Journal of Plant Nutrition

ISSN: 0190-4167 (Print) 1532-4087 (Online) Journal homepage: https://www.tandfonline.com/loi/lpla20

Analysis of the variations in dry matter yield and resource use efficiency of maize under different rates of nitrogen, phosphorous and water supply

Ali Momen, Alireza Koocheki & Mehdi Nassiri Mahallati

To cite this article: Ali Momen, Alireza Koocheki & Mehdi Nassiri Mahallati (2020): Analysis of the variations in dry matter yield and resource use efficiency of maize under different rates of nitrogen, phosphorous and water supply, Journal of Plant Nutrition, DOI: 10.1080/01904167.2020.1729802

To link to this article: https://doi.org/10.1080/01904167.2020.1729802

JOURNAL OF PLANT NUTRITION
https://doi.org/10.1080/01904167.2020.1729802

Analysis of the variations in dry matter yield and resource use efficiency of maize under different rates of nitrogen, phosphorous and water supply

Ali Momen[a], Alireza Koocheki[b], and Mehdi Nassiri Mahallati[b]

[a]Ferdowsi University of Mashhad, Faculty of Agriculture, Mashhad, Iran (the Islamic Republic of); [b]Ferdowsi University of Mashhad, Mashhad, Iran (Islamic Republic of)

ABSTRACT

Increasing resources use efficiency in intensive cultivation systems of maize (*Zea mays* L.) can play an important role in increasing the production and sustainability of agricultural systems. The objectives of the present study were to evaluate DM yield and the efficiency of inputs uses under different levels of water, nitrogen (N) and phosphorus (P) in maize. Therefore, three levels of irrigation including 80 (ETc_{80}), 100 (ETc_{100}) and 120% (ETc_{120}) of crop evapotranspiration were considered as the main plots, and the factorial combination of three levels of zero (N_0), 200 (N_{200}) and 400 (N_{400}) kg N ha^{-1} with three levels of zero (P_0), 100(P_{100}) and 200 (P_{200}) kg P ha^{-1} was considered as the sub plots. The results showed that increasing the consumption of water and P was led to the reduction of N and P utilization efficiency, while RUE increased. WUE was also increased in response to application of N and P, but decreased when ET_C increased. DM yield under ETc_{80} treatment reduced by 11 and 12%, respectively, compared to ETc_{100} and ETc_{120} which was due to reduction of cumulative absorbed radiation (R_{abs}(cum)) and RUE. Under these conditions, changes of stomatal conductance (gs) had little effect on DM yield. It was also found that N limitation caused 11 and 20% reduction in DM yield compared to N_{200} and N_{400}, respectively. This yield reduction was mainly the result of decrease in RUE. By decreasing R_{abs}(cum), P deficiency also reduced DM yield by 5 and 9%, respectively, relative to P_{100} and P_{200} treatments.

ARTICLE HISTORY
Received 20 October 2018
Accepted 30 December 2019

KEYWORDS
high input systems; nitrogen nutrition index; resource use efficiency; resources limitation; stomatal conductance

Introduction

The world population is likely to reach up to 10.5 billion by 2050, a fact that rapidly increases food demands of the world from the existing agricultural lands (Tilman et al. 2011; Bouwman et al. 2017; Bai and Tao 2017). Provision of more land to supply these food requirements seems unlikely (Pretty and Bharucha 2014). Therefore, there is a need for some intensification in agricultural systems (Mueller et al. 2012). Systems with intensive management and high yield require more irrigation and fertilization, but it is evidenced that efficiency of using inputs is reduced due to the excessive increase in plant's requirements (Teixeira et al. 2014; Bai and Tao 2017). In addition, excessive use of chemical fertilizers brings about many environmental problems, such as air, soil, and water pollution, and emission of greenhouse gases (Maris et al. 2015; Loick et al. 2016). Hence, determining the best management operations in order to optimize yield and to understand how use efficiency of resources change in response to limitation or adequacy of water

CONTACT Alireza Koocheki ✉ akooch@um.ac.ir Ferdowsi University of Mashhad, Mashhad, Iran (Islamic Republic of).

and nutrients can be a crucial step in achieving sustainable intensification of agricultural systems (Sadras and Angus 2006; Teixeira et al. 2014; Bai and Tao 2017).

Total biomass production depends on the amount of accumulated intercepted radiation and the efficiency to convert intercepted radiation into dry matter (RUE) when other factors are unconstrained (Monteith 1977). However, water and nutrient deficiency often restrict growth and production potentials of agricultural ecosystems in arid and semi-arid environments (Cao et al. 2007).

Nitrogen (N) is the major mineral nutrient in plants and strongly influences crop production (Sinclair and Weiss 2010). The photosynthetic capacity of leaves and canopy depends directly on the concentration of nitrogen in leaves (SLN) (Sinclair and Horie 1989). Photosynthetic responses of leaves are presented at crop level by RUE (Monteith 1977), which is reduced as a result of nitrogen deficiency. Similarly, leaf area decreases by nitrogen deficiency (Sinclair and Horie 1989; Massignam et al. 2009). However, nitrogen deficiency in crops can give three responses: (i) reduced LAI expansion and maintained RUE; (ii) reduced RUE and maintained LAI expansion; or (iii) a combination of these responses (Lemaire et al. 2008). In the experiment, RUE and leaf area (radiation intercepted) by maize and sunflower decreased in response to nitrogen reduction. However, in maize, the effect of nitrogen on RUE was higher than that of leaf area, while in sunflower, these results were in contrast (Massignam et al. 2009). In relation to the effect of N supply on WUE Caviglia and Sadras (2001) showed that when N use was increased, 60% of the observed changes in WUE of wheat based on the biological performance were related to the improvement in RUE, and crop conductance did not show significant effect on WUE.

After nitrogen, phosphorus (P) is the most important nutrient that limits plant growth by influencing intercepted photosynthetically active radiation (IPAR) and RUE (Fletcher et al. 2008). However, experimental results showed that RUE of maize was unaffected by phosphorus application (Plenet, Mollier, and Pellerin 2000). Contrary to these results, it has been observed that photosynthesis changes are related to phosphorus supply (Jacob and Lawlor 1991; Usuda and Shimogawara 1992), so that even slight reduction in RUE of maize was observed in response to phosphorus deficiency (Mollier and Pellerin 1999). Additionally, Fletcher et al. (2008) found that the variations in maize biomass accumulation in response to P supply were explained mainly by Differences in accumulated intercepted solar radiation ($\mathrm{RI_{cum}}$).

It has been widely reported that water stress in crops reduces foliar development and expansion, primarily due to a reduction of the stomatal conductance that inhibits the C assimilation and hence decreases photosynthesis and RUE (Jamieson et al. 1995; Plauborg et al. 2010). It was found by Teixeira et al. (2014) that water deficiencies reduce DM of maize both through reductions in resource capture (radiation interception and N uptake) and RUE. Results from Goyne et al. (1993) and Robertson and Giunta (1994) indicated that, both IPAR and RUE in spring wheat and barley were reduced when water was limited. However, the major factor was the reduced IPAR. However, there is limited comprehensive information about the variations in dry matter yield and resource use efficiency of maize when water and nutrients are supplied simultaneously at different levels. Such studies would give us a better understanding of the mechanisms affecting crop production changes in order to balance the need to increase yields and the efficiency of resource use under different rates of inputs in field.

Therefore, the primary objective of the present study was to evaluate the DM yield and the efficiency of inputs uses under different levels of irrigation water, N and P in maize. Then, the reasons for changes in DM yield and formation of these relationships were studied by evaluating some related physiological and morphological characteristics such as stomatal conductance (gs), SPAD index, nitrogen nutrition index (NNI), cumulative absorbed radiation (R_{abs}(cum)) and maximum leaf area index ($\mathrm{LAI_{max}}$).

Table 1. Soil physicochemical properties of the experimental site at 0–30 cm depth during 2014 and 2015.

		Available							
Soil texture	Total N (%)	P (ppm)	K (ppm)	OC (%)	OM (%)	EC (dS m^{-1})	B.D (g cm^{-3})	CEC (meq lit^{-1})	pH
2014 Loam	0.09	13.1	134.6	0.19	0.33	1.3	1.28	13.4	7.4
2015 Silt loam	0.084	10.3	112.7	0.16	0.27	1.2	1.33	12.2	7.2

Materials and methods

Description of the site and experimental design

This study was carried out at the research farm of Ferdowsi University of Mashhad, located 10 km east of Mashhad, Iran at 36.16° North latitude, 59.36° East longitude, and height of 985 m above sea level, in two growing years of 2014 and 2015. Soil characteristics at the 0 to 30 cm depth, as well as the average values of temperature and precipitation during the two years of the experiment are shown in Table 1 and Figure 1, respectively.

The experiment was conducted as split plot based on randomized complete block design with three replications. The main plot consisted three levels of irrigation water including %80 (ETc_{80}), %100 (ETc_{100}) and %120 (ETc_{120}) of plant evapotranspiration, and sub plot included factorial combination of three N levels (0, 200 and 400 kg ha^{-1}) and three P levels (0, 100 and 200 kg ha^{-1}).

Determination of plant water requirement

Water requirement of plant was calculated using evaporation pan. Then, based on the pan and crop coefficients, the amount of water consumed at each interval of irrigation was estimated using Eq. (1) (Allen et al. 1998).

$$ET_c = E_{pan} \times K_p \times K_c \tag{1}$$

where E_{pan} is evaporation from the pan (mm), K_p is pan coefficient (.6), and K_c is crop coefficient of maize. Crop coefficient is different during the growth period and was determined and corrected at each stage, according to FAO publication, number 56 (Allen et al. 1998). Plots were irrigated by polyethylene tubes, and volume of water entering the plots was controlled by the water meter. Irrigation efficiency under these conditions was 90%, and the irrigation interval was 7 days. Accordingly, ET_{80}, ET_{100} and ET_{120} treatments were irrigated as much as 739.92, 924.9, and 1109.88 mm ha^{-1} in 2014, and 814.5, 1018.12, and 1221.74 mm ha^{-1} in 2014, respectively.

Crop management

Primary tillage operations, including plowing, ground leveling and creating 70 cm furrows were performed in early May of each year. Then, 4 × 3.5-m plots, each consisting of five rows, were prepared. The seeds of maize cv. Single Cross 704 were cultivated in rows with the space of 20 cm apart. P fertilizer levels (triple superphosphate) were applied uniformly in the form of the strip under the root zone in all the plots. Urea fertilizer (46% N) was added to the soil at three stages: at sowing, three-leaf stage and flowering time. Planting operations were carried out on May 14th and 18th of 2014 and 2015, respectively. Weed was removed twice manually.

Measurements

During the growing season, sampling was performed six times every 14 days in both experimental years starting 35 days after planting. At each sampling total aboveground parts of 3 plants were

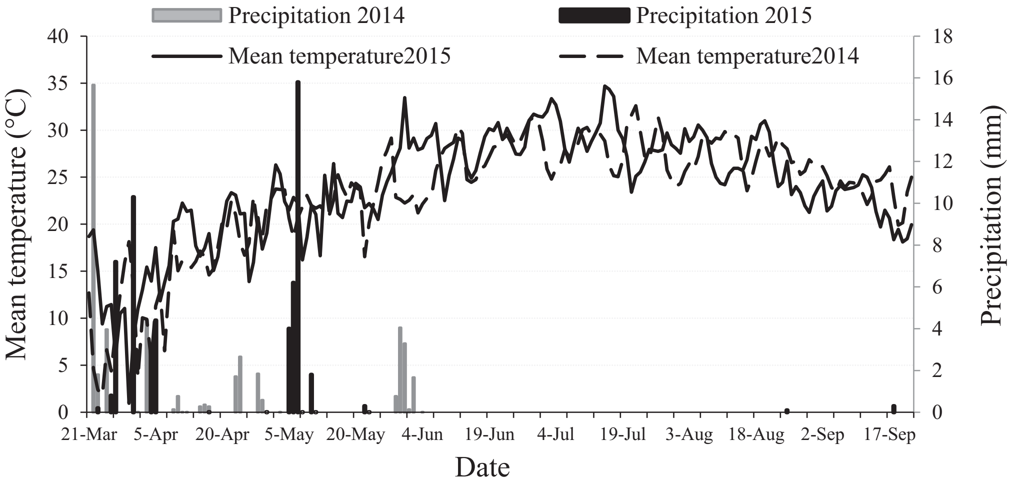

Figure 1. Mean daily air temperature and daily precipitation during 2014 and 2015 growing seasons.

harvested randomly from each plot and leaf area was determined by using Leaf Area Meter, DeltaT Ltd., UK. The harvested materials were dried at 70 °C for 48 hours and the dry weight of each sample was measured. To measure the grain yield and dry matter of each plot at ripening (September 27, 2014 and September 21, 2015), the whole plants were harvested from 4 m^2 area and dried.

N and P contents of grain and straw were determined separately at the end of growth season by using micro-Kjeldahl and spectrophotometer devices, respectively. Accordingly, nitrogen nutrition index (NNI) was determined at the end of the growing season by using Eq. (2) (Lemaire and Gastal 2009).

$$\mathrm{NNI} = \mathrm{N}_a/\mathrm{N}_c \tag{2}$$

where N_a and N_c show the measured and critical N concentration, respectively. N_c at the range of 1 to 22 ton ha^{-1} maize dry matter (W) was determined by Eq. (3) (Plenet and Lemaire 2000).

$$\%\ \mathrm{Nc}\ = 3.40\ (W)^{-0.37} \tag{3}$$

Stomatal conductance (gs) and SPAD index in three plants per plot were measured at silking stage in the top fully developed leaf by the promoter (Leaf Prometer, Model SC-1, Decagon Devices) and chlorophyll meter (SPAD-502, Konica Minolta, Japan), respectively. Time of gs measurements was between 10 and 14 pm and the place of measurement was in the middle of leaf lamella.

Calculation of resources use efficiency

In this study, we investigate resources use efficiency at the crop scale with a physiological focus.

N and P utilization efficiency (NUtE and PUtE)

NU_tE (kg DM kg^{-1} N_{uptake}) and PU_tE (kg DM kg^{-1} P_{uptake}) were calculated based on the ratio of DM yield (Y_{DM}) to N_{uptake} and P_{uptake} by shoot biomass of maize according to Eqs. (4) (López-Bellido and López-Bellido 2001) and (5).

$$\mathrm{NU_tE} = Y_{\mathrm{DM}}/\mathrm{N_{uptake}} \tag{4}$$

$$\mathrm{PU_tE} = Y_{\mathrm{DM}}/\mathrm{P_{uptake}} \tag{5}$$

Water use efficiency (WUE)

WUE was obtained from the ratio of DM yield ($\mathrm{Y_{DM}}$) to total evapotranspiration ($\mathrm{ET_c}$) according to Eq. (6) (Cossani, Slafer, and Savin 2012).

$$\mathrm{WUE} = Y_{\mathrm{DM}}/\mathrm{ET_c} \tag{6}$$

Radiation use efficiency (RUE)

Daily values of LAI were estimated by fitting the measured data of LAI in each sampling to the Eq. (7).

$$\mathrm{LAI_t} = a + b \times 4 \times (e^{(-(x-c)/d)})/(1 + e^{(-(x-c)/d)})^2 \tag{7}$$

where a is y-intercept, b is the maximum LAI, c is the time when LAI reaches its maximum amount, d is the turning point of the curve in which the growth of the leaf area enters the linear stage, and x is the time on the basis of the day after planting.

The daily values of incoming radiation for Mashhad latitude were calculated by the method proposed by Goudriaan and Laar (1994). Then, these values were modified based on the number of sunshine hours taken from Mashhad meteorological station according to Angstrom Eq. (8) (Goudriaan and Laar 1994).

$$I/I_0 = A + B(n/N) \tag{8}$$

where I is daily simulated radiation, I_0 is daily radiation above the canopy based on sunny hours, n and N are sunshine hours and day length, respectively, and A and B are Angstrom coefficients. The values of A and B in Mashhad were considered equal to .3 and .37, respectively (Kamkar et al. 2011). Then, based on the values of $\mathrm{LAI_t}$, I_0 and light extinction coefficient of maize ($K = .65$) the amount of daily absorbed radiation (I_{abs}) by the plant was calculated in MJ $\mathrm{m^{-2}\,day^{-1}}$ by using Eq. (9) (Fletcher et al. 2013), and 50% of which was considered as photosynthetically active radiation (PAR).

$$I_{\mathrm{abs}} = I_0(1 - e^{-k\times \mathrm{LAI}_t}) \tag{9}$$

Radiation use efficiency (g DM $\mathrm{MJ^{-1}}$) was estimated as the slope of the regression line between cumulative I_{abs} and dry matter.

Statistical analysis

After testing for homogeneity of error mean squares of two year (Levene's test), combined analysis of variance (ANOVA) was performed by SAS 9.4 software (SAS Inc., Carey, NC), and means of different treatments were compared by Tukey test at the probability level of 5%. Slicing of interaction effects was performed by using the LS Means method. Equations were fitted by using the Slidwrite 7.01 software. Stepwise regression analysis was separately performed by using SAS 9.4 software on each level of N, P and ETc treatments in order to identify the variables that had the highest effect on DM yield. Input variables included $\mathrm{LAI_{max}}$, R_{abs}(cum), SPAD index, gs, and RUE. Considering that N_c in the calculation of NNI was calculated directly from maize DM yield, and the index also had a high correlation with other variables, it was not used in the stepwise regression analysis in order to avoid multicolinearity.

Results and discussion

NU_tE and PU_tE in response to N, P and ETc

The results of combined ANOVA on data collected during two consecutive years showed that NU_tE and PU_tE were significantly affected by different levels of N, P and water (ETc) (Table 2). However, the interaction effect of experimental factors on the nutrients use efficiency was not significant. The highest NU_tE and PU_tE with the values of 124.2 kg DM $kgkg^{-1}$ N_{uptake} and 633.1 kg DM kg^{-1} P_{uptake} were obtained in treatment of ETc_{80} at N_0P_0 and $N_{400}P_0$, respectively, while the lowest NU_tE and PU_tE of 73.5 kg DM kg^{-1} N_{uptake} and 432.2 kg DM kg^{-1} P_{uptake} were obtained in treatment of ETc_{100} at $N_{400}P_{200}$ and $N_{200}P_{200}$, respectively (Table 3).

The results showed that increasing water availability was led to significant reduction in NU_tE and PU_tE (Figure 2a). Moderate water stress (ETc_{80}) compared to optimal irrigation (ETc_{100}), significantly increased NU_tE and PU_tE by 10 and 9%, respectively (Figure 2a). To explain this, we can refer to the results of NNI (1.01 and .99) in full irrigation (ETc_{100}) and ETc_{120} (20% excessive water), which was significantly higher than that of moderate stress level (ETc_{80}) with NNI of .87 (Table 4). Under such conditions, plants use N with lower efficiencies. In this regard, it has been reported that NU_tE was higher under drought stress conditions than full irrigation (Teixeira et al. 2014).

PU_tE in response to N levels increased from 514.4 in N_0 treatment to 544 kg DM Kg^{-1} P_{uptake} in N_{400} treatment (Figure 2b). PU_tE was also influenced by different levels of P ranging from 470.5 to 570.1 kg DM Kg^{-1} P_{uptake}, with the highest and the lowest efficiencies obtaining in P_0 and P_{200} treatments, respectively (Figure 2c).

Increasing the use of both N and P brought about a reduction in NU_tE (Figure 2b,c). It seems that an increase in the absorption of N is higher than the increase in DM yield, ultimately leading to the reduction of NU_tE. In this context, it has been reported that high levels of N application caused a significant reduction in N utilization efficiency of wheat (*Triticum aestivum* L.) due to the greater response of the plant to increased N uptake relative to plant yield (López-Bellido and López-Bellido 2001).

WUE in response to N, P, and ETc

The effect of different levels of N, P and irrigation water (ETc) on maize WUE was significant but it was not affected by the interaction between experimental factors (Table 2). WUE varied

Table 2. Results of variance analysis (mean of squares) for NUtE, PUtE, WUE, RUE and DM yield of maize under different treatments of nitrogen, phosphorous and water (based on ETc).

Sources of variation	*df*	NU_tE	PU_tE	WUE	RUE	Dry matter yield
Year	1	423*	22.6^{ns}	381.9**	1.294**	$59,084,610^{ns}$
REP (year)	4	32.1	2260.8	14.3	0.048	13,007,575
ETc	2	1292.6***	38366.6***	375.0***	0.368***	91,331,141***
Year × ETc	2	48.2^{ns}	3248.7^{ns}	0.9^{ns}	0.031^{ns}	$2,021,221^{ns}$
REP × ETc (year)	8	77.0	1862.8	3.1	0.012	2,560,124
N	2	87.9***	371.8***	8.0***	0.121***	8,450,607***
P	2	24.0***	478.6***	0.5***	0.020***	974,910***
N × P	4	9.5^{ns}	395.7^{ns}	0.2^{ns}	0.001	$135,522^{ns}$
ETc × N	4	18.8^{ns}	478.8^{ns}	0.7^{ns}	0.048**	$10,645,42^{ns}$
ETc × P	4	10^{ns}	708.3^{ns}	$0.1n^{s}$	0.001^{ns}	$43,194^{ns}$
ETc × N × P	8	13.7^{ns}	212^{ns}	0.5^{ns}	0.007^{ns}	$423,156^{ns}$
Year × N	2	14103.2^{ns}	19888.2^{ns}	252.8^{ns}	3.400^{ns}	$230,754,935^{ns}$
Year × P	2	1568.3^{ns}	134519^{ns}	47.2^{ns}	0.240^{ns}	$43,415,234^{ns}$
Year × N × P	4	8.6^{ns}	531.6^{ns}	1.4^{ns}	0.003^{ns}	$1,169,851^{ns}$
Year × ETc × N	4	1^{ns}	113.2^{ns}	8.7^{ns}	0.247^{ns}	$5,236,233^{ns}$
Year × ETc × P	4	0.7^{ns}	1598.7^{ns}	3.9^{ns}	0.015^{ns}	$2,461,169^{ns}$
Year × ETc × N × P	8	12.9^{ns}	313.3^{ns}	0.9^{ns}	0.003^{ns}	$740,212^{ns}$

ns, *, ** and *** are non-significant and significant at 5, 1 and 0.1% probability levels, respectively.

Table 3. NU_tE, PU_tE, WUE, RUE and DM yield of maize under various applied irrigation water (based on ETc), N and P application rates.

Treatments							
ETc	N (kg ha^{-1})	P (kg ha^{-1})	NU_tE (kg DM kg^{-1} N_{uptake})	PU_tE (kg DM kg^{-1} P_{uptake})	WUE (kg DM mm^{-1})	RUE (g DM MJ^{-1})	Dry matter yield (kg ha^{-1})
ETc_{80}	0	0	124.2 ± 4.4[a]	592.5 ± 22.8	19.45 ± 0.86	1.81 ± 0.1	150,67.2 ± 515
		100	114.1 ± 5.2	545.3 ± 25.5	19.55 ± 0.78	1.86 ± 0.02	151,45.4 ± 445
		200	113.1 ± 4.6	485.8 ± 11.7	20.28 ± 1.11	1.85 ± 0.09	15,712.6 ± 727
	200	0	101 ± 3.5	592.3 ± 23.6	20.71 ± 1.19	2.01 ± 0.05	160,31.3 ± 731
		100	91 ± 3.4	546.7 ± 17.7	21.32 ± 1.33	2.08 ± 0.07	16,523.3 ± 929
		200	85.8 ± 3.4	494.2 ± 16.2	22.84 ± 1.27	2.09 ± 0.08	17,677.5 ± 763
	400	0	92.6 ± 3.7	633.1 ± 32.7	22.38 ± 0.96	2.13 ± 0.07	17,354.3 ± 677
		100	86 ± 2.9	579.6 ± 18.1	23.56 ± 1.14	2.22 ± 0.07	18,251.6 ± 687
		200	80.5 ± 2.5	503.7 ± 11.1	24.75 ± 1.6	2.20 ± 0.09	19,149.1 ± 1016
ETc_{100}	0	0	116.8 ± 4.2	538.7 ± 12.8	15.83 ± 0.65	1.81 ± 0.08	15,331.9 ± 445
		100	110.1 ± 5.1	501.5 ± 18.9	16.79 ± 0.9	1.83 ± 0.07	16,255.7 ± 749
		200	105 ± 3.3	451.7 ± 18.2	17.74 ± 1.01	1.94 ± 0.11	17,161.3 ± 777
	200	0	88.0 ± 2.8	542.2 ± 18.8	18.55 ± 1.01	2.10 ± 0.06	17,963.2 ± 826
		100	80.8 ± 3.5	485.5 ± 13.2	19.33 ± 1.19	2.15 ± 0.09	18,709.3 ± 1010
		200	77 ± 3	432.2 ± 11.8	20.41 ± 1.56	2.25 ± 0.12	19,740.7 ± 1307
	400	0	82.2 ± 1.9	564.2 ± 19.4	21.34 ± 1.48	2.42 ± 0.07	20,639.4 ± 1188
		100	75.4 ± 2.1	531.7 ± 18.7	22.72 ± 1.54	2.54 ± 0.06	21,981.0 ± 1295
		200	73.5 ± 3.1	480 ± 18.1	23.79 ± 1.48	2.60 ± 0.09	22,991.8 ± 1084
ETc_{120}	0	0	112.4 ± 5.1	542.1 ± 18.5	14.09 ± 0.64	1.80 ± 0.02	16,371.5 ± 547
		100	104 ± 3.2	514.5 ± 12.2	14.95 ± 0.56	1.89 ± 0.04	17,391.1 ± 508
		200	104 ± 3.5	457.4 ± 14.5	15.29 ± 0.58	1.97 ± 0.04	17,776.4 ± 542
	200	0	87.8 ± 2.5	542.4 ± 17.1	15.39 ± 0.99	2.08 ± 0.11	17,865.3 ± 1014
		100	83 ± 3.3	485.9 ± 18	16.35 ± 0.77	2.17 ± 0.1	19,000.7 ± 723
		200	80.1 ± 4	450.7 ± 15	17.37 ± 1.04	2.27 ± 0.11	20,136.5 ± 878
	100	0	86 ± 4.1	583.2 ± 16.7	16.91 ± 0.85	2.30 ± 0.08	19,622.2 ± 663
		100	80.8 ± 3.3	541.9 ± 24.4	18.44 ± 1.16	2.38 ± 0.1	21,372.9 ± 1013
		200	77.3 ± 3	478.4 ± 16.6	19.00 ± 1.11	2.48 ± 0.11	22,036.0 ± 904

[a] Standard error of means.

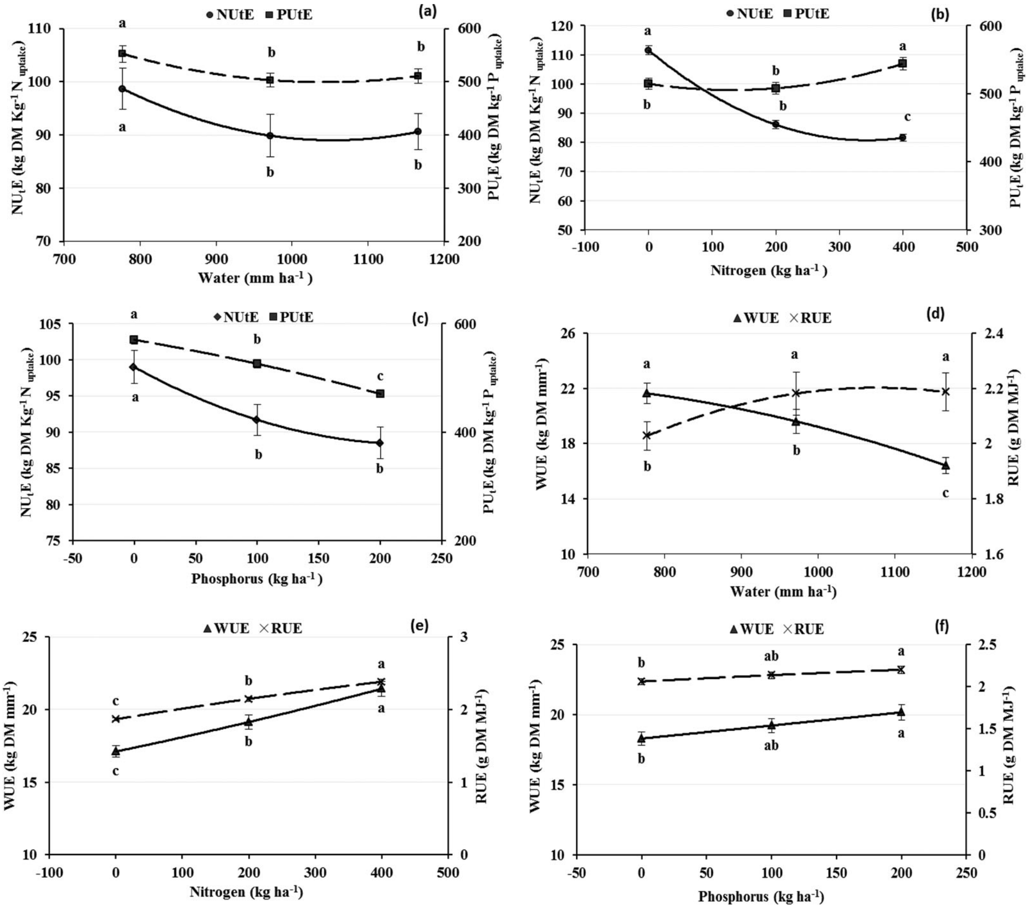

Figure 2. NU_tE, PU_tE (a–c), WUE and RUE (d–f) in maize crop under various irrigation water (based on ETc), N and P application rates. Error bars are standard error of means.

from 14.1 kg DM mm^{-1} in ETc$_{120}$ (N_0P_0) to 24.8 kg DM mm^{-1} in ETc$_{80}$ ($N_{400}P_{200}$) (Table 3). ETc$_{80}$ with the value of 24.05 kg DM mm^{-1} showed the highest WUE, however, in ETc$_{100}$ and ETc$_{120}$ treatments WUE reduced by 9 and 24%, respectively (Figure 2d). It has been reported that an increase in water use increased plant transpiration, leading to the reduction of WUE (Patterson, Guy, and Dang 1997). It has also been shown that under water stress conditions, stomatal resistance to the reduction of transpiration is higher than to carbon dioxide absorption, resulting in an increase in WUE under stress compared to non-stress conditions (Hay and Porter 2006).

WUE increased significantly as a result of increase in N application (Figure 3e), hence N_{200} and N_{400} treatments caused 12% and 25% increases in WUE, respectively, compared to control (N_0). These results are consistent with the previous studies on temperate cereals such as wheat and barley (*Hordeum vulgare* L.) (Cooper, Keatinge, and Hughes 1983; Cabrera-Bosquet et al. 2007). Two mechanisms seem to be involved: 1) positive response of photosynthesis to N supply increases RUE, which explains the main mechanism for improving WUE at high N levels (Teixeira et al. 2014). In our experiment, N_{200} and N_{400} treatments increased RUE by 15% and 28%, respectively (Figure 2e). Higher NNI and SPAD readings in N fertilized treatments along with increased RUE compared to control support this hypothesis (Table 4). Evaluation of the relationship between WUE and RUE also showed that this relationship was negative only along

Table 4. Dry matter, LAI_{max}, cumulative absorbed radiation ($R_{abs(cum)}$), nitrogen nutrition index (NNI), SPAD index and stomatal conductance (gs) of maize under various irrigation water (based on ETc), N and P application rates.

Treatment		Dry matter (kg ha^{-1})	LAI_{max}	R_{abs}(cum) (MJ m^{-2})	NNI	SPAD index	gs (mmol CO_2 m^{-2} s^{-1})
ETc	ETc_{80}	16768b	3.76b	1635.9b	0.87b	50.8a	41.9b
	ETc_{100}	18974.9a	4.12a	1747.4a	1.01a	50.6a	43.4ab
	ETc_{120}	19063.6a	4.09a	1695.6a	0.99a	52.2a	44.9a
HSD		884.3	0.19	54	0.06	2.7	2
p value		$\leq$0.0001	$\leq$0.01	$\leq$0.001	$\leq$0.001	0.25 (NS)	$\leq$0.01
Nitrogen (kg ha^{-1})	N_0	16245.9c	3.84b	1679.7b	0.75c	47.1c	44.3a
	N_{200}	18183.1b	4.02ab	1682.6b	1.01b	52.1b	43.8a
	N_{400}	20377.6a	4.12a	1716.6a	1.11a	54.4a	42.2a
HSD		953.5	0.18	28.11	0.06	2.25	2.13
p value		$\leq$0.0001	$\leq$0.001	$\leq$0.01	$\leq$0.001	$\leq$0.001	0.05 (NS)
Phosphorus (kg ha^{-1})	P_0	17360.7b	3.81b	1657.1c	0.88b	49.9a	42.3a
	P_{100}	18292.3ab	3.98b	1692.9b	0.97a	51.4a	43.8a
	P_{200}	19153.5a	4.19a	1728.9a	1.03a	52.2a	44.2a
HSD		953.5	0.18	28.11	0.06	2.25	2.13
p value		$\leq$0.0001	$\leq$0.001	$\leq$0.001	$\leq$0.001	0.06 (NS)	0.09 (NS)

Means with different letters differ significantly by Tukey HSD ($\alpha = 0.05$).

the water use slope (Figure 2d), but WUE and RUE increased proportionately along with the increase in soil N and P (Figure 2e,f). It was reported that WUE and RUE of wheat were directly inter-related (Caviglia and Sadras 2001). 2) It has been reported that increase of N leads to decreased plant stomatal conductance (gs) and therefore increased WUE (Cabrera-Bosquet et al. 2007). Our results showed that changes in gs of maize in response to N application rates, despite the slight reduction, were not significant (Table 4). The limited response of gs to N reported for sunflower (*Helianthus annuus* L.) and sorghum (*Sorghum bicolor* L.) (Jacob, Udayakumar, and Prasad 1990) is in accordance with the results of the present experiment. Hence, it can be concluded that variations in WUE in response to N supply are largely controlled by non-stomatal limitations.

The effect of P on WUE was incremental, but only P_{200} treatment with 10% improvement in WUE showed a significant difference from P_0 (Figure 2f). Stomatal conductance (gs), despite the slight increase, was not significantly affected by P (Table 4). Similar results are also reported for changes in gs and photosynthesis in response to other nutrients (Jacob and Lawlor 1991; Jin et al. 2011). It thus seems that changes of WUE under different levels of P cannot be associated with the opening or closure of stomata. On the other hand, it was reported that P deficiency can be effective on WUE by increasing mesophilic resistance and reducing RUE (Singh et al. 2013). By contrast, the results of the present study exhibited that RUE of maize showed slight changes in response to P deficiency (Figure 2f). Therefore, it seems that the main reason for improving WUE was the increase of maize yield as a result of an increase in LAI_{max} and R_{abs}(cum) (Table 4). Parallel to our results, Singh et al. (2013) found that LAI and dry matter of cotton were more sensitive to P deficiency than photosynthesis per unit area.

RUE in response to N, P and ETc

RUE of maize in response to different levels of irrigation water, N and P was changed significantly (Table 2). A slight but significant increase (about 7%) was observed in RUE under full irrigation (ETc_{100}) and 20% excessive water (ETc_{120}) (Figure 2d), which can be due to the increase in gs and consequently the increase in intracellular CO_2 concentration, as well as an increase in NNI as a result of water supply (Table 4).

As previously stated, maize RUE was increased with increasing N application rate, so that treatments N_{400} and N_0 with the values of 2.38 and 1.87 g DM MJ^{-1} showed the highest and the lowest RUE, respectively (Figure 2e). Considering the small changes in maximum leaf area index (LAI_{max}) in response to N compared to DM yield of maize, the increase in RUE as a result of N

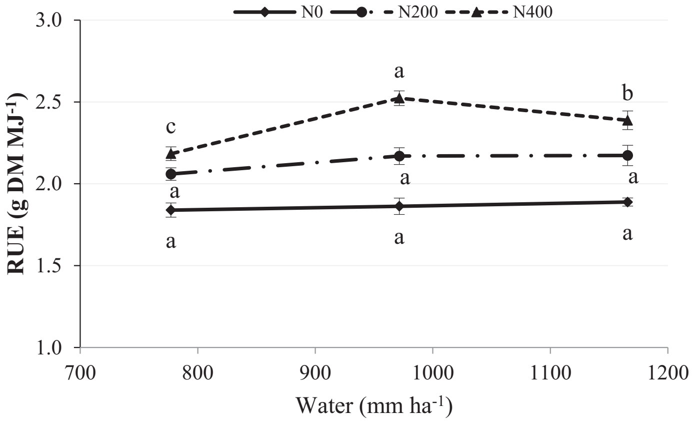

Figure 3. Interaction between amount of applied water (based on ETc) and N on RUE of the maize. Error bars are standard error of means.

application can be associated with the increase in the leaf chlorophyll and nitrogen content (Table 4). It has been shown that maize, when facing N deficiency, maintained the development of its leaf by reducing N per unit leaf area, and therefore its photosynthesis reduced (Lemaire et al. 2008). Strategy of maize for development of leaf area in response to N deficiency is different with that of potato (*Solanum tuberosum* L.), which reduces its leaf area and maintaining the amount of available N (Vos, van der Putten, and Birch 2005).

The interaction between amount of irrigation water and N on RUE was significant (Table 2), so that the highest and the lowest RUE with the values of 2.52 and 1.84 g DM MJ^{-1} observed in $ETc_{100}(N_{400})$ and $ETc_{80}(N_0)$ treatments, respectively (Figure 3). When water supply increased, no significant difference was observed in RUE in N_0 and N_{200} treatments, but N_{400} treatment caused 16% increase ($p < .05$) in RUE when applied water increased up to 100% evapotranspiration. However, with excessive water use (ETc_{120}) RUE decreased in N_{400} treatment (Figure 3). It seems that under these conditions, higher leaching was ultimately led to the reduction of RUE. According to these findings, irrigation waters more than ETc_{100} was led to lower NNI (Table 4). These results are in agreement with the previous studies reporting the increase in nitrate leaching when irrigation was higher than plant water requirement (Cameira, Fernando, and Pereira 2003; Gheysari et al. 2009).

The effect of P on the increase of maize RUE was negligible and only 6% increase in RUE was observed at the highest level of P application (Figure 2f). Mollier and Pellerin (1999) also reported a slight reduction in RUE under the conditions of P deficiency. Furthermore, the results of Colomb, Bouniols, and Delpech (1995) on sunflower and Rodriguez, Andrade, and Goudriaan (2000) on wheat showed that P caused a significant increase in RUE. Contrary to these results, Plenet, Mollier, and Pellerin (2000) reported that maize RUE was not affected by phosphorus. Fletcher et al. (2008) found the same result for sweet maize and reported that the stability of RUE in different levels of P was not the result of differences in yield, but it was the result of the amount of absorbed radiation, because the yield was low under P deficiency.

Variation in DM yields in response to N, P and ETc

The impacts of irrigation level (ETc), N and P on DM yield of maize were significant (Table 2). However, the interaction effects of factors on DM yield were not. $ETc_{120}(N_{400}P_{200})$ treatment showed the highest DM yield of 22,992 kg ha^{-1} compared to ETc_{80} (N_0P_0) treatment with the lowest DM yield of 15,067 kg ha^{-1} (Table 3).

Table 5. Summary of stepwise regression between DM yield and LAI_{max}, SPAD index, stomatal conductance (gs), $R_{abs(cum)}$ and RUE in each level of N, P, and irrigation water (based on ETc).

Treatments	Variable entered	p value	Partial R^2 (%)	Model R^2 (%)	Equation
ETc (mm ha^{-1})	R_{abs} (cum)	0.0001	64	78	DM = −22,583 + 265 gs
	RUE	0.0315	9		+5137 RUE
	gs	0.1487	5		+10.91 R_{abs} (cum)
Nitrogen (kg ha^{-1})	RUE	0.0001	77	77	DM = 2917 + 7239 RUE
Phosphorus (kg ha^{-1})	R_{abs}(cum)	0.0001	78	78	DM = −29614 + 28.28 R_{abs}(cum)

Alpha to enter and remove = 01.15.

DM yield of maize under ETc_{80} decreased by 11% and 12%, respectively, compared to ETc_{100} and ETc_{120} treatments (Table 4). The results of stepwise regression indicated that R_{abs}(cum) ($p < .01$, partial $R^2 = .64$) and RUE ($p < .05$, partial $R^2 = .09$) were the most important factors determining the variation in maize yield in response to water application, and gs variations showed little effect ($p > .05$, partial $R^2 = .05$) on DM yield (Table 5). Liu et al. (2010) showed that under water limited conditions, R_{abs}(cum) determined 96 and 72% of the changes in biological and grain yield of maize, respectively. Moreover, the results showed that ETc_{120} and ETc_{80} treatments had the highest and the lowest gs values of 44.9 and 41.9 mmol CO_2 m^{-2} s^{-1}, respectively, and no significant difference was observed between ETc_{80} and ETc_{100} treatments (Table 4). It has been reported that plant growth was affected more than gas exchange under moderate stress conditions, and plant gas exchanges became compatible to moderate and continued stress during growth (Cabrera-Bosquet et al. 2007). Therefore, it seems that the changes in plant DM yield in response to different levels of applied water show little dependence on the changes in gs (Tables 4 and 5).

Under N limitation, DM yield of maize showed 11% and 20% reduction when compared with N_{200} and N_{400}, respectively (Table 4). The results showed that RUE solely determined 77% ($p < .01$) of maize yield variation in response to N (Table 5). These findings are in consistent with the results reported by other researchers, who found that reduction of RUE was the most important factor in the yield reduction due to N deficiency (Caviglia and Sadras 2001; Vos, van der Putten, and Birch 2005; George et al. 2013).

Higher P rates (P_{100} and P_{200}) caused 5% and 9% increases in maize DM yield compared to P_0, respectively (Table 4). The relatively favorable conditions of soil P in both experimental years (Table 1) and low P uptake efficiency in the field can be considered as the probable reasons for this. Johnston and Syers (2009) reported that P uptake efficiency in direct application method in agricultural systems rarely exceeds 25%. In addition, the results of stepwise regression indicated that R_{abs}(cum) ($p < .01$, $R^2 = .78$) was the most important factor affecting variation of maize yield in response to different levels of P (Table 5). Fletcher et al. (2008) reported that LAI and leaf emergence were involved in calculating absorbed radiation, and the total absorbed radiation in treatments containing P was 12–28% higher than non-phosphorus treatment. These researchers argued that P limitation in the early stages of growth may cause a delay in leaf emergence and a reduction in leaf development and cumulative absorbed radiation, because plant roots are weak and unable to absorb P, but in mature stages when the roots are fully developed, P concentrations in plants exposed to P deficiency reached critical levels and photosynthesis was performed reasonably, provided that RUE was not changed but the yield reduced as a result of P deficiency. This mechanism explains the role of P application in early stages of crops growth (Barry and Miller 1989; Lauznon and Miller 1997; Grant et al. 2001).

Conclusion

The results indicated that resource use efficiency of maize has been closely related to crop productivity. Although the lowest N, P and water uses were associated with increased NU_tE, PU_tE and

WUE, this issue may seem misleading because DM yield of maize reduced under these conditions. This shows the importance of optimization of inputs application in agricultural systems. According to our results, DM yield of maize reduced under moderate water stress and P deficiency mainly owing to the reduction of R_{abs}(cum), which was related to the leaf area index. N limitation reduced DM yield mainly by decreasing RUE, while a reduction in the LAI_{max} and R_{abs}(cum) was of less importance. These findings are important for understanding the mechanisms of yield reduction by reducing N, P and water use. Furthermore, in agreement with our proposition, WUE and RUE were directly inter-related. It is hoped that this results will be useful in order to increase yield and reduce the environmental impacts of using inputs in intensive production systems of maize.

References

Allen, R., L. Pereira, R. Dirk, and M. Smith. 1998. Crop evapotranspiration guidelines for computing crop water requirements. In *FAO irrigation and drainage paper 56*. Rome: Food and Agriculture Organization of the United Nations.

Bai, H., and F. Tao. 2017. Sustainable intensification options to improve yield potential and eco-efficiency for rice-wheat rotation system in China. *Field Crops Research* 211:89–105. doi: 10.1016/j.fcr.2017.06.010.

Barry, D. A. J., and M. H. Miller. 1989. Phosphorus nutritional requirement of maize seedlings for maximum yield. *Agronomy Journal* 81 (1):95–9. doi: 10.2134/agronj1989.00021962008100010017x.

Bouwman, A. F., A. H. Beusen, L. Lassaletta, D. F. van Apeldoorn, H. J. van Grinsven, J. Zhang, and M. K. Ittersum van. 2017. Lessons from temporal and spatial patterns in global use of N and P fertilizer on cropland. *Scientific Reports* 7 (1):40366. doi: 10.1038/srep40366.

Cabrera-Bosquet, L., G. Molero, J. Bort, S. Nogués, and J. L. Araus. 2007. The combined effect of constant water deficit and nitrogen supply on WUE, NUE and 13C in durum wheat potted plants. *Annals of Applied Biology* 151 (3):277–89. doi: 10.1111/j.1744-7348.2007.00195.x.

Cameira, M. R., R. M. Fernando, and L. S. Pereira. 2003. Monitoring water and NO_3-N in irrigated maize fields in the Sorraia watershed, Portugal. *Agricultural Water Management* 60 (3):199–216. doi: 10.1016/S0378-3774(02)00175-0.

Cao, H. X., Z. B. Zhang, P. Xu, L. Y. Chu, H. B. Shao, Z. H. Lu, and J. H. Liu. 2007. Mutual physiological genetic mechanism of plant high water use efficiency and nutrition use efficiency. *Colloids and Surfaces B: Biointerfaces* 57 (1):1–7. doi: 10.1016/j.colsurfb.2006.11.036.

Caviglia, O. P., and V. O. Sadras. 2001. Effect of nitrogen supply on crop conductance, water- and radiation-use efficiency of wheat. *Field Crops Research* 69 (3):259–66. doi: 10.1016/S0378-4290(00)00149-0.

Colomb, B., A. Bouniols, and C. Delpech. 1995. Effect of various phosphorus availabilities on radiation-use efficiency in sunflower biomass until anthesis. *Journal of Plant Nutrition* 18 (8):1649–58. doi: 10.1080/01904169509365010.

Cooper, P. J. M., J. D. H. Keatinge, and G. Hughes. 1983. Crop evapotranspiration - a technique for calculation of its components by field measurements. *Field Crops Research* 7:299–312. doi: 10.1016/0378-4290(83)90038-2.

Cossani, C. M., G. A. Slafer, and R. Savin. 2012. Nitrogen and water use efficiencies of wheat and barley under a Mediterranean environment in Catalonia. *Field Crops Research* 128:109–18. doi: 10.1016/j.fcr.2012.01.001.

Fletcher, A., P. R. Johnstone, E. Chakwizira, and H. E. Brown. 2013. Radiation capture and radiation use efficiency in response to N supply for crop species with contrasting canopies. *Field Crops Research* 150:126–34. doi: 10.1016/j.fcr.2013.06.014.

Fletcher, A. L., D. J. Moot, and P. J. Stone. 2008. Radiation use efficiency and leaf photosynthesis of sweet corn in response to phosphorus in a cool temperate environment. *European Journal of Agronomy* 29 (2-3):88–93. doi: 10.1016/j.eja.2008.04.002.

Fletcher, A. L., D. J. Moot, and P. J. Stone. 2008. Solar radiation interception and canopy expansion of sweet corn in response to phosphorus. *European Journal of Agronomy* 29 (2–3):80–7. doi: 10.1016/j.eja.2008.04.003.

George, M. J., E. I. Teixeira, T. F. Herreman, and H. E. Brown. 2013. Understanding nitrogen and water stress mechanisms on maize crops. *Agronomy Society of New Zealand* 43:27–32.

Gheysari, M., S. M. Mirlatifi, M. Homaee, M. E. Asadi, and G. Hoogenboom. 2009. Nitrate leaching in a silage maize field under different irrigation and nitrogen fertilizer rates. *Agricultural Water Management* 96 (6): 946–54. doi: 10.1016/j.agwat.2009.01.005.

Goudriaan, J., and H. H. V. Laar. 1994. *Modelling potential crop growth processes: Textbook with exercises*. Dordrecht: Kluwer Academic Publishers.

Goyne, P. J., S. P. Milroy, J. M. Lilley, and J. M. Hare. 1993. Radiation interception, radiation use efficiency and growth of barley cultivars. *Australian Journal of Agricultural Research* 44 (6):1351–66. doi: 10.1071/AR9931351.

Grant, C. A., D. N. Flaten, D. J. Tomasiewicz, and S. C. Sheppard. 2001. The importance of early season phosphorus nutrition. *Canadian Journal of Plant Science* 81 (2):211–24. doi: 10.4141/P00-093.

Hay, R. K. M., and J. R. Porter. 2006. *The physiology of crop yield*. Oxford, UK: Blackwell Publishing.

Jacob, J., and D. W. Lawlor. 1991. Stomatal and mesophyll limitations of photosynthesis in phosphate deficient sunflower, maize and wheat plants. *Journal of Experimental Botany* 42 (8):1003–11. doi: 10.1093/jxb/42.8.1003.

Jacob, J.,. M. Udayakumar, and T. G. Prasad. 1990. Mesophyll conductance was inhibited more than stomatal conductance in nitrogen deficient plants. *Plant Physiology and Biochemistry* 17:55–61.

Jamieson, P. D., R. J. Martin, G. S. Francis, and D. R. Wilson. 1995. Drought effects on biomass production and radiation use efficiency in barley. *Field Crops Research* 43 (2–3):77–86. doi: 10.1016/0378-4290(95)00042-O.

Jin, S. H., J. Q. Huang, X.Q. Li, B. S. Zheng, J. S. Wu, Z. J. Wang, G. H. Liu, and M. Chen. 2011. Effects of potassium supply on limitations of photosynthesis by mesophyll diffusion conductance in *Carya cathayensis*. *Tree Physiology* 31 (10):1142–51. doi: 10.1093/treephys/tpr095.

Johnston, A. E. J., and J. K. Syers. 2009. A new approach to assessing phosphorus use efficiency in agriculture. *Better Crops Plant Food* 93:14–6.

Kamkar, B., A. Koocheki, M. N. Mahallati, J. A. Teixeira da Silva, P. R. Moghaddam, and M. Kafi. 2011. Fungal diseases and inappropriate sowing dates, the most important reducing factors in cumin fields of Iran, a case study in Khorasan provinces. *Crop Protection* 30 (2):208–15. doi: 10.1016/j.cropro.2010.11.007.

Lauznon, J. D., and M. H. Miller. 1997. Comparative response of corn and soybean to seedplaced phosphorus over a range of soil test phosphorus. *Communications in Soil Science and Plant Analysis* 28 (3–5):205–15. doi: 10.1080/00103629709369785.

Lemaire, G., and F. Gastal. 2009. Quantifying crop responses to nitrogen deficiency and avenues to improve nitrogen-use efficiency. In *Crop physiology: Applications for genetic improvement and agronomy*, ed V. O. Sadras and D. F. Calderini, 171–211. San Diego: Academic Press.

Lemaire, G., E. van Oosterom, M. Jeuffroy, F. Gastal, and A. Massignam. 2008. Crop species present different qualitative types of response to N deficiency during their vegetative growth. *Field Crops Research* 105 (3):253–65. doi: 10.1016/j.fcr.2007.10.009.

Liu, J., E. Pattey, J. R. Miller, H. McNairn, A. Smith, and B. Hu. 2010. Estimating crop stresses, aboveground dry biomass and yield of corn using multi-temporal optical data combined with a radiation use efficiency model. *Remote Sensing of Environment* 114 (6):1167–77. doi: 10.1016/j.rse.2010.01.004.

Loick, N., E. R. Dixon, D. Abalos, A. Vallejo, G. P. Matthews, K. L. McGeough, R. Well, C. J. Watson, R. J. Laughlin, and L. M. Cardenas. 2016. Denitrification as a source of nitric oxide emissions from incubated soil cores from a UK grassland soil. *Soil Biology and Biochemistry* 95:1–7. doi: 10.1016/j.soilbio.2015.12.009.

López-Bellido, R. J., and L. López-Bellido. 2001. Efficiency of nitrogen in wheat under Mediterranean conditions: Effect of tillage, crop rotation and N fertilization. *Field Crops Research* 71 (1):31–46. doi: 10.1016/S0378-4290(01)00146-0.

Maris, S. C., M. R. Teira-Esmatges, A. Arbones, and J. Rufat. 2015. Effect of irrigation, nitrogen application, and a nitrification inhibitor on nitrous oxide, carbon dioxide and methane emissions from an olive (*Olea europaea* L.) orchard. *Science of the Total Environment* 538:966–78. doi: 10.1016/j.scitotenv.2015.08.040.

Massignam, A. M., S. C. Chapman, G. L. Hammer, and S. Fukai. 2009. Physiological determinants of maize and sunflower grain yield as affected by nitrogen supply. *Field Crops Research* 113 (3):256–67. doi: 10.1016/j.fcr.2009.06.001.

Mollier, A., and S. Pellerin. 1999. Maize root system growth and development as influenced by phosphorus deficiency. *Journal of Experimental Botany* 50 (333):487–97. doi: 10.1093/jxb/50.333.487.

Monteith, J. L. 1977. Climate and the efficiency of crop production in Britain. *Philosophical Transactions of the Royal Society B* 281:277–94.

Mueller, N. D., J. S. Gerber, M. Johnston, D. K. Ray, N. Ramankutty, and J. A. Foley. 2012. Closing yield gaps through nutrient and water management. *Nature* 490 (7419):254–7. doi: 10.1038/nature11420.

Patterson, T. B., R. D. Guy, and Q. L. Dang. 1997. Whole-plant nitrogen and water-relations traits, and their associated trade-offs, in adjacent muskeg and upland boreal spruce species. *Oecologia* 110 (2):160–8. doi: 10.1007/s004420050145.

Plauborg, F., P. Abrahamsen, B. Gjettermann, M. Mollerup, B. V. Iversen, F. Liu, M. N. Andersen, and S. Hansen. 2010. Modelling of root ABA synthesis stomatal conductance, transpiration and potato production under water saving irrigation regimes. *Agricultural Water Management* 98 (3):425–39. doi: 10.1016/j.agwat.2010.10.006.

Plenet, D., and L. Lemaire. 2000. Relationships between dynamics of nitrogen uptake and dry matter accumulation in maize crops. Determination of critical N concentration. *Plant and Soil* 216:65–82. doi: 10.1023/A:1004783431055.

Plenet, D., A. Mollier, and S. Pellerin. 2000. Growth analysis of maize field crops under phosphorus deficiency. II. Radiation use efficiency, biomass accumulation and yield components. *Plant and Soil* 224:259–72. doi: 10.1023/A:1004835621371.

Pretty, J., and Z. P. Bharucha. 2014. Sustainable intensification in agricultural systems. *Annals of Botany* 114 (8):1571–96. doi: 10.1093/aob/mcu205.

Robertson, M. J., and F. Giunta. 1994. Responses of spring wheat exposed to pre-anthesis water stress. *Australian Journal of Agricultural Research* 45 (1):19–35. doi: 10.1071/AR9940019.

Rodriguez, D., F. H. Andrade, and J. Goudriaan. 2000. Does assimilate supply limit leaf expansion in wheat grown in the field under low phosphorus availability? *Field Crops Research* 67 (3):227–38. doi: 10.1016/S0378-4290(00)00098-8.

Sadras, V. O., and J. F. Angus. 2006. Benchmarking water-use efficiency of rainfed wheat in dry environments. *Australian Journal of Agricultural Research* 57 (8):847–56. doi: 10.1071/AR05359.

Sinclair, T. R., and T. Horie. 1989. Leaf nitrogen, photosynthesis, and crop radiation use efficiency: A review. *Crop Science* 29 (1):90–8. doi: 10.2135/cropsci1989.0011183X002900010023x.

Sinclair, T. R., and A. Weiss. 2010. *Principles of ecology in plant production*. Wallingford, UK: CAB International.

Singh, S. K., G. Badgujar, V. R. Reddy, D. H. Fleisher, and J. A. Bunce. 2013. Carbon dioxide diffusion across stomata and mesophyll and photo-biochemical processes as affected by growth CO_2 and phosphorus nutrition in cotton. *Journal of Plant Physiology* 170 (9):801–13. doi: 10.1016/j.jplph.2013.01.001.

Teixeira, E. I., M. George, T. Herreman, H. Brown, A. Fletcher, E. Chakwizira, J. de Ruiter, S. Maley, and A. Noble. 2014. The impact of water and nitrogen limitation on maize biomass and resource-use efficiencies for radiation, water and nitrogen. *Field Crops Research* 168:109–18. doi: 10.1016/j.fcr.2014.08.002.

Tilman, D., C. Balzer, J. Hill, and B. L. Befort. 2011. Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences United States of America* 108 (50):20260–4. doi: 10.1073/pnas.1116437108.

Usuda, H., and K. Shimogawara. 1992. Phosphate deficiency in maize. III Changes in enzyme activities during the course of phosphate deprivation. *Plant Physiology* 99 (4):1680–5. doi: 10.1104/pp.99.4.1680.

Vos, J., P. E. L. van der Putten, and C. J. Birch. 2005. Effect of nitrogen supply on leaf appearance, leaf growth, leaf nitrogen economy and photosynthetic capacity in maize (*Zea mays* L.). *Field Crops Research* 93 (1):64–73. doi: 10.1016/j.fcr.2004.09.013.