Crop rotation effect on wheat grain yield as mediated by changes in the degree of water and nitrogen co-limitation

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Abstract. Theoretically, growth of stressed plants is maximised when all resources are equally limiting. The concept of co-limitation could be used to integrate key factors affected by crop rotation. This paper tested the hypothesis that the effect of crop rotation on the yield of wheat is partially mediated by changes in the degree of co-limitation between nitrogen and water.

Four rotations were established on a sodic, supracalcic, red chromosol in a Mediterranean-type environment of southern Australia. Rotations included wheat grown after (a) faba bean harvested for grain, (b) faba bean incorporated as green manure, (c) ryegrass pasture, or (d) medic pasture; barley was grown after wheat in all cases. The response of wheat to the rotations during 3 growing seasons was analysed in terms of nitrogen and water co-limitation, and the response of barley was taken as a measure of the persistence of rotation effects.

Daily scalars quantifying water and nitrogen stress effects on tissue expansion were calculated with a crop simulation model. These scalars were integrated in a series of seasonal indices to quantify the intensity of water \((S_W)\) and nitrogen stress \((S_N)\), the aggregated intensity of water and nitrogen stress \((S_{WN})\), the degree of water and nitrogen co-limitation \((C_{WN})\), and the integrated effect of stress and co-limitation \((S_{CWN} = C_{WN}/S_{WN})\). The expectation is that grain yield should be inversely proportional to stress intensity and directly proportional to degree of co-limitation, thus proportional to \(S_{CWN}\).

Combination of rotations and seasons generated a wide variation in the amount of water and inorganic nitrogen in the 1-m soil profile at the time of wheat sowing. Plant-available water ranged from 33 to 107 mm, and inorganic nitrogen from 47 to 253 kg N/ha. Larger amounts of nitrogen were found after green-manured faba bean, and smaller after grass pasture. There was a consistent effect of rotation on wheat yield and grain protein content, which persisted in subsequent barley crops. Measured grain yield of wheat crops ranged from 2.5 to 4.8 t/ha. It was unrelated to water or nitrogen stresses taken individually, inversely related to the aggregated stress index \(S_{WN}\), and directly related to the \(C_{WN}\) index of co-limitation. The combination of stress and co-limitation in a single index \(S_{CWN}\) accounted for 65% of the variation in measured crop yield. This is a substantial improvement with respect to the stress effect quantified with \(S_{WN}\), which accounted for 43% of yield variation. It is concluded that rotation effects mediated by changes in the relative availability of water and nitrogen can be partially accounted for by degree of resource co-limitation.

Additional keywords: barley, fertiliser, grain protein, legumes, modelling, pastures, resource limitation, stress, water-use efficiency.

Introduction

Agriculturalists have used crop rotations for thousands of years. Pliny described rotations involving cereals, legumes, and \textit{Brassica} spp. in ancient Greece and Rome, which are comparable with those currently used in the wheat growing regions of Australia. Despite their long history, the effect of rotations is only partially understood because of the many interacting factors that this practice modifies. Karlen \textit{et al.} (1994) reviewed the mechanisms underlying the effects of rotations on the yield of target crops, highlighting the myriad of changes involving communities of plant pathogens, weeds, and insects, availability of water and nutrients, soil structure, soil microbial activity, and phytotoxic or growth promoting compounds. They concluded that determining how the factors associated with crop rotations interact and contribute to the currently undefined ‘rotation effect’ will remain a major research challenge.

Co-limitation occurs when the response of a biological system to 2 or more factors is greater than its response to each factor in isolation. According to this operational definition,
co-limitation has been identified in systems spanning organisation levels from cell to ecosystem (Chapin et al. 1987; Mooney et al. 1991; Takeda et al. 1995; Sadras et al. 1998; Sih et al. 1998; Maberly et al. 2002; Vyn and Hooker 2002). In contrast to this view of co-limitation, Blackman’s law of limiting factors states that crop production is only responsive to one, the most limiting, factor (Kho 2000). Studies in both agricultural and natural ecosystems highlight the inadequacy of the single limiting factor paradigm, as co-limitation could arise from (a) the sequential influence of factors at different time scales, (b) the influence of different factors on different components of the system, and (c) pseudo-substitution of inputs (Sinclair and Park 1993; Sadras and Roget 2004). The response of a crop to the multiple factors altered by crop rotation can be considered a particular case of the more general problem of living systems constrained by multiple factors and their interactions. The concept of co-limitation could therefore be used to integrate key factors affected by crop rotations.

Water and nitrogen are key resources constraining primary production in sown and arid ecosystems (Mazzarino et al. 1998; Alon and Steinberger 1999). The effects of crop rotation on the water and nitrogen economies of dryland farming systems in Australia have been widely researched (Dunin et al. 2001; Evans et al. 2001; Fillery 2001; Ridley et al. 2001), but few studies looked at the interactions between these resources in the light of co-limitation theories (Sadras 2004; Sadras and Roget 2004). Here we propose that crop yield is (a) inversely proportional to the intensity of water and nitrogen stress and (b) proportional to the degree of nitrogen and water co-limitation. The expected proportionality between crop yield and degree of co-limitation is a corollary of the Blom et al. (1985) theorem stating that plant growth is maximised when all growth resources are equally limiting. To account for the combined effect of total stress (\(S_{WN}\)) and degree of co-limitation (\(C_{WN}\)), we defined a coefficient \(SC_{WN}\):

\[
SC_{WN} = C_{WN} / S_{WN}
\]

(1)

This paper tested the hypothesis that the effect of crop rotation on the yield of wheat is partially mediated by changes in total stress and degree of co-limitation between nitrogen and water, as characterised with \(SC_{WN}\).

Methods

Field experiment

The experiment, including a full account of agronomic practices, is described by Baldock and Cox (2004). Four rotations were established on a sodic, supracalcic, red chromosol (Isbell 1996) at Roseworthy, South Australia (34° S, 134° W). Rotations were of the form \(x_{s}wheat/barley\), where \(x_{s}\) = faba bean (cv. Fiord, 150 kg/ha) harvested for grain, \(x_{f}\) = faba bean incorporated as green manure at flowering, \(x_{r}\) = ryegrass pasture (cv. Guard, 14-31 kg/ha), and \(x_{p}\) = medic pasture (cv. Paraggio, 40-48 kg/ha). The experiment involved 2 phases, i.e. Phase 1 initiated with \(x_{s}\) in 1994 and Phase 2 initiated with \(x_{s}\) in 1995. Treatments were laid out in a completely randomised block design with 3 replicates; individual experimental plots were 50 by 100 m to allow for grazing (10 sheep/ha) and use of farm machinery in commercial practice. The response of wheat (cv. Janz, 85–104 kg/ha) to rotations during 3 growing seasons was analysed in terms of nitrogen and water co-limitation, and the response of barley (cv. Chebec, 82 kg/ha) was taken as a measure of the persistence of rotation effects. Wheat was sown on 30 June 1995; 15 June 1996, 15 May 1998, and 2 June 1999. The 1996 crop was excluded from the analysis due to atypically late re-sowing following herbicide damage of the original crop. Only low rates of nitrogen fertiliser (10-20 kg N/ha) were applied to the cereal crops to accentuate any influence of rotation treatments on the availability of inorganic nitrogen.

Three soil profile cores (70 mm diam., 1 m depth) were taken from each experimental plot to determine the soil chemical and physical properties summarised in Table 1. Soil profile cores were also extracted at 3 locations within each experimental plot within the week prior to sowing to determine gravimetric water content and inorganic nitrogen (ammonium-N plus nitrate-N). Inorganic nitrogen was measured in dried soil samples ground to \(\leq 2\) mm using a 2 M KCl extraction procedure (1 h at 25°C) (Kalra and Maynard 1991). Yield was determined from machine-harvested grain collected from 4 sections (1.8 by 80 m) per plot. Grain nitrogen concentration was measured on ground samples (\(\leq 2\) mm) using a LECO CNS2000 dry combustion analyser (Raymont and Higginsom 1992). Grain protein (% by mass) was calculated using a conversion factor of 0.625 g N/kg. Shoot biomass was measured 1–3 times during the growing cycle of the crop in four 0.6-m row samples per plot; these data were used in conjunction with grain yield in testing the model as explained below.

The effects of rotation on response variables including grain yield and its components, grain protein, plant-available water, and inorganic nitrogen in the soil at sowing were analysed using separate ANOVAs for each season, as equality of variance F-tests (SAS Institute 1999) indicated non-homogeneous variance among seasons for all variables.

Modelling analysis

The APSIM model (ver. 2.1) including the wheat, water, and nitrogen modules described by Meinke et al. (1998) and Probert et al. (1998) was used to explore the hypothesised association between measured yield and degree of nitrogen and water co-limitation. Grain yield and shoot biomass measured in the field experiment were compared with model estimates, and statistics of the comparison were calculated with the BRNE software (Filipe et al. 2003). Inputs included weather records measured at Roseworthy, actual amounts of inorganic nitrogen and water in the 1 m soil profile, sowing dates, and dose of nitrogen fertiliser. Soil parameters were derived from Table 1. To account for the effect of subsoil salinity (Table 1), we used lower limits of plant-available water measured on soils as explained in Sadras et al. (2003). All other parameters were model defaults.

Model scalar accounting for the effect of water (\(w_{o} = 2\)) and nitrogen deficit (\(n_{o} = 2\)) on plant tissue expansion range from 0 (maximum stress) to 1 (no stress), and are defined daily using relationships between water supply and demand (\(w_{o} = 2\)), and actual and critical leaf nitrogen concentration (\(n_{o} = 2\)). These scalars were combined in a series of indices to account for the degree of co-limitation between water and nitrogen, and for the intensity of stresses. Degree of co-limitation (\(C_{WN}\)) was calculated as:

\[
C_{WN} = \sum_{t=1}^{2} 1 - w_{o}(2 - n_{o}(2))
\]

(2)

The \(C_{WN}\) index was calculated for 3 periods of 2 days between times \(t_{1}\) and \(t_{2}\) sowing to harvest, 10–90% of shoot biomass accumulation, and the 30-day period bracketing anthesis (Fischer 1985). Hereafter, the...
seasonal index from sowing to harvest will be used, as it proved to be the most robust in its relationship with grain yield, i.e. it accounted for about half of the variation in crop yield, whereas the other indices accounted for one-third of the variation in yield. Co-limitation, as defined in Eqn 2, tends to 1 when both stresses are of similar magnitude; the index for one-third of the variation in yield. Co-limitation, as defined in

\[ S_S = 1 - \text{seasonal average (mm/2) } \]

\[ S_W = 1 - \text{seasonal average (mm/2) } \]

\[ S_P = S_S + S_W \]

The expectation is that grain yield should be inversely proportional to stress intensity and directly proportional to degree of co-limitation, thus proportional to \( S_S \) \( S_W \) and \( S_P \) had frequency distributions not different from normal \( (P > 0.94) \) (SAS Institute 1999).

**Results**

**Field experiment: rotation and seasonal effects on available nitrogen and soil water, and wheat and barley yield and grain protein concentration**

Rainfall between sowing and harvest ranged from 191 to 274 mm, and accounted for 0.36-0.61 of reference evapotranspiration (Table 2). Figure 1 shows the variation in plant-available water and inorganic nitrogen in the 1 m soil profile at sowing. There was a strong seasonal effect on plant-available water, which ranged from 33 to 107 mm, but no consistent effect of rotation. The amount of inorganic nitrogen varied from 47 to 253 kg N/ha. Rotation effect on soil inorganic nitrogen at sowing was significant only in 1999 \( (P = 0.007) \), when larger amounts of nitrogen were found after green-manured faba bean, and smaller amounts after grass pasture. There was a very weak, positive association between inorganic nitrogen and plant-available water \( (r^2 = 0.16; P = 0.018) \).

Table 3 summarises the effects of rotations and seasons on grain yield, its components, and grain protein concentration. Grain number accounted for most of the variation in grain yield \( (r^2 = 0.71, P < 0.0001) \), and was unrelated to individual grain mass \( (P > 0.94) \). Sowing date contributed to the large seasonal effect on grain yield, which declined at an average rate of 30 ± 4.3 kg/ha per day delay in sowing between 13 May and 30 June \( (P < 0.001) \). Wheat crops sown after faba bean generally out-yielded their counterparts grown after pasture.

Attainable yield can be defined as the best yield achieved through skilful use of available technology (Loomis and

**Table 1. Soil properties at Roseworthy**

<table>
<thead>
<tr>
<th>Layer (cm)</th>
<th>Bulk density ( \rho_b ) (g/cm(^3))</th>
<th>pH(CaCl(_2))</th>
<th>pH(C(_2)CO(_3))</th>
<th>EC (dS/m)</th>
<th>Total C ( C_T ) (g/kg)</th>
<th>Inorg. C ( C_{IN} ) (g/kg)</th>
<th>Org. C ( C_{OR} ) (g/kg)</th>
<th>Total N ( N_T ) (g/kg)</th>
<th>P ( P ) (mg/kg)</th>
<th>K ( K ) (mg/kg)</th>
<th>UL ( UL ) (mm/mm)</th>
<th>LL ( LL ) (mm/mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0–10</td>
<td>1.30</td>
<td>7.7</td>
<td>7.2</td>
<td>0.14</td>
<td>15.9</td>
<td>3.1</td>
<td>13.3</td>
<td>1.17</td>
<td>45</td>
<td>467</td>
<td>0.24</td>
<td>0.04</td>
</tr>
<tr>
<td>10–20</td>
<td>1.33</td>
<td>8.3</td>
<td>7.5</td>
<td>0.12</td>
<td>17.7</td>
<td>11.2</td>
<td>6.3</td>
<td>0.53</td>
<td>6</td>
<td>211</td>
<td>0.32</td>
<td>0.09</td>
</tr>
<tr>
<td>20–40</td>
<td>1.24</td>
<td>8.7</td>
<td>7.9</td>
<td>0.13</td>
<td>32.7</td>
<td>29.1</td>
<td>4.3</td>
<td>0.35</td>
<td>6</td>
<td>134</td>
<td>0.16</td>
<td>0.09</td>
</tr>
<tr>
<td>40–60</td>
<td>1.26</td>
<td>9.2</td>
<td>8.1</td>
<td>0.26</td>
<td>53.7</td>
<td>50.1</td>
<td>3.6</td>
<td>0.27</td>
<td>5</td>
<td>120</td>
<td>0.29</td>
<td>0.07</td>
</tr>
<tr>
<td>60–80</td>
<td>1.38</td>
<td>9.6</td>
<td>8.3</td>
<td>0.62</td>
<td>59.2</td>
<td>57.1</td>
<td>2.3</td>
<td>0.20</td>
<td>3</td>
<td>202</td>
<td>0.22</td>
<td>0.09</td>
</tr>
<tr>
<td>80–100</td>
<td>1.35</td>
<td>9.8</td>
<td>8.4</td>
<td>0.84</td>
<td>58.8</td>
<td>56.0</td>
<td>2.0</td>
<td>0.15</td>
<td>2</td>
<td>282</td>
<td>0.24</td>
<td>0.11</td>
</tr>
</tbody>
</table>

\(^a\)Measured after oven-drying soil cores extracted with a 70-mm-diam. push tube.


\(^e\)Measured using LECO CNS2000 dry combustion furnace.

\(^f\)Measured using a calcimeter according to Loveday (1974).

\(^g\)Calculated as the difference between total C and inorganic C.

\(^h\)Measured using the same method and instrumentation as used for total carbon.


\(^j\)Upper and lower limits of plant-available water determined using field-measured soil water content during 3 cropping seasons.

**Table 2. Rainfall (mm) and reference evapotranspiration (mm) at Roseworthy during 3 wheat-growing cycles**

<table>
<thead>
<tr>
<th>Variable</th>
<th>Period</th>
<th>1995</th>
<th>1998</th>
<th>1999</th>
<th>Long-term (^a)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rainfall</td>
<td>April–October</td>
<td>305 (0.54)(^b)</td>
<td>298 (0.50)</td>
<td>265 (0.42)</td>
<td>317 (0.53)</td>
</tr>
<tr>
<td></td>
<td>Sowing–harvest</td>
<td>191 (0.36)</td>
<td>274 (0.61)</td>
<td>262 (0.55)</td>
<td></td>
</tr>
<tr>
<td>Evapotranspiration(^c)</td>
<td>April–October</td>
<td>569</td>
<td>594</td>
<td>632</td>
<td>594</td>
</tr>
<tr>
<td></td>
<td>Sowing–harvest</td>
<td>532</td>
<td>450</td>
<td>478</td>
<td></td>
</tr>
</tbody>
</table>

\(^a\)1997–2002 average.

\(^b\)Rainfall-to-exposure evapotranspiration ratio.

\(^c\)Calculated with the method of Priestly and Taylor (1972), with constant = 1.26.
Fig. 1. Rotation and seasonal effects on (a) the amount of plant-available water and (b) inorganic nitrogen in the 1-m soil profile at the time of wheat sowing during 3 seasons at Roseworthy. Error bars are ± s.e.m. (c) Relationship between inorganic nitrogen and plant-available water at sowing. Rotations are x/wheat/barley, where x is faba bean harvested for grain (faba_g), faba bean incorporated as green manure (faba_gm), ryegrass pasture (grass), or medic pasture (medic).

Connor 1996). The scatter plot of grain yield v. plant-available water plus growing season rainfall indicated substantial departures from attainable yield calculated as a function of attainable water-use efficiency (Fig. 2a). The gap between attainable and actual yield increased with decreasing amount of nitrogen per unit available water at sowing (Fig. 2b). Departures from attainable yield were more pronounced in crops grown after grass and medic pasture, as indicated

Table 3. Rotation and seasonal effects on yield, yield components, and grain protein concentration of wheat crops

<table>
<thead>
<tr>
<th>Rotation</th>
<th>Yield (kg/ha)</th>
<th>Grain number (per m²)</th>
<th>Grain mass (mg/grain)</th>
<th>Grain protein (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1995</td>
<td>1998</td>
<td>1999</td>
<td></td>
</tr>
<tr>
<td>Faba grain</td>
<td>2875 (137.9)</td>
<td>9158 (446.3)</td>
<td>31 (0.1)</td>
<td>15.0 (0.22)</td>
</tr>
<tr>
<td>Faba green manured</td>
<td>3120 (32.6)</td>
<td>10173 (112.5)</td>
<td>31 (0.1)</td>
<td>14.8 (0.16)</td>
</tr>
<tr>
<td>Grass pasture</td>
<td>2547 (202.6)</td>
<td>8019 (525.6)</td>
<td>32 (0.5)</td>
<td>14.3 (0.10)</td>
</tr>
<tr>
<td>Medic pasture</td>
<td>2887 (87.7)</td>
<td>9135 (125.4)</td>
<td>32 (1.3)</td>
<td>14.8 (0.44)</td>
</tr>
<tr>
<td>*P</td>
<td>0.082</td>
<td>0.018</td>
<td>0.722</td>
<td>0.378</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Faba grain</td>
<td>4782 (64.0)</td>
<td>12307 (1376.7)</td>
<td>39 (0.8)</td>
<td>13.0 (0.15)</td>
</tr>
<tr>
<td>Faba green manured</td>
<td>4579 (49.4)</td>
<td>11771 (242.6)</td>
<td>39 (0.9)</td>
<td>13.8 (0.18)</td>
</tr>
<tr>
<td>Grass pasture</td>
<td>4664 (123.5)</td>
<td>9489 (424.8)</td>
<td>44 (0.7)</td>
<td>10.8 (0.38)</td>
</tr>
<tr>
<td>Medic pasture</td>
<td>3621 (123.3)</td>
<td>8096 (135.4)</td>
<td>42 (0.8)</td>
<td>13.4 (0.74)</td>
</tr>
<tr>
<td>*P</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.008</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Faba grain</td>
<td>4568 (88.8)</td>
<td>11618 (402.2)</td>
<td>38 (0.5)</td>
<td>14.7 (0.15)</td>
</tr>
<tr>
<td>Faba green manured</td>
<td>4506 (35.9)</td>
<td>12137 (112.1)</td>
<td>37 (0.4)</td>
<td>15.5 (0.12)</td>
</tr>
<tr>
<td>Grass pasture</td>
<td>3515 (172.5)</td>
<td>7386 (461.0)</td>
<td>43 (0.4)</td>
<td>11.3 (0.26)</td>
</tr>
<tr>
<td>Medic pasture</td>
<td>3142 (96.2)</td>
<td>8274 (423.3)</td>
<td>38 (1.1)</td>
<td>15.7 (0.19)</td>
</tr>
<tr>
<td>*P</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.001</td>
<td>0.0001</td>
</tr>
</tbody>
</table>

Rotations are x/wheat/barley, where x is faba bean harvested for grain (faba_g), faba bean incorporated as green manure (faba_gm), ryegrass pasture (grass), or medic pasture (medic). Standard errors are in parentheses; *P values are from ANOVA.
Crop rotation effect on wheat grain yield

**Fig. 2.** (a) Relationship between measured grain yield and plant-available water at sowing plus rainfall in the sowing to harvest period. The reference attainable yield (solid line) assumes transpiration efficiency = 20 kg/ha.mm, and soil evaporation = 80 mm. (b) Difference between attainable and actual yield as a function of the ratio between inorganic nitrogen and plant-available water in the 1-m soil profile at sowing. The solid line is the linear regression fitted to all data ($r^2 = 0.58$, $P = 0.004$). The dotted lines are linear regressions fitted to crops grown after faba bean (circles) or pasture (triangles); numbers are slopes of the lines.

Grain protein concentration was much lower in wheat crops grown after grass pasture than in their counterparts grown after grain or pasture legumes, particularly in the higher-yielding seasons 1998 and 1999 (Table 3). Grain yield and protein content were unrelated ($P > 0.20$).

The yield and grain protein content of barley grown after wheat was used to evaluate the persistency of rotation effects (Table 4). Barley crops grown in rotations including faba bean, out-yielded their counterparts grown in rotations including grass pasture (1999) and grass and medic pasture (2000). Rotation and season both had marked effects on protein content, which was positively associated with yield in 1996 and 1999, and negatively associated with yield in 2000 (Table 4).

**Table 4.** Rotation and seasonal effects on the yield and grain protein concentration of barley crops

<table>
<thead>
<tr>
<th>Rotation</th>
<th>Yield (kg/ha)</th>
<th>Protein (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1996</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Faba grain</td>
<td>3114 (50.5)</td>
<td>14.3 (0.49)</td>
</tr>
<tr>
<td>Faba green manured</td>
<td>3130 (57.6)</td>
<td>14.4 (0.81)</td>
</tr>
<tr>
<td>Grass pasture</td>
<td>2934 (16.2)</td>
<td>12.0 (0.56)</td>
</tr>
<tr>
<td>Medic pasture</td>
<td>3187 (39.4)</td>
<td>14.0 (0.26)</td>
</tr>
<tr>
<td>$P$</td>
<td>0.008</td>
<td>0.050</td>
</tr>
<tr>
<td>1999</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Faba grain</td>
<td>2345 (76.6)</td>
<td>9.4 (0.17)</td>
</tr>
<tr>
<td>Faba green manured</td>
<td>2420 (89.2)</td>
<td>10.5 (0.25)</td>
</tr>
<tr>
<td>Grass pasture</td>
<td>1965 (44.7)</td>
<td>8.3 (0.13)</td>
</tr>
<tr>
<td>Medic pasture</td>
<td>2334 (38.1)</td>
<td>10.0 (0.23)</td>
</tr>
<tr>
<td>$P$</td>
<td>0.005</td>
<td>0.001</td>
</tr>
<tr>
<td>2000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Faba grain</td>
<td>4633 (28.8)</td>
<td>10.8 (0.30)</td>
</tr>
<tr>
<td>Faba green manured</td>
<td>4604 (72.1)</td>
<td>10.5 (0.68)</td>
</tr>
<tr>
<td>Grass pasture</td>
<td>4034 (64.1)</td>
<td>11.1 (1.24)</td>
</tr>
<tr>
<td>Medic pasture</td>
<td>3781 (184.6)</td>
<td>12.0 (0.68)</td>
</tr>
<tr>
<td>$P$</td>
<td>0.001</td>
<td>0.603</td>
</tr>
</tbody>
</table>

**Modelling analysis: wheat grain yield and degree of water and nitrogen co-limitation**

Reported tests of the model used in this study indicate that it is able to capture the major effects of water and nitrogen availability on crop growth and yield (Keating _et al._ 2003; Sadras _et al._ 2003). Figure 3, comparing measured and modelled growth and yield of wheat crops in our rotation trial, reinforces this conclusion.
Measured grain yield was unrelated to indices accounting for the individual effects of water (SW, \( P > 0.19 \)) and nitrogen stress (SN, \( P > 0.86 \)). Figure 4 shows the relationships between measured grain yield and the index SWN combining water and nitrogen stress (\( r = -0.66, P = 0.02 \)), the co-limitation index CWN (\( r = 0.71, P = 0.01 \)), and the SCW2N index combining stress intensity and degree of co-limitation (\( r = 0.81, P = 0.001 \)). SWN and CWN were unrelated (\( P > 0.23 \)).

Discussion

This study reinforces previously reported, general effects of rotations on cereal yield and grain protein content (Fig. 1, Tables 3 and 4), highlights rotation effects that are not mediated by availability of water and nitrogen (Fig. 2), and presents a novel interpretation of water and nitrogen effects in terms of degree of co-limitation between these resources (Fig. 4).

General effects of rotations on cereal yield and grain protein content

The improvement in yield and grain protein content of winter and summer cereals grown after legumes is widely documented, and is partially attributed to increased availability of nitrogen (Karlen et al. 1994; Galantini et al. 2000; Angus 2001; Evans et al. 2001; Sadras et al. 2002a, 2002b). Recent reviews emphasise the highly variable but dominantly positive contribution of legumes to available soil nitrogen in Australian cropping systems. The reported net change in soil nitrogen content after the legume phase of rotations ranges from -67 to 271 kg N/ha for grain species (Evans et al. 2001) and from 59 to 268 kg N/ha for pastures (Peoples and Baldock 2001). Mineralisation of organic nitrogen after legume phases can result in the accumulation of up to 150 kg N/ha, chiefly as nitrate (Fillery 2001). Some components of rotations such as fallow or deep-rooted perennials can have dramatic and consistent effects on plant-available water but patterns, if any, are less clear in rotations involving continuous sequences of annual crops and pastures (Cantero-Martinez et al. 1995; O’Leary and Connor 1997; O’Connell et al. 2002). Importantly, seasonal conditions and the interaction between rotation and season strongly affect both soil inorganic nitrogen and plant-available water (Karlen et al. 1994).

Results in our field experiment are consistent with the responses outlined above: yield and grain protein content of wheat grown after faba bean increased in comparison with crops grown after pasture; grain legumes increased inorganic soil nitrogen, particularly when green manured; there was no detectable effect of rotation on plant-available water at sowing; and there were substantial interactions between season and rotation for key response variables (Fig. 1, Table 3). The significant responses of barley grown after wheat are an indication of the persistence of rotation effects (Table 4). This finding is consistent with the conclusion of Angus et al. (1998) that legume nitrogen fixation can sustain the yields of several subsequent crops in regions with Mediterranean-type climates.
Rotation effects unrelated to availability of water and nitrogen

For the pooled data, the gap between actual and attainable grain yield declined linearly with the amount of inorganic nitrogen per unit available water in the range of about 1–5 kg N/ha.mm (Fig. 2). A non-linear response, however, could have been expected due to ‘haying-off’ and large yield gaps for crops with high nitrogen to water ratios in extremely dry seasons (van Herwaarden et al. 1998; Sadras 2002). Rainfall close to average during the experiments (Table 2) may have prevented this extreme response. Simulations involving long-term rainfall allowed for the identification of a non-linear response, with a broad optimum around 2 kg N/ha.mm for both simulated yield and deviations with respect to attainable yield (not shown).

The most striking feature of the data in Fig. 2b is that, after accounting for the effect of initial soil inorganic nitrogen relative to plant-available water, a 2-fold difference remained between wheat crops grown after faba bean or pasture. This sharp difference could be partially associated with variation in the rate of in-season nitrogen mineralisation, but it is also possible that factors unrelated to resource availability could have been involved. Reported biological effects of rotations include changes in soil microbial activity, phytotoxic or growth promoting compounds, and populations of plant pathogens, weeds, and insects (Karlen et al. 1994). In our experiment, take-all (Gaeumannomyces graminis var. tritici) and Pratylenchus neglectus were more abundant in soil where wheat was grown after medic pasture than when wheat was grown after grass pasture or faba bean (J. A. Baldock, unpublished data). This could account for part of the difference between crops grown after grain or pasture legumes, but unaccounted effects remain for crops grown after grass pasture. Cropping system models need to be developed that account for major biological effects of rotations.

Water and nitrogen co-limitation

Measured yield was unrelated to water or nitrogen stresses taken individually, inversely related to the aggregated stress index $S_{WN}$, and directly related to the $C_{WN}$ index of co-limitation (Fig. 4). The combination of stress and co-limitation in a single index $S_{WN}$ accounted for 65% of the variation in measured crop yield. This is a substantial improvement with respect to the stress effect quantified with $S_{WN}$, which accounted for 43% of yield variation. Although all these indices are derived from simulations, and modelling artefacts cannot be discarded, the results are consistent with theory (Bloom et al. 1985) and lend primary support to the hypothesis that the degree of co-limitation between nitrogen and water can account for part of the variation in the response of crop yield to rotation and seasonal effects. The decline in yield with increasing stress intensity is not surprising (Fig. 4), but is indicative of the ability of modelled indices to explain part of the variation in grain yield measured in field crops. The association of yield with degree of co-limitation is not trivial and provides a new perspective in the understanding of plant responses to stresses. Although Bloom et al. (1985) formulated their theorem relating plant growth and co-limitation almost 2 decades ago, there have been few, if any, attempts to test this hypothetical relationship. Part of the difficulty in testing the putative link between plant growth and resource co-limitation stems from the lack of appropriate methods to quantify co-limitation. In fact, the dominant approach in ecological studies is semiquantitative, with typical experiments looking at co-limitation in yes/no terms, rather than degrees (Verhoeven et al. 1996; Venterink et al. 2001; Maherly et al. 2002). Despite many limitations, this study illustrated how crop simulation models could be useful in providing a quantitative basis to develop co-limitation indices for nitrogen and water. Using curves relating crop production ($P$) and availability of resource ($r(A_r)$), Kho (2000) defined an index of limitation $L_r$ as the slope of the $W/A$ curve normalised by the ratio $W/A$. This definition allows for the quantification of degree of co-limitation between 2 resources $a$ and $b$, i.e. $1 - |L_a - L_b|$, which is conceptually comparable to our index in Eqn 2. Notwithstanding an unavoidable element of circularity in relating back $W$ and $L_r$ or derived indices (which are related to $W$ by definition), the approach of Kho (2000) is a substantial step forwards in quantifying co-limitation, and can be applied to a broad range of resources. Conversely, model-derived indices such as $C_{WN}$ provide a largely independent measure of co-limitation to be related with measured crop responses, but most models only allow for few resources, i.e. water, nitrogen, and radiation.

Assessments of crop fertiliser requirements are often based on estimates of nutrient demand and supply (Angus et al. 1998; Angus 2001). Where high variation in rainfall determines high variation in nitrogen requirements to sustain crop growth, the problem of matching nitrogen supply and demand can be formulated in terms of matching nitrogen supply and water availability (Sadras and Roget 2004). There is a reinforcing convergence, therefore, between the agronomic perception that high crop yield in low rainfall environments requires close matching of nitrogen supply and water availability, and the conclusion supported by theory and the analysis in this paper that, for a given level of stress, a high degree of resource co-limitation maximises crop production.

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