the same as when no allowance for protein concentration reduction has been made, and certainly well within the limits of error. This only increases by about 0·7 days if the cost of increasing protein concentration doubles. The only difference to crop management is that, when the reduction in GPC is being accounted for, the delay in senescence of 5·6 days also justifies the use of 20 kg N/ha as late-season foliar urea.

The most marked reductions in protein concentration on a bread-making quality wheat were in 2000 on cv. Hereward. Here the yield response to GFLAD was less than the average ($b_y = 0{\cdot}0887$ t/ha/day, S.E. 0·00922) while the reductions in GPC were greater than the average ($b_{cp} = -0{\cdot}0832$% GPC/day, S.E. 0·0048). Using costs described above in Eqn 1 would suggest that flag leaf senescence would need to be delayed by 7·2 days to justify the expense of the fungicide programme. Incorporating a cost for protein concentration reductions in Eqn 2 increases this requirement to 8·2 days. Again this is well within errors associated with estimating the coefficients involved.

It appears, therefore, that in the special cases where *S. tritici* is the main foliar pathogen controlled, reductions in grain protein concentration following fungicide use should not greatly alter decisions on their adoption for farmers targeting bread-making quality markets. Small expenditure increases associated with greater amounts of foliar urea are sufficient to maintain protein concentrations where high yields of high value crops have been successfully protected from severe disease. The same conclusion is reached by analysing the results from individual experiments assessing factorial combinations of fungicide treatments, foliar urea sprays and cultivars (Ruske *et al.* 2001).

CONCLUSIONS

The use of foliar fungicides in wheat production provides large benefits to both growers and the marketplace in terms of business stability and enhanced security of supply. In addition to yield gains, large increases in nitrogen accumulation and protein yield can be obtained, and most aspects of grain quality are either improved or unaffected by fungicide use. This has been shown to be the case for GPC where rusts (*Puccinia* spp.) and powdery mildew (*E. graminis*) are the main foliar diseases controlled. The use of fungicides where *Septoria* spp. are the dominant pathogens can reduce GPC, but such losses are usually small, and can be diminished or eliminated through application of foliar urea during grain filling at a low cost relative to the overall economic benefits of fungicides. There is no evidence that fungicide effects on GPC should influence choice of either fungicide chemistry or application programme.

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