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Is time to flowering in wheat and barley influenced by nitrogen?: A critical appraisal of recent published reports

Antonio J. Hall[a], Roxana Savin[b,*], Gustavo A. Slafer[b,c]

[a] IFEVA, Facultad de Agronomía UBA/CONICET, Av. San Martín 4453, C1417DSE Buenos Aires, Argentina
[b] Department of Crop and Forest Sciences, AGROTECNIO (Center for Research in Agrotechnology) University of Lleida, Av. Rovira Roure 191, 25198 Lleida, Spain
[c] ICREA (Catalonian Institute for Research and Advanced Studies), Spain

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ABSTRACT

The literature includes a number of reports, relating to both crop and non-crop species, showing conflicting responses of developmental plasticity to nitrogen availability. We reviewed 1130 papers published from 1990 to 2010 drawn from 14 agriculture-themed journals and conducted a critical appraisal of the effects of fertiliser nitrogen on time to heading or anthesis in barley and wheat, species for which there is a good deal of data. Features of the analysis were the use of relative responses (respect to unfertilised controls) of yield and time to flowering to nitrogen as a proxy for crop nitrogen status and developmental differences, respectively, and the standardisation of the start point for calculating time (in both calendar and thermal units) to flowering in autumn-sown winter cultivars to March 1 (N Hemisphere). The resulting database (180 cases) covered a broad range of unfertilised crop yields (1–8 Mg ha^{-1}), and times to flowering (47–168 days). In very few cases (19 out of 118), the relative time to flowering in fertilised crops differed by more than 5% from those of unfertilised crops across a range of yield responses to fertiliser nitrogen from negligible to three-fold. Currently available evidence does not provide solid support to a plastic response of time to flowering to nitrogen in these two species.

1. Introduction

Timing of flowering is critically important in determining yield of grain crops (Evans, 1993), because it defines crop adaptation, a property reflecting the best match between the seasonal dynamics of environmental conditions (which may be either positive or negative in their effects) and crop requirements for yield formation and realisation (Araus et al., 2002; Slafer, 2003). Shifts in timing can alter both the number of grains set per unit area (e.g., Fischer, 1985; Slafer and Rawson, 1994; Slafer et al., 2009) and their average weight (e.g., Fischer, 1984; Chimenti et al., 2001; Poggio et al., 2005). These effects can arise, even under irrigated conditions, through the crops being exposed to more or less favourable combinations of radiation and temperature or temperature alone during the windows of development for grain number and grain weight determination, respectively. If grain number determination and grain filling take place under increasingly stressful conditions (e.g., terminal drought, increasing seasonal temperatures) and if flowering is delayed, impacts on yield can be even greater than under non-stressed conditions (e.g., Stapper and Fischer, 1990).

The most important environmental factors regulating time to flowering in wheat and barley are daylength and temperature (via both the positive effects of temperature and those operating through vernalisation). A large body of literature describes the effects of these two factors on cereal development (e.g., Miralles and Slafer, 1999; García del Moral et al., 2002; Slafer et al., 2009 and references cited therein). However, in several studies aimed at exploring yield responses to nitrogen (N) fertilisation in cereals and other crops, effects of N availability on time to anthesis have also been reported (e.g., Birch and Long, 1990; Fischer et al., 1993; Williams and Angus, 1994; Prystupa et al., 2003; Guarda et al., 2004; Massignam et al., 2009; Van Oosterom et al., 2010). Characteristically, in these and other reports, the effects of N on crop phenology are noted, but there has not been any systematic attempt to analyse the occurrence and importance of these effects across a broad spectrum of reports.

It has been argued, from the viewpoint of evolutionary ecology (e.g., Bradshaw and Hardwick, 1989; Sultan, 2000; Pierce et al., 2005), that plastic responses of development in annual species to stress, including both water and nutrient stresses, could improve ecotype fitness (i.e., the ability to contribute the next generation). In this context, the expected response to a restriction in resource availability is an increase in the rate of development, which translates into a reduced time to flowering and a shorter overall life

* Corresponding author. Tel.: +34 973 702853; fax: +34 973 702690.
E-mail address: savin@pvcf.udl.cat (R. Savin).

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cycle. Attempts to demonstrate the existence of a response of this nature in several species have revealed a rather more complex picture. To cite a few examples, Pigliucci and Byrd (1998) found low N *lengthened* the duration of the germination-to-bolting phase in two out of 17 *Arabidopsis thaliana* ecotypes, but had no effect on development in the remaining ecotypes; and Pigliucci and Schlichting (1995) found that reductions in the dose of slow-release N–P–K fertiliser produced a shortening of between 2 and 22 days in time to bolting in 6 out of 26 *A. thaliana* accessions, an increase of 60 days in one accession, and no response in the remaining ones. Sorensen (1954) found that nutrient stress reduced time to flowering in sand dune populations of *Capsella bursa-pastoris* but had no effect on development in populations from a fertile grassland. Galloway (1995) found flowering in clonally reproduced populations of *Mimulus guttatus* to occur earlier in low resource availability environments (a categorisation which probably confounded water and nutrient effects). Volis et al. (2002) found a slight acceleration of development under low nitrogen treatment, both under water-stressed and non-water stressed conditions, in all 4 ecotypes of *Hordeum spontaneum* obtained across a rainfall transect spanning a 90–1600 mm y^{-1} range. In what is possibly the most detailed study published to date on nutrient effects on development in *A. thaliana*, Kolar and Senkova (2008) found that extreme nitrogen deficiency produced a strong (equivalent to 29% of the control values) shortening of time to bud appearance.

The responses of development to N in cultivated species appear to be equally varied. Williams and Angus (1994) found that application of 250 kgN ha^{-1} delayed flowering in rice by 8–19 days in 11 out of 12 treatment combinations of cultivar by time-of-sowing by floodwater depth. In this example, the early-sown 0 N treatments yielded in the order of 6–8 Mg ha^{-1} of grain, which suggests that the N-stress in this treatment, although real, was moderate. By contrast, Van Oosterom et al. (2010) reported a reduction in time to anthesis in three sorghum hybrids of between 6 and 9 days in response to the addition of 353 kgN ha^{-1}, with yields of the unfertilised control in the order of 4 Mg ha^{-1} of grain. Gungula et al. (2003) reported reductions in times to silking of between 3 and 10 days in response to the application of 120 kgN ha^{-1} in seven maize cultivars; and Massignam et al. (2009) reported reductions of time to anthesis in maize (9–10 days) and sunflower (16 days) in response to applications, before anthesis, of between 50 and 250 kgN ha^{-1}. In controlled environment conditions, and for wheat, Angus and Moncur (1985) reported a slight acceleration of rate of development when plants were subjected to low levels of N in the nutrient solution after floral initiation, and Nerson et al. (1990) found that 85 ppm of N in the nutrient solution shortened the time to terminal spikelet initiation (with respect to 5 ppm N) by between 16 and 22 days, depending on the levels of P in the solution. By contrast, Longnecker et al. (1993) found little effect of N level on timing of anthesis in micro-plots grown outdoors. In sunflower, Steer and Hocking (1983) found that levels of nitrogen supply low enough to severely curtail plant leaf area at anthesis had only minor effects on timing of anthesis.

Changes in timing of anthesis in response to nitrogen as large as those reported by Williams and Angus (1994), Massignam et al. (2009), Gungula et al. (2003) or Van Oosterom et al. (2010), or those found by Kolar and Senkova (2008) or Nerson et al. (1990) certainly have the potential to impact yield quite markedly if these changes lead to crops being exposed to changed environmental conditions during the grain number determination and grain filling phases. A further dimension of this issue is the possibility that substantial differences in nutrient supply within a given experiment might produce effects on yield that were mediated by indirect effects of nitrogen on development rather than the more usually considered effects of this nutrient on spike biomass accumulation at anthesis

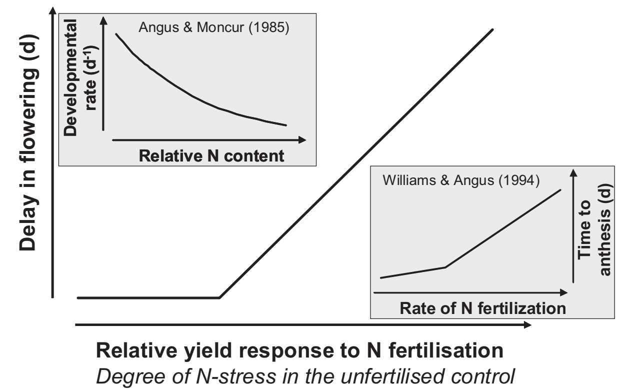

Fig. 1. Hypothetical response function for delay in flowering (heading or anthesis) in wheat and barley to the degree of N-stress experienced by the unfertilised control (reflected in the relative magnitude of the yield response to N). Insets show schematic response functions embodied in data reported for wheat (upper-left inset; Angus and Moncur, 1985) and rice (bottom-right inset; Williams and Angus, 1994). Note that development rate (*y*-axis, upper-left inset) is the inverse of time to anthesis.

(Stockman et al., 1983; Fischer, 1993; Abbate et al., 1995; Prystupa et al., 2004) and on floret survival (Ferrante et al., 2010, 2013).

Information on N effects on flowering time is highly dispersed in the literature, and even when those effects were large, researchers have often noted them in passing, without attempting to consider the subject in a broader context or trying to link the effects with some indicator of crop nitrogen response. This paper attempts to shed light on this issue through a critical appraisal of reports, published during the last twenty years in high-impact journals specialising in agriculture, of the effects of fertiliser nitrogen on time to either heading or anthesis in wheat and barley, using crop yield responses as a proxy for crop nitrogen status. We have focussed on the responses to nitrogen in wheat (both bread and durum) and barley (both two- and six-row) because of the more abundant (with respect to other crop species and nutrients) volume of experiments in which both variables (time to flowering and yield) have been recorded.

Given conflicting reports about the effects of nitrogen on development (slowing or accelerating rates of development), we were particularly interested in trying to establish whether there was a consistent pattern of flowering time response to nitrogen in these cereals. We also sought to test the ideas of Angus and Moncur (1985) and Williams and Angus (1994) who, in the only detailed published model proposed for these responses in wheat, suggested a non-linear response of flowering time to N application (Fig. 1). A response function of this form might explain why in some cases (highly N-stressed controls) there is a developmental response while in others (mildly to moderately N-stressed controls) phenology is largely unaffected by fertilisation. A further feature of our analysis is that we used the relative (to unfertilised control) response of yield to nitrogen (rather than relative N content of the crop or the rate of N fertilisation) as a rough proxy for the degree of N-stress the unfertilised crop was subjected to.

The reports considered in this appraisal cover both winter and spring forms of these three species. Because much of the growth and development of crops of the winter forms takes place during the spring–summer that follows an autumn sowing, we have used time from the beginning of March (N Hemisphere) to heading/anthesis as an indicator of development in order to avoid undue bias (through diminution) against the relative developmental rate of the winter forms. We restricted our coverage to field-grown crops or micro-crops grown in large containers under field conditions to avoid the effects on development and yield which frequently occur in the low-irradiance conditions typical of controlled environment