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

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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

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

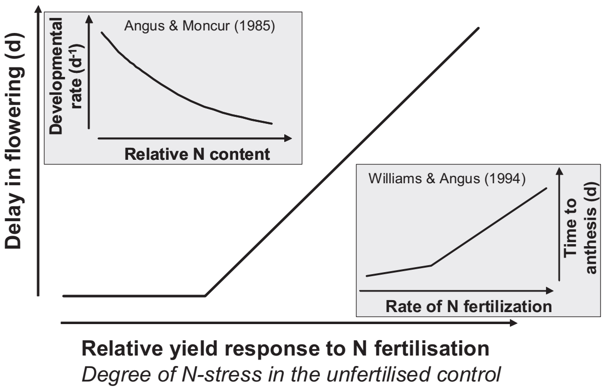

Fig. 1. Hypothetical response function for delay in flowering (heading or anthesis) in wheat and barley to the degree of N-stress experienced by the unfertilised control (reflected in the relative magnitude of the yield response to N). Insets show schematic response functions embodied in data reported 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.

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

Table 1
Journals scanned for relevant articles during the 1990–2010 period and number of tagged articles per journal. Search strings used: TITLE ("nitrogen and wheat") and TITLE ("nitrogen and barley").

Journal	Number of articles meeting search criteria
Agricultural and Forest Meteorology	4
Agronomy Journal	142
Agronomy and Sustainable Development	267
Agricultural Water Management	15
Annals of Applied Biology	11
Australian Journal of Agricultural Research	56
Australian Journal of Experimental Agriculture	43
Crop Science	37
European Journal of Agronomy	52
Field Crops Research	78
Journal of Agricultural Science (Cambridge)	120
Journal of Agronomy and Crop Science	112
Journal of Plant Nutrition and Soil Science	19
Plant and Soil	174
Total	1130

experiments (as well as in many glasshouse studies). In addition, we have only covered experiments in which nitrogen was applied at (rarely, before) sowing or up to the onset of stem elongation. Although some reports that we reviewed included data on developmental stages other than heading/anthesis, there were too few of these to allow for any substantial analysis of the effects of N on the timing of these stages.

Other responses of crop development to N than those summarised in Fig. 1 have been proposed. Thus, the STICS (Brisson et al., 2003) crop simulation model includes a N stress effect (a delay in flowering) as part of its phenology module, and this effect only comes into to play at very high levels of stress. In this, STICS differs from other widely used crop simulation models (e.g., CERES-Wheat in DSSAT-CSM (Jones et al., 2003); APSIM-Wheat (Wang and Engel, 1998); AFRCWHEAT2 (Ewert et al., 1996); and Sirius (Jamieson et al., 2007), all of which assume phenology is not affected by N. It should also be noted that the response function included in STICS, unlike those shown in Fig. 1, assumes that added N hastens, rather than delays, flowering.

2. Materials and methods

2.1. Literature search

To select papers reporting yield and time to heading or anthesis in response to N fertilisation in wheat and barley following objective criteria, we searched (using the search engines provided by each journal) the indexes of selected journals for article titles that included the words "nitrogen" and "wheat" or "barley" published in all years between 1990 and 2010. The selected journals were those included in the top quartile (impact factor ranked) of the ISI Web of Science (consulted September 14, 2010) for the categories of "Agronomy" and "Agriculture, Multidisciplinary". Within these top quartiles, we removed journals we judged as unlikely to contain reports of the kind we were searching for (e.g., journals specialising in weeds, insect pests, plant diseases, soil science, livestock husbandry and nutrition, basic breeding and biology, cropping systems, ecology, modelling, and so on), and ended up with a selection of 14 journals (Table 1). A total of 1130 articles in the selected journals met the search criteria.

Articles meeting the search criteria (Table 2) were reviewed, and those relating to experiments that included treatments involving more than one level of N applied between sowing (or immediately previous to planting) and the onset of stem elongation and which also reported the timing of heading or anthesis and grain yield were used to construct the database used in this critical appraisal. In the cases in which there were uncertainties of interpretation of the published data and/or in which we had to estimate yield or date of heading/anthesis from the published figures, we consulted with the authors, many of whom very generously invested their time in satisfying our queries. In some instances, we extracted data for some of our key variables from one paper and data for other variables (obtained in the same experiment) from a companion paper or a paper by other authors whose data had been used in the article retrieved by our literature search. This led us to occasionally use data published outside the 1990–2010 period and/or from journals not included in Table 1. In one case, we added to our database unpublished results provided by researchers we had consulted (Table 2).

2.2. Data standardisation and filtering

We standardised the time to heading or anthesis (whichever was provided by the authors) of treatments receiving additional N by expressing these values relative to that of the unfertilised controls. For simplicity, we refer to either of these stages as "flowering", assuming that time to heading (the phasic development variable most frequently reported) is a reasonable approximation to time to anthesis, particularly if expressed in relative (to unfertilised control) terms. In all cases these phenostages were reported for the crop, with no distinction being made between the main culm and tillers. In order to make the comparisons between autumn-sown winter cultivars and winter-sown facultative/spring cultivars more realistic, times to anthesis or heading for experiments involving the former category were recalculated as from March 1 (N Hemisphere). This standardisation is physiologically reasonable insofar as fully vernalised winter cultivars flower after producing a similar number of leaves to that of vernalisation insensitive spring cultivars (e.g., Wang et al., 1995), and there is very little plant growth during the winter period. Omitting this standardisation would have resulted in reducing any possible difference in relative time to flowering in autumn-sown winter cultivars. The use of relative values (to unfertilised controls) for time to heading/anthesis and the adjustment for winter/spring cultivar types, though necessarily approximate, should also remove much of the effects of earliness per se, vernalisation and photoperiod controls on crop development (crop cycle duration), together with those of geographical variation in climate (temperature) and time of sowing.

In order to compare the relative effects of N on crop development across experiments, we linked these to the relative (to the unfertilised treatment in each experiment) effects on yield. This standardisation procedure is agronomically reasonable since the dominant reason for N fertiliser application is to increase yield. Additionally, and although yield responses to N are not linear, the use of relative values moderates the differences between experiments in initial available soil N stock and mineralisation capacity, as well as those caused by experiment effects, which can be quite marked in rainfed crops in water limited environments. In order to establish the significance of differences between species in the variability of their response to fertilisation we used homogeneity of variance test (Levene, 1960).

To assess the association between variables we used linear regression analysis. As in our data sets the values of both "x" and "y" variables are subject to error (neither of them was controlled by the experimenters), we used Model II regression (Niklas, 1994; Ludbrook, 2012) to fit functions.

3. Results

Yields of unfertilised controls ranged from less than 1 to around 7 Mg ha^{-1} in wheat, and from ca. 1.5 to almost 8 Mg ha^{-1} in barley

Table 2
List of articles published during the 1990–2010 interval and personal communication from which data was extracted.

Reference	Main treatments
Abbate et al. (1995)	1 wheat genotype × 2 years × 4 N levels
Arisnabarreta and Miralles (2004)	2 years × 4 barley genotypes × 2 N levels
Arisnabarreta and Miralles (2006)	
Arisnabarreta and Miralles (2010)	2 barley genotypes × 2 N levels
Barraclough et al. (1989)	1 wheat genotype × water × 2 N levels
Porter (1993)	
Birch and Long (1990)	3 barley genotypes × 5 N levels
Delogu et al. (1998)	3 years × 1 barley genotype × 1 wheat genotype × 3 N levels
Dreccer et al. (2000)	1 wheat genotype and 3 N levels
Ferrise et al. (2010)	1 wheat genotype × 2 years × 2 sowing dates × 4 N levels
Fischer (1993)	2 exps × 1 wheat genotype × different N
Fischer et al. (1993)	levels × timing of N applications
Guarda et al. (2004)	4 years × 16 wheat genotypes × 3 N levels
Hocking and Stapper (2001)	1 wheat genotype × 3 sowing dates × 2 N levels
Kernich and Halloran (1996)	2 exps × 2 barley genotypes × 2 N levels
Martre et al. (2006)	1 wheat genotype × 3 initial N conditions
Triböı et al. (2003)	
Newton (2001)	1 wheat genotype × 4 stubble conditions × 2 N levels
Peltonen (1993)	2 wheat genotypes × 2 N levels
Prystupa et al. (2003)	1 barley genotype × 2 N levels × 3 P levels
Prystupa et al. (2004)	1 barley genotype × 2 N levels × 3 P levels
Rodriguez et al. (2005)	1 wheat genotype × 2 water treatments × 4 N levels × 2 sowing densities
Salvagiotti and Miralles (2007)	2 exps: (i) field 1 wheat genotype × 2 years × 4 N levels × 2 S levels, (ii)
Salvagiotti and Miralles (2008)	containers 1 wheat genotype × 2 N levels × 2 S levels
Smith et al. (2000)	1 wheat genotype × 2 N levels
Subedi et al. (2007)	1 wheat genotype × 2 locations × 3 sowing dates × 3 N levels
Valle and Calderini (pers. comm.)	1 wheat genotype × 2 N levels

(Fig. 2a). Calendar or thermal times from either 1 March (winter cultivars) or sowing (facultative/spring cultivars) to flowering also ranged widely (Fig. 2a). Across experiments and as expected, there was no relationship between yield of unfertilised crops (heavily influenced by resource availability and management in each experiment) and duration of pre-flowering growth (heavily influenced by photoperiodic and thermal conditions of each experiment) for any of these cereals (Fig. 2a).

In most cases, fertilisation increased yields of both wheat and barley (Fig. 2b). Although there was a good deal of dispersion among data points, the magnitude of this response tended to be positively related to the yield level of the unfertilised control (see line of best fit with Model II regression for both crops in Fig. 2b). The response to N appeared (see Fig. 2b) to have been slightly more variable in barley than in wheat ($F = 1.49$, $P = 0.07$), implying that yield responded to N fertilisation in barley similarly to, or even more markedly than, in wheat. Yield responsiveness to N varied very widely, ranging from negligible values to extremely large responses of several tonnes of grain/ha representing, depending on the yield of the control, yield increases of up to 300%. The range actually extended into negative yield responses, although these were exceptional (only 4 out of the 118 responses analysed were negative, and only 2 of them departed substantially from the 1:1 ratio line in Fig. 2b). In addition, the intercept of the regression line fitted to the pooled data points did not differ significantly from 0.

Taking all data points included in the database together, and unlike what was hypothesised, there were very small, mostly negligible, changes in absolute time to flowering in response to added N (Fig. 3a). Even in those cases in which the unfertilised controls were severely N-stressed, leading to relative yield increases with added N that exceeded 100%, there was little or no change in relative responses to flowering (Fig. 3b). The lack of relationship between relative responses of flowering and of yield was not simply a consequence of lumping all the data points from the different sources together: analysing the data from each of the papers separately showed there were no cases in which the relative response of flowering to N fertilisation were related to that of yield (i.e., the slopes of the relationship between the two variables within each data set did not differ significantly from 0; data not shown).

When the responses to N fertilisation of relative time to flowering are examined in greater detail via alteration of the scales of the "*y*" and "*x*" axes (Fig. 3b, inset), it was found that only 19 out of 118 cases for relative response to N of time to flowering departed more than 5% from the line representing complete insensitivity, and in the majority of cases (12 out of 19) in which these departures occurred they were positive. In neither of the two subsets of departures (i.e., positive or negative) from insensitivity was there any indication of an association between relative responses of flowering and of yield. Thus, for the subset of positive departures, the response functions posited in Fig. 1 do not appear apply, something which applies even more strongly for the negative-departure subset. This subset, in which flowering was advanced (by up to 15%, or almost 200 °C d) in response to N-fertilisation derived from a single set of two experiments (Arisnabarreta and Miralles, 2004, 2006) and they contrast with results from another independent study by the same authors (Arisnabarreta and Miralles, 2010) in which time to flowering in these same barley lines did not respond to N-fertilisation at all. In both studies the controls were severely N-stressed and yield responded markedly to N-fertilisation.

Time to flowering can, in first approximation, be viewed as the summation of two developmental phases (sowing or emergence to awn initiation [barley] or terminal spikelet [wheat], and from these stages to heading/flowering) or as the product of final leaf number by phyllochron (or subsets of these variables). Only two of the papers reviewed in the present exercise included data guided by these approaches (Kernich and Halloran, 1996; Salvagiotti and Miralles, 2007). In both sets of experiments, the fertilised treatment yielded between 11% and 94% more than the unfertilised controls. Contrasts between these extreme treatments for durations of the two pre-anthesis subphases, for final leaf number and for phyllochron revealed that in most cases there was no effect of N fertilisation on any of the developmental traits considered and in the few cases in which there was a response, it showed to be rather small and with no consistent patterns. There was, however,

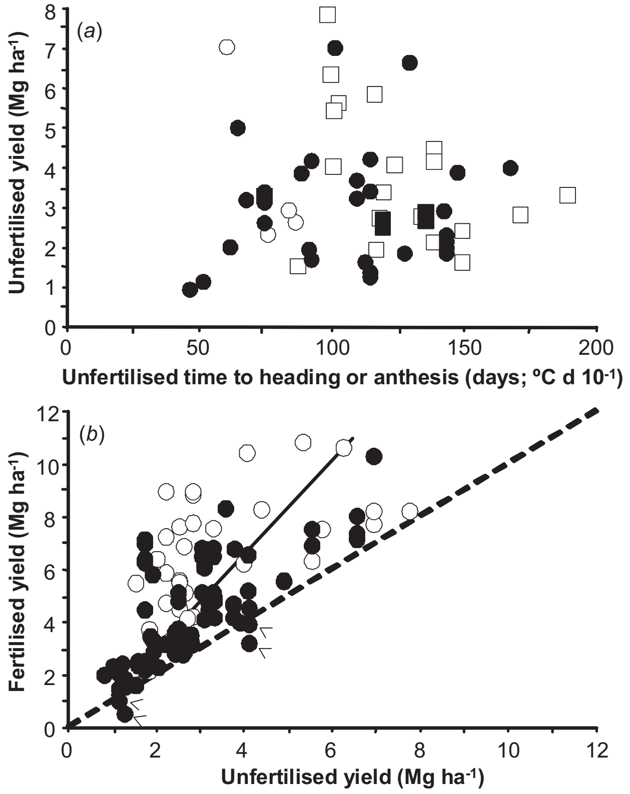

Fig. 2. Relationships between grain yield in the unfertilised control crops and calendar (circles) or thermal (squares) times to heading or anthesis (a); and the relationship of yields in fertilised and unfertilised crops of both cereals (b). In both panels, closed symbols are wheat and open symbols are barley. The times to heading or anthesis in (a) are in days or degree-days from March 1 for winter types sown in autumn in the Northern hemisphere and from sowing in all other cases. In (b) yield responsiveness to fertilisation is the vertical distance from a data point to the dashed line standing for the 1:1 ratio. The continuous line represents the line of best fit (Model II regression) to the fertilised to unfertilised relationship for both species (−0.82 (±0.66) + 1.85 (±0.19), $r^2 = 0.44$, $P < 0.01$). Many data points (in (a) $n = 65$; in (b) $n = 118$) are not visible as they overlap. The arrow-heads in (b) indicate the 4 cases in which yield of the fertilised crop was lower than that of the unfertilised control.

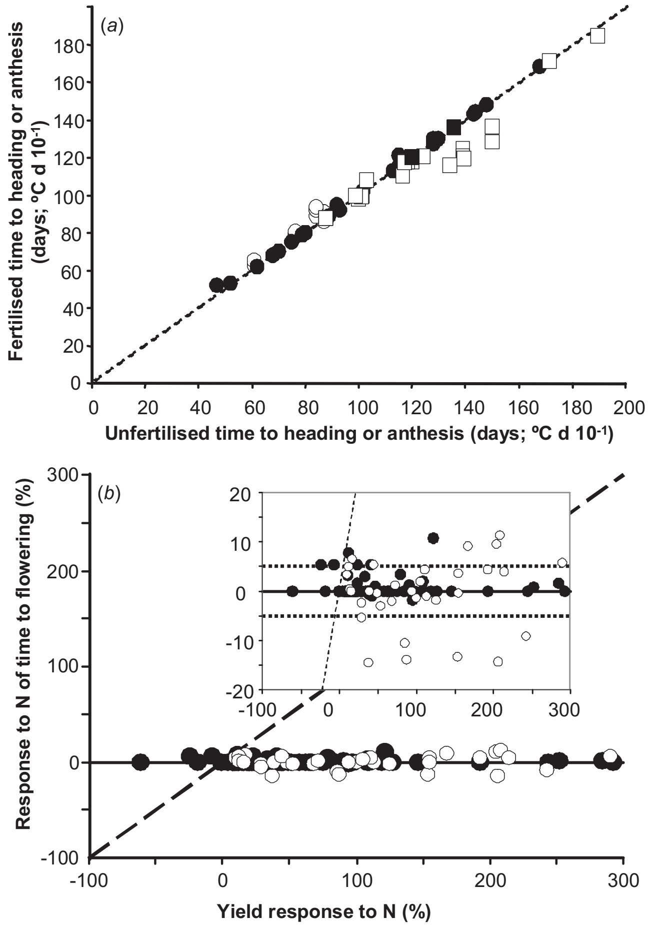

Fig. 3. Time to heading or anthesis in fertilised vs. unfertilised treatments (a), and relationship of the relative responses to fertilisation of time to heading or anthesis and grain yield with the same scale for both variables (b). Inset in (b) shows a detail of the main panel with an expanded "y" axis scale, and horizontal lines (thin dashes, thick continuous, and thin continuous) indicate +5%, 0% and −5% responses, respectively. Results for wheat (closed symbols) and barley (open symbols). In panel a, time is in calendar (circles) or thermal units (squares). In all cases, times are days or degree-days from March 1 for winter types sown in autumn in the Northern hemisphere and from sowing in all other cases. Dashed lines stand for the 1:1 ratio. Many data-points ($n = 118$) are not visible as they overlap. The Model II regression function in panel a is $y = 5.84\ (\pm 1.82) + 0.94\ (\pm 0.01x)$, $r^2 = 0.97$, $P < 0.01$.

some indication of counteracting responses to N of leaf number and phyllochron (data not shown).

4. Discussion

The data set we constructed was well suited to testing the hypothesis that the responsiveness of wheat and barley development to N fertilisation might be related to the magnitude of N stress in the unfertilised plots. The range of yields in the unfertilised controls was very broad (Fig. 2a) and responsiveness to fertilisation varied widely across experiments and treatments from negligible to three-fold (Fig. 2b). This implies that the controls in the various experiments included in the dataset effectively explored conditions from no soil N stress through moderate to extremely severe stress. Within the extremely wide range of yield responsiveness to N, negative responses to yield occurred only exceptionally (Fig. 2b, arrows). It is likely these negative responses were due to haying-off (a negative yield response to N fertiliser in which vigorous vegetative growth leading to enhanced consumption of water early in the season is followed by terminal drought resulting in pinched grains (see Van Herwanarden et al. (1998) and references therein).

Although not central to our aim, it is worth noting that our appraisal revealed that yield responsiveness to N fertilisation in barley was at least similar to that of wheat (Fig. 2b). This observation conflicts with the belief, generalised in the Mediterranean region, that barley is more adapted to marginal areas (Ryan et al., 2008) and that its yield responds to fertilisation less and more erratically than that of wheat. On the other hand, the similarity in responsiveness of barley and wheat found in the current analysis is consistent with the results of recent comparative studies of the two cereals across different water by N treatments in Mediterranean Spain (Cossani et al., 2007, 2009).

The papers used to construct our database only exceptionally included information on the components (time to awn initiation or terminal spikelet formation and time from then to flowering; or final leaf number and phyllochron) of time to flowering. In these exceptional cases, there seemed to be small effects on leaf number and phyllochron which compensated each other and consequently did not affect total time to flowering, something which has been reported by others (Prystupa et al., 2003; Longnecker et al., 1993; Longnecker and Robson, 1994). On this limited basis, it seems clear that the lack of clear effects of N fertilisation on time-to-flowering in wheat and barley also reflects the fact that its components were also insensitive to N or exhibit very small responses in opposite directions. In a recently published paper reporting the development of floret primordia in durum wheat it was clear that N fertilisation did not affect the rate of development, nor the timing of pollination, of the florets which became fertile in any of the four cultivars analysed (Ferrante et al., 2013). This finding is consistent with the notion that N can hardly affect time to flowering if the developmental patterns of the florets which become fertile, and whose pollination mark the flowering stage, are rather insensitive to N.

Although our database covered a broad range of yield responses to fertiliser N, we found no indication of a substantial plastic response to applied N of time to flowering in wheat and barley, independently of the level of N stress in which the unfertilised control had been subjected to (Fig. 3 b). In few cases some positive departures from developmental insensitivity to N supply were found (Fig. 3b, inset, values above the 5% line), a result that is partly consistent with the proposed response functions set out in Fig. 1. But these departures were categorical (i.e., fertilised vs. non-fertilised) across the whole range of relative yield responses to N rather a graduated response to increased fertiliser levels as suggested in Fig. 1. There were also few negative departures from insensitivity, whose magnitude again seemed unrelated to the level of N stress in the unfertilised control (Fig. 3b, inset). It is important to note that although few in number, coming from a single paper, and inconsistent with another paper published by the same authors and with the same genotypes, these negative responses are consistent with what has been observed in crops such as maize, sorghum, and sunflower (Gungula et al., 2003; Massignam et al., 2009; Van Oosterom et al., 2010). It may be that determination, by the observer, of flowering in these latter species, with less inflorescences per unit crop area, is more straightforward than in small-grain cereals in which the dispersion of flowering across main stems and tillers may make it harder to define the precise timing of crop flowering.

A clearer resolution of the issue of the magnitude and sense of possible plastic responses to N of time-to-flowering in wheat and barley will require much more focused, careful and detailed experimentation and observation than that which characterised the reports included in this appraisal, in which yield rather than phenology was the main objective. In spite of the almost complete absence of evidence suggesting that tillers (a very N-responsive component of crop yield) reach anthesis at times very different to the main culm (e.g., Ewert et al., 1996 and references therein) under conditions of good N nutrition, careful distinction of flowering in main culms and tillers, especially under N-stress, should be included in these more detailed experiments. Absent work of that kind, our conclusion of limited or no effect of N on time-to-flowering in wheat and barley remains the interpretation of available data with the most evidential support and is consistent with the decision of modellers interested in these crops who have not included a response of phenology to N in their models.

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