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Unravelling environmental and genetic relationships between grain yield and nitrogen concentration for wheat

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Abstract

The analysis of the evolution of crop yield reveals a change in grain composition: increases in yield have led to a decrease in the protein to starch or oil ratios. This negative relationship reflects the higher increase of C assimilation compared with N assimilation. For wheat (*Triticum aestivum* L.), flour protein concentration is the main quality criterion, especially for bread making. Therefore, a critical question for the future is how to manage the relationship between yield and N concentration, where the objective is to increase both the level and stability of yield and N concentration. To answer these questions, we need a better understanding of the mechanisms involved in the variations of yield and of its composition. First of all, we need to analyse genetic variability in different environments that allow the identification of genetic sources of variation that can be used for breeding or in more reductionist approaches. In this paper, we used data from controlled environment and field experiments, at canopy and plant level, and at different sink:source ratios to analyse the genetic and environmental relationship between grain productivity and composition. These experiments confirmed the strong negative relationship between grain yield and N concentration. Post-anthesis temperature and water deficit had significant effects on grain yield and protein concentration, but they did not modify the negative relationship between these variables. However, pre-anthesis water deficit decreased the sink:source ratio resulting in a lower intercept, while the slope was unchanged. Nitrogen deficiency also modified the intercept of the negative relationship, but more importantly it decreased the slope three to four-fold. Thus under limiting N conditions, grain N concentration is more sensitive to yield variation than under non-limiting N conditions. Genetic variation of single grain dry mass and of the sink:source ratios had similar effects to the environmental variation. Three major conclusions can be drawn from these results: (1) the negative relationship between grain yield and protein concentration is primarily determined at the stem level; (2) the grain itself is more limiting for starch synthesis than for protein synthesis and (3) overall any increase in yield is followed by an increase of N utilisation and use efficiency.

Keywords: Environmental effect; Genetic variability; Genotype by environment interaction; Grain yield; Grain nitrogen concentration; Sink:source ratio; *Triticum*

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1. Introduction

Over the last 50 years, the yield for various crops has increased by 0.5–2% per year (Cassman, 1999, 2001). This continuous yield increase, due to genetic and crop management progress, has been accompanied by significant changes in grain composition (e.g., Calderini et al., 1995; Simmonds, 1995; Oury et al., 2003). Regardless of the species, the increase in grain yield leads to a decrease in the protein to starch or oil ratio (Triboi and Triboi-Blondel, 2002). For example, in France, average wheat (*Triticum aestivum* L.) yields increased from 2.3 $\mathrm{Mg\,ha^{-1}}$ in 1961 to 7.6 $\mathrm{Mg\,ha^{-1}}$ in 2004, at a constant annual rate of 0.12 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$ (FAOSTAT, 2005). Similar increases occurred in the United Kingdom (Austin, 1999). Concomitantly, grain N concentration decreased by approximately 10 $\mathrm{mg\,g^{-1}}$ DM for a 1 Mg increase in yield (Le Buanec, 1999; Oury et al., 2003). At the local level, year-to-year variations of the climate also induce important variations of both grain yield and N concentration.

Protein concentration in flour is the main quality criterion for wheat, especially for bread making. Therefore, a critical question for the future is how to manage the relationship between yield and N concentration, where the objective is to increase both the level and stability of yield and N concentration. In order to fulfil this objective, through varietal and crop management improvement, we need a better understanding of the effects and mechanisms involved in the variations of yield and yield composition by genotype and environment, and their interactions.

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Agronomists and breeders often use field experiments across different sites and years to evaluate the genotype behaviour in different environments and to identify the best management techniques required for the expression of genetic potential. The negative relationship between yield and N concentration is highly variable and often genetic differences are masked by environmental factors (Oury et al., 2003). To better evaluate the genetic effects, Oury et al. (2003) proposed to reduce environment influences in comparison to genetic effects by examining large genetic variations in a single environment, or to average out environmental effects by using mean values obtained from a network corresponding to a wide range of environments. However, while it is valuable to analyse genetic variability, this statistical approach produces little information about the physiological origins of the observed variations.

Yield realisation is a dynamic process, and is a balance between genetically determined plant demand for growth and development, and the environment supply. There are multiple interactions between biological processes at different levels of organisation that involve competition and compensation mechanisms, which lead to modifications of the size and number of organs. This means that the effect of an environmental factor depends on the developmental stage of the plant. For example, leaf size is modified by factors such as N and light acting during cell division (Gastal and Nelson, 1994; Triboi and Ntonga, 1993). The number of grains, which determines the storage capacity and often reflects the genetic potential, is dependent on C and N availability between meioses and anthesis (Triboi and Ntonga, 1993). Hence, ecophysiological and physiological approaches which describe the dynamics of the relationships between demand and supply or between source and sink are useful tools for improving understanding of genotype × environment interactions. To understand these variations field experiments may be complemented by experiments in controlled conditions, because these allow the separation of environmental factors and studies of their interactions.

At the plant level, this negative relationship between yield and N concentration reflects the fact that C assimilation and accumulation has increased faster than that of N (Lawlor, 2002; Triboi and Triboi-Blondel, 2002). Genetic or environmental effects on the C supply are due mostly to increases in growth duration, especially after anthesis, and not to any improvement in the basic mechanisms of C assimilation (Loomis and Amthor, 1999; Horton, 2000; Richards, 2000). Experimental and modelling results have shown that grain N accumulation is mostly source determined (Martre et al., 2003). Under non-limiting N supply conditions, about 80% of the N accumulated in the grains come from the N stored in the plant at anthesis. To increase the N:C ratio we must increase the capacity of plants to store N or/and to uptake more N after anthesis. Even though these processes are highly conservative and their regulations are not so well understood, genetic differences for N uptake and utilisation have been shown for wheat (Le Gouis et al., 2000).

To progress in this area, first of all we need to analyse the genetic variability in different environments in order to identify the genetic sources of variation for breeding or use in a more reductionist approach. In this paper, we report several experiments carried out to analyse at the canopy and whole plant levels the genetic and environment relationship between grain yield and N concentration for different varieties of wheat (*Triticum aestivum* L.). Two hypotheses were tested: (a) the negative correlations between yield and protein concentration describe the variability induced by both genetic and environment factors and their interactions; (b) these relations are conservative with few genetic variations.

2. Materials and methods

2.1. Plant material and growth conditions

In 1997–1998 and 2001–2002, wheat crops were grown in semi-controlled conditions and in the field with different N supply, temperature and watering regimes. In 2002–2003, the genetic variability of the negative relationship between grain yield and N concentration was assessed for 17 cultivars grown in pots. In this latter experiment, the effect of an artificial reduction of the sink:source ratio by ear halving was also analysed. All the experiments were done at Clermont-Ferrand, France (45°47′N, 3°10′E, 329 m elevation).

2.1.1. Effects of water deficit at different developmental stages, and temperature × water deficit interactions during grain filling (Experiment 1)

The effects of temperature and water deficit were studied in 1998 for the winter wheat cultivar Thésée (Table 1). Crops were grown outside in 2 m^2 containers 0.5 m deep, filled with a 2:1 mixture of black soil:peat. Compared with field conditions, these semi-controlled conditions allowed a better control of the quantity of water and nitrogen available to the crops in relation to developmental stage. Seeds were sown at a density of 500 seed m^{-2}, resulting in 371–463 ear m^{-2} at anthesis. Nitrogen was supplied as ammonium–phosphate (N:P, 18:46); 3 g N m^{-2} was applied about 1 week after the beginning of tillering, 10 g N m^{-2} when the stem started to elongate, 10 g N m^{-2} at meiosis, and 10 g N m^{-2} at anthesis. The high plant density inhibited the development of axillary tillers, which co-ordinated the development of the crops within the containers. From sowing to anthesis, the crops received an average of 226 and 238 mm of rainfall and watering, respectively.

The interaction between water deficit and crop developmental stage was studied by withholding water during six different periods of time (Table 1): from 28 d (393 °Cd) before anthesis to anthesis (i.e., the period during which grain number is set; treatment DW), from 28 d (393 °Cd) or 16 d (253 °Cd) before anthesis to harvest maturity (DD and dD, respectively), from anthesis to harvest maturity (WD), or only during the linear grain filling period (from 11 d [170 °Cd] to mature harvest, Wd). The control treatment (WW) received sufficient water to replace measured crop evapotranspiration (measured at crop level under outdoor controlled-environment chambers). To control the crop water supply, the six containers were transferred under a mobile rain shelter. The effect of the rain shelter on incident radiation and canopy temperature was negligible since it covered the crops only during rainfall. During the period when water was withheld,