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Influence of Soil Nitrogen and Water Supply on Canola Nitrogen Use Efficiency

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ABSTRACT

Nitrogen fertilizer requirements for economic optimization of spring canola (*Brassica napus* L.) production in eastern Washington varies with yield potential. Recent research has revealed that more N is needed per unit of grain (UNR) as yield potential decreases. Because UNR is the inverse of N use efficiency (NUE) at optimal yield, the implication of this research is that canola becomes less efficient at using N as yield potential decreases. Our research goal was to identify the NUE components that contribute to higher potential yields with more available water. In both years of a two-location experiment, grain yield (Gw), grain N (Ng), and N supply (Ns) were significantly greater with increasing available water supply. The NUE component analysis indicated that differences in water-enhanced yields were associated with higher N uptake (plant N [Nt]/Ns) and utilization (Gw/Nt) efficiencies, which in turn were attributed to a higher grain N utilization efficiency (Gw/Ng) component, followed by higher N retention (available N [Nav]/Ns). Differences in grain N accumulation due to a greater availability of water was mostly attributed to greater N retention efficiency. With increasing available water and fertilization, spring canola became more efficient at accumulating (i) grain biomass per unit grain N and (ii) grain N per unit of available N supply. These results emphasize the need to develop breeding and management strategies to improve water use efficiency and to select canola cultivars capable of coping with water stress that limits grain biomass production per unit plant N accumulation.

Core Ideas

- Spring canola exhibited Mitscherlich response to soil N and Liebig response to plant N.
- Water availability limited yields by restricting N utilization, retention, and uptake.
- Water availability limited grain N accumulation by lowering N uptake from soil.

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Regional interests in canola as a rotational crop for agronomic and market diversification have stimulated agronomic research to fit canola into the unique environments and soils of eastern Washington. Despite early notions to manage canola similarly to wheat (*Triticum aestivum* L.), Pan et al. (2016) found that spring canola's fertilizer N requirement (UNR) varied with yield potential, which was relatively greater for lower yield potentials. The UNR is important for two reasons. First, yield-based N recommendations are commonly calculated by applying a predefined UNR at optimum yield (Fiez et al., 1995). Second, the UNR is the inverse of N use efficiency (NUE) at optimal yield, which is a measurement of the system's production efficiency.

The NUE of cropping systems is a major agronomic concern due to the extensive environmental and economic consequences of N loss from agricultural systems. Increased global inputs of natural and synthetic N sources, in addition to biological N_2 fixation by expanded cultivation of legumes, have largely contributed to the enhancement of N transport that results in the accumulation of alarming amounts of N in the hydrosphere and atmosphere. Negative environmental effects include tropospheric ozone production, N deposition above critical thresholds, acidification, eutrophication, and stratospheric ozone depletion (Galloway et al., 2003). Growers faced with rising fertilizer, chemical, fuel, and land costs will benefit from the application of N at economically optimum rates. Economic fertilizer rates are based on cost/price ratios and maximize profitability according to the law of diminishing returns (Spillman, 1923).

Optimizing N fertility management and NUE is challenged by the interactive effects of physiological, ecological, agronomic, economic, social, and political factors (Cassman et al., 2002; Dawson et al., 2008; Lea and Azevedo, 2006; Weih et al., 2011). Globally, an estimated 30 and 50% of fertilizer N is recovered within the grain (Conant et al., 2013; Raun and Johnson, 1999; Smil, 1999) and aboveground crop biomass (Cassman et al., 2002), respectively, and the unrecovered fertilizer N is often assumed to be lost from the system (Galloway et al., 2003; Raun and Johnson, 1999). Weather, water availability, tillage practices, residue retention, crop rotation, and fertilizer rate, timing, placement, and source are the important management factors that affect the NUE in a given crop production system (Cassman et

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Abbreviations: Ns, nitrogen supply; Nav, available nitrogen supply; Nt, plant nitrogen; Ng, grain nitrogen; Gw, grain weight; H_2Ot, total available water; NUE, nitrogen use efficiency; UNR, unit nitrogen requirement; WUE, water use efficiency.

al., 2002; Dawson et al., 2008; Huggins and Pan, 1993; Lea and Azevedo, 2006; Raun and Johnson, 1999).

Huggins and Pan (1993) expanded the NUE component analysis, defined by Moll et al. (1982), as a framework to evaluate differences in NUE among cropping systems, which is linked to soil and plant processes. This procedure attributes differences in grain yield to the soil and plant components of NUE, as calculated from measured grain yield, grain N, aboveground plant N, fertilizer N inputs, and post-harvest inorganic soil N. The NUE components, or ratios, include N retention efficiency, available N uptake efficiency, NUE, grain N accumulation efficiency, and N harvest index (Fig. 1). The NUE component analysis identifies plant and soil processes that contribute to yield differences in response to N. In the component analysis, NUE is calculated based on N supply as a means to compare the performances of any two cropping systems.

Nitrogen use efficiency generally declines with increasing N supply (Dawson et al., 2008; Huggins and Pan, 1993; Sowers et al., 1994), which is simply an outcome of nutrient responses that follow Mitscherlich's law of diminishing returns in agricultural systems (Pan et al., 2016). A decrease in N retention, N uptake, or N utilization may correlate with the reduction in NUE (Dawson et al., 2008). For instance, under limited water availability, low uptake efficiency may result from impaired root growth (Pan et al., 2007), while a low N utilization efficiency may be caused by a shortened grain filling period (Asplund et al., 2014).

Pan et al. (2016) recently demonstrated that UNRs vary across a range of canola yield goals in eastern Washington, as a function of N supply and available water, by using the Harmsen–Mitscherlich model (Harmsen, 2000a, 2000b). The underlying plant and soil mechanisms contributing to differences in the NUE of spring canola remain unclear. The goal of this study was to define the relationships between yield potential, water availability, and NUE components. The objectives were to identify NUE components that contribute to differences in (i) water-limited yields of spring canola and (ii) grain N accumulation at limiting, optimal, and excessive N supply.

MATERIALS AND METHODS

Details for the locations, experimental design, and baseline characteristics of this experiment were provided by Pan et al. (2016). Briefly, 2.3- by 15.2-m (34.7-m^2) plots were established in a randomized complete block design in quadruplet with five N rates (0, 45, 90, 134, and 179 kg ha^{-1}) as urea. Sulfur was applied at a rate of 17 kg ha^{-1} as $(NH_4)_2SO_4$. Spring canola (Dekalb cultivar 30-42 in 2011 and 55-55 in 2012) was direct seeded at a rate of 8 kg ha^{-1} with a Fabro plot drill (Fabro Enterprises Ltd.) into winter wheat stubble, and all urea fertilizer was deep banded 10 cm beneath the seed at planting. Glyphosate [*N*-(phosphonomethyl) glycine] was used at a rate of 0.59 L ha^{-1} to control weeds before planting and at the six-leaf stage for in-season weed control.

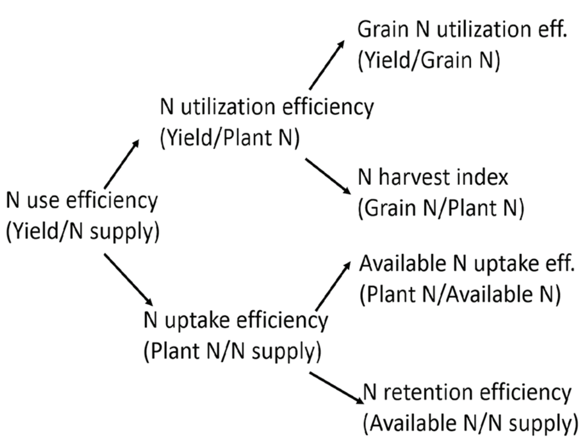

Fig. 1. Nitrogen use efficiency (NUE) and NUE components.

Initial soil characteristics are presented in Table 1. Data from this study represent spring canola planted in 2011 and 2012, serving as the initiation year of a 3-yr cropping sequence study. Soil samples were collected from each replicate block prior to fertilization and planting to a depth of 120 cm in 30-cm increments for the analysis of available water and 1 mol L^{-1} KCl exchangeable NH_4^+–N and NO_3^-–N. Preplant soil pH, organic matter, and available P and K fertility tests were conducted on the top 30-cm increment. Plots were resampled after harvest for inorganic N analysis. Samples were collected with a tractor (John Deere 5425) mounted hydraulic probe (Giddings) and stored at –15°C prior to inorganic N flow injection autoanalysis (Quickchem 8000 Series FIA+ system, Lachat Instruments).

Canola grain was harvested in whole plots using a plot combine (Kincaid); the seed was recleaned using a 2-mm sieve, air dried, and weighed to determine yield. Prior to harvest, 1.5 m were trimmed from each plot end to avoid an "edge effect." Harvested length and width were measured after harvest for more accurate estimation of yield.

At physiological maturity prior to seed harvest, biomass samples were collected from 3-m lengths selected from different inner rows staggered along the length of the plot. Plots were selected from the 0, 89, and 179 kg N ha^{-1} treatments in each replicate block in 2011 and from 0, 45, 89, 134, and 179 kg N ha^{-1} treatments in 2012. The biomass samples were dried at 50°C for 48 h prior to weighing. Whole samples were threshed with a Vogel stationary grain thresher to separate seeds, chaff, and stems. Seeds were weighed for harvest index determination and then ground with a Cyclone sample mill (Thomas Scientific) for C and N analysis with a C/N autoanalyzer (Leco Corporation). Residue yields were calculated from the combined seed yields by applying the harvest index. Residue samples were ground with a Thomas Wiley mill (Thomas Scientific) prior to C and N analysis.

Nitrogen use efficiency was assessed with the calculations listed in Table 2, and the NUE component analysis was performed according to the steps outlined by Huggins and Pan (1993). For individual site years, yield or grain N maxima were

Table 1. Site-year available pH, organic matter, P, K, S in the upper 0 to 90 cm, N supply in 0 to 120 cm, total available water (H_2Ot), and in-season precipitation (ppt) as a proportion of annual precipitation.

Year	pH†	OM	P‡	K‡	S	N supply	H_2Ot	In-season ppt
		%	–mg kg^{-1}–		—kg ha^{-1}—		mm	%
Pullman (annual cropping zone)								
2011	5.7	3.2	38	611	30	93	675	31
2012	5.5	3.0	28	352	23	65	497	25
Davenport (grain–fallow transition zone)								
2011	6.2	2.2	15	401	26	85	406	35
2012	5.7	2.8	23	602	34	82	279	44

† 1:1 soil/H_2O.
‡ $NaHCO_3$ extraction.

determined by regressing the yield response or grain N accumulation of replicate data to N supply, available N supply, plant N, and grain N with the best-fit Mitscherlich growth factor response model or quadratic functions using Sigmaplot (Systat Software, Inc.) as outlined by Pan et al. (2016).

The water use efficiency of yield and grain N accumulation were determined for each of the N components by fitting the relationship between maximum yield divided by grain N and available water supply for each N component as outlined by Pan et al. (2016).

After the completion of all site years, the overall yield and grain N accumulation response to increasing N was characterized with the Harmsen–Mitscherlich growth factor response model (Pan et al., 2016):

$$Y = \mathrm{WUE}(\mathrm{H_2Ot} - 61)\left\{1 - 10^{d(X)\left[\mathrm{WUE}(\mathrm{H_2Ot}-61)^{n-1}\right]}\right\} \quad [1]$$

where Y is grain weight (Gw), X is N applied, WUE(H_2Ot) is the available water supply with a minimum threshold for canola germination of 61 mm yr^{-1}, d is an efficiency constant for soil N availability, and n is a moisture-dependent power constant.

An analysis of variance was performed using the mixed model provided by the nlme package in R to determine statistical differences in NUE components. Because site and year had a significant interaction, data are reported for each year and site. Nitrogen rate × site was the main fixed effect, with blocking as the random effect. Post hoc mean comparisons were assessed using Tukey's honest significant difference (p value < 0.05). The goodness of fit of the Harmsen–Mitscherlich equation was assessed by comparing the significance, root mean square error, and R^2 values for observed vs. predicted Gw and grain N (Ng).

RESULTS

Water and Site-Year Effects on Nitrogen Use Components

Several NUE component variations resulted in significant three-way year × site × N interactions (Table 3). Therefore, data are presented and discussed by year and site. In both years, grain yield (kg Gw ha^{-1}), grain N (kg Ng ha^{-1}), and N supply (kg Ns ha^{-1}) were significantly greater at Pullman, which lies in the annual cropping zone, than Davenport, located in a flex-cropping transitional zone between annual cropping and grain–fallow cropping. These results corresponded with greater available water supply at Pullman than Davenport. At Pullman, available water was 675 mm yr^{-1} in 2011 and 497 mm yr^{-1} in 2012. In comparison, the available water at Davenport was 406 mm yr^{-1} in 2011 and 297 mm yr^{-1} in 2012. In 2011, the aboveground plant N (kg Nt ha^{-1}) and available N supply (kg Nav ha^{-1}) were significantly greater at Pullman, corresponding with the greatest available water during the study period. Post-harvest residual N was significantly greater at Davenport than Pullman in 2011. In both years, more residual N was recovered in the 60- to 120-cm depth at Davenport than Pullman (Fig. 2). Additions of fertilizer N significantly increased all measured values.

Nitrogen use efficiency (Gw/Ns) was significantly greater at Pullman than Davenport for both years (Table 4). Nitrogen use efficiency can be partitioned into uptake efficiency (Nt/Ns = Nav/Ns × Nt/Nav) and utilization (Gw/Nt = Ng/Nt × Gw/Ng) components and subcomponents (Fig. 1). Of the subcomponents, N harvest index (Ng/Nt) and grain N utilization efficiency (Gw/Ng) components were also significantly greater at Pullman with higher water availability than at Davenport for both years. Nitrogen retention efficiency (Nav/Ns) and available N uptake efficiency (Nt/Nav) were greater at Pullman in 2011. The addition of fertilizer decreased all efficiency factors with the exception of available N uptake efficiency.

Mitscherlich-Modeled Nitrogen Response and Component Relationships

The relationship of grain yield to N supply, available N supply, plant N, and grain N were fitted by the Harmsen–Mitscherlich equation (Fig. 3). Yield maxima were determined according to the best fit by the classic Mitscherlich equation or quadratic functions for individual site years with a significant response to increasing N (Table 5), where yield maxima served as parameters to model the overall responses with the Harmsen–Mitscherlich equation (Eq. [1]). The Harmsen–Mitscherlich regression model was statistically

Table 2. Nitrogen use efficiency terminology and calculations.

Component or ratio	Calculation
Grain yield (Gw)	
Aboveground plant N (Nt)	
Grain N (Ng)	
Post-harvest inorganic N (Nh)	
Fertilizer N (Nf)	
N supply (Ns)	mineralizable N + preplant N + Nf
Available N (Nav)	Nt + Nh
Available N retention efficiency	Nav/Ns
N use efficiency	Gw/Ns
N uptake efficiency	Nt/Ns
N utilization efficiency	Gw/Nt
Available N uptake efficiency	Nt/Nav
N harvest index	Ng/Nt
Grain N utilization efficiency	Gw/Ng
N uptake efficiency components	Nav/Ns × Nt/Nav
N utilization efficiency components	Ng/Nt × Gw/Ng
N use efficiency components	Nav/Ns × Nt/Nav × Ng/Nt × Gw/Ng

Table 3. Grain yield (Gw), grain N (Ng), N supply (Ns), available soil N (Nav), aboveground plant N (Nt), and post-harvest soil N (Nh) for spring canola in response to N rate at Pullman (Pull) and Davenport (Dav) in 2011 and 2012. Values are means of observations in both years (n = 4).

	Gw		Ng		Ns		Nav		Nt		Nh	
N rate	Pull	Dav	Pull	Dav	Pull	Dav	Pull	Dav	Pull	Dav	Pull	Dav
	kg ha^{-1}											
	2011											
0	1785.2	336.5	54.0	10.4	92.6	43.5	87.4	35.9	75.0	19.7	12.5	16.2
89	2210.5	520.9	70.1	18.4	181.6	132.5	125.4	53.4	109.4	32.8	16.0	20.6
179	2045.2	690.7	66.7	32.3	271.6	222.5	147.0	76.0	117.7	45.1	29.3	30.9
HSD(0.05)	796.4		15.3				35.0		27.1		11.7	
EONR†	2313	531	73	18	178	114	150	57	125	33	25	24
	Analysis of variance											
N rate (N)	*		**				***		***		***	
Site (S)	***		***		***		***		***		***	
N × S	NS		NS				NS		***		***	
CV, %	17.6		17.6				20.8					
	2012											
0	786.8	677.3	24.6	25.1	65.0	84.7	51.1	60.1	30.7	34.6	20.4	25.5
89	1553.2	968.8	51.3	42.2	154.0	173.7	80.0	83.0	66.8	63.9	13.2	44.0
179	1466.7	768.8	54.6	36.0	244.0	262.7	97.6	103.1	72.2	57.5	25.4	45.6
HSD(0.05)	443.5		18.9				63.5		30.6		42.0	
EONR	1497	659	50	26	171	87	85	48	64	34	21	14
	Analysis of variance											
N	***		***				*		***		NS	
S	***		*		***		NS		NS		NS	
N × S	***		NS				NS		NS		NS	
CV, %	20.0		22.7				37.5		26.0		79.0	

* Significant at the 0.05 probability level; NS, not significant.
** Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.
† EONR, economically optimum N rate.

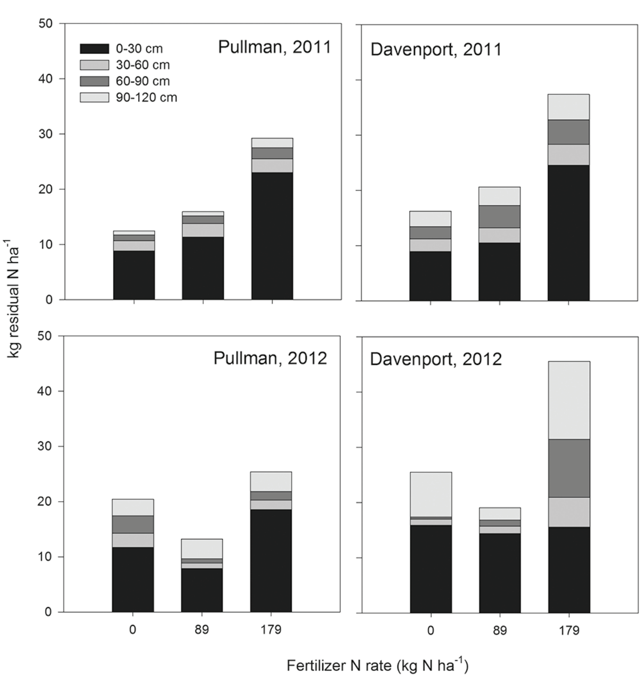

Fig. 2. Residual inorganic N (NH_4^+ + NO_3^- in 0–30 cm, NO_3^- in 30–120 cm) at 30-cm incremental depths within the soil profile following the harvest of spring canola at Pullman and Davenport in 2011 and 2012.

significant, explaining 75 to 99% of the variation in yield response (Table 6). The WUE of spring canola was 3.2 kg grain kg^{-1} Ns, 4.5 kg grain kg^{-1} Nav, 4.9 kg grain kg^{-1} Nt, and 13.0 kg grain kg^{-1} Ng. The moisture-dependent constant (n value) was >1 when yields were regressed against N supply but decreased to near zero when regressed against plant N (Nt) and grain N (Ng).

The responses of grain N to N supply, available N, and plant N were also modeled by the Harmsen–Mitscherlich equation (Fig. 4). The Harmsen–Mitscherlich regression model was statistically significant, explaining 64 to 93% of the variation in grain N accumulation (Table 6). The WUE of spring canola was 0.12 kg grain N kg^{-1} Ns, 0.19 kg grain N kg^{-1} Nav, and 0.26 kg grain N kg^{-1} Nt. Similar to the yield response, the moisture dependent n value was near 1 when grain N was regressed against N supply but decreased to close to zero when regressed against plant N.

Component Attribution to Water-Related Yield Differences at Economic Optimums

The NUE component analysis was conducted to partition yield differences at various water-limited yield potentials observed during the study period. For this analysis, yield responses were compared among 675, 497, and 297 mm available water yr^{-1} (Table 7). These levels of available water corresponded to observed availabilities at Pullman 2011, Pullman 2012, and Davenport 2012, respectively.

Table 4. Nitrogen use efficiency (Gw/Ns), available N retention efficiency (Nav/Ns), available N uptake efficiency (Nt/Nav), N harvest index (Ng/Nt), and grain N utilization efficiency (Gw/Ng) ratios for spring canola at Pullman (Pull) and Davenport (Dav). Values are means of observations for 2011 and 2012 (*n* = 4).

	Gw/Ns		Nav/Ns		Nt/Nav		Ng/Nt		Gw/Ng	
N rate	Pull	Dav	Pull	Dav	Pull	Dav	Pull	Dav	Pull	Dav
	kg ha^{-1}									
					2011					
0	19.3	7.7	0.94	0.82	0.86	0.54	0.72	0.53	33.1	33.6
89	12.2	3.9	0.69	0.40	0.87	0.61	0.64	0.56	31.6	28.5
179	7.5	3.0	0.54	0.34	0.81	0.58	0.57	0.54	30.6	27.3
HSD(0.05)	3.0		0.18		0.11		0.06		4.7	
EONR†	13.0	4.6	0.84	0.50	0.83	0.58	0.59	0.55	31.3	29.5
					Analysis of variance					
N rate (N)	***		***		NS		***		**	
Site (S)	***		***		***		***		*	
N × S	***		NS		NS		***		NS	
CV, %	15.7		13.9		7.5		4.7		7.2	
					2012					
0	12.1	8.0	0.79	0.71	0.64	0.66	0.81	0.74	31.9	27.5
89	10.1	5.6	0.52	0.48	0.83	0.81	0.77	0.67	30.4	23.9
179	6.0	2.9	0.4	0.39	0.75	0.58	0.76	0.64	26.9	21.5
HSD(0.05)	2.6		0.49		0.33		0.11		4.0	
EONR	8.7	7.6	0.50	0.55	0.75	0.71	0.78	0.76	29.9	25.3
					Analysis of variance					
N	***		*		NS		*		***	
S	***		NS		NS		**		***	
N × S	NS		NS		NS		NS		NS	
CV, %	16.6		41.7		22.0		7.3		7.0	

* Significant at the 0.05 probability level; NS, not significant.
** Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.
† EONR, economically optimum N rate.

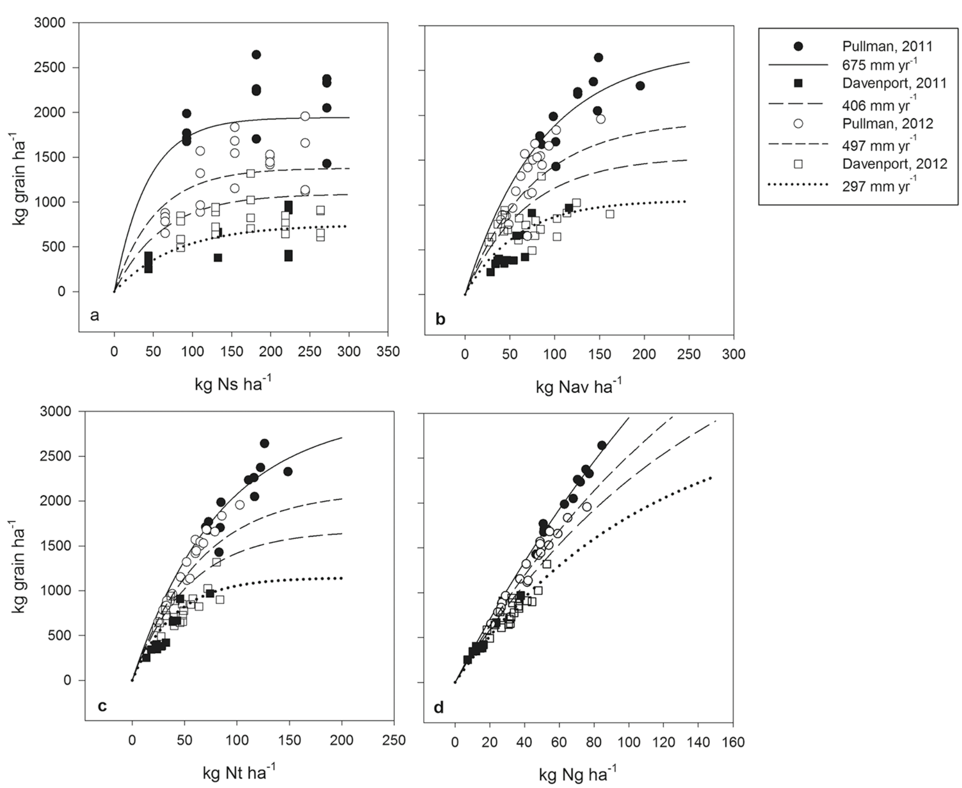

Fig. 3. Relationship between grain yield (Gw) and (a) N supply (Ns), (b) available N (Nav), (c) aboveground plant N (Nt), and (d) grain N at Pullman and Davenport in 2011 and 2012.

Table 5. Results for regression analysis for determining yield (Gw) and grain N (Ng) maxima in response to N supply (Ns), available N (Nav), and aboveground plant N (Nt).

Parameter	Gw maxima				Ng maxima		
	Ns	Nav	Nt	Ng	Ns	Nav	Nt
	kg grain yield ha^{-1}				kg grain N ha^{-1}		
				Pullman, 2011 (675 mm available water yr^{-1})			
	2014	2421	2539	9684	72	108	131
Equation	average	$y = -0.067x^2 + 25.40x$	$y = -0.081x^2 + 28.57x$	$y = 9684(1 - 10^{-0.0037x})$	$y = -0.0018x^2 + 0.72x$	$y = -0.0011x^2 + 0.69x$	$y = 131(1 - 10^{-0.0067x})$
R^2	ns	0.6528	0.7375	0.9681	0.2942	7964	0.8372
p value	0.1572	0.0015	0.0003	<0.0001	0.0685	<0.0001	<0.0001
				Davenport, 2011 (406 mm available water yr^{-1})			
	674	2077	2277	3602	26	84	52
Equation	$y = 674(1 - 10^{-0.014x})$	$y = -0.012x^2 + 10.07x$	$y = 2277(1 - 10^{-0.0081x})$	$y = 3602(1 - 10^{-0.0088x})$	$y = 26(1 - 10^{-0.0102x})$	$y = -0.0017x^2 + 0.75x$	$y = -0.0026x^2 + 0.76x - 3.49$
R^2	0.345	0.7731	0.878	0.9363	0.45	0.7703	0.9864
p value	0.0446	0.0002	<0.0001	<0.0001	0.017	0.0002	<0.0001
				Pullman, 2012 (497 mm available water yr^{-1})			
	1530	2086	2262	4271	57	84	176
Equation	$y = -0.0379x^2 + 15.23x$	$y = -0.063x^2 + 23.00x$	$y = -0.093x^2 + 29.03x$	$y = 4271(1 - 10^{-0.0085x})$	$y = -0.0009x^2 + 0.45x$	$y = -0.0024x^2 + 0.96x - 11.53$	$y = -0.001x^2 + 0.84x$
R^2	0.5644	0.7731	0.9613	0.9651	0.5939	0.8072	0.9946
p value	0.0001	<0.0001	<0.001	<0.0001	<0.0001	<0.0001	<0.0001
				Davenport, 2012 (297 mm available water yr^{-1})			
	899	846	1149	2580	36	43	72
Equation	$y = -0.027x^2 + 9.91x$	average	$y = 1149(1 - 10^{-0.0263x})$	$y = 2580(1 - 10^{-0.0112x})$	$y = -0.0009x^2 + 0.36x$	$y = 43(1 - 10^{-0.0237x})$	$y = 72(1 - 10^{-0.0135x})$
R^2	0.1531	ns	0.4965	0.7682	0.3001	0.4656	0.8897
p value	0.088	0.1572	0.0005	<0.0001	0.0124	0.0009	<0.0001

Table 6. Results of regression analysis for fitting the response of grain yield and grain N accumulation to N supply (Ns), available N (Nav), aboveground plant N (Nt), and grain N (Ng) with the Harmsen–Mitscherlich equation (Eq. [1]).

Parameter†	Ns	Nav	Nt	Ng
		Grain yield		
WUE	3.166	4.465	4.856	13.02
d	0.0001	0.1346	2.8035	1.3144
n	1.6303	0.5854	0.2112	0.2781
R^2	0.7531	0.8429	0.9236	0.9862
RMSE	314	250	174	74
p value	<0.0001	<0.0001	<0.0001	<0.0001
		Grain N accumulation		
WUE	0.1165	0.1918	0.2593	
d	0.0087	0.2433	1.112	
n	0.9103	0.072	–0.2215	
R^2	0.6437	0.8105	0.9292	
RMSE	12	8	5	
p value	<0.0001	<0.0001	<0.0001	

† WUE, water use efficiency; *d*, efficiency constant for soil N availability; *n*, moisture-dependent power constant.

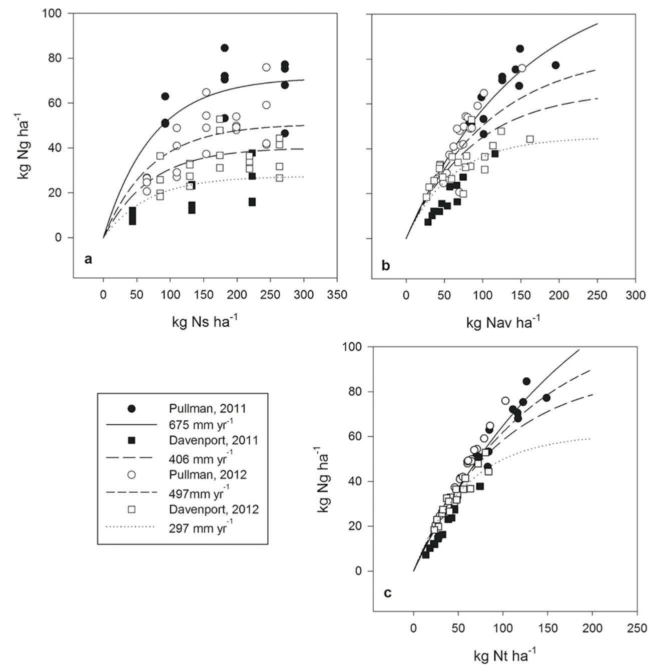

Fig. 4. Relationship between grain N accumulation (Ng) and (a) N supply (Ns), (b) available N (Nav), and (c) aboveground plant N (Nt) at Pullman and Davenport in 2011 and 2012.

Pullman 2011 vs. Pullman 2012

Grain yields were 574 to 748 kg ha^{-1} greater when 675 mm of water was available compared with 497 mm and decreased with increasing N supply (Table 7). At the economically optimum yield, the yield difference was 589 kg ha^{-1}. Only a small fraction of the yield differences was attributed to a greater N supply, which accounted for 22% of the differences when no fertilizer was added but 0% of yield differences at the highest rate of fertilization. Therefore, 78 to 100% of the yield differences was attributed to differences in NUE (Gw/Ns). When NUE was broken down into its uptake and utilization components, 17 to 38% of the yield differences was attributed to the N uptake efficiency (Nt/Ns) component, which decreased with increasing N supply. In contrast, 40 to 82% of the yield differences was associated with the N utilization (Gw/Nt) component, which increased with fertilization.

The N uptake efficiency component was further delineated into the available N retention efficiency (Nav/Ns) and available N uptake efficiency (Nt/Nav) subcomponents. Between 0 and 25% of the yield differences at Pullman was attributed to the available N retention efficiency (Nav/Ns) subcomponent, which decreased with fertilization. In comparison, the available N uptake efficiency (Nt/Nav) subcomponent accounted for 13 to 18% of yield differences and was unaffected by fertilization. At economically optimum yields, only 27 and 18% of yield differences were attributed to the N retention efficiency (Nav/Ns) and available N uptake efficiency (Nt/Nav) components, respectively (Fig. 5a). The N utilization efficiency component (Gw/Nt) was also further divided into the N harvest index (Ng/Nt) and grain N utilization (Gw/Ng) subcomponents, both of which increased with N supply. Between 12 and 35% of grain yield differences was attributed to the N harvest index (Ng/Nt) subcomponent, whereas the greatest proportion of differences in grain yield was attributed to the grain N utilization efficiency (Gw/Ng) subcomponent, accounting for 28 to 47% of the overall difference. At economically optimum yields, only 18 and 38% of yield differences were attributed to the N harvest index (Ng/Nt) and grain N utilization (Gw/Ng) components, respectively (Fig. 5a).

Table 7. Nitrogen use component analysis of yield differences, determined as the changes in grain yield (Gw), N supply (Ns), N use efficiency (Gw/Ns), N uptake efficiency (Nt/Ns), N utilization efficiency (Gw/Nt), available N retention efficiency (Nav/Ns), available N uptake efficiency (Nt/Nav), N harvest index (Ng/Nt), and grain N utilization efficiency (Gw/Ng) at different fertilizer N rates (Nf).

Nf	ΔGw	ΔNs	ΔGw/Ns	ΔNt/Ns	ΔGw/Nt	ΔNav/Ns	ΔNt/Nav	ΔNg/Nt	ΔGw/Ng
				Pullman 2011 minus Pullman 2012					
0	748	166	582	281	301	176	105	89	212
89	611	31	580	142	439	61	81	155	284
179	574	6	568	100	468	–2	102	200	269
EONR†	589	–1	590	260	330	157	103	106	224
				Pullman 2012 minus Davenport 2012					
0	481	–73	554	367	187	207	161	42	145
89	638	–23	661	225	436	170	55	109	328
179	645	–7	652	182	470	90	92	118	351
EONR	695	42	653	274	379	177	97	116	263

† EONR, economically optimum N rate.

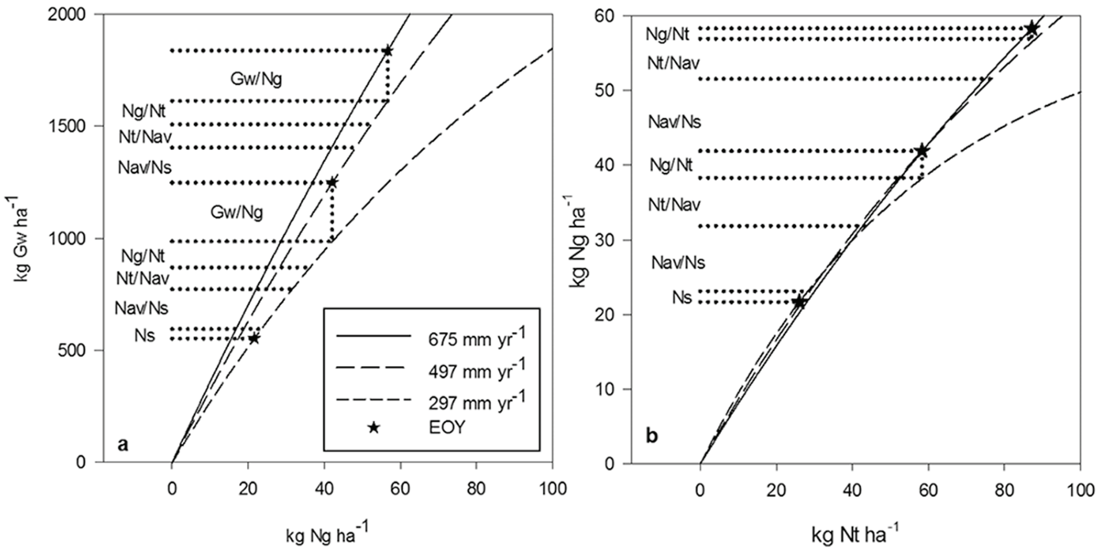

Fig. 5. Attribution of N use efficiency components grain N utilization (Gw/Ng), N harvest index (Ng/Nt), available N uptake efficiency (Nt/Nav), available N retention efficiency (Nav/Ns), and N supply (Ns) to differences in (a) grain yield (Gw) and (b) grain N accumulation (Ng) at economically optimum yields (EOY) for 297, 497, and 675 mm available water yr^{-1}.

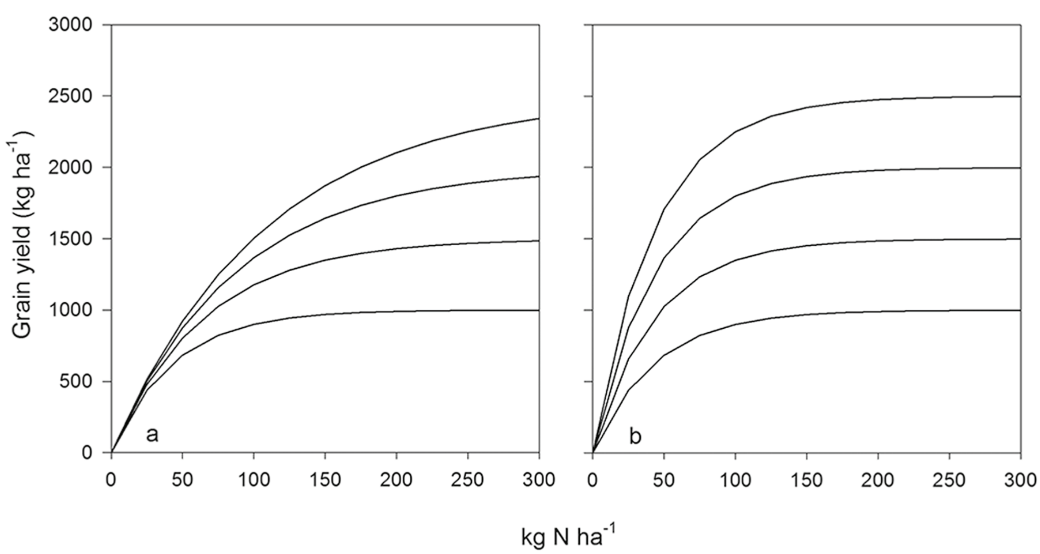

Fig. 6. Yield curves following (a) Liebig and (b) Mitscherlich relationships with respect to N across various yield potentials. When $n = 0$, the Harmsen–Mitscherlich equation (Eq. [1]) reduces to the Liebig function, defined as $y = A(1 - 10^{-cx/A})$. When $n = 1$, the Harmsen–Mitscherlich equation reduces to the classic Mitscherlich function, defined as $y = A(1 - 10^{-cx})$ (Harmsen, 2000a, 2000b).

Table 8. Nitrogen use component analysis of grain N accumulation differences as the changes in grain N (Ng), N supply (Ns), grain N use efficiency (Ng/Ns), N uptake efficiency (Nt/Ns), N harvest index (Ng/Nt), available N retention efficiency (Nav/Ns), available N uptake efficiency (Nt/Nav), and N harvest index (Ng/Nt) at different fertilizer N rates (Nf).

Nf	ΔNg	ΔNs	ΔNg/Ns	ΔNt/Ns	ΔNg/Nt	ΔNav/Ns	ΔNt/Nav	ΔNg/Nt
				Pullman 2011 minus Pullman 2012				
0	21	7	14	13	1	8	5	1
89	21	3	19	15	4	9	6	4
179	21	1	20	16	5	8	7	5
EONR†	16	1	16	15	1	10	5	1
				Pullman 2012 minus Davenport 2012				
0	11	–3	13	14	0	8	6	0
89	20	–1	20	15	5	10	5	5
179	22	0	22	16	6	9	7	6
EONR	20	1	19	15	4	9	6	4

† EONR, economically optimum N rate.

Pullman 2012 vs. Davenport 2012

In 2012, grain yields were 481 to 645 kg ha^{-1} greater at Pullman than Davenport, corresponding with 497 mm of available water vs. 297 mm (Table 7). At the economically optimum yield, the yield difference was 695 kg ha^{-1}. Davenport had a greater N supply than Pullman in 2012, and therefore differences in N supply contributed to negative differences in yield. Nevertheless, at economically optimum yields, 6% of yield differences was attributed to differences in N supply. A large proportion of yield differences between Davenport and Pullman was attributed to the N uptake efficiency (Nt/Ns) component, which ranged from 28 to 76% and decreased with increasing N supply. In contrast, 39 to 73% of yield differences was associated with the N utilization (Gw/Nt) subcomponent, which increased with fertilization. At economically optimum yields, 39 and 55% of yield differences were attributed to the N uptake efficiency and N utilization efficiency components, respectively.

The available N retention efficiency (Nav/Ns) subcomponent accounted for 14 to 43% of yield differences and the available N uptake efficiency (Nt/Nav) subcomponent 14 to 33%. Both components decreased with increasing N supply. At economically optimum yields, only 26 and 14% of yield differences were attributed to the N retention efficiency (Nav/Ns) and available N uptake efficiency (Nt/Nav) components, respectively (Fig. 5a). The N harvest index (Ng/Nt) and grain N utilization (Gw/Ng) subcomponents increased with N supply. The least proportion of grain yield differences between the two sites was attributed to the N harvest index (Ng/Nt) component, which ranged from 9 to 18%, whereas the greatest proportion of differences in grain yield was attributed to the grain N utilization efficiency (Gw/Ng), accounting for 30 to 54% of the overall difference. At economic optimums, 17 and 38% of yield differences were attributed to the N harvest index (Ng/Nt) and grain N utilization (Gw/Ng) components, respectively (Fig. 5a).

Grain Nitrogen-Based Nitrogen Use Efficiency Component Analysis

The NUE component analysis was conducted to partition differences in grain N (Table 8). Trends in differences in grain N accumulation were similar among the various levels of available water (675, 497, and 297 mm available water yr^{-1}). As available water increased from 297 to 497 mm yr^{-1}, grain N accumulation increased by 11 to 22 kg N ha^{-1}, and differences became more prominent with a greater soil N supply. However, the majority of grain N accumulation was not attributed to differences in soil N supply. Of the NUE components, 68 to 125% of the differences was attributed to the N uptake efficiency (Nt/Ns) component. Differences exceeding 100% indicate that the N supply component was greater for the lower yielding site, attributed to negative yield differences. Forty to 71% of grain N differences was attributed to the N retention efficiency (Nav/Ns) component and 24 to 56% to the available N uptake efficiency (Nt/Nav) component. Less than 29% of the differences in grain N accumulation was attributed to the N harvest index (Ng/Nt) component (Fig. 5b).

DISCUSSION

In eastern Washington, the yield potential of spring canola is significantly correlated to available water, and a relationship between yield potential and available water supply is emerging for the region (Pan et al., 2016). In addition, the UNR (Ns/Gw) varied with canola's yield potential, which increased as available water decreased. The major implication of this research is that the NUE of canola diminishes as available water decreases, even when optimum yields were attained. In the subset of data presented here, the UNR at economic yields was 0.07 kg Ns kg^{-1} grain at 675 mm yr^{-1}; 0.13 kg Ns kg^{-1} grain at 497 mm yr^{-1}, and 0.19 kg Ns kg^{-1} grain at 297 mm yr^{-1}.

The Harmsen–Mitscherlich equation enables the modeling of N responses across a range of yield potentials through the addition of a moisture-dependent n term in the classical Mitscherlich formula (Eq. [1]). When n is near 1, the Harmsen–Mitscherlich closely resembles the classic Mitscherlich response (Harmsen, 2000a, 2000b; Fig. 6). As a result, UNR varies across a range of economically optimum yields (Pan et al., 2016), as confirmed with the subset of data presented here. However, when $n = 0$, the Harmsen–Mitscherlich equation reduces to a Liebig relationship (Harmsen, 2000a, 2000b). With n values close to zero, N partitioning within the plant for this subset of data followed a Liebig-like response to N. As a result, the quantity of N in the plant and grain was similar at optimum yield: 0.044 to 0.048 kg plant N kg^{-1} grain and 0.031 to 0.039 kg grain N kg^{-1} grain.

Changes in Nitrogen Use Efficiency with Increasing Yield Potential

Spring canola was less efficient at retaining, recovering, partitioning, and utilizing N as yield potential decreased with a lower water supply across sites and between years in eastern Washington. Seventeen to 76% of the reduction in yield under lower available water was attributed to a diminishing uptake efficiency (Nt/Ns) component, while 39 to 73% was associated with a lower utilization efficiency (Gw/Nt).

Multiple soil and plant processes can contribute to these inefficiencies in N uptake and utilization. As water became more limiting, the available N retention efficiency and available N uptake efficiency subcomponents decreased. Furthermore, the yield response to soil N supply was relatively greater with increasing available water (i.e., greater c value in the Mitscherlich-like response), whereas the yield response to available N was relatively lower (i.e., lower c value in the Mitscherlich–Liebig-like response). Therefore, the data suggest that more N supply was accessible with a greater water supply, which seems counterintuitive because leaching losses are generally associated with higher available water (Pan et al., 2007). Possible explanations include (i) a decrease in effective rooting depth, (ii) an overestimation of net N mineralization, and/or (iii) enhanced NH_4^+ fixation under lower available water. First, canola's root system has a high surface area characterized by long root hairs, which plays an important role in nutrient acquisition in water-limited soils (Hammac et al., 2011), and the extensiveness of the canola root system correlates with genotypic variation in NUE (Zhang et al., 2010). Second, net N mineralization was embedded in the estimate of soil N supply, which was similar among the various levels of water supply. However, in laboratory incubations, Maaz (2014) found that the net N mineralization potential was greater in the top 15 cm of soil collected at Pullman than Davenport, which was significantly correlated with volumetric soil water content. Third, NH_4^+ fixation may reduce the excess of added N fertilizer, which may be enhanced in dry soils (Nieder et al., 2011).

The majority of the yield differences were attributed to the N utilization efficiency, and specifically the grain N utilization efficiency (Gw/Ng) component, which accounted for as much as 54% of the yield reduction under greater water stress. Grain N utilization efficiency is the inverse of grain N concentration (Ng/Gw), which increased significantly with decreasing water availability. Drought stress has been linked to a reduction in the grain filling period (Gooding et al., 2003; Kiliç and Yağbasanlar, 2010) and duration of flowering, resulting in high protein content (Gooding et al., 2003). Hocking et al. (2002) observed greater N concentration in canola seeds at a warmer, drier site (430 mm) than a cooler, wetter location (540 mm). Moisture stress during canola flowering or seed set may result in a decrease in oil percentage coupled with an increase in protein (Champolivier and Merrien, 1996; Bouchereau et al., 1996; Brennan et al., 2000; Mingeau, 1974). Despite a greater N concentration in seeds, less N accumulated in the canola grain as the available water supply became more limiting, highlighting uptake limitations in the quantity of N recovered. This finding is in agreement with Hocking et al. (1997a, 2002), who reported greater grain N accumulation as the yield potential increased. Our results indicate that the selection of *Brassica* species exhibiting high nutrient acquisition patterns, early and prolonged flowering, post-anthesis drought tolerance, and yield stability are important factors in adaptable oilseed crops (Gan et al., 2008).

Changes in Nitrogen Use Efficiency with Increasing Nitrogen Supply

Under N-limiting conditions, a high proportion (76%) of yield differences between Pullman and Davenport was attributed to N uptake efficiency. Various environmental processes affect the supply of N and its retention. Dry spring conditions may leave soil N "stranded" as root activity near the surface is impaired, thus restricting available N uptake. With impaired root activity, the retention of N located lower in the profile may be reduced.

At economically optimum N supplies, similar proportions of yield differences were attributed to the N uptake (39–44%) and N utilization (55–56%) components. However, as N fertilization became excessive, the majority of yield differences were attributed to N utilization efficiency. Although fertilization resulted in greater amounts of unaccounted for N and residual N at harvest, particularly under lower available water, plant physiological processes became increasingly influential on yield differences with increasing fertilization.

Post-anthesis N uptake and mobilization from leaves and taproot to grain are emphasized as determinants of overall N use efficiency (Malagoli et al., 2005). Genotypic variation in N efficiency at flowering is not necessarily indicative of efficiencies observed at maturity (Balint and Rengel, 2008). This is due to variability in N mobilization and N uptake during grain filling during source–sink competition between grain and roots, whereby a high grain sink demand in prolific maize (*Zea mays* L.) was demonstrated to curtail post-anthesis N uptake and increase N mobilization from vegetative plant parts (Pan et al., 1995). Source–sink competition coupled with N source limitations were shown to advance leaf senescence. The mobilization of N from canola leaves and stems is crucial during pod development (Papantoniou et al., 2013), accounting for >50% of the seed N at maturity (Hocking et al., 1997b), and mid-season leaf senescence and abscission limit the mobilization of vegetative N to developing grain (Malagoli et al., 2005). These mechanisms may explain the reduction in the N harvest index with excessive fertilization and limitations on water availability. Between 9 and 35% of yield differences was attributed to the N harvest index (Ng/Nt) subcomponent, or source N limitations, which became more prominent under excessive fertilization.

The results further highlight the importance of environmental stress during flowering and grain filling under increasing N supply. The reduction in N utilization efficiency with less available water, coupled with excessive fertilization, was mostly attributable to the grain N utilization efficiency (Gw/Ng) subcomponent. A reduction in grain N utilization has been previous linked to shortened flowering and grain filling periods due to water stress (Champolivier and Merrien, 1996; Bouchereau et al., 1996; Brennan et al., 2000; Mingeau, 1974), which became increasingly apparent at excessive levels of fertilization.

A greater amount of N accumulated in canola grain with fertilization, in agreement with Hocking et al. (1997a, 2002). Differences in canola N partitioning contributed to <29% of the differences in grain N accumulation, which increased with excessive fertilization. However, most differences in grain N accumulation were attributed to the N uptake efficiency components, which also increased with fertilization. Therefore, with increasing fertilization and water supply, spring canola was not only more efficient at utilizing grain N to produce grain but was also more efficient at accumulating grain N from the N supply.

CONCLUSION

Nitrogen use efficiency estimates are useful for (i) establishing yield-based N recommendations and (ii) characterizing a system's productivity efficiency. In the Mediterranean-like climate of the inland Pacific Northwest, spring canola becomes more efficient at using N as yield potential increases. Available water is a major determinant of yield potential in this environment, which leads to higher grain yield (Gw), grain N (Ng), N supply (Ns), available N supply (Nav), and plant N (Nt). The NUE component analysis indicates that differences in water-limited yields were associated with N uptake and utilization efficiencies. The majority of the yield differences were attributed to grain N utilization efficiency (Gw/Ng) component, while most grain N differences were attributed to N uptake efficiency (Nt/Ns). By increasing the available water supply and fertilization, spring canola was more efficient at accumulating grain N and utilizing grain N from the N supply. Therefore, we recommend that canola cultivars should be screened for high water use efficiency, N utilization efficiency, and grain N accumulation in environments with water limitations. Furthermore, soil and residue management strategies that improve soil water availability and crop water use efficiency will probably improve NUE and reduce UNRs by enhancing N uptake efficiency in these semiarid production systems.

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