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Review

Interactions between water and nitrogen in Australian cropping systems: physiological, agronomic, economic, breeding and modelling perspectives

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Abstract. This paper reviews the interactions between water and nitrogen from physiological, agronomic, economic, breeding and modelling perspectives. Our primary focus is wheat; we consider forage crops, sorghum and legumes where relevant aspects of water–nitrogen interactions have been advanced.

From a physiological perspective, we ask: How does nitrogen deficit influence the water economy of the crop? How does water deficit influence the nitrogen economy of the crop? How do combined water and nitrogen deficit affect crop growth and yield? We emphasise synergies, and the nitrogen-driven trade-off between the efficiency in the use of water and nitrogen. The concept of nitrogen–water co-limitation is discussed briefly.

From agronomic and economic perspectives, the need to match supply of nitrogen and water is recognised, but this remains a challenge in dryland systems with uncertain rainfall. Under-fertilisation commonly causes gaps between actual and water-limited potential yield. We discuss risk aversion and the role of seasonal rainfall forecasts to manage risk.

From a breeding perspective, we ask how selection for yield has changed crop traits relating to water and nitrogen. Changes in nitrogen traits are more common and profound than changes in water-related traits. Comparison of shifts in the wheat phenotype in Australia, UK, Argentina and Italy suggests that improving yield per unit nitrogen uptake is straightforward; it requires selection for yield and allowing grain protein concentration to drift unchecked. A more interesting proposition is to increase nitrogen uptake to match yield gains and conserve protein in grain. Increased stomatal conductance is a conspicuous response to selection for yield which partially conflicts with the perception that reduced conductance at high vapour pressure deficit is required to increase water- use efficiency; but high stomatal conductance at high vapour pressure deficit may be adaptive for thermal stress.

From a modelling perspective, water and nitrogen are linked in multiple ways. In crops where water limits growth, reduced biomass reduces nitrogen demand. Reciprocally, nitrogen limitation during crop expansion reduces leaf area index and increases the soil evaporation : transpiration ratio. Water–nitrogen interactions are also captured in the water-driven uptake of nitrogen by mass flow and diffusion and in the water-driven processes of nitrogen in soil (e.g. mineralisation).

The paper concludes with suggestions for future research on water-nitrogen interactions.

Additional keywords: drought, nitrogen use efficiency, profit, rain, yield gap.

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Introduction

Management practices that increased the availability of nitrogen and water have been major drivers of gains in crop yield on historical time scales (Sinclair and Rufty 2012). Except for some regions of high rainfall and fertile soil, water and nutrient scarcity are widespread features of Australian dryland farming (Angus 2001; Connor 2004; Fischer 2009).

Interactions between water and nitrogen influence processes from ecosystem to molecular levels. Water–nitrogen interactions modulate the geochemical cycling of nitrogen, shape functional diversity of plants and niche segregation, and affect crop yield, grain size and protein, root demography, leaf stoichiometry, photosynthesis and senescence, root-to-shoot translocation and microbial enzyme activity in soil (Cossani *et al*. 2010, 2011; Sadras and Rodriguez 2010; Dijkstra *et al*. 2012; Gonzalez-Dugo *et al*. 2012; Lü *et al*. 2012; Ye *et al*. 2013; Bermúdez and Retuerto 2014; Errecart *et al*. 2014; Teixeira *et al*. 2014; Wang *et al*. 2015).

Understanding the interactions between water and nitrogen over a range of time scales and organisation levels (from ecosystem to molecular) is important for dryland cropping (Sadras and Richards 2014). Yield gains, however, arise from improved agronomy, better varieties and their synergy (Fischer 2009). Therefore, for water–nitrogen interactions to be exploited they must be linked to agronomy, breeding or both. Agronomically, the need to match supply of water and nitrogen is recognised and the interactions have therefore received attention in both rainfed and irrigated cropping systems worldwide (Dalal *et al*. 1997; Angus and van Herwaarden 2001; Asseng *et al*. 2001*b*; Sadras 2005; Cossani *et al*. 2010; Albrizio *et al*. 2010; Hernández *et al*. 2015).

The links between water and nitrogen are less developed in plant breeding (Sadras and Richards 2014). Breeding for drought adaptation has partially focused on nitrogen metabolism, including the use of N-isotope signature as a phenotyping tool (Yousfi *et al*. 2012) and the maintenance of N_2 fixation in water-stressed legumes (Sinclair *et al*. 2007; Sinclair 2011). Attempts to improve efficiency in the use of nitrogen genetically have paid less attention to the interaction with water (Cao *et al*. 2007; Huang *et al*. 2007).

This paper reviews interactions between nitrogen and water from physiological, agronomic, economic, breeding and modelling perspectives. Synergies between water and nitrogen (Box 1) and trade-offs are emphasised. Environmental aspects of the water–nitrogen interaction are important (e.g. Christianson and Harmel 2015; Norse and Ju 2015) but are not considered here. Our primary focus is wheat, the main crop in Australia. We discuss other species for comparison, including forage crops, where advanced notions on the physiology of water and nitrogen have been proposed, sorghum, where current understanding of stay-green illuminates some of the connections between nitrogen and water, and legumes, where intra-specific variation in N_2 fixation under drought seems relevant for crop yield. Directions for further research are identified.

Background: aspects of Australia's climate and soil related to the economies of water and nitrogen of crops

Climate

We first consider the climate drivers of potential yield. Then, we focus on rainfall as the main constraint to achieve potential yield; we highlight the value of quantitative patterns accounting for the timing, intensity and duration of stress in relation to the critical period of yield determination. We conclude with a brief

Box 1. Synergies between efficiencies

Efficiency in the use of resources can be defined at different levels of organisation and time scales (Sinclair *et al*. 1984; Wang *et al*. 2013). To highlight synergies, here we focus on efficiencies defined as a function of crop shoot biomass (B) as follows: transpiration efficiency, WUE (B,T) is biomass per unit transpiration (T); nitrogen-conversion efficiency (NCE) is biomass per unit nitrogen uptake (Nupt); and radiation-use efficiency (RUE) is biomass per unit intercepted photosynthetically active radiation (PARi). Hence:

$$\mathrm{WUE}\ (\mathrm{B,T}) = \mathrm{RUE} \times \mathrm{PARi} \times \mathrm{T}^{-1} \qquad (1.1a)$$

taking the ratio T : PARi as a coarse approximation to canopy conductance g_c (Sadras *et al*. 1991; Caviglia and Sadras 2001):

$$\mathrm{WUE}\ (\mathrm{B,T}) = \mathrm{RUE} \times g_c^{-1} \qquad (1.1b)$$

Also:

$$\mathrm{WUE}\ (\mathrm{B,T}) = \mathrm{NCE} \times \mathrm{Nupt}\ \mathrm{T}^{-1} \qquad (1.2)$$

$$\mathrm{NCE} = \mathrm{RUE} \times \mathrm{Nupt}^{-1} \times \mathrm{PARi} \qquad (1.3)$$

Enhanced radiation use efficiency, e.g. as associated with stay-green, sink-driven or nitrogen-driven enhancement of photosynthesis (Stockle and Kemanian 2009) could increase transpiration efficiency, provided canopy conductance does not increase much (Eqn 1.1b). Caviglia and Sadras (2001) provide empirical evidence for the enhancement in water-use efficiency driven by higher radiation-use efficiency in response to nitrogen supply. Transpiration efficiency can increase with both higher nitrogen-conversion efficiency and higher uptake of nitrogen per unit transpiration (Eqn 1.2). Enhanced radiation-use efficiency per unit nitrogen uptake can increase nitrogen-conversion efficiency for a given PAR interception (Eqn 1.3). In pot-grown plants, transpiration efficiency and nitrogen-conversion efficiency both increased with increasing level of ploidy in a comparison of wheats: three diploid (*Triticum boeoticum*, AA; *Aegilops speltoides*, BB and *Ae. tauschii*, DD), two tetraploid (*T. dicoccoides*, AABB and *T. dicoccon*, AABB) and one hexaploid (*T. vulgare*, AABBDD) (Huang *et al*. 2007).

discussion of extreme temperatures and their interaction with water and nitrogen.

The photothermal environment

The photothermal environment is the primary limit to potential yield, as defined by Evans and Fischer (1999). Fischer (1985) showed that wheat kernel number, the main yield component, correlates with a photothermal quotient (PTQ) during the critical period for grain set. The PTQ relates solar radiation (Rad) and mean temperature (T_{mean}) above a base temperature (Tb):

$$\mathrm{PTQ} = \mathrm{Rad}/(\mathrm{T_{mean}} - \mathrm{Tb}) \quad (1)$$

Associations between PTQ, seed number and yield were later verified in rice (Islam and Morison 1992), sunflower (Cantagallo *et al*. 1997), maize (Didonet *et al*. 2002), field pea (Poggio *et al*. 2005), barley (Francia *et al*. 2011), canola (Faraji 2014) and chickpea (Sadras *et al*. 2015). The robustness of the PTQ as a major driver of yield derives from its physiological basis; it captures the positive association between seed number and radiation, mediated by photosynthesis, and the negative association between seed number and temperature, mediated by the shortening of the critical window with increasing temperature. Refinements of this index include corrections for incomplete canopy cover affecting the radiation component (Fischer 1985) and corrections for vapour-pressure deficit and the fraction of diffuse radiation (Rodriguez and Sadras 2007). Doherty *et al*. (2010) mapped vapour-pressure deficit and PTQ normalised for vapour-pressure deficit and diffuse radiation at shire-level for the Australian wheatbelt, thus highlighting latitudinal and costal variation in climate drivers of potential yield.

Rainfall patterns

In rainfed systems, the amount of rainfall, seasonality and frequency distribution of size of events have implications for yield as related to the water and nitrogen economy of crops.

The amount of precipitation (P) in relation to evaporative demand (E) sets the broad pattern of land use, separating pastoral and cropping areas. Trumbell (1939) defined the limit of safe wheat growth in South Australia based on P/E ≈0.33 for the period May–September. French (1993) identified P/E = 0.26 for April–October based on Minnipa (33°S, 135°E) on the upper Eyre Peninsula. An isoline of P/E = 0.26 extended around the Australian grains belt effectively fits the current boundary between grain and pastoral land use from Western Australia to southern Queensland (Nidumolu *et al*. 2012). This fit is surprising given the different soil types, seasonality of rainfall and land-use policies.

For a given amount of rainfall, seasonality sets the scope of cropping options. In the winter-rainfall areas of the south and west of Australia, cropping is constrained to wheat-based systems in rotation with pasture, barley, grain legumes and canola. In the Northern Grains Region, the combination of summer-dominant rainfall and deep soils with high water-holding capacity offers the possibility of growing winter and summer crops, as well as opportunistic double cropping (e.g. sorghum–chickpea). Owing to the marked seasonality of rainfall, stored soil water is a larger component of water supply for wheat in the northern region than the winter-rainfall regions (Sadras and Rodriguez 2007).

For a given amount and seasonality, size of rainfall events influences the fate of water; that is, large events favour runoff and deep drainage, whereas small events favour soil evaporation (Sadras 2003*b*). High frequency of small events also favours nitrogen mineralisation. The amount, seasonality and size distribution of rainfall events interact with temperature, soil properties and management to determine the fate of soil nitrogen. Figure 1 illustrates the annual dynamics of modelled nitrogen mineralisation in response to rainfall and temperature, highlighting differences among locations with different rainfall patterns. The section *A modelling perspective* discusses limitations to simulate nitrogen mineralisation with current models.

Rainfall events of different size and frequency drive different biological processes (Schwinning and Ehleringer 2001; Schwinning and Sala 2004). Schwinning and Sala (2004) emphasise the two elements defining ‘pulse size’: pulse depth, the depth to which soil water potential is elevated to levels that promote specific biological activities; and pulse duration, the time over which soil-water potential remains at biologically relevant levels. In the space defined by pulse depth and duration, those authors outline a hierarchy from small, short pulses triggering processes such as nitrogen mineralisation to large, long pulses driving pest outbreaks and shifts in community structure (Fig. 2*a*). The size distribution of rainfall events in Australia in the winter semester is mapped in Fig. 2*b*, highlighting the latitudinal shift from large events in the north to smaller events in the south. The concept of pulses has been used to analyse the fate of water in cropping systems, particularly in relation to the role of stubble (Sadras 2003*b*; Monzon *et al*. 2006; Verburg *et al*. 2012).The perspective of water pulse can provide further insight on the connections between the dynamics of water and nitrogen in cropping systems.

Supply and demand of water and nitrogen in relation to critical periods of yield determination

Crop response to stress depends on the intensity and duration of stress and the timing in relation to the critical period for yield determination. Adaptive traits and agronomic practices to mitigate the effect of stress thus require an understanding of the probabilistic spatial and temporal patterns of stress in relation to crop development. The pioneering work of Chapman *et al*. (2000) modelled the patterns of water supply : demand ratio for sorghum in northern Australia. A similar approach has been used to characterise the patterns of water stress for Australian wheat, maize, field pea and chickpea (Sadras *et al*. 2012*b*; Chauhan *et al*. 2013; Chenu *et al*. 2013; Lake *et al*. 2016). For wheat, environment types 3 and 4 in the classification of Chenu *et al*. (2013) are widespread geographically, represent an important share of the total diversity of environments (≥50% in many important growing regions), and cause the strongest reduction in yield. In both of these environment types, the onset of water stress occurs at ~500 degree-days before anthesis. This challenges the ambiguous label of ‘terminal drought’ often used to characterise wheat-growing environments of Australia and other Mediterranean-type regions (Savin *et al*. 2015). Patterns of water stress need to be quantified for other important crops in Australia including barley, canola, lentil, faba bean and lupin.

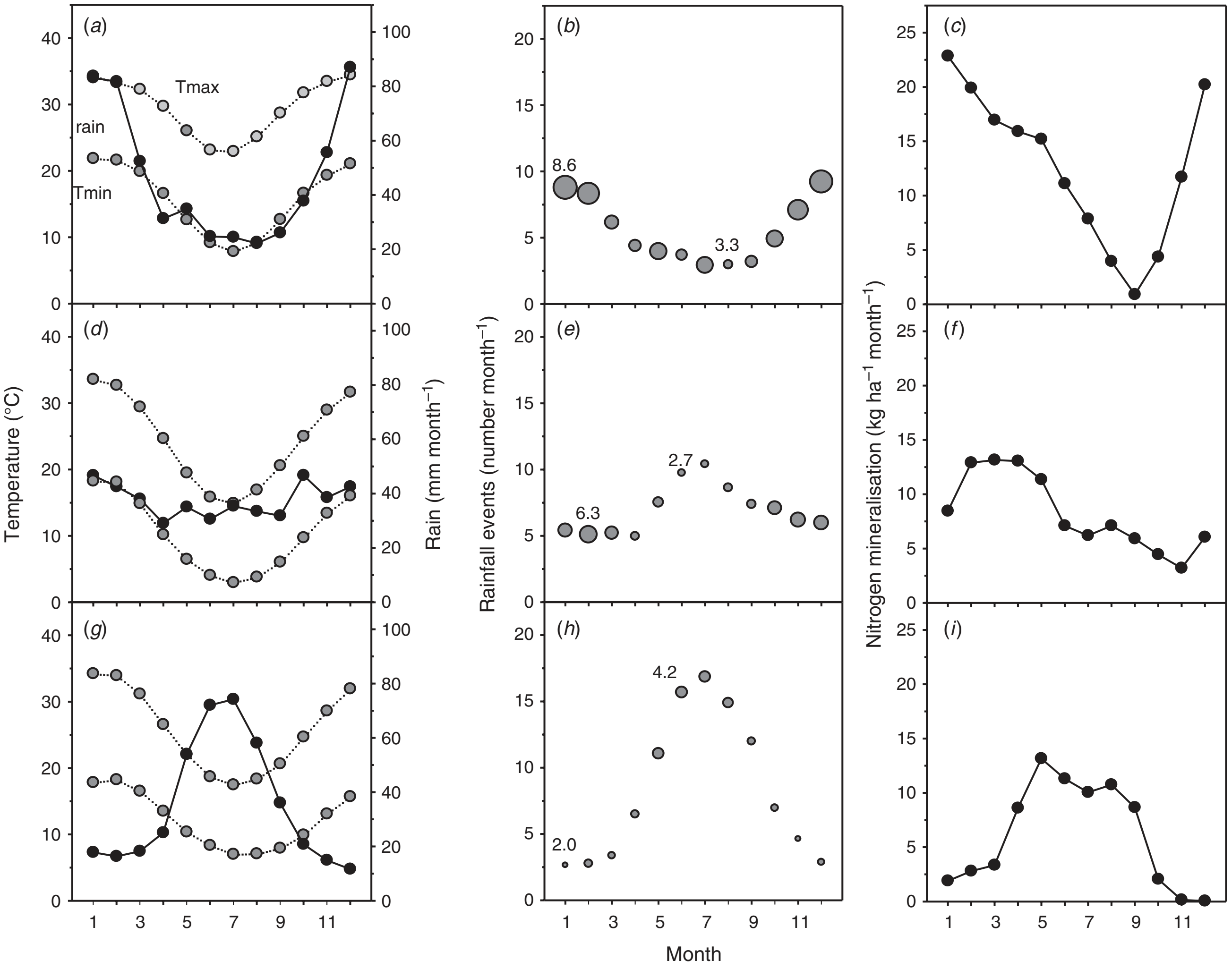

Fig. 1. Annual dynamics of modelled nitrogen mineralisation in response to amount, seasonality and size of rainfall events interacting with temperature. Locations represent summer-dominant rainfall (Emerald: 23°50′S, 131°62′E; annual rainfall 561 mm), uniform rainfall distribution during the year (Condobolin: 33°02′S, 147°23′E; annual rainfall 450 mm) and winter-dominant rainfall (West Moora: 30°64′S, 115°92′E; annual rainfall 419 mm). In *b*, *e*, *h*: the size of the points represents the average size of events, and the numbers indicate the smallest and largest (mm event^{-1}). Mineralisation was modelled with APSIM, assuming an initially dry soil (plant-available water 10% of maximum on 1 January 1957) and a continuous soil-water balance for the period 1957–2014. A wheat crop (cv. Hartog) was sown according to a rule combining a sowing window (15 May–10 July) and rainfall conditions (25 mm accumulated in seven events); if these conditions are not met in a given season, the crop is sown at the end of the window. Stubble is reset to 1 t ha^{-1} on 1 January every year and crop fertilisation is set to 150 kg N ha^{-1} at sowing each season. A single soil was used to remove soil effects, and thus capture the climatic drivers of mineralisation.

The spatial and temporal characterisation of the patterns of supply and demand of nitrogen has received less attention (Angus 2001). Modelling tools can be used to relate soil, crop, and climate as illustrated in Fig. 1. Next, it would be interesting to link the spatial and temporal patterns of supply and demand for water and nitrogen as background for agronomic and breeding applications.

Extreme temperatures

Heat (Barlow *et al*. 2015) and frost (Zheng *et al*. 2012; Frederiks *et al*. 2015) events in spring can disrupt reproduction and thus reduce crop yield. The dates of the last spring frosts and first heat events vary spatially in the Australian grain-growing regions (Zheng *et al*. 2012) and influence the target flowering window that farmers manipulate with sowing date and cultivar choice. The actual response to heat and frost depends on timing, intensity and duration of the event, history (acclimation), conditions for compensation after the event, and the interaction of these factors with nitrogen and water supply. For example, a severe heat event around flowering caused no visible damage to well-watered wheat crops, whereas in rainfed crops, ear damage ranged from 10% in low density, low nitrogen crops to 60% in their high density, high nitrogen counterparts (Table 1).

Under the modelling assumptions of Zheng *et al*. (2015), the direct effect of frost was about a 10% reduction in yield of the annual Australian wheat crop, and a further 10% reduction in yield due to conservative sowing time to avoid frost. These

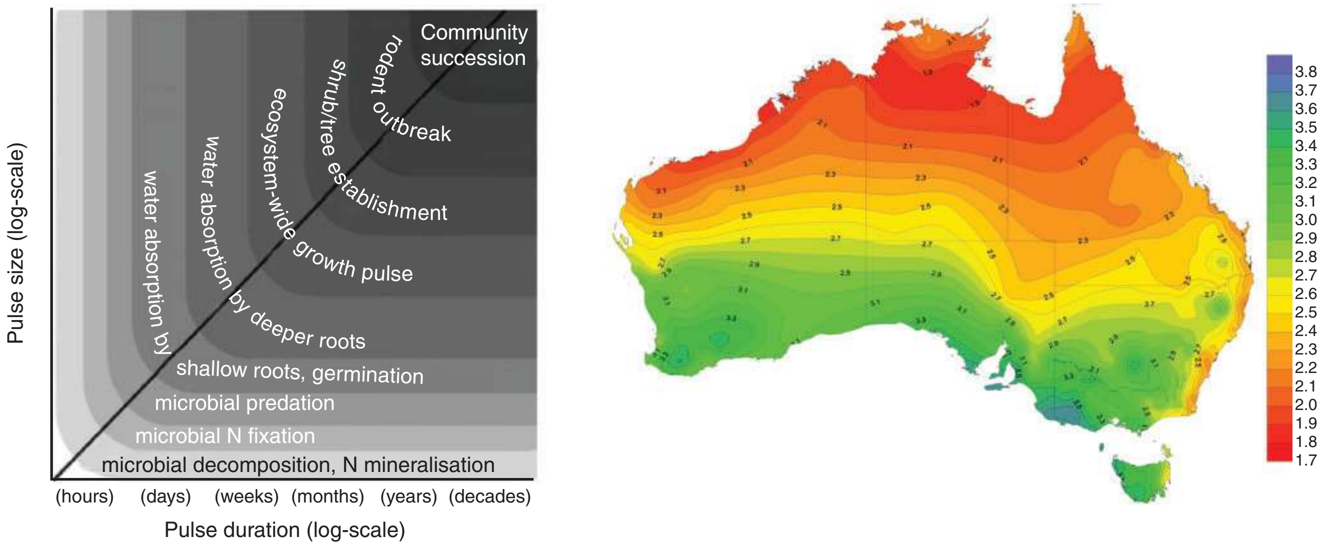

Fig. 2. The 'water-pulse' perspective. Left: Response hierarchy to soil moisture pulses of variable size and duration. The solid line shows an approximately linear relationship between size and duration on a log–log scale. Small, short pulses can activate the physiology of microbes at the soil surface. Larger and longer pulses trigger physiological responses of larger organisms, first of soil invertebrates, then of plants. Size of events differentially affects water absorption by shallow or deep roots. Seed germination usually requires smaller pulses than plant establishment. Rainfall clusters, producing pulse events from weeks to months, add up to a wet season, which usually triggers ecosystem-wide vegetation growth that could in turn trigger outbreaks of herbivores or granivores (e.g. small rodents). Wet periods spanning several years may trigger large-scale shifts of entire communities. Right: Power-law coefficient of rainfall for the winter semester in Australia. Power low coefficients are the unitless slope of the relationship between frequency and size of non-zero rainfall events on a log–log scale; a high coefficient indicates dominance of small events. Sources: left, Schwinning and Sala (2004); right, Williamson (2007).

risks are not well simulated in models and decision-support systems (Barlow *et al*. 2015). Zheng *et al*. (2015) assumed adequate nitrogen fertiliser, so the only indirect cost related to yield loss due to delayed sowing. A further indirect cost of spring frost and heat is likely to be conservative nitrogen rates, whereby farmers concerned about these events diminish crop inputs to reduce the financial loss. The perception that a vigorous crop is more vulnerable to frost damage might further constrain nitrogen rates in frost-prone environments despite unclear connections between crop vigour and frost damage (Whaley *et al*. 2004).

Soil

Soil water directly influences the availability of mineral nitrogen for crop uptake, and reciprocally, nitrogen influences crop water use but, more importantly, canopy size and thus the partitioning of evapotranspiration between soil evaporation and transpiration. The response to nitrogen of yield per unit water use is larger than the response to water of yield per unit available nitrogen, as discussed later from a physiological perspective. Here, we outline the role of soil texture in determining the upper and lower limits for soil water and nitrogen storage and their implications for crop growth. We then consider water as the primary driver of soil nitrogen mineralisation and the influence of nitrogen availability on crop water uptake. We then examine coarse regional differences in soils with implications for the water and nitrogen economies of crops.

Soil texture, soil water and soil nitrogen

Potential water storage is a function of soil texture, an inherent soil property which is not under the influence of management except for practices such as clay spreading, which seeks to ameliorate surface water repellence (Müller and Deurer 2011), and delving, which changes the textural profiles of texture-contrast (or 'duplex') soils (Betti *et al*. 2015). Owing to the association between clay content and soil porosity, soils with higher clay content have greater soil-water storage capacity than sandy soils. However, clay soils hold onto their water more tightly and there is a trade-off between soil-water storage capacity and the availability of that water for crops. The plant-available water capacity (PAWC) is the difference between the drained upper limit, which is the maximum amount of water that a soil can hold against gravity, and the crop lower limit, the residual amount of water in a soil that is inaccessible to crops. The drained upper limit is a soil property, whereas the lower limit depends on both soil and crop, because the depth, distribution and functionality of roots affect water uptake (Ritchie 1981).

Soils with a clay content ≈30% are able to store about double the amount of water of sandy soils (Oliver and Robertson 2009). However, such difference is important for crops only when the soil-water content is close to the drained upper limit for the sandy soil, at which point finer textured soils become advantageous. Therefore, under low rainfall, differences in PAWC between soils may not be critical. There is thus an interaction between climate and seasonal conditions with soil texture, which means that in wetter conditions soil texture may modulate yield whereas it exerts less influence under drier conditions. The exception would be under very low rainfall, when soils with lower clay content can be more productive because they hold soil water less tightly.

Soil clay content correlates with soil organic matter and soil organic nitrogen stock. This is because the clays offer physical

Table 1. Interaction between water and nitrogen supply, sowing density, frost and heat in wheat (cv. Chara) crops on a Grey Vertosol at Horsham, south-eastern Australia (36.65°S, 142.10°W)

Rainfed crops received 270 mm and irrigated crops 390 mm during the growing season. Ear tipping is a visual assessment of damaged ears attributable to stress. Growth rate is for the period from 12 days before anthesis to anthesis. Anthesis started at 115 days after emergence (DAE) for all rainfed crops and irrigated, low nitrogen (N) treatments, and at 121 DAE for the irrigated, high N plots. At 114 DAE, temperature was ≤ 0°C for ~4 h from midnight. At 115 DAE, temperature was >31°C from 11 : 40 until 19 : 00 and peaked at 37°C; average daily vapour-pressure deficit was 1.5 kPa, with an absolute maximum of 6 kPa at 16 : 00. Yield correlated with ear tipping for rainfed crops ($r^2 = 0.23$) and with pre-flowering growth rate for the pooled data ($r^2 = 0.81$). Source: Rodriguez *et al.* (2005)

Sowing density (kg seed ha^{-1})	N rate (kg N ha^{-1})	Ear tipping (%)	Yield (kg ha^{-1})	Growth rate (g m^{-2} day^{-1})
		Rainfed		
52	0	10	1245	0.0
	16	20	1446	–0.1
	39	27	2043	–4.5
	163	33	1005	0.7
102	0	22	1341	3.0
	16	28	1537	1.5
	39	37	1845	8.8
	163	60	525	2.0
		Irrigated		
52	0	0	4181	16.5
	16	0	4505	12.0
	39	0	3889	12.6
	163	0	3200	10.1
102	0	0	3361	11.0
	16	0	4862	11.6
	39	0	4767	11.2
	163	0	4174	10.9

protection to organic matter, reducing the likelihood that it is broken down by organisms. Hence, there is a tendency for finer textured soils to maintain higher organic fertility than coarser textured soils under the same management and climate. Over a single annual cropping season, 5–10% of organic nitrogen might be mineralised (Murphy *et al.* 1998*a*), and finer textured soils with higher organic matter densities are therefore likely to mineralise more nitrogen within a cropping season than coarse-textured soils, even though the organic matter is less protected on the finer textured soil. Finer textured soils have a greater hysteresis, more slowly unlocking legacy water and organic nitrogen, and at the same time providing a more buffered mineral nitrogen supply. Soil organic matter also has a small positive influence on the ability of soils to hold and to conduct water, primarily through the formation of soil aggregates, although the effect is significant only at higher soil-water content, with soil texture being the primary determinant at lower, perhaps more relevant, soil-water content (Saxton and Rawls 2006).

Although it is generally thought that nitrogen is primarily taken up from superficial soil layers, deeper soil nitrogen provides an additional source of nitrogen in sandy soils (Anderson *et al.* 1998), and possibly on some finer textured soils (Page *et al.* 2003). Management of nitrogen becomes more critical as PAWC decreases (Oliver and Robertson 2009). Soils with low PAWC are typically sandier and crops grown on these soils are more responsive to nitrogen than finer textured soils (Oliver and Robertson 2009; Unkovich 2014), probably because organic nitrogen reserves are lower, the soil is more often dry, and nitrate cannot be held in the profile against leaching. Fields with low PAWC (<75 mm) (Oliver and Robertson 2009) might be economically more sensitive to nitrogen management because the margin between nitrogen deficiency, sufficiency and excess is small compared with soils with higher PAWC where water and nitrogen buffers are larger.

Soil texture can influence processes leading to loss of nitrogen from the crop–soil system. In soils with low oxygen availability, usually caused by high soil-water content, nitrate can be converted to gaseous N_2O or N_2 (Dalal *et al.* 2003). Because this also requires a readily available supply of carbon for microbial growth, it tends to be a greater problem on finer than coarser textured soils. Waterlogging also causes transient nitrogen deficiency, where recovery is a function of available nitrogen after the waterlogging rather than antecedent nitrogen availability (Robertson *et al.* 2009). Coarse-textured soils are also more prone to leaching of nitrate (Anderson *et al.* 1998).

Soil water and nitrogen mineralisation

A strong, short-term interaction between available soil water and available nitrogen derives from moisture pulses that sustain the activity of microorganisms involved in the mineralisation of soil organic nitrogen and turnover of microbial biomass and carbon (Murphy *et al.* 1998*a*). Small and frequent rainfall events favour superficial soil moisture and nitrogen mineralisation (Sadras 2003*a*; Sadras and Baldock 2003), resulting in mineralisation of native organic matter and microbial turnover but not decomposition of fresh organic matter (Sparling *et al.* 1995). Hence, soil organic matter stock is likely to be eroded under regular wetting and drying of surface soils. Most (>70%) nitrogen mineralisation is likely to occur in the surface 5 cm of soil (Murphy *et al.* 1998*b*) where the organic matter typically resides. Whether modern, reduced tillage, stubble retention systems have stratified this organic matter nearer the surface, increasing the potential effects of short wetting and drying cycles on organic matter cycling and nitrogen mineralisation is unclear.

Recently, the primary nitrogen supply for cereal crops in Australia has shifted to fertiliser and away from that mineralised from legumes in rotations (Angus 2001), or from historical soil nitrogen reserves in the northern grain growing regions (Herridge 2013); this is further developed below in the section *An agronomic perspective*. This has likely also been associated with a decline in soil organic matter stocks. As soil organic matter declines, so too does the ability to retain nutrients via the microbial biomass and other organic matter. High temperature favours mineralisation but not immobilisation of nitrogen (Luxhøi *et al.* 2008); hence, mineral nitrogen can build up over a warm fallow period provided the topsoil is wet, a condition more likely to occur in northern Australia (Fig. 1). The size of the soil microbial biomass further modulates the magnitude of mineralisation (McNeill *et al.* 1998).

Soil nitrogen and crop water use

Annual crops tend to root to the depth of available water in south-eastern Australia (Norton and Wachsmann 2006; Kirkegaard *et al*. 2007). Rooting depth and access to water and nutrients could be curtailed by pathogens (Lorimer and Douglas 2001) or by physical or chemical soil constraints (Dracup *et al*. 1992; Nuttall *et al*. 2003; Sadras *et al*. 2005; Rodriguez *et al*. 2006; McDonald *et al*. 2012).

Increased available nitrogen can increase root density directly by stimulation of growth near the nitrogen-rich zone (Officer *et al*. 2009), and indirectly through crop vigour (Palta *et al*. 2011). The impact of a nitrogen-driven larger root system on crop water uptake depends on the availability and distribution of water in the soil, the distribution of roots in the soil profile and the crop demand for water. Increased availability of nitrogen can increase crop water extraction, but this effect is generally modest (typically ~10 mm) in southern Australia (Angus 2001; Norton and Wachsmann 2006; Sadras *et al*. 2012*c*), perhaps because of lack of water at depth, soil chemical constraints or a combination of both. In the Middle East, fertilisation increased seasonal evapotranspiration by up to 16% in rainfed barley (Cooper *et al*. 1987) and by 8% in irrigated durum wheat (Karam *et al*. 2009) in relation to unfertilised controls. In environments where crops depend on stored water in deeper soils layers, increased nitrogen availability may have larger effects on rooting depth and water use. Brown (1971) showed a large response of seasonal evapotranspiration of winter wheat, increasing from 221 mm in unfertilised crops to 315 mm in their fertilised counterparts (268 kg N ha^{-1}) on a silt-loam soil developed on deep loess in a summer-rainfall region of USA. Soil-water extraction was constrained to 0.9 m in the unfertilised crops and increased to 1.8 m under fertilisation. In the deep soils of the Loess Plateau in China, seasonal water use of winter wheat increased up to 19% in response to nitrogen fertilisation, mostly by enhanced water uptake between depths 1.2 and 2.4 m (Zhong and Zhouping 2014). Increasing water use through improved nitrogen nutrition may increase grain yield (Norton and Wachsmann 2006), but the combinations of crop, soil, climate, and management that are more likely to be responsive are unknown.

Regional differences in soils

We have used the Australian three-dimensional soil grid (Rossel *et al*. 2015) to estimate the soil clay content, bulk density and soil organic carbon stock across the croplands for each state (Fig. 3). There is a trend of decreasing topsoil clay content from the north-east (Queensland) to the south-west (Western Australia). This correlates with a decrease in soil organic fertility and coincides with a shift from summer-dominant to equi-seasonal and then strongly winter-dominant rainfall from the north-east to south-west of the cropping zone (Sadras and Rodriguez 2007; Unkovich *et al*. 2009).

These broad changes in texture have implications for water and nitrogen, as outlined above. The magnitude of availability and release of soil nitrogen is likely greater in the east and north and is thus a pivotal variable for nitrogen management. By contrast, the lower capacity of soils to store and supply nitrogen and water, and the strong seasonality of rainfall, increase the focus on matching fertiliser nitrogen input to seasonal rainfall in the southern and western regions. The amount of total nitrogen required per unit yield seems consistent across the southern and northern cropping regions (Bell *et al*. 2013). There is a strong tendency for coarse-textured soils to produce lower protein wheat, perhaps because those soils have difficulty supplying both nitrogen and water during grain filling, although regional differences in the cultivar grown would also be implicated.

A physiological perspective: reciprocal influences between water and nitrogen and co-limitation

Here we address the questions of how nitrogen deficit influences the water economy of the crop, how water deficit influences the nitrogen economy of the crop, and how combined water and nitrogen deficit affect crop growth and yield.

Effect of nitrogen deficit on the water economy of crops

This effect can be interpreted in light of the equation (Cooper *et al*. 1987):

$$\mathrm{WUE}(\mathrm{Y}, \mathrm{ET}, \mathrm{s}) = \frac{\mathrm{WUE}(\mathrm{B}, \mathrm{T}, \mathrm{s})}{1 + \frac{\mathrm{E}}{\mathrm{T}}} \times \mathrm{HI} \qquad (2)$$

where, using the nomenclature of Sinclair *et al*. (1984), WUE (Y, ET, s) is yield (Y) per unit evapotranspiration (ET) on a seasonal basis (s); WUE (B, T, s) is biomass (B) per unit seasonal transpiration (T); E is seasonal soil evaporation; and HI is harvest index. Owing to the links between foliar nitrogen and radiation-use efficiency (Stockle and Kemanian 2009) and between radiation-use efficiency and transpiration efficiency (Box 1), nitrogen deficit reduces biomass per unit transpiration. Brueck (2008) compiled the response of biomass per unit transpiration to nitrogen supply for major crop species. Nitrogen deficit slows canopy growth and increases the ratio of soil evaporation to transpiration (Cooper *et al*. 1987; Angus and van Herwaarden 2001). Often, shortage of nitrogen reduces crop transpiration, which could be reflected in residual water in the soil at maturity (see the previous section *Soil nitrogen and crop water use*). Nitrogen deficit can be neutral, positive or negative for HI (Albrizio *et al*. 2010; Bandyopadhyay *et al*. 2010) and it can respond to the interaction between water and nitrogen; that is, high nitrogen supply can increase HI under favourable water conditions, but decrease it under water deficit (Hernández *et al*. 2015). However, the effects of nitrogen on HI are small compared with those on biomass in agronomically meaningful conditions (Fig. 4*d v*. Fig. 4*b*). Thus, nitrogen deficit reduces yield per unit evapotranspiration (Eqn 2) primarily by reducing biomass per unit transpiration, increasing soil evaporation and reducing transpiration, with a minor effect of HI reinforcing or partially counteracting this reduction. Owing to the law of diminishing returns, the yield per unit nitrogen supply declines with increasing nitrogen supply (Gastal *et al*. 2015). From these, a nitrogen-driven trade-off between the efficiency in the use of water and the efficiency in the use of nitrogen emerges irrespective of species, soil, climate and management. Experimental and modelling evidence for this trade-off can be found for wheat and barley in southern

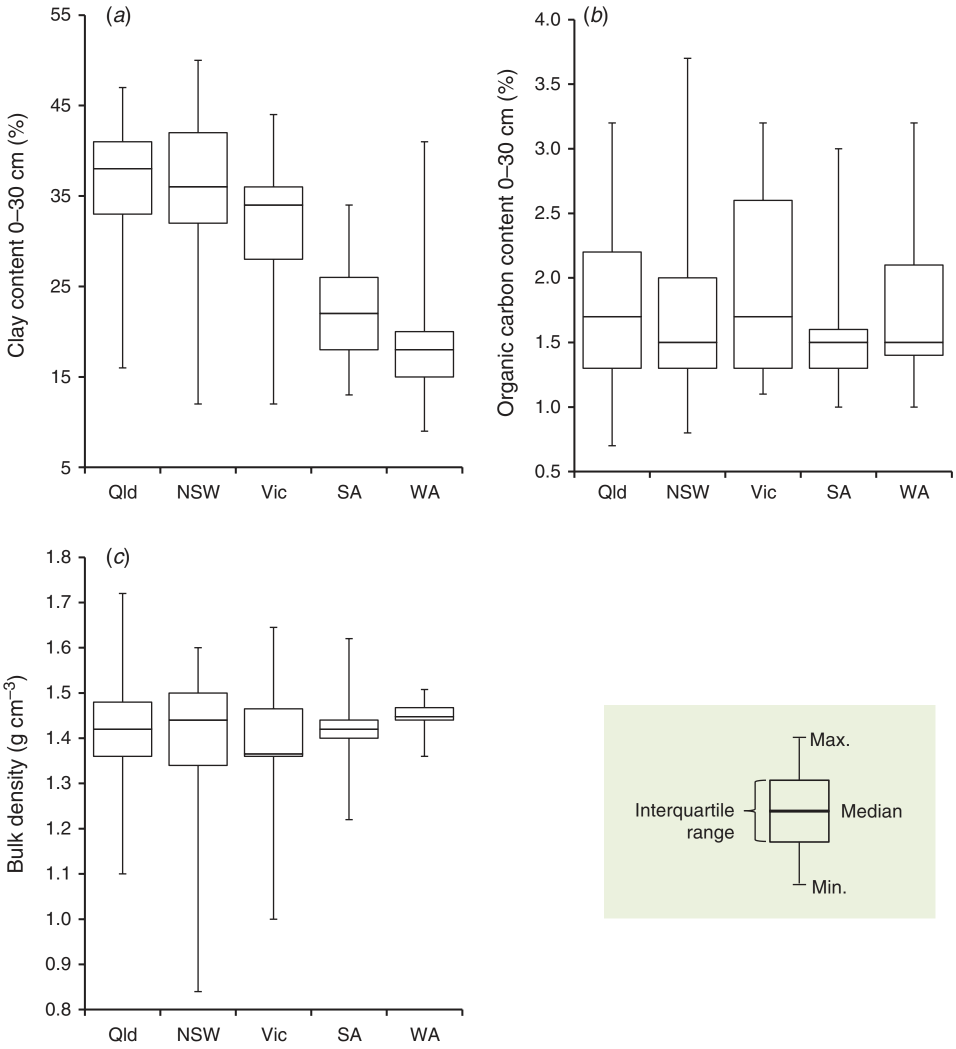

Fig. 3. State-level frequency distribution of spatially averaged soil properties for the Australian croplands: (*a*) clay content, (*b*) organic carbon content and (*c*) bulk density. Croplands are as defined in the national land-use map (ABARE 2010*b*) and the carbon stock calculated as in Valzano *et al.* (2005). Clay and organic carbon are for the top 0.3 m and bulk density for the top 0.1 m.

Italy, USA and Australia (Brown 1971; Albrizio *et al.* 2010; Sadras and Rodriguez 2010), maize in USA and Argentina (Kim *et al.* 2008; Albarenque 2015), rice in Philippines (Belder *et al.* 2005), and potato in Egypt (Badr *et al.* 2012), thus highlighting the universality of this trade-off.

Effect of water deficit on the nitrogen economy of crops

The effect of water deficit on the nitrogen economy of crops is complex because water deficit affects the growth-driven nitrogen demand (i.e. potential crop biomass × critical nitrogen concentration), critical nitrogen concentration, and supply (i.e. nitrogen availability at the root surface), assimilation and partitioning of nitrogen. Gonzalez-Dugo and colleagues have investigated the influence of water on nitrogen-related processes in forages, and they advanced a conceptual framework for the interpretation of experiments (Gonzalez-Dugo *et al.* 2005, 2010, 2011, 2012; Durand *et al.* 2010; Debaeke *et al.* 2012). In drying soil, three processes—mineralisation, mass flow and diffusion of nitrogen—are impaired and collectively this can reduce the availability of nitrogen at the root surface; a high root : shoot ratio may partially compensate these effects. In parallel, drying soil reduces crop growth primarily by reducing the capture of resources (radiation, water and nutrients), hence reducing nitrogen demand. Water deficit can also impair transport of nitrogen from root to shoot and activity of nitrate reductase. Although water deficit could reduce the nitrogen status of plants, the actual response depends on the relative effect of water deficit on growth-driven demand and supply. However, the lack of allometric relationships of nitrogen concentration and biomass under water deficit to derive a reliable nitrogen-nutrition index (Sadras and Lemaire 2014) means that we have little or no reliable information on the nitrogen status of water-stressed crops.

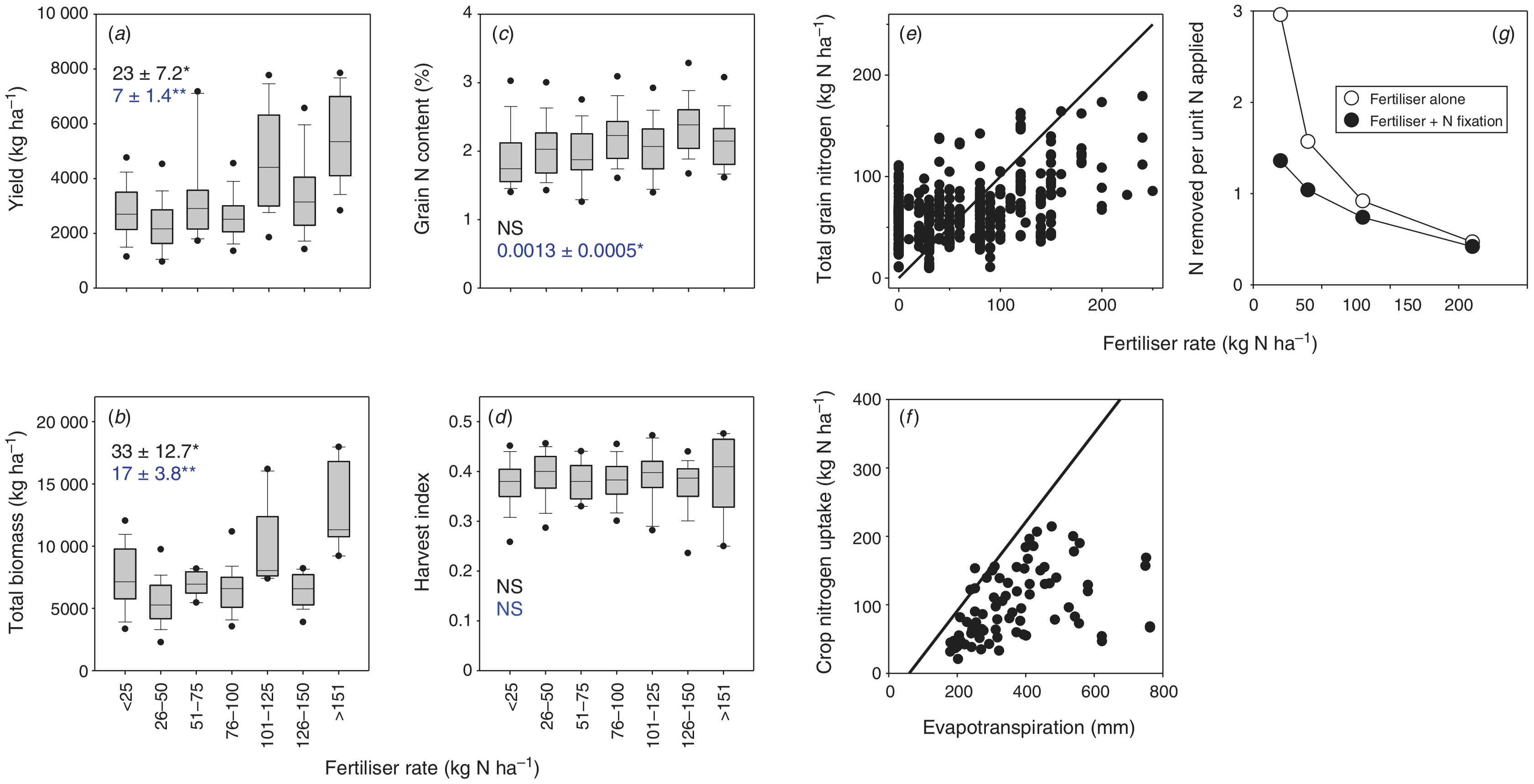

Fig. 4. Frequency distribution of wheat (*a*) grain yield, (*b*) shoot biomass, (*c*) grain nitrogen concentration, and (*d*) harvest index in relation to nitrogen fertiliser rate. Boxes indicate 5th, 10th, 50th, 90th and 95th percentiles. Values are the slope of regression between fertiliser rate and the trait for the 90th (upper values, black) and 10th (lower values, blue) percentiles with *$P < 0.05$ and **$P < 0.01$. (*e*) Relationship between export of nitrogen in grain and input of nitrogen as fertiliser; the reference line is $y = x$. (*f*) Relationship between crop nitrogen uptake and seasonal evapotranspiration; the reference line has slope of 0.65 kg N ha^{-1} mm^{-1} (French and Schultz 1984*b*) and *x*-intercept of 60 mm (Sadras and Roget 2004). (*g*) Ratio of nitrogen exported in grain and nitrogen input as a function of fertiliser rate in a long-term experiment at Dahlen, Victoria. Data sources: *a*–*f*, see Appendix 1; *g*, Norton *et al*. (2015).

Two knowledge gaps thus require attention in relation to the influence of water on nitrogen processes: nitrogen availability and the quantification of crop nitrogen status. The concept of plant-available water is well established (see the previous section *Soil*). By contrast, particularly for management purposes, we assume that all inorganic nitrogen in soil is available for the crop. In dry soil, however, part of the inorganic nitrogen may not be available if root growth, nitrogen diffusion and mass flow are constrained. Beyond water, chemical and physical subsoil constraints can also reduce nitrogen availability (Sadras 2005). By analogy with plant-available water, the concept of plant-available nitrogen needs to be developed for management applications.

Quantification of crop nitrogen status requires dilution curves to account for the allometry between shoot nitrogen concentration and biomass (Gastal *et al*. 2015). However, nitrogen dilution curves have been parameterised in well-watered crops, whereas theory and limited experimental evidence indicates that the parameters of the curve shift with water deficit (Bélanger *et al*. 2001; Gonzalez-Dugo *et al*. 2010; Errecart *et al*. 2014). Further, dilution curves assume two compartments, metabolic, with high nitrogen concentration, and structural, with lower concentration (Gastal *et al*. 2015). In some crops such as wheat, water-soluble carbohydrates are an important part of crop biomass, with zero nitrogen concentration. Where cultivar or growing conditions alter the amount of water-soluble carbohydrates, dilution curves based on total biomass will be biased (Hoogmoed and Sadras 2016); we further discuss this topic below in the section *A breeding perspective*.

A gap in the assessment of nitrogen-nutrition status of legumes relates to the lack of appropriate dilution curves ensuring nitrogen supply that maximises growth; published curves have relied on nitrogen-fixing crops where this condition might not have been met (Lemaire *et al*. 1985; Ney *et al*. 1997; Divito *et al*. 2016).

Combined effect of water and nitrogen deficit on crop growth and yield: co-limitation

Plants in the field are often exposed to multiple stresses (Mooney *et al*. 1991). Because a single limiting factor is unlikely, the Liebig paradigm is generally inappropriate to understand and manage crops (Sinclair and Park 1993; Kaspari and Powers 2016; Sperfeld *et al*. 2016). Bloom *et al*. (1985) used economic analogies to formulate testable hypotheses on plant acquisition and allocation of resources, and proposed that plant growth is maximised when it is equally limited by all resources. This notion was tested in studies combining modelling and experimental data in Mediterranean-type environments of Australia and Spain where it was concluded that, for a given intensity of stress, a high degree of water and nitrogen co-limitation favours wheat grain yield (Sadras 2005; Cossani *et al*. 2010). Savin *et al*. (2015) recently reviewed the co-limitation perspective to integrate nitrogen and water limitations quantitatively in wheat and barley.

Albarenque (2015) used the concept of water–nitrogen co-limitation to explore maize response to within-field spatial variation in availability of resources in the eastern Pampas of Argentina. She combined field experiments and modelling to test two hypotheses: there is variation in water–nitrogen co-limitation at the scale of management zones within paddocks, and yield per unit evapotranspiration is more responsive to co-limitation than yield per unit available nitrogen. The second hypothesis stems from the observation that the response to nitrogen of yield per unit water use is larger than the response to water of yield per unit available nitrogen. Experiments were conducted in two fields (12–14 ha) with either four management zones corresponding to levels of soil erosion or three management zones corresponding to soil types, where each management zone was fertilised with rates from 0 to 210 kg N ha^{-1}. The study supported the working hypotheses, and the author concluded that co-limitation can be used for zone-management of fertilisation accounting for both water and nitrogen-use efficiency.

Current methods to calculate co-limitation require involved experiments, modelling or a combination of these. Practical methods to quantify the degree of co-limitation, such as using remote sensing to quantify the nitrogen and water status of the crop, and its application for management are worth exploring.

An agronomic perspective: yield gap and management practices

Many practices influence the fate of both water and nitrogen at field to regional scales. Rotations, tillage, stubble, disease and weed management can all affect the amount of water and nitrogen stored in the soil, their availability to the crop and partitioning between unproductive losses (e.g. soil evaporation, nitrogen leaching) and productive plant uptake. Here, we present an overview of management practices that provides explicit crop and cropping-system perspectives, followed by consideration of the interaction between water and nitrogen from the perspective of yield gap. After establishing that shortage of nitrogen is a proximal cause underlying part of the yield gap of wheat crops in Australia, we revise tactical and strategic approaches to manage the water–nitrogen interaction of wheat, with an emphasis on the winter-rainfall regions of south-eastern and Western Australia. Wheat and sorghum in the northern region are briefly discussed to contrast winter- and summer-rainfall regions.

Overview

Recent reviews relevant to the agronomy of water–nitrogen interactions in Australia include Kirkegaard and Hunt (2010) and Kirkegaard *et al*. (2014), with a primary focus on water and a broad view on management options; Angus and Peoples (2012), assessing the contribution of pastures to the nitrogen economy of annual crops; Angus *et al*. (2015), on the impact of break crops on wheat yield, including the contribution of nitrogen from previous grain crops; and Scott *et al*. (2010), on the role of stubble management for water storage. A series of papers (Bell *et al*. 2013; Conyers *et al*. 2013; Watmuff *et al*. 2013) analysed soil nitrogen test and its value as a diagnostic tool for fertilisation, primarily based on yield–nitrogen response curves. Gastal *et al*. (2015) dissected the problems of yield–nitrogen curves and highlighted the nitrogen-nutrition index as a benchmark for the assessment of crop nitrogen status. Readers are referred to these reviews.

In a dataset of crops across diverse soils, climates and managements in Australia, median wheat yield was 2.7 t ha^{-1} and median grain nitrogen concentration 1.7% where fertilisation was <25 kg N ha^{-1}; by comparison, median yield was 5.3 t ha^{-1} and median grain nitrogen concentration 2.1% where fertilisation was >151 kg N ha^{-1} (Fig. 4*a, c*). Despite this trend, there was large scatter in the response of yield to nitrogen, as expected from the effects of other factors. Likewise, there is well-established, large scatter in the relationship between yield and water use (French and Schultz 1984*a*; Grassini *et al*. 2009, 2011). Variation in yield was mostly related to variation in biomass, whereas median HI was relatively stable, ranging from 0.38 with <25 kg N ha^{-1} to 0.41 at $\geq$151 kg N ha^{-1} (Fig. 4*b, d*). The data were further analysed by using percentile regression to capture the top and bottom boundaries of crop responses to fertiliser (Cade and Noon 2003). This is summarised in the slopes of regressions for the 10th and 90th percentiles in Fig. 4*a–d*. Yield and biomass response to fertiliser was 2–3 times larger under favourable conditions (90th percentile) than under stressful conditions (10th percentile). Grain nitrogen concentration correlated with nitrogen fertiliser rate under favourable conditions but not under conditions conducive to low grain protein. The relationship between HI and fertiliser had slopes undistinguishable from zero for both 90th and 10th percentiles ($P > 0.60$). Interactions between available soil nitrogen and seasonal water supply may influence HI (Kirkegaard and Ryan 2014). In this context, it is interesting to note the stability of HI in response to nitrogen fertilisation across soils, management, varieties and climates (Fig. 4*d*).

Comparisons of nitrogen export in grain and the input of nitrogen fertiliser across these environments indicate an export-input balance around 50 kg N ha^{-1} (Fig. 4*e*); below this rate, export exceeds input, suggesting likely soil mining. This coarse estimate of partial nutrient balance is consistent with a detailed, long-term experiment at a single site in Victoria where the ratio nitrogen removed : applied was 1 for rates of fertilisation 40–80 kg N ha^{-1} (Fig. 4*g*). Empirical information on the rate of nitrogen fertiliser required to match export for specific combinations of sites and management is an interesting reference for management.

Yield gap

The previous section (*A physiological perspective*) highlighted the low water-use efficiency of nitrogen-deficient crops; here, we look at the same association from the perspective of yield gaps. Where soils with low fertility combine with uncertain rainfall that makes fertiliser investment a risky proposition, nitrogen availability accounts for an important part of the gap between water-limited potential yield and actual yield of wheat (French and Schultz 1984*b*; Sadras and Roget 2004; Hochman *et al.* 2009, 2013). Nitrogen deficiency also accounts for part of the yield gap in other rainfed systems, e.g. sunflower in Argentina (Grassini *et al*. 2009) and millet in Sub-Saharan Africa (Sadras *et al*. 2012*a*). Where irrigation eliminates the uncertainty in water supply, the yield gap attributable to nitrogen can be negligible (Grassini *et al*. 2011).

Figure 5 illustrates the nitrogen-driven yield gap for an experiment involving two locations in South Australia, two rates of fertiliser and 13 wheat varieties. For crops with 187 kg N ha^{-1} in the soil profile at sowing, the yield gap across varieties averaged 890 kg ha^{-1} and protein concentration in grain averaged 10.7%; increasing initial nitrogen to 284 kg ha^{-1} reduced the average yield gap to 375 kg ha^{-1} and increased protein to 14.3% (Fig. 5*b, c*). For a given nitrogen supply, varieties with higher capacity to absorb nitrogen had a smaller yield gap (Fig. 5*d, e*); this varietal effect is discussed in a later section (*A breeding perspective*). Closing the yield gap in the experiments in Fig. 5 required 0.7 ± 0.11 kg N ha^{-1} mm^{-1} for grain with 14.3% protein, and 0.5 ± 0.07 kg N ha^{-1} mm^{-1} for grain with 10.7% protein. For the data of French and Schultz (1984*b*), yield gaps were closed at an uptake of 0.65 kg N ha^{-1} mm^{-1}. This ratio is physiologically and agronomically meaningful, and can be explored further for practical applications linking water and nitrogen.

Finding the causes of yield gaps is a necessary first step to close them. In this context, it is important to separate the proximate and ultimate causes of gaps. For example, shortage of nitrogen is a common proximate cause of yield gaps for wheat in Australia and millet in the Sahel in Africa, but the ultimate causes, and therefore the solutions, are different. Shortages of nitrogen inputs in Africa relate to underdeveloped markets and infrastructure, concerns about perceived and realised risks, inaccessibility of input services and credit, and/or inconsistency with personal aspirations (Tittonell and Giller 2013), whereas financial risk is the main constraint to fertiliser use in Australia (Monjardino *et al*. 2013, 2015).

Wheat in winter-rainfall environments

Seasonal variation in rainfall is a major driver of seasonal variation in yield (Box 2). For example, in a latitudinal transect in the Eyre Peninsula, the coefficient of variation of wheat yield at the shire level was 20–40% in the higher rainfall southern region and increased to 80–100% in the lower rainfall, northern boundary of the grain region (Doherty *et al*. 2010). Hence, different farming practices have evolved in the low- and high-rainfall districts of south-eastern and Western Australia. We compiled the following information directly from local experts—mostly advisors; this information is largely undocumented, hence the scarcity of supporting references compared with the other sections of this paper.

In South Australia, low–medium-rainfall districts are loosely defined as those receiving >400 mm annual rainfall and crop yield generally >2.5 t ha^{-1} (Doherty *et al*. 2010). The low-rainfall districts of the north and east of Western Australia often feature short growing season, <4 months. These regions have traditionally been low users of nitrogen fertiliser, and rotations incorporating ley pastures, predominantly self-regenerating medics, have been a major source of nitrogen. In recent decades, however, nitrogen from pastures has declined because of reductions in both fixation per unit land area and the proportion of land allocated to pastures (Angus and Peoples 2012). In the Mallee and Wimmera regions, land allocated to pastures decreased by 63% whereas cropping increased by 66% between 1975 and 2005 (Duncan and Dorrough 2009). This combination of increased intensification of cropping and reduced nitrogen fixation per unit land has increased the focus

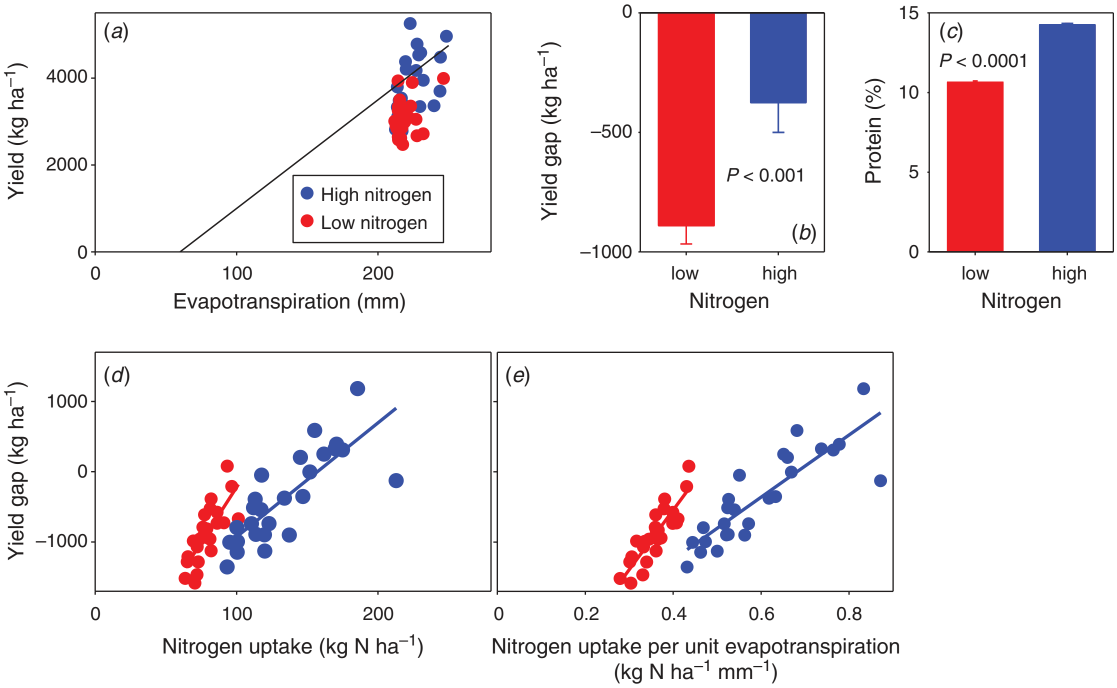

Fig. 5. Nitrogen-driven gap between water-limited potential yield and actual yield of wheat. (*a*) Yield and seasonal evapotranspiration compared with a boundary line representing the water-limited potential yield. Parameters of the line are *x*-intercept 60 mm (Sadras and Roget 2004) and slope 25 kg ha^{-1} mm^{-1} accounting for the potential of the newest variety in the experiment (Sadras and Lawson 2013). (*b*) Average yield gap across varieties. (*c*) Average protein concentration in grain across varieties. (*d*) Yield gap as a function of nitrogen uptake. (*e*) Yield gap as a function of nitrogen uptake per unit evapotranspiration. Data from experiments combining low (187 kg N ha^{-1}) and high (284 kg N ha^{-1}) nitrogen availability (initial mineral nitrogen + fertiliser), 13 varieties and two locations in South Australia. In *b* and *c*, error bars are 1 s.e. Source: Sadras and Lawson (2013).

on the importance of effective nitrogen management in these environments.

Current advice in low-rainfall areas is to apply nitrogen early, either at seeding or by tillering. The main difficulty with this approach is that information available to assess water-limited potential yield is often limited. The trend to earlier seeding, which may translate to dry seeding before the season break (Fletcher *et al*. 2015), further compounds these difficulties.

Advisors increasingly accept the need to overcome the tactical difficulties of nitrogen management in low-rainfall environments by a more strategic approach focusing on increased share of high-quality, well-managed leguminous pastures (Kirkegaard *et al*. 2014). The current profitability of livestock provides additional impetus for this approach. What is an adequate share of pastures in the cropping mix remains unresolved; modelling for a cropping farm in southern New South Wales indicated that a pasture intensity of ~40% would overcome historical nitrogen deficiency (Angus and Peoples 2012). In low-rainfall cropping regions of South Australia, 25–33% of land area apportioned to leguminous pastures is more common. In cropping rotations incorporating leguminous pastures, there is an inter-seasonal trade-off between maximising pasture biomass for N_2 fixation and plant-available water for the next crop. Brown manuring involving early termination of a pasture (usually vetch) in spring, resulting in some residual carryover of water, can become important in the nitrogen–water management decisions for the following season.

Logistics may further contribute to strategic approaches. Recent history involving substantial losses on fertiliser stock held by importers has seen an increased reluctance on behalf of suppliers to hold uncommitted stock, resulting in a decline in the flexibility of supply of urea at reseller and farmer level. Although actual shortages have been uncommon and only temporary in recent years, there is a trend for (usually) larger users of urea to lock-in supplies early in the season to avoid supply risks. This can compromise flexibility in the face of variable seasons and encourage more strategic thinking.

The increased intensification of cropping noted earlier has seen a decline in the traditional long fallow. However, recent work has highlighted the importance of summer-fallow management and its influence on water and nitrogen (Kirkegaard *et al*. 2014); control of summer weeds is now accepted best practice even after allowing for the reduction in summer grazing from sheep (Hunt *et al*. 2013).

The shift in cultural practice towards stubble retention and direct drilling has been undertaken to deal with soil erosion and decline in soil structure, as well as allowing quicker and earlier crop establishment. Whereas farmers' perception is that these practices favour soil-water storage by reducing unproductive water loss, the evidence does not fully support this view (Ward *et al*. 2009; Scott *et al*. 2010; Sadras *et al*. 2012*c*).

In South Australia, high-rainfall districts receive >400 mm annual rainfall. Crop yields are typically >3.0 t ha^{-1} (Doherty *et al*. 2010). The traditional approach has been to apply nitrogen

Box 2. Climatology of rainfall in Australia and crop yield

Nix (1975) drew attention to the relative importance of rainfall as a climatic constraint in Australian grain production compared with cold temperatures in North America, Europe and Asia and high temperatures and high humidity in India. Australian grain farmers thus face a higher production volatility than most other grain-exporting countries (Kimura and Le Thi 2011). According to Podbury *et al*. (1998), the coefficient of variation of de-trended Australian wheat yield from 1960 to 1997 was 19%, compared with 7% for the USA. The major source of the year-to-year rainfall variation is the El Niño Southern Oscillation (ENSO) (McBride and Nicholls 1983; Manton *et al*. 2006; Risbey *et al*. 2009). Australian national wheat yields were more strongly related to broad-scale ENSO indices than any other major grain crop in the world (Garnett and Khandekar 1992).

Although ENSO is dominant, the Indian Ocean, position of the subtropical ridge and the Southern Annular Mode are additional sources of climate variation for the Australian grain belt (Fig. Box 2.1).

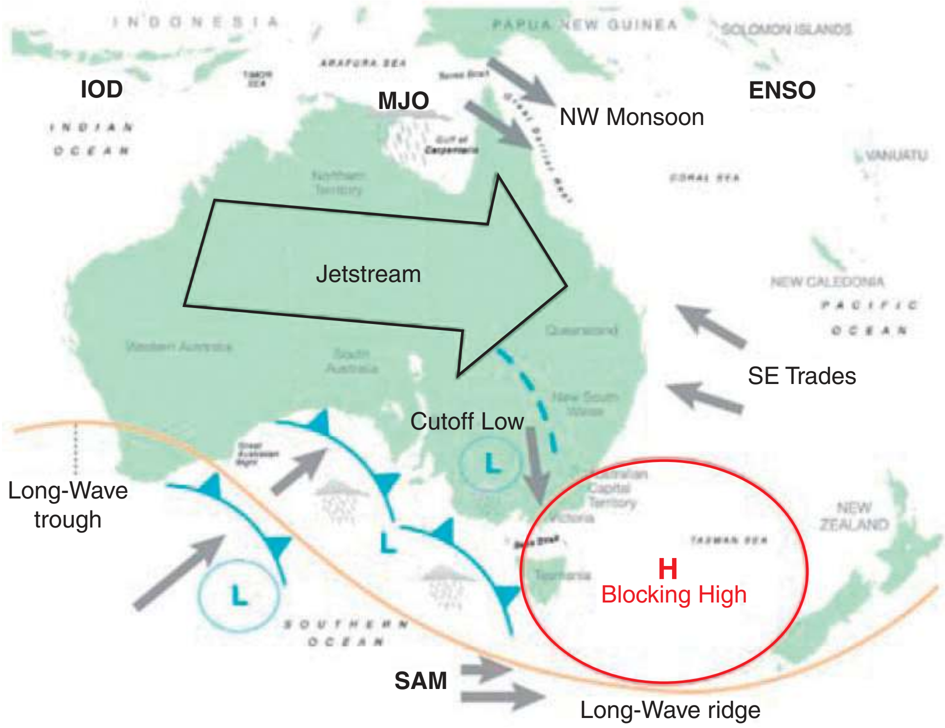

Fig. Box 2.1. Main drivers of rainfall variation in Australia. The dominant features originate in the tropics and include El Niño Southern Oscillation (ENSO), the Indian Ocean Dipole (IOD) and the Madden Jullian Oscillation (MJO). The Southern Annular Mode and blocking modify the impact of these tropical drivers. Other important features include the subtropical jet and a cut-off low shown in a typical position to influence south-eastern Australian rainfall. In this schematic, the long-wave pattern in the mid-troposphere consistent with the blocking high is also indicated with a trough over Western Australia and a ridge in the Tasman Sea. Dynamic climate models such as POAMA capture some climate drivers and interactions better than do others. Improvements will come from better input data of the state of oceans and atmosphere, more accurate representation of processes in the model and improved computing power. Source: Risbey *et al.* (2009).

A recent manifestation of these multiple sources of variation is the Millennium Drought from late 1996 to mid-2010, which had a measurable effect on the aggregated output of Australia's agriculture (Fig. Box 2.2). Although 2002 and 2006 were El Niño years and the Southern Oscillation Index was negative in spring of 2004, there were aspects of this drought that could not be explained by ENSO alone (Timbal *et al.* 2010).

Climate change will present further challenges for the Australian grains industry. It will change the interaction between water and nitrogen in complex ways, and is likely to increase pressure on agronomic and genetic improvement in the capture of both resources. Confidence from climate science is highest for elevated CO_2, followed by increased temperature and then

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Box 2. *Continued*

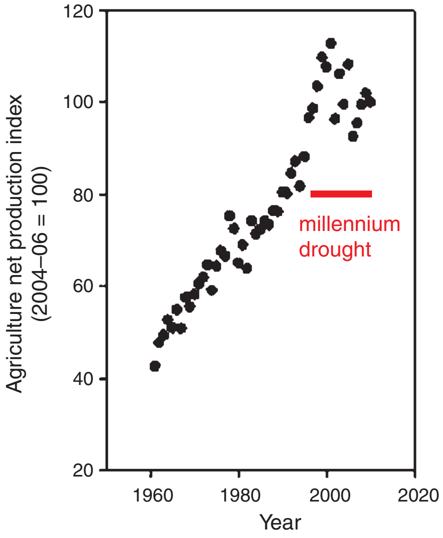

Fig. Box 2.2. Time trend in FAO's Net Production Index in Australia, highlighting the sustained increase in productivity and the disruption caused by the Millennium Drought. Source: Sadras *et al.* (2015).

changes to rainfall (Howden *et al*. 2010; Karoly 2014). Over the last 150 years, the amount of reactive nitrogen on Earth's land and in fresh water has more than doubled, primarily from anthropogenic sources (Galloway *et al*. 2008). In common with CO_2, emissions of NO_2 and NO_x have global implications, but other aspects of the altered nitrogen cycle (e.g. atmospheric nitrogen deposition) are strongly local. Elevated CO_2 would contribute to higher wheat yield and lower grain protein concentration (Bloom *et al*. 2014; Fitzgerald *et al*. 2010). The decrease in protein is partially associated with a dilution effect but complicated by reduced nitrogen uptake (Bloom *et al*. 2014). Warming will have the dual impact of hastening crop development and increasing the frequency and intensity of hot days (Sadras and Dreccer 2015). The shifts in phenology may increase the risk of frost at vulnerable crop stages (Zheng *et al*. 2015), and this can be compounded by increased frost risk in parts of southern Australia (Crimp *et al*. 2014).

The high variability of rainfall on annual and decadal scales makes detection and attribution of trends difficult, but recent studies have attributed some of the decline of rain in southern Australia to human-induced climate changes (Timbal *et al.* 2010; Delworth and Zeng 2014). The impact on grain crops of changes to the water balance from rainfall and evaporative demand are relatively well understood and modelled (Potgieter *et al*. 2013; Yang *et al*. 2014). The impact and adaptation options arising from changes in seasonality of rainfall and changes to rainfall intensity are an area for future research. How grain crops respond to the interaction of CO_2, temperature and rainfall along with changes in ozone and radiation is an ongoing challenge for modelling (Asseng *et al*. 2015). Further, we have little understanding of the effects of climate change on crop yield mediated by changes in pests, diseases and soil microorganisms (Sadras and Dreccer 2015). Seasonal variability rather than climate-change signals dominate farmers' decisions on fertiliser use. However, climate change may add a level of uncertainty to a risky decision. For advisers, crop modellers and developers of decision tools, climate change raises questions of appropriate historical timeframes to assess the analysis of risk.

based on target yield, with a substantial portion applied as a separated band at seeding, and follow-up applications depending on seasonal conditions. In the longer season, higher rainfall districts of South Australia and Western Australia, a third application is considered if the crop is growing well and is free of weed and disease, and if water has accumulated in the soil. Current best practice is largely strategic, based initially on testing for nitrogen in the root-zone before seeding. Logistics and cost means that not all paddocks are tested; therefore, untested paddocks require extrapolation from tested paddocks based on rotation history and soil type.

Rates of nitrogen fertiliser in high-rainfall environments, up to 160 kg N ha^{-1}, are based on rules-of-thumb relating to nitrogen requirements and yield; for example, wheat at 11% protein requires 40 kg N ha^{-1} t^{-1} grain yield. Yield is analysed in terms of frequency distribution of alternative outcomes depending on how the season evolves, for example by using the decision-support tool Yield Prophet.

Timing of nitrogen application in high-rainfall districts relates to managing crop vigour to ensure sufficient plant-available water at anthesis, hence the importance of methods to model or measure plant-available water. Work undertaken by the Mid-North High Rainfall Group in South Australia has found that a wheat crop of 4 t ha^{-1} requires 50 mm plant-available water at anthesis. Canopy-management techniques may include lower seeding rates for early-sown crops, delaying nitrogen application, grazing to delay biomass accumulation and the use of plant growth regulators to prevent lodging.

Owing to the large uncertainties in matching nitrogen and water supply, advice and rules have been mostly generic, but there is an emergent interest in tailoring practices to varieties, which might reflect the impact of breeding for yield on the nitrogen economy of the crop (see later section *A breeding perspective*). Further, tailoring nitrogen management to variety might be important to reach malt specifications in barley (Browne and Walters 2015).

Wheat and sorghum in summer-rainfall environments

In the northern region, where the shorter seasons are associated with higher winter temperature, opportunities for in-crop fertilisation in wheat are limited by the reliance on stored soil water and scarce rainfall events in autumn (Fig. 1). Nitrogen fertiliser is usually incorporated up to 1 month before sowing. Some farmers define fertiliser rates based on the initial availability of nitrogen and water. There is an increasing interest in the use of cover crops to reduce nitrogen costs, control herbicide resistance and improve soils. Preliminary trials in the Darling Downs showed that 60-day-old legumes used as cover crops contributed ~30 kg N ha^{-1} for wheat and sorghum crops, compared with a common fertilisation rate of 100 kg N ha^{-1}. However, trade-offs with water use by the cover crop can be significant, particularly in dry seasons. For example, at Jimbour (26°57′S, 151°13′E), summer legumes consumed more than half of the available soil water compared with a bare fallow after 46 days of growth, where dry matter production was 3.7 t ha^{-1} for mungbean, 3.4 t ha^{-1} for lablab and 2.7 t ha^{-1} for guar (D. Rodriguez, unpubl. data). At the time that the cover crop was killed, there was a 59% chance of obtaining a full profile before the winter sowing window following mungbean, and a 68% chance in the case of lablab and guar based on current soil-water content and historical climate records.

Owing to variation in hybrids, environments and agronomic options, there is an opportunity for the improvement of sorghum yield by developing specific genotype × environment × management (G × E × M) combinations (Hammer *et al*. 2014). Hybrids vary in tillering (Kim *et al*. 2010), maturity (Ravi Kumar *et al*. 2009), root angle (Singh *et al*. 2012) and stay-green (see later section *A breeding perspective*). Management options including plant population, row configuration (i.e. solid, single or double skip row; Whish *et al*. 2005) and sowing date affect the pattern of canopy development and water use during the growing season. Modelling showed that single- and double-skip arrangements and reduced plant densities reduced pre-anthesis water use and helped to sustain HI and yield in years with below-average rainfall (Whish *et al*. 2005).

In contrast to the local breeding effort in sorghum, Australia's maize hybrids derive mostly from lines developed in the USA, where maize is usually grown in more favourable environments and often at higher plant populations (Grassini *et al*. 2015). In Australia, rainfed maize is sown at wide row spacing and low densities (2.5–3.5 plants m^{-2}) where current hybrids produce fertile and infertile tillers but do not develop a secondary cob in the main stem (J. Eyre, A. Ferrante, E. Ortelli, J. L. McLean, D. Rodriguez, unpubl. data 2015). Unproductive tillering with the current combination of hybrids, environments, crop configuration and population density is likely to compromise efficiency in the use of water and nitrogen. A comparative analysis of sorghum and maize would improve understanding of the differences in plant phenotype in relation to the water and nitrogen economies of the crop and its responses to management.

An economic perspective: dealing with risk

Jobbágy and Sala (2014) quantified the inputs and outputs of nutrients across cropping industries on a global scale. They found that the difference between input and output increases with farm-gate value of produce (Fig. 6*a*). This suggests that a declining share of fertiliser on the production costs encourages higher fertilisation rates, irrespective of their agronomic benefit and despite their environmental consequences. The largest surplus of both nitrogen and phosphorus corresponds to fruits and vegetables. By comparison, economic return in the grains industry is smaller and the associated nutrient balance is closer to neutral.

The Australian grains industry is characterised by relatively low use of fertiliser due to a combination of (*i*) relatively low grain yield; (*ii*) unsubsidised inputs and outputs; (*iii*) trends of increased farm size and, hence, more extensive operations; and (*iv*) erratic rainfall leading to uncertain return from fertiliser. Not only is nitrogen a significant portion of variable costs, it is an easily observed cost compared with other costs such as machinery depreciation and maintenance (GRDC 2014). The overriding influence of economic considerations thus sets the scene for our analysis of nitrogen management in a context of risk, largely driven by uncertain water availability.

Here, we outline some principles of production economics and risk as background to the specific consideration of the consequences of risk and risk aversion in handling the interactions between water and nitrogen in grain production. We briefly consider the role of seasonal climate forecasts (SCF) in nitrogen decision making.

Production economics

The relationship between the inputs and the resulting yield output is a response or production function, which conforms to the law of diminishing returns whereby an additional unit of input results in a less-than-proportional increase in grain production. This is illustrated in simulated yield response to nitrogen in Fig. 6*b*.

When combined with price and cost data, a production function results in a payoff or profit function. The additional income generated by the addition of a unit of input is the marginal return (MR) and the associated additional cost is the marginal cost (MC). The economically optimum nitrogen rate (EONR) occurs when MR = MC. For the 30 years in Fig. 6*b* and *c*, the EONR is 100 kg N ha^{-1} and it varies from 140 kg N ha^{-1} in the seasons with above-median rainfall to 40 kg N ha^{-1} in the seasons with below-median rainfall.

The EONR varies with climate, soil nitrogen and the cost of nitrogen relative to the price of grain. Between 1985 and 2015, there has been a 5-fold variation in the nitrogen : wheat price ratio (Fig. 6*d*). Nitrogen price depends on global supply and demand, the price of energy and feedstock gas, the exchange rate and shipping costs (Angus 2001; Prudhomme 2015). Decisions on nitrogen rate thus need to consider the relative price of wheat and cost of nitrogen (Abadi and Farre 2015), in addition to agronomic information.

Although the concept of EONR is common in the literature, a rate lower than the profit-maximising rate can be justified for two reasons, seasonal uncertainty and opportunity costs, i.e. better uses of scarce funds than maximising the profit from nitrogen fertiliser. The benefit : cost ratio (BCR) is the benefit in extra grain yield divided by the cost of applying nitrogen. A BCR of, say, 2.0 has the straightforward understanding that a farmer will get back \$2 for each \$1 invested in nitrogen. An associated expression is return on investment (ROI), which is the net return found by subtracting the cost of investment from the benefit of the investment and dividing by the cost of

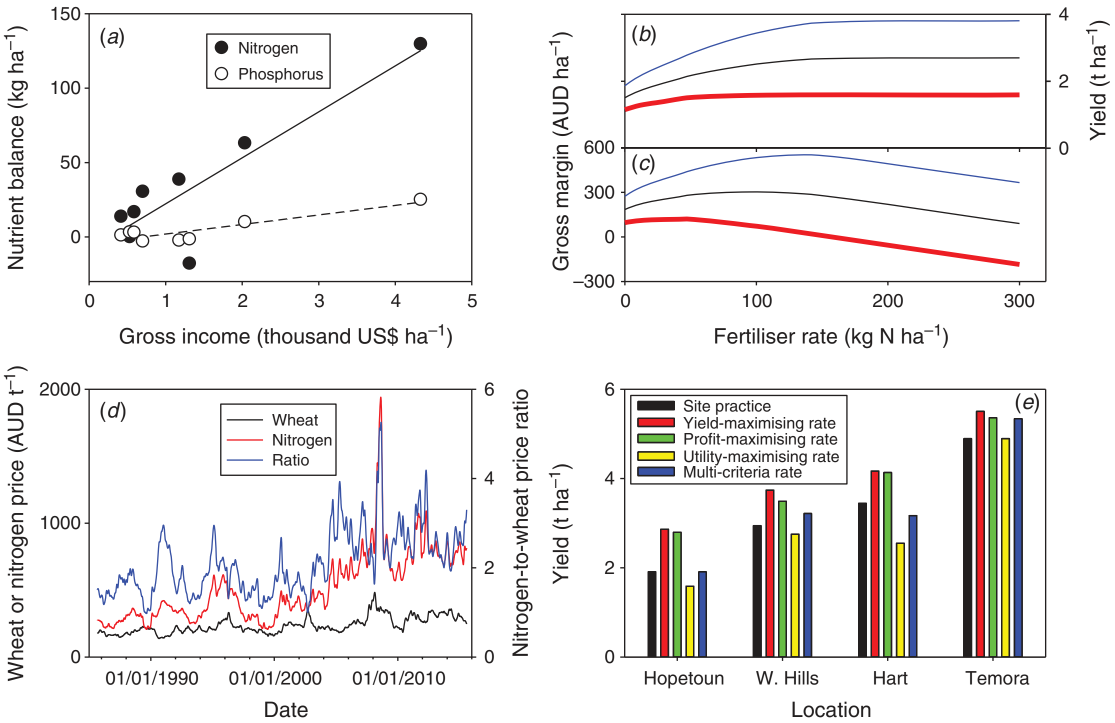

Fig. 6. Some economic factors with implications for nitrogen management. (*a*) Association between nutrient balance (fertilisation – withdrawal) and farm-gate value across crops on a global scale. (*b*) Modelled yield and (*c*) gross margin of wheat in response to rate of nitrogen fertiliser at Brinkworth, South Australia (33°S, 138°E); curves are simulated averages for all years between 1981 and 2010 (middle, black lines), average of the 15 below-median years (lower, red lines) and average of the 15 above-median years (upper, blue lines). (*d*) Grain price (based on ASW wheat), fertiliser price (based on the cost of urea at 46% N) and nitrogen : wheat price ratio between 1979 and 2009 in Australia. (*e*) Modelled mean (1957–2011) wheat yield with five nitrogen fertiliser rates: site practice, yield maximising, profit maximising, utility maximising and multi-criteria in four Australian locations. Sources: *a*, Jobbágy and Sala (2014); *b*–*c*, Hayman *et al.* (2015); *d*, ABARE (2010*a*); *e*, Monjardino *et al.* (2015).

investment (commonly expressed as a percentage). Both expressions are valid, and they are related as ROI = 1 + BCR. Both ROI (Asseng *et al.* 2012; McIntosh *et al.* 2015) and BCR (Angus 1998; Hayman *et al.* 2015) have been used in economic analysis of nitrogen management. The key point is to understand what farmers mean when they refer to requiring a return of say 2 to 1 (Browne and Walters 2015); if the definition is not explicit, this could be interpreted as an extra two (BCR) or three (ROI) dollars income from grain per dollar invested in nitrogen.

Although the agricultural economics literature emphasises inputs to maximise profit, large deviations from optimal management often make little difference to the payoff because flat payoff functions are common (Anderson 1975; Pannell 2006). For nitrogen, a flat payoff curve means that there is a ‘margin for error’, i.e. a set of alternative rates that are only slightly less attractive than the maximum payoff for nitrogen applications (say, within 5% of the maximum), thereby lowering the risk of not selecting the best rate, or allowing for rate adjustments when considering other factors such as the environment. However, the flatness of the curve is reduced with increasing price ratio of nitrogen to grain. Figure 6*c* illustrates the relative flatness around the optimal rate of ~100 kg N ha^{-1}, suggesting that farmers may be better off only taking informed guesses (based on soil, seasonal and economic indicators) instead of employing costly methods for identifying the appropriate fertiliser rate (Robertson *et al.* 2008). Further, the degree of flatness depends on soil properties, as discussed for soils with low PAWC where a limited buffering capacity for both water and nitrogen would lead to sharper payoff functions (see earlier section *Soil texture, soil water and soil nitrogen*). Overall, the degree of flatness in payoff functions has implications for risk management, precision farming and the value of research.

Risk and uncertainty

Yield variability, market volatility and financial debt are major risks faced by dryland farmers in Australia (Hardaker *et al.* 2004). The inherent riskiness of grain production is often high (Hayman *et al.* 2010) and the variance in wheat revenue has increased between 1992 and 2009 (Kingwell 2011) in response to both climate drivers and cropping intensification (Llewellyn *et al.* 2012).

Farmers in low-rainfall regions are conservative in the use of fertiliser, partially because the chance of downside risk is perceived as far greater than that of upside gain. Nevertheless, higher nitrogen rates may pay off by increasing yield and grain quality, and by reducing the probability of missing out in the better years (Asseng *et al.* 2001*a*; Sadras 2002; Anderson 2010; Monjardino *et al.* 2013; Monjardino *et al.* 2015). Strategies and tools have been developed to manage the riskiness of nitrogen fertiliser decisions, but investment in fertiliser remains a challenge in variable environments (Hochman and Carberry 2011).

The average wheat yield gap in Australia of ~2.0 t ha^{-1} in the period 1996–2012 estimated by Hochman *et al.* (2012) is partially attributable to intentional under-fertilisation with nitrogen, due to risk, risk-aversion and trade-offs between efficiency in the use of nitrogen and water, particularly in low-rainfall regions (Monjardino *et al.* 2015). The role of risk management in yield gaps is illustrated in Fig. 6*e*, which highlights the difference in mean wheat yield response between nitrogen rate according to site practice, a yield-maximising rate, profit-maximising rate, utility-maximising rate and multi-criteria rate in four sites. Here, utility-maximising rate is the nitrogen rate that allows farmers to maximise their utility (or certainty equivalents) for a given level of risk-aversion, and multi-criteria rate is the result of a set of yield–risk–return and risk-aversion criteria that would need to be met for a nitrogen-management practice to be selected as the most preferred (Monjardino *et al.* 2015). In all cases, the preferred multi-criteria management strategy was neither the yield-maximising nor the profit-maximising strategy; it generated higher mean yield than the utility-maximising strategy, and in three of the four sites it resulted in a similar mean yield to site practice. On average, yield-maximising rate was only 3% greater than profit-maximising rate, with the biggest yield gap between these strategies at Wongan Hills. Importantly, site practice and multi-criteria rate achieved ~20% less than potential yield, and in two sites, yield with site practice was 8% less than with multi-criteria rate, all of which emphasises the role of farmer risk-aversion in limiting the closure of yield gaps in the management of fertilisation. Overall, site practice, particularly at Hopetoun, Wongan Hills and Hart appeared close to optimal when risk was considered.

A discussion of the economics of nitrogen for dryland grains concentrates on the rate of nitrogen as the controlling variable that comes with a cost, and often treats the supply of water as zero cost and uncertain. The supply of water is closely linked to the cost of purchasing or leasing land. Weed control over the fallow is a cost with benefits in water and nitrogen available to the subsequent wheat crop (Hunt *et al.* 2013). McMaster *et al.* (2015) refer to the process of 'buying a spring' in central New South Wales with a BCR of up to 8.0 for summer weed control. This increased the BCR of nitrogen topdressing from 1 with no weed control to 3 with complete weed control. Stored soil water at sowing will increase the confidence farmers can have in applying higher rates of nitrogen.

Seasonal climate forecasts

Given the risk and costs associated with uncertain seasonal conditions, there is an interest in SCF, which are defined as probabilistic statements about the climate of the coming season (WMO 2006). SCF rely on the memory of the climate system captured in the slower moving variable of ocean temperatures, especially the Pacific and Indian Ocean (Box 2). SCF have been available since the 1990s and many studies have shown their potential benefit to agricultural decisions (Easterling 1999; Hammer 2000; Mase and Prokopy 2014).

The requirements for a forecast to be beneficial include (*i*) a climate-sensitive decision, (*ii*) a prediction that is skilful and timely, (*iii*) the ability to adjust the decision in light of the forecast, and (*iv*) the communication and support for the forecast (Hansen 2002). The ongoing challenge is to have acceptable accuracy or skill of the forecast, and in some cases, the timing of the forecast. Closely linked to the skill of the forecast is the effective communication of the forecast. A more accurate forecast would solve many of the communication problems (Hayman *et al.* 2007; Mase and Prokopy 2014).

Many studies have assessed the application of SCF for the management of nitrogen on wheat in Australia (Hammer *et al.* 1996; Marshall *et al.* 1996; Moeller *et al.* 2008; Asseng *et al.* 2012; Hayman *et al.* 2015; McIntosh *et al.* 2015). The early focus on the Southern Oscillation Index has shifted to POAMA (*Predictive Ocean Atmosphere Model for Australia*) (Box 2). By using ENSO phases, Marshall *et al.* (1996) found that a Goondiwindi grain grower benefited from SCF about as much from wheat breeding (\$3–\$4 ha^{-1} year^{-1}). However, adopting a new wheat variety is likely to provide a modest gain each year, whereas the returns from adopting SCF are more variable. This is because in some years (and for many locations, the majority of years) the forecast will be no different from climatology, and when the forecast is emphatic (say 70% chance of exceeding median), a significant minority of years (up to 30%) when acting on the forecast may lead to losses. McIntosh *et al.* (2015) calculated that it takes on average 3–8 years for a forecast to be of value in representative grain sites around Australia. Hayman *et al.* (2015) compared two strategies in the medium-rainfall zone of South Australia: topdressing a wheat crop with the same amount of nitrogen every year, and tactically changing the rates for topdressing by using information from POAMA. Over the 30-year period from 1981 to 2010, POAMA would have produced the correct guidance 19 times and incorrect guidance 11 times. Under the assumptions of this modelling study, depending on the amount of nitrogen used, following POAMA increased the gross margin by \$23 ha^{-1} or 9%.

A common assumption in these evaluations is that all the benefit of nitrogen is realised in the season when it is applied; however, residual nitrogen in the soil (e.g. in dry seasons) can be of value to the next crop. In a long-term (1996–2004) trial on a Vertosol in the medium-rainfall cropping zone of Victoria, systems with a fertiliser input of 40 kg N ha^{-1} year^{-1} built up a surplus of ~150 kg N ha^{-1} with the onset of the Millennium Drought (Box 2). This surplus was drawn down in the better years from 2009 (Norton *et al.* 2015). The soil, climate and management conditions that favour the carryover of nitrogen need to be identified. Economic assessments at the whole-farm level need to account for the multiple benefits of legumes in rotations, including their potential contribution to the soil nitrogen budget (Preissel *et al.* 2015).

Most analyses of the value of SCF for nitrogen on wheat assume that a farmer has to make the decision before the uncertain season. However, in-crop application of nitrogen is common in southern and Western Australia (see above *An agronomic perspective*). By delaying the application of nitrogen, farmers are applying the principles of 'real options', sometimes referred to as purposeful procrastination. The idea of making a decision and then waiting to see what happens compared with waiting to see what is starting to happen and then deciding or adjusting is central to the intuitive value of real options (Luehrman 1998). Real options have been applied to agriculture and natural resource management (Hertzler 2007; Nelson *et al.* 2013; Sanderson *et al.* 2015).The essence of real options is to use the analogy of financial options to consider the value of waiting for better, but not complete, information. Almost all decisions can be delayed, with costs and benefits changing as the delay continues. The benefit of applying nitrogen later in the season is extra information including the status of the crop and stored soil water, improved information on the rest of the season because the skill of climate forecasts in winter for spring is superior to the low skill in autumn for the coming spring, and more information on the price of grain. The costs of delaying fertilisation include application costs and the risk of low rates of uptake in a dry season.

A breeding perspective: the water and nitrogen economies of high-yielding varieties

The pioneering experiments of Austin *et al.* (1980) compared the phenotypes of wheats released in the UK between 1908 and 1978. This approach returns a rate of yield gain and identifies the traits driving yield improvement. Worldwide comparison of similar studies reinforces the early conclusion that genetic gain in wheat yield is proportional to the potential of the environment (Fig. 7). Although breeders primarily select for yield, grain quality and disease resistance (Richards *et al.* 2014), this selective pressure can lead to extraordinary changes in phenotype. By using this information, we ask: what are the changes in traits related to the water and nitrogen economy of crops in response to selection for yield? Our primary focus is wheat, and rates of change are calculated as percentage of the newest varieties for comparison of traits (Fischer *et al.* 2014). We briefly discuss other crops, including sorghum and maize, where current understanding of stay-green illuminates some of the connections between nitrogen and water, and soybean, where the role of nitrogen fixation under drought has been evaluated in detail.

Water- and nitrogen-related traits of wheat

Two studies have quantified the changes in the wheat phenotype in the winter-rainfall regions of Australia from early breeding until the mid1980s (Siddique *et al.* 1989, 1990*a*, 1990*b*) and for the period 1958–2007 (Sadras and Lawson 2011, 2013; Sadras *et al.* 2012*d*). Yield improvement in Australia over these periods aligns with a global benchmark accounting for the potential of the environment (Fig. 7). Richards *et al.* (2014) provide further insight in an extended assessment of agronomic and breeding contributions to wheat-yield improvement in Australia, where they highlight the higher rates of yield gain under more favourable, wetter conditions.

Early selection returned shorter season varieties with better adaptation to local conditions and reduced seasonal evapotranspiration in parallel with shorter cycles (Fig. 8*a*); mean daily evapotranspiration did not vary among varieties ($P = 0.91$) and averaged 1.3 mm day^{-1}. Soil evaporation accounted for 40% of the seasonal evapotranspiration irrespective of cultivar ($P = 0.50$). Seasonal evapotranspiration remained unchanged for the varieties released between 1958 and 2007 (Fig. 8*b*). Because of the increase in yield and largely unchanged water use after accounting for phenology, yield per unit water use of Australian wheats increased linearly over a century to 2007 (Fig. 8*c*). The 20 kg ha^{-1} mm^{-1} benchmark

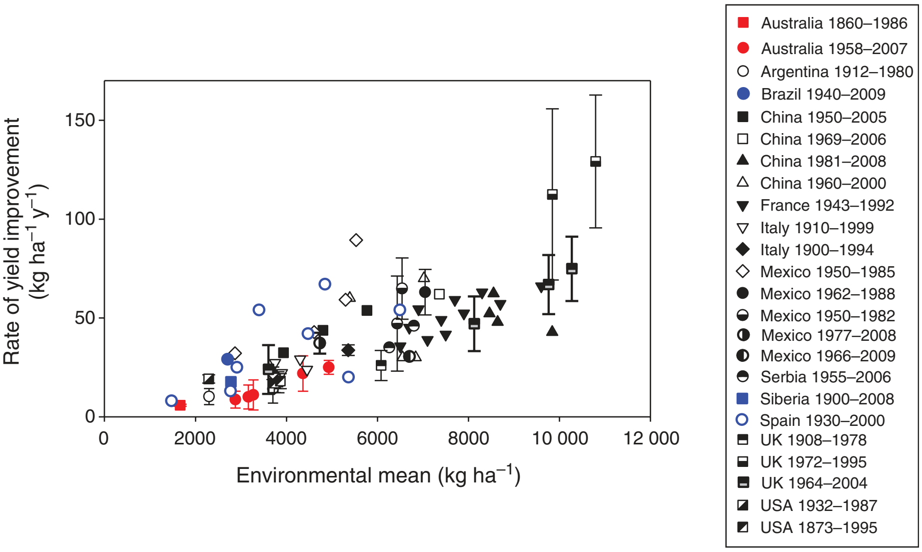

Fig. 7. The rate of genetic gain in wheat yield is proportional to the environmental potential. Sources: Australia, Siddique *et al.* (1989), Sadras and Lawson (2011); Argentina, Slafer and Andrade (1989); Brazil, Beche *et al.* (2014); China, Zhou *et al.* (2007), Tian *et al.* (2011), Zheng *et al.* (2011), Xiao *et al.* (2012); France, Brancourt-Hulmel *et al.* (2003); Italy, Guarda *et al.* (2004), Giunta *et al.* (2007); Mexico, Ortiz-Monasterio *et al.* (1997), Sayre *et al.* (1997); Waddington *et al.* (1986), Lopes *et al.* (2012), Aisawi *et al.* (2015); Serbia, Mladenov *et al.* (2011); Siberia, Morgounov *et al.* (2010); Spain, Sanchez-Garcia *et al.* (2013); UK, Austin *et al.* (1980), Shearman *et al.* (2005); USA, Jensen (1978), Cox *et al.* (1989), Donmez *et al.* (2001).

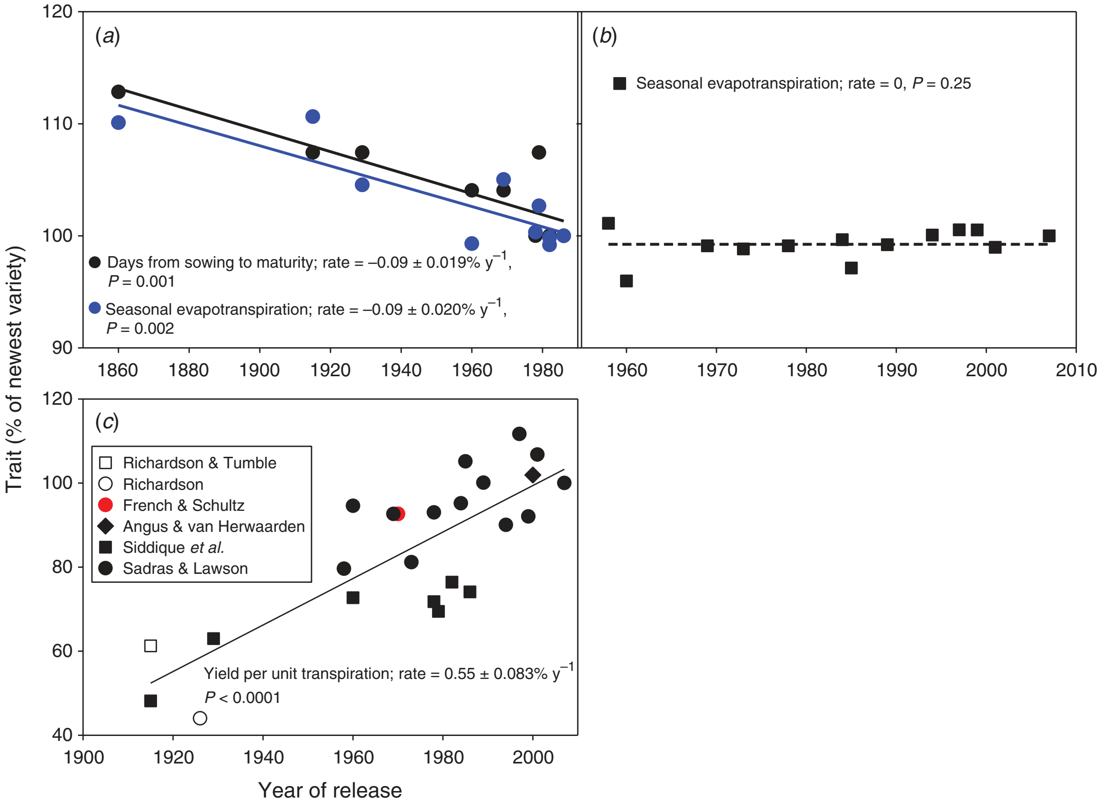

Fig. 8. Changes in phenology and water-related traits of bread wheat in response to selection for yield in south-eastern and Western Australia. (*a*) Shorter cycle and parallel reduction in seasonal evapotranspiration between 1860 and 1986. (*b*) Stable seasonal evapotranspiration between 1958 and 2007. (*c*) Increase in yield per unit transpiration; the red circle is cv. Halberd, with an assumed ratio of 20 kg grain ha^{-1} mm^{-1} (French and Schultz 1984*a*). Solid lines are regressions with significant slopes, and the dashed line shows slope ≈0. Sources: Richardson (1923), Richardson and Trumble (1928), French and Schultz (1984*a*), Angus and van Herwaarden (2001), Siddique *et al*. (1989) and Sadras and Lawson (2011).

of French and Schultz (1984*a*) was largely based on Halberd or earlier cultivars (red point in Fig. 8*c*), hence the need to update this benchmark to account for contemporary varieties, which are close to 25 kg ha^{-1} mm^{-1}.

Selection for yield between 1958 and 2007 increased wheat stomatal conductance but did not increase the rate of photosynthesis per unit leaf area (Sadras and Lawson 2011; Sadras *et al*. 2012*d*). Higher stomatal conductance is a conspicuous response to selection for yield reported for spring and winter bread wheat, durum wheat, rice, cotton and soybean in diverse breeding settings worldwide (Roche 2015). Often, the increase in stomata conductance has been associated with small (or no) change in photosynthesis, thus the apparent decline in intrinsic water-use efficiency (assimilation : conductance ratio). Roche (2015) analysed the possible causes for these responses, and Sadras *et al.* (2012*e*) advanced the hypothesis that where heat stress is prevalent, evaporative cooling, requiring maintenance of stomatal conductance at high vapour pressure, overrides water-use efficiency, which requires stomatal closure. In common to cereals, cotton and grapevine, important physiological and behavioural traits in birds and mammals can be explained in terms of the trade-off between water economy and thermal regulation mediated by evaporative cooling (Piersma and van Gils 2011).

Early selection for yield of wheat in Australia reduced root biomass with no effect on root depth or water uptake (Siddique *et al*. 1990*a*). In field-grown crops, root dry matter at anthesis decreased from 397 g m^{-2} in the old variety Purple Straw to 280 g m^{-2} in the 1986 variety Kulin, and the root : shoot ratio declined from 0.64 to 0.55. Under controlled conditions, root biomass seemed to decline further in response to selection for yield between 1958 and 2007 (Aziz *et al*. 2016). Both studies focused on varieties adapted to the winter-rainfall environments of the west and south-east of Australia where crops rely primarily on in-season rainfall and stored soil water is minor (see earlier section *Climate*). Selective pressure for yield in northern environments where crops rely on soil-stored water might have modified wheat phenotype differently, favouring deeper roots (Manschadi *et al*. 2006). Experiments comparing historic sets of wheat varieties adapted to the northern region would be of interest as a cost-effective means to unravel adaptive traits.

Selection for yield increased shoot water-soluble carbohydrates at anthesis in both stressful Australian conditions and high-yielding UK environments (Shearman *et al*. 2005; Sadras and Lawson 2011). Our understanding of the role of carbohydrate reserves is fragmented, particularly in relation to the interaction between genotype, water and nitrogen (Hoogmoed and Sadras

2016). It is often assumed that reserve carbohydrates contribute to the maintenance of grain size under water stress during grain filling; intra-specific variation for this trait is large, narrow-sense heritability is moderate to high, and complex genetic control across up to 10 quantitative trait loci has been reported (Fischer 2011). Direct selection for water-soluble carbohydrates can thus be achieved with genetic tools, high-throughput phenotyping (Dreccer *et al*. 2014), or a combination of these. The main impediment to selection for this trait is, however, not technical but conceptual, because its adaptive value remains uncertain in relation to both environmental influences and trade-offs. The role of labile carbohydrate in grain filling under stress needs to be reconciled with the enhancement of this trait in response to selection for yield in wet, high-yielding (>10 t ha^{-1}) environments. Storage of labile carbohydrates involves apparent trade-offs with tillering, grain number, root growth and nitrogen uptake (van Herwaarden *et al*. 1998; Dreccer *et al*. 2009, 2013; Lopes and Reynolds 2010). Yield response to the interaction between water and nitrogen supply is partially mediated by responses in partitioning of carbon and nitrogen between yield components and reserves (van Herwaarden *et al*. 1998; Dreccer *et al*. 2009). Dreccer *et al*. (2009) showed that resource-based models are insufficient to capture these interactions. This conclusion arises mostly from studies with lines with different combinations of tillering and patterns of resource allocation, and the recognition that the allocation of resources is bounded by the fate of meristems in the plant. Whether a meristem is inactive, grows a new shoot or transitions to reproduction depends on genetic and environmental influences, and to some extent, the fate of meristems precedes and drives the allocation of resources (Bonser and Aarssen 1996, 2001; Zhang *et al*. 2008). Understanding the controls of meristem fate and crop morphology, coupled with resource-based models, is thus necessary to untangle these important interactions (Dingkuhn *et al*. 2006; Dreccer *et al*. 2009, 2013; Luquet *et al*. 2012).

During the last five decades, the rate of increase in nitrogen uptake of Australian wheats matched the rate of increase in grain yield with breeding; yield per unit nitrogen uptake thus remained stable (Fig. 9). In the absence of changes in nitrogen harvest index, protein concentration in grain remained stable (Fig. 9). The increase in nitrogen uptake was accompanied by shifts in the profile of foliar nitrogen, whereby newer varieties were greener at flowering, particularly at the bottom of the canopy. The increase in uptake and the shift in the distribution of nitrogen contributed to higher radiation-use efficiency, biomass and yield of newer varieties (Sadras *et al*. 2012*d*).

The large increase in nitrogen uptake in this historic set of Australian varieties is unique. Comparison with bread wheat in UK and Argentina, and durum wheat in Italy, shows that nitrogen uptake did not increase in response to selection for yield, or where it did, that increase did not match the rate of yield gain (Figs 10–12). Hence, yield per unit nitrogen increased in all of those breeding settings. With little or no increase in nitrogen harvest index, grain protein declined. Figure 13 summarises the four datasets; the condition for the increase in yield per unit nitrogen is that yield increases faster than nitrogen uptake, and this is reflected in a reduction in grain protein content. Reduced grain protein content in response to breeding for yield was reported for other crops, e.g. maize in the USA (Egli 2015).

In conclusion, selection for yield in the dry, nitrogen-scarce environments of Australia had, arguably, a larger impact on the nitrogen economy of the crop than on traits with putative value for adaptation to water deficit. If anything, some of the more consistent trends in water-related traits have been contrary to expectations; stomatal conductance increased with an apparent decline in assimilation : conductance ratio, and root biomass decreased. The enhanced capacity for nitrogen uptake, despite the putative reduction in root biomass, in newer varieties is of particular interest in the light of the findings of Liu *et al*. (2015). Those authors compared two wheat lines, XY107 and XY6, under low and high nitrogen supply in a glasshouse experiment. Despite its lower root biomass, particularly in the low nitrogen treatment, XY107 absorbed more nitrogen than XY6 and this was associated with the differential expression of nitrate and ammonium transporter genes, especially *TaNRT2.1*.

Water- and nitrogen-related traits of other crops

Stay-green in sorghum and nitrogen fixation in legumes involve links between the water and nitrogen economy of

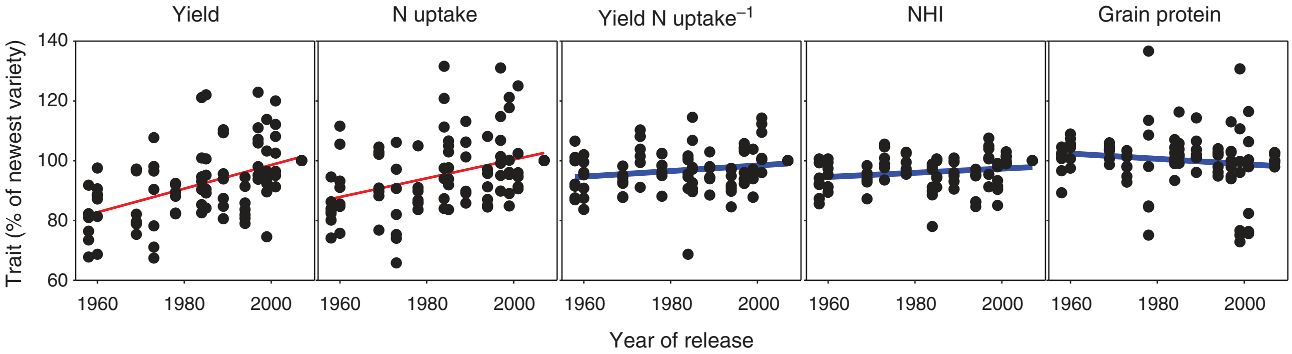

Fig. 9. Changes in yield and nitrogen-related traits of bread wheat in response to selection for yield in Australia. Data are from experiments comparing 13 cultivars in seven environments of South Australia, including locations, seasons and nitrogen rates. Traits are relative to the newest variety. Red lines (for yield and N uptake) are regressions with non-zero slope ($P < 0.05$) and blue lines (for yield N uptake^{-1}, N harvest index (NHI) and grain protein) are regressions with slope not different from zero ($P > 0.05$). Source: Sadras and Lawson (2013).

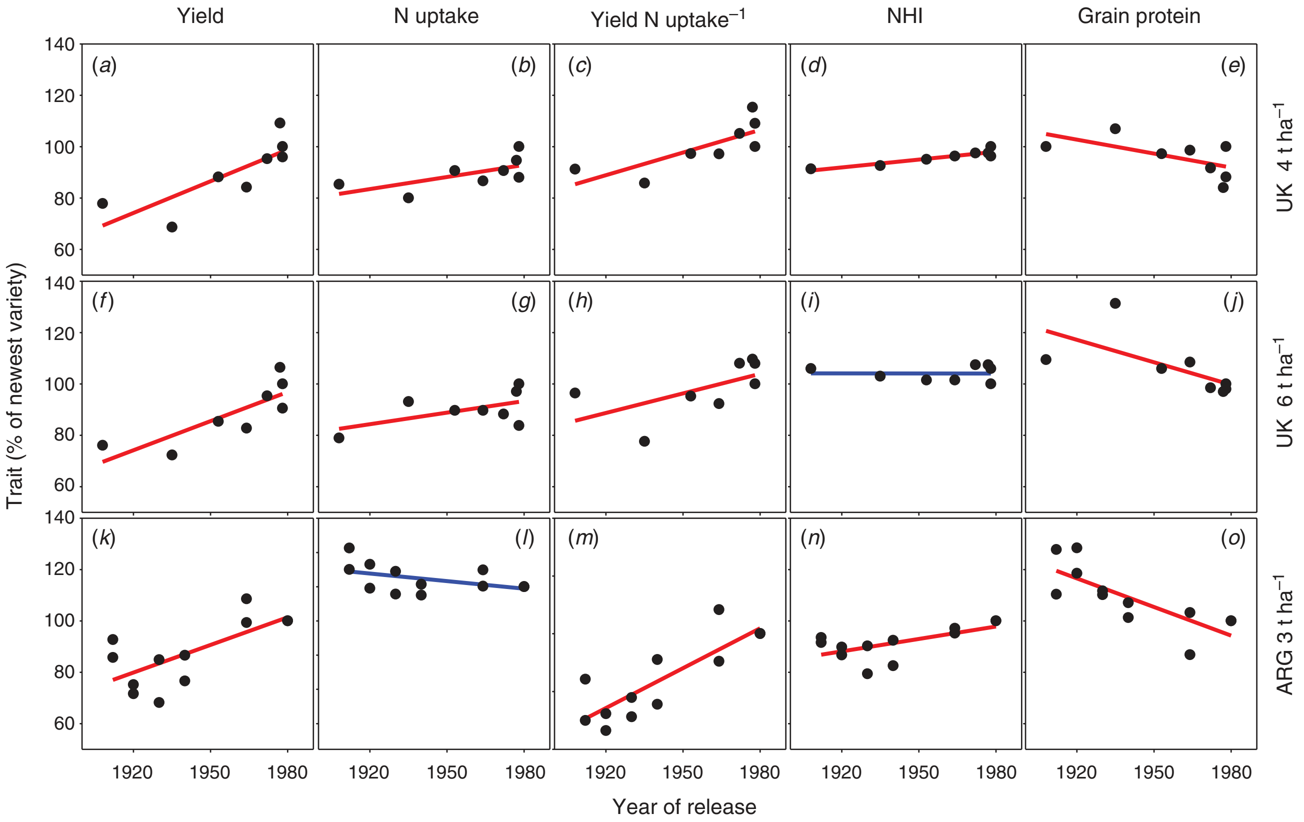

Fig. 10. Changes in yield and nitrogen-related traits of bread wheat in response to selection for yield in the UK and Argentina between 1900s and 1980s. The first and second rows are from two fields in the UK, yielding an average of 4 or 6 t ha^{-1}. The third row is the experiment in Argentina where average yield was 3 t ha^{-1}. Traits are relative to the newest variety in each series. Red lines (*a–h*, *j*, *k*, *m–o*) are regressions with non-zero slope ($P < 0.05$) and blue lines (*i*, *l*) are regressions with slope not different from zero ($P > 0.05$). Sources: Austin *et al.* (1980) and Slafer *et al.* (1990).

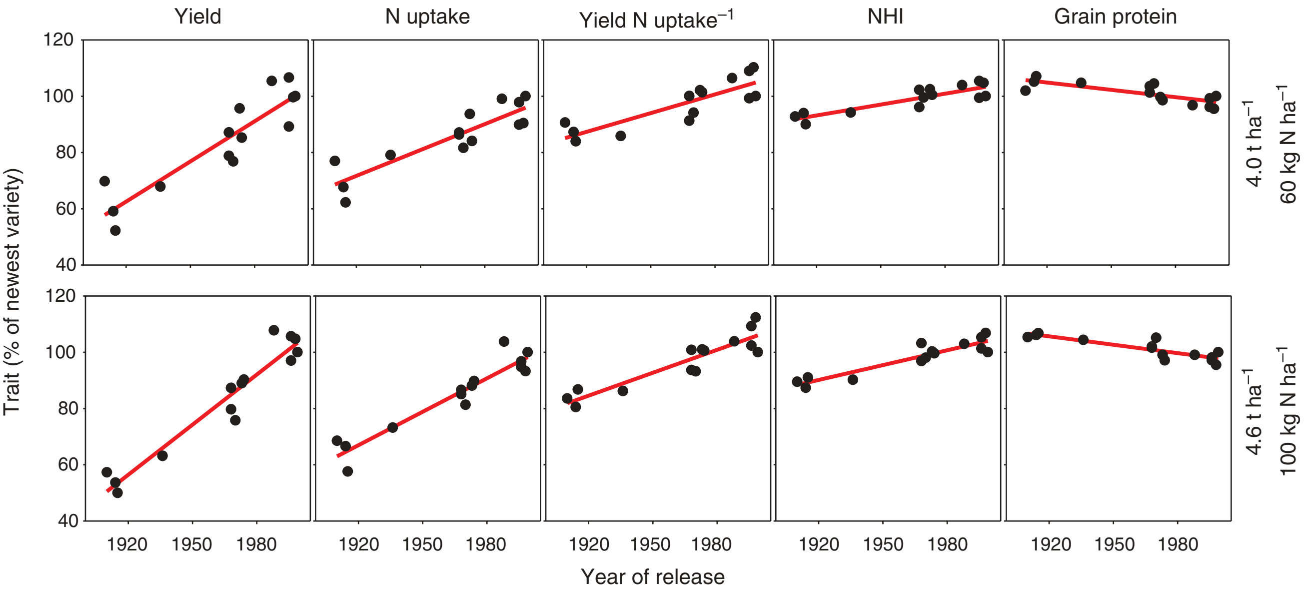

Fig. 11. Changes in yield and nitrogen-related traits of durum wheat in response to selection for yield in Italy between 1900s and 1980s. The top row is from crops fertilised with 60 kg N ha^{-1} and the second 100 kg N ha^{-1}, returning average yields of 4.0 and 4.6 t ha^{-1}, respectively. Traits are relative to the newest variety. All regressions have non-zero slope ($P < 0.05$). Source: Giunta *et al.* (2007).

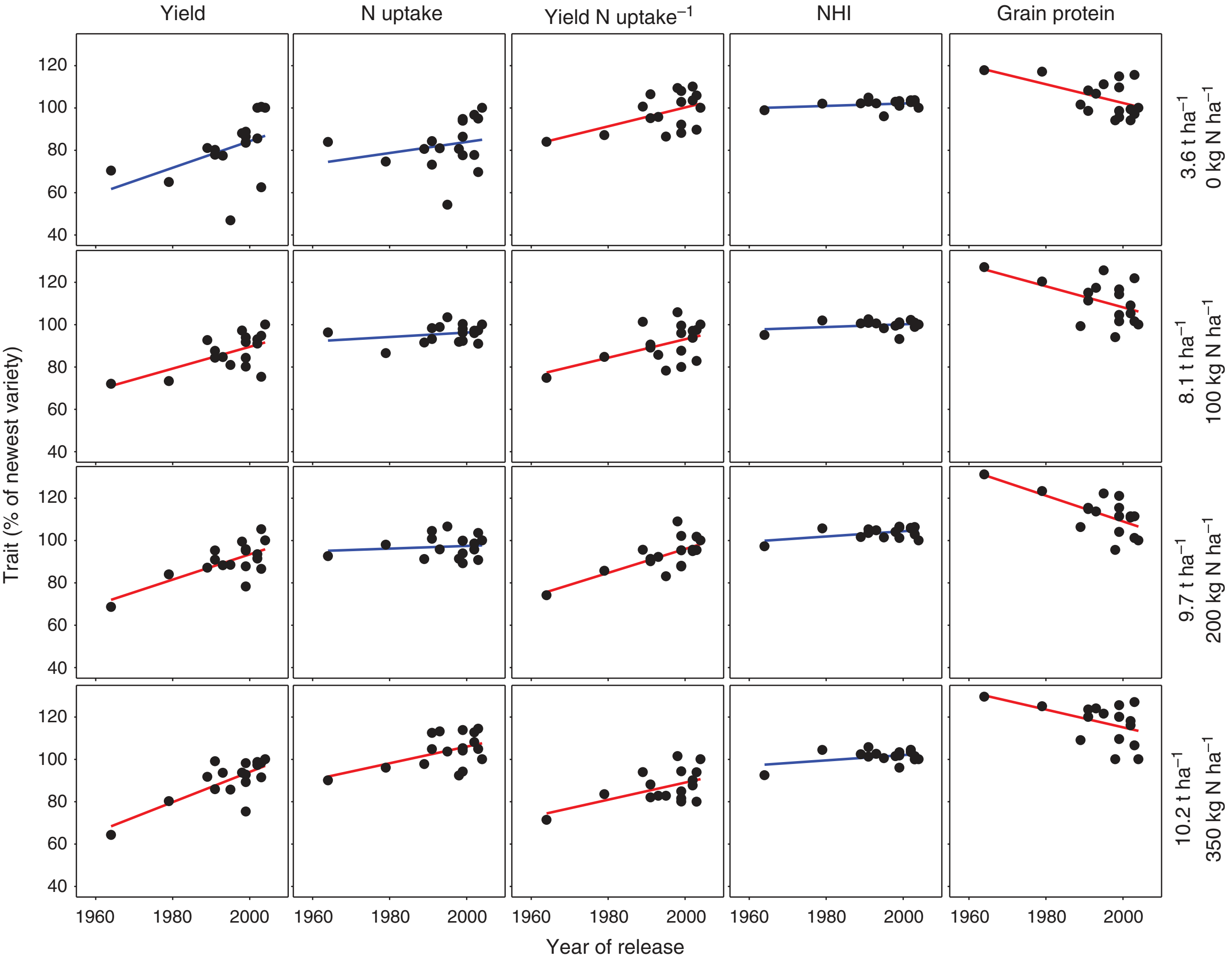

Fig. 12. Changes in yield and nitrogen-related traits of bread wheat in response to selection for yield in the UK between 1964 and 2004. Each row is a rate of nitrogen fertiliser and mean yields from 3.6 to 10.2 t ha^{-1}. Traits are relative to the newest variety. Red lines are regressions with non-zero slope ($P < 0.05$) and blue lines are regressions with slope not different from zero ($P > 0.05$). Source: Barraclough *et al.* (2010).

the crop that have been summarised by Sadras and Richards (2014). Stay-green in sorghum integrates several lower level traits and is mostly expressed where water stress during grainfill increases the rate of nitrogen remobilisation and leaf senescence; hence, its expression strongly depends on how the trait interacts with other traits, and with environmental and management factors (Jordan *et al.* 2012). Five combinations of traits and environments would contribute to stay-green in sorghum: (*i*) traits that contribute to water saving and less severe stress during grainfill, such as early maturity, small leaves and few tillers, high stomatal sensitivity to drying soil and high vapour-pressure deficit; (*ii*) traits that contribute to enhanced water uptake, such as deep roots in the right combination of soil and rainfall; (*iii*) life-history (i.e. high perenniality) or metabolic traits (e.g. higher carbon and nitrogen allocation to roots during grain filling); (*iv*) traits that favour high source : sink ratio (e.g. few grains); and (*v*) developmental traits that change the seasonal pattern of water use for the same maturity type. For plant breeding, (*i*) and (*ii*), and maybe (*iii*), are of interest, but usually not (*iv*) or (*v*) because these may involve trade-offs with HI and yield.

Selection for yield in the USA has often favoured stay-green traits in maize (Duvick 2005). In a comparison of single-cross hybrids released between 1967 and 2006, the rate of yield increase was 56 kg ha^{-1} year^{-1} in unfertilised crops, 79 kg ha^{-1} year^{-1} in crops fertilised with 67 kg N ha^{-1}, and 86 kg ha^{-1} year^{-1} in crops with 252 kg N ha^{-1} (Haegele *et al.* 2013). The relative increase in nitrogen uptake matched the relative increase in yield at the low fertiliser rate but not at the higher rate, and this was reflected in a reduction in protein content with year of release (Haegele *et al.* 2013), in a process similar to that described above for wheat in Europe and Argentina. Modern hybrids require higher fertiliser rates to express their enhanced yield capacity, and this is partially related to more subtle changes in the kinetics of nutrient uptake in response to selection for yield. Saccomani *et al.* (1984) evaluated the two kinetic parameters of sulfate uptake in maize seedlings spanning the period 1930–75 and found that $V_{\max}$ increased 1.37% year^{-1} and K_m 3.24% year^{-1} in

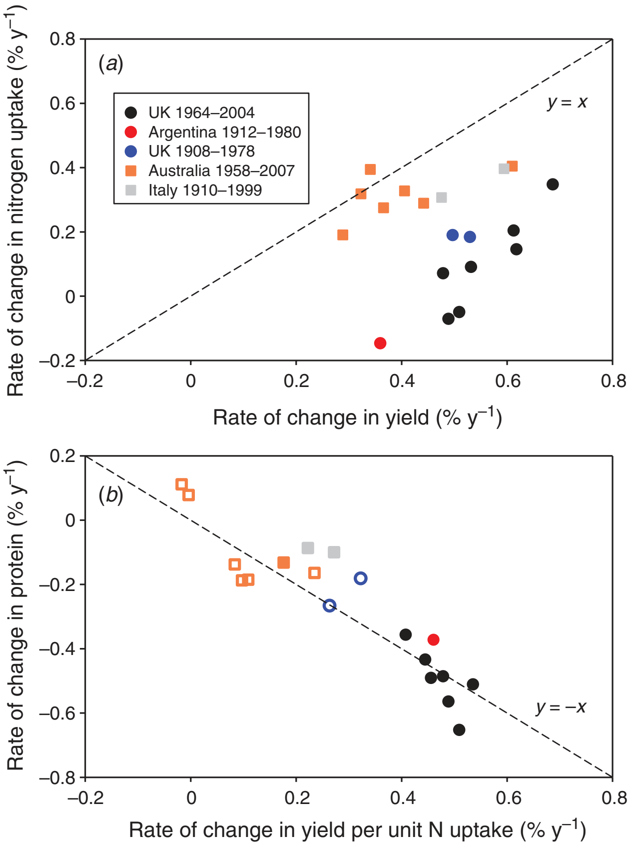

Fig. 13. Comparison of rates of change in wheat traits in response to selection for yield. (*a*) Rate of change of nitrogen uptake *v.* rate of change in yield. (*b*) Rate of change in grain protein concentration *v.* rate of change in yield per unit nitrogen uptake. In *b*, open symbols indicate rates of change in protein not different from zero, and solid symbols indicate significant rates ($P = 0.05$). Sources: Austin *et al.* (1980), Slafer *et al.* (1990), Giunta *et al.* (2007), Barraclough *et al.* (2010), Sadras and Lawson (2013).

relation to the oldest varieties. Thus, the gain in uptake efficiency associated with higher V_{max} was counteracted by the loss of affinity of the transport system for sulfate, thus explaining why recent hybrids are handicapped with respect to older ones at lower nutrient concentration.

A genotype-driven link between the maintenance of N_2 fixation under stress and drought adaptation has been proposed for soybean (Sinclair *et al.* 2007; Sinclair 2011). Selected lines with enhanced maintenance of N_2 fixation were compared with high-yielding commercial cultivars under broad environmental conditions. Two lines were identified that outperformed commercial checks under water deficit, but trade-offs were apparent under high-yielding conditions. In a glasshouse experiment comparing the normalised acetylene reduction activity of 10 cowpea lines in response to soil drying, the fraction of transpirable soil water at which N_2 fixation rate began to decline was 0.33 in the most sensitive line, whereas in another line there was no decline in N_2 fixation rate (Sinclair *et al.* 2015). Whereas the sensitivity to water deficit in legume N_2 fixation is recognised, intra-specific variation is significant and has putatively adaptive value. Similar studies are lacking for temperate legumes.

A modelling perspective

Diverse modelling approaches aim to match model complexity, error and applications (Passioura 1996). Here, we outline aspects of the water and nitrogen economy of crops from a modelling perspective with a primary focus on APSIM (Probert *et al.* 1998; Holzworth *et al.* 2014).

The typical approach for modelling crop growth is to simulate the potential growth first, followed by its reduction due to water and nitrogen limitations and other stresses. Net biomass growth or carbon assimilation at whole-crop level is modelled by using species-specific parameters (e.g. radiation-use efficiency or maximum photosynthesis rate, extinction coefficient) together with canopy size, CO_2 concentration, radiation and temperature. Potential growth of individual organs (leaf, root, or grain) is mostly temperature-driven and defines the demand for carbohydrates. It can be limited by the partition of available biomass or assimilates (supply), which is controlled by progression of phenological stages driven by temperature and photoperiod.

Impact of water deficit on growth is simulated by comparing the water demand of the crop and the water supply from the root–soil system. Demand is the amount of water required to maintain potential growth and is determined by crop type, canopy size and weather. APSIM converts the potential biomass growth rate to water demand by using the vapour-pressure-deficit-corrected transpiration efficiency. Water supply is limited by the amount of plant-available water in soil and further reduced by the size of root system. APSIM simulates water supply as a fraction of plant-available water in the rooted soil layers, considering this fraction and the maximum rooting depth as both crop- and soil-dependent. Other models link water supply to root-length density and plant-available water. Soil water content at saturation, drained upper limit, crop lower limit, and parameters related to water conductivity control water movement in soil and availability to crops. If water supply cannot meet water demand, biomass growth rate is scaled down from potential by the supply : demand ratio. Impact on processes that are more-or-less sensitive to water stress is simulated by using higher or lower thresholds of the supply : demand ratio.

Crop nitrogen relations are simulated by using a similar supply–demand approach. In APSIM, maximum (N_{cx}), critical (N_{cc}) and minimum (N_{cm}) nitrogen concentrations are defined as species-specific attributes dependent on phenological stages. Crop nitrogen demand is the sum of the demand from the pre-existing biomass to reach N_{cc} plus the nitrogen required by the new growth to maintain N_{cc}. The nitrogen supply (root N uptake) is the total of N transported into roots via mass flow (passive uptake) and by diffusion (active uptake), with the former linked to transpiration and the latter affected by the fraction of available water in soil, both limited by available mineral nitrogen in rooted soil layers. Actual nitrogen uptake is the smaller of demand and supply, and it is partitioned to different organs proportional to their nitrogen demand. Re-translocation of nitrogen from leaf and stem to grain occurs during grain filling, which can lower the nitrogen concentrations in leaves and stems to their minima (N_{cm}). Nitrogen stress is calculated as the relative difference between actual leaf N concentration (N_{ca}) and leaf N_{cc} as:

$$f_n = a(N_{ca} - N_{cm})/(N_{cc} - N_{cm}) \quad (3)$$

An f_n with $a = 1.5$ is used to scale down biomass growth, and $a = 1.0$ is used for leaf expansion because of its higher sensitivity to nitrogen stress. Available mineral nitrogen in soil is updated daily by the soil nitrogen module, which simulates soil nitrogen processes including mineralisation, immobilisation, nitrification, denitrification, movement in soil and leaching (Probert *et al.* 1998).

APSIM and similar process-based models capture several aspects of the interactions between water and nitrogen. Water and nitrogen are primarily linked by applying the minimum of the water and nitrogen stress to reduce the rate of different processes (tissue expansion, biomass growth). Further, in crops where water limits growth, reduced biomass would reduce nitrogen demand. Reciprocally, nitrogen limitation during crop expansion would reduce leaf area index and evaporative demand. The modulation of canopy size by nitrogen also affects the partitioning of water use between transpiration and soil evaporation. Water and nitrogen interactions are also captured in the water-driven uptake of nitrogen by mass flow and diffusion and in the water-driven fate of nitrogen in soil (e.g. leaching, mineralisation).

In general, the precision and accuracy of current models is superior for the components of the water budget than for the components of the nitrogen budget of soils and crops (Asseng *et al.* 1998; Mohanty *et al.* 2010; Sharp *et al.* 2011*a*, 2011*b*; do Nascimento *et al.* 2012). To support research on the effect of water–nitrogen interactions on crop yield and grain protein, models need to have improved capacity to simulate nitrogen-related processes. The model SiriusQuality2 is improving simulation of the protein content of the wheat grain, and incorporating allometric relations accounting for the proportions of structural nitrogen, gliadins and glutenins in grain, and their responses to source : sink ratio, temperature, radiation, ambient CO_2 concentration, water and nitrogen (Aguirrezábal *et al.* 2015; Martre *et al.* 2015). An alternative modelling framework is being developed to improve capture of genotype-dependent traits in APSIM (Hammer *et al.* 2010), including the demand for structural, non-structural and metabolic nitrogen pools of different organs. An example is the calculation of leaf nitrogen demand based on a critical specific leaf nitrogen (van Oosterom *et al.* 2010). This, together with a canopy photosynthesis model, can help to capture the genotypic differences in nitrogen demand and uptake and their impact on radiation-use efficiency and potential growth rate (Fig. 9). Better understanding of genotype-dependent root water and nitrogen uptake in different soils is needed. Modelling nitrogen mineralisation requires methods to quantify better the composition and decomposition of soil organic matter (e.g. more or less labile fractions) in response to soil conditions (Luo *et al.* 2014) and crop residues and their management (Mohanty *et al.* 2010; do Nascimento *et al.* 2012). The characteristically large error in the measurement of soil organic carbon and nitrogen mineralisation challenges the parameterisation and validation of soil carbon and nitrogen mineralisation models (Sadras and Baldock 2003). Improved modelling of denitrification losses during wets period can improve soil and crop nitrogen budgets (Huth *et al.* 2010).

Conclusions: further research

From the previous discussion, the following lines of research are suggested.

(1) Nitrogen dilution curves for water-stressed crops. Plant-based diagnostic of crop nitrogen status must capture the allometry between shoot nitrogen concentration and biomass. With few exceptions, these curves have been developed for well-watered crops. Thus, we propose to develop nitrogen-dilution curves for major crops accounting for the effects of water deficit. In wheat, these curves also need to include explicitly a compartment of water-soluble carbohydrates. These dilution curves will allow for unequivocal assessment of the nitrogen status of crops, which is in turn necessary for calibration of diagnostic tools in crop management, high-throughput methods in breeding and model parameterisation.

(2) Tailoring fertiliser to variety. Fertiliser recommendations are generic, but there is an increasing interest in variety-specific differences in response to nitrogen. Thus, we propose to assess the nitrogen demand and responsiveness to fertiliser, in terms of yield and protein, of new wheat varieties, and explore the benefits of tailoring fertiliser management to specific varieties.

(3) Nitrogen uptake *v.* evapotranspiration relationship. The French and Schultz model has been instrumental for benchmarking and management of rainfed wheat in Australia and has recently been expanded to other crops and regions. By analogy to the yield–evapotranspiration relationship, we propose to investigate the nitrogen uptake *v.* evapotranspiration relationship; the nitrogen : water ratio required to close the yield gap, at a certain grain protein, has potential benchmarking applications.

(4) Plant-available nitrogen. Growers are familiar with the concept of plant-available water but there is no equivalent for nitrogen; estimates of fertiliser requirements assume that all mineral nitrogen in the soil root-zone is available for the crop. We thus propose to develop the concept of plant-available nitrogen and field methods to measure it. Practical aspects of soil sampling need some attention, e.g. transport from the farm to the laboratory, timeliness of laboratory results to support decisions.

(5) Influence of nitrogen supply on water uptake. There is large variation in the impact of nitrogen supply on water uptake. We suggest that there is a need to establish the combination of crops, soils and growing conditions where additional nitrogen can enhance soil-water uptake. This is more likely to be relevant in the northern region, where stored soil water is important.

(6) Water–nitrogen trade-offs associated with cover crops and pastures. Some components of cropping systems contribute nitrogen but may reduce the water available to subsequent crops. We therefore need to quantify the trade-offs between nitrogen supply and water consumption by pastures and

green manures in different combinations of soil, climate and rotations in both winter- and summer-rainfall regions.

(7) Carryover of nitrogen and risk analysis. Risk analysis of fertiliser decisions generally assumes that all of the benefit of nitrogen application is limited to a single season. Given emerging experimental evidence, we need to determine the size of the carryover effect for different combinations of crop, soil, climate and management and update risk analysis to account for carryover of nitrogen beyond the application season.

(8) Genotype-dependent nitrogen uptake in wheat. Breeding for yield in Australian wheat adapted to winter-rainfall regions has increased crop nitrogen uptake. Following on from this finding, it is of interest to determine the physiological and genetic basis of nitrogen uptake in old and new wheat varieties with proven differences in nitrogen uptake.

(9) Nitrogen fixation in water-stressed temperate pulses. Superior soybean lines have been selected for maintenance of N_2 fixation under drought. Research in temperate legumes lags behind soybean and other subtropical species. Hence, there is a need to screen temperate pulses for N_2 fixation in soil dry-down experiments, and establish the adaptive value (in terms of yield) of this trait.

(10) G × E × M in sorghum and maize. Sorghum is the more important summer cereal in Australia and is supported by local breeding, whereas growers rely on putatively less adapted maize hybrids developed overseas. We propose to compare sorghum and maize to understand the relevant phenotypic differences (e.g. tillering, stomatal sensitivity, response to sowing density) and to determine the profitability and risk of different G × E × M combinations (hybrids, plant density, row configuration, sowing time, soil type and nitrogen fertilisation).

(11) Probabilistic patterns of supply and demand of water and nitrogen. Modelling is a cost-effective approach to generate agronomically interesting information across regions and climates. We propose to model and map the nationwide, probabilistic patterns of supply and demand of water and nitrogen for major crops as background for agronomic (e.g. timing of fertilisation) and breeding (e.g. root patterns) studies. Nationwide patterns of water stress have been produced for wheat, maize, sorghum, field pea and chickpea; remaining crops to be modelled are barley, canola, lentil, lupin and faba bean. The patterns of demand and supply for nitrogen need to be developed for all crops. To support this, we need improved modelling of genotype-dependent nitrogen processes.

(12) The role of stomatal conductance in the adaptation to drought and heat. Increasing stomatal conductance is a conspicuous response to selection for yield. This is in conflict with the view that stomatal closure at high vapour-pressure deficit favours transpiration efficiency and growth under drought. Thus, there is need to explore the role of stomatal conductance in view of the trade-off between evaporative cooling and water-use efficiency against the backdrop of the probabilistic patterns of thermal and water regimes in the cropping regions.

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