HAYING-OFF IN WHEAT: ENDURING MYTH OR CURRENT PROBLEM?

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Summary. Nitrogen (N) fertiliser applied to wheat growing at three sites in southern NSW produced contrasting yield responses, ranging from a large positive response to a large negative response. In all cases additional N led to increased tillering and greater biomass at anthesis. However, at each site, water soluble carbohydrate reserves (WSC) at anthesis were negatively correlated with anthesis biomass. This finding contrasts with previous studies which estimated greater remobilisable reserves with greater biomass. In the absence of post-anthesis water stress, grain yield increased with additional N while remobilisation of WSC and protein did not change. When there was severe post-anthesis water stress, additional N led to reduced yields accompanied by reduced remobilisation of WSC and protein. A model for haying-off in wheat is presented which takes account of WSC, N status and post-anthesis water stress.

INTRODUCTION

Most generally, haying-off is regarded as the phenomenon in which cereal crops fail to yield grain in accordance with their vegetative potentia*l* (16). Early research attributed the negative yield response to exhaustion of soil water by the vigorous vegetative growth stimulated by high soil nitrogen levels (15). Haying-off is also induced by the use of nitrogen (N) fertiliser (2, 11, 15). The belief that water stress is an essential factor contributing to haying-off has persisted (14). However, studies in the field (15) and controlled environments (9) showed reductions in kernel weight with the addition of N fertiliser in the absence of grain filling water stress. Clearly factors in addition to water stress are also involved in haying-off (8).

The aim of the field experiments presented in this paper was to determine the physiological responses to increasing soil mineral N which contribute to, or predispose a wheat crop to, haying-off. The study is based on field experiments at sites with contrasting mean temperatures, evaporative demand and water-stress conditions during grain filling.

MATERIALS AND METHODS

Experiments were sown at three sites in late May or June of 1991 at CSIRO Experiment Station, Ginninderra, ACT, at *Harmon's Tank*, Pucawan, NSW and at Charles Sturt University, Wagga Wagga, NSW. The experimental sites followed a breakcrop (3) to minimise the detrimental effects of soil-borne disease on N response (11). All experiments were 4-replicate, randomised complete block designs. Nitrogen fertiliser as urea (46% N) was topdressed at sowing or late tillering. Time of N application had minimal impact on yield and N uptake, so data for the two application times were combined for each level of N.

At anthesis, quadrats were harvested at the soil surface to estimate total above-ground dry matter production (biomass). Samples were counted for fertile shoots, oven dried at 70?C and ground in a Wiley mill to pass a 1-mm sieve. These subsamples were used to determine WSC levels (7). N concentration was determined using a semi-micro-Kjeldahl method. At physiological maturity ten random grab samples were taken from each plot to estimate harvest index, and quadrats, as at anthesis, were harvested to calculate biomass at maturity. Grain yield was calculated from a machine harvest. Harvest index samples were separated into spikes and straw, oven dried at 70?C and weighed. Spikes were threshed, and the glumes, awns and rachis put with the straw, the grain redried at 70?C and weighed. Kernel weight was calculated from the mean weight of 3 lots of 100 kernels. Grain was ground using a Cyclotec mill with an 0.5 mm sieve and the non-grain dry matter ground in a Wiley mill to pass a 1-mm sieve. WSC remaining in the non-grain biomass were also estimated. N concentration in the grain and non-grain biomass was analysed by near infrared reflectance spectroscopy using locally determined calibrations.

RESULTS AND DISCUSSION

Maximum and minimum temperatures were comparable between Wagga Wagga and Pucawan while Ginninderra was the coldest. April to December rainfall was below the mean at Pucawan and Wagga Wagga. The proportion of sowing to maturity rain which fell after anthesis was 23% at Ginninderra, 13% at Pucawan and only 7% at Wagga Wagga. In the present study, greater biomass production to anthesis resulted in vastly different grain yield responses at the three sites (Table 1).

Table 1. Effect of N fertiliser on the growth, water soluble carbohydrate (WSC) and grain yield of wheat at sites in southern NSW and ACT.

	Anthesis			Maturity			
N rate	Biomass	Spike density	WSC	Biomass	WSC	Grain yield	Kernel weight
(kgN/ha)	(g/m^2)	(g/m^2)	(g/m^2)	(g/m^2)	(g/m^2)	(g/m^2)	(mg)
Ginninderra (15.6.91, Janz)[a]							
0	989	515	244	1366	31	607	40.1
40	1089	603	222	1578	25	723	39.1
80	1167	627	227	1615	25	729	37.7
120	1134	606	210	1619	19	765	36.8
160	1166	633	204	1683	15	781	37.4
200	1197	646	181	1670	15	777	36.3
240	1190	644	172	1676	13	798	37.1
(l.s.d., P = 0.05)	97	70	20	131	9	78	1.6
Pucawan (19.6.91, Janz)							

0	653	372	122	995	34	420	34.2
40	-	-	-	1052	-	446	31.4
80	787	459	96	1074	17	458	29.3
120	836	485	98	1097	16	463	27.4
160	-	-	-	1084	-	444	25.9
200	843	525	86	1069	15	432	25.4
(l.s.d., P = 0.05)	58	43	13	ns	4	22	1.9
			Wagga Wagga (25.5.91, Matong)				
0	984	377	214	1086	20	374	28.6
40	-	-	-	1158	-	366	24.4
80	1075	421	167	1148	20	345	22.2
120	1092	416	151	1163	18	328	20.9
160	-	-	-	1132	-	283	17.6
200	1097	420	123	1106	18	284	17.6
(l.s.d., P = 0.05)	ns	31	21	ns	ns	30	1.9

[a] Sowing date and variety.

At Ginninderra the yield response to N was positive with decreasing returns of yield to applied N. At Pucawan, the yield response was positive to low rates of N but negative at high rates. At Wagga Wagga addition of N led to reduced yield. At all sites grain-yield responses to N fertiliser were associated with increased spike density and more kernels per square metre. However, kernel weight fell in response to N at all sites, varying from an 8% decrease at Ginninderra to 39% at Wagga Wagga. Harvest index increased by 9% at Ginninderra, but decreased by 5% at Pucawan and by 25% at Wagga Wagga (data not shown).

Although additional N promoted leaf area development (data not shown) and hence the photosynthetic potential, the amount of WSC in the crop at anthesis fell with increasing N (Table 1). This reduction in WSC with increased biomass is most likely due to assimilates being used to a greater extent for structural materials (13) and increased respiration rates due to higher N concentration (1). Mean WSC reserves at anthesis over the three sites decreased from 13.5 mgWSC/kernel for the control treatment to 6.5 mgWSC/kernel for the highest rate of N.

Retranslocation from the non-grain biomass to grain was estimated by two methods. The simpler, termed *apparent retranslocation*, assumes weight loss between anthesis and maturity equates with retranslocation (10). This method takes no account of leaf fall (4) or saprophytic decay of lower leaves (6) during grainfilling, and is therefore prone to overestimating the pre-anthesis contribution to grain yield. However, in the absence of water stress, continued growth of the stem after anthesis (7) and cell-wall thickening and lignification (12) can lead to an increase in structural biomass thereby reducing apparent retranslocation. A more complete estimate, termed *estimated retranslocation*, is the decrease in WSC and protein in the non-grain biomass between anthesis and maturity. This calculation assumes that once laid down WSC is not turned over (18) and that post-anthesis respiration is supplied by current rather than stored assimilates (5). Both estimates of retranslocation are presented in Table 2.

Table 2. Comparison between apparent and estimated retranslocation (g/m^2) to the grain from non-grain biomass.

Rate of N	Apparent retranslocation	Estimated retranslocation		
(kg N/ha)		WSC	Protein	Total
		Ginninderra		
0	230	214	53	267
240	312	159	113	272
		Pucawan		
0	78	88	28	116
200	206	71	68	139
		Wagga Wagga		
0	272	194	36	230
200	275	105	55	160

Apparent retranslocation increased in response to N with moderate or no post-anthesis water stress, while under severe water stress at Wagga Wagga it remained constant. In contrast, estimated retranslocation remained relatively constant at Ginninderra and Pucawan in response to N but decreased in association with haying-off at Wagga Wagga.

CONCLUSIONS

The results of these experiments lead to an improved model of the development of haying-off. Firstly, high N status leads to decreased WSC reserves at anthesis. Provided there is little or no water stress, a high N crop can then fill grain from current photosynthesis and call on WSC reserves during the periods of peak assimilate demand. However, in the event of water stress, reduced current photosynthesis and the lack of WSC reserves leads to haying-off. A low N crop does not face the same water stress due to lower anthesis biomass and is able to achieve a higher yield through greater current photosynthesis and its greater reserves of pre-anthesis WSC.

This model also accounts for high levels of WSC in low plant density canopies in the accompanying poster (17). It proposes that the worse reputation for haying-off by tall varieties is explained by low pre-anthesis reserves of WSC due to the greater assimilate demand by larger stems. It also leads to speculation that while haying-off is a problem in the closed-canopy crops of the south-eastern wheatbelt, it is not recognised as a problem in the north-eastern or Western wheatbelt where the open-canopy crops are likely to contain higher levels of pre-anthesis stored WSC.

In the south-eastern wheatbelt, haying-off is likely to be a continuing problem when crops of a high N status reach anthesis with low levels of soluble carbohydrate and subsequently encounter water stress. The problem could be reduced by breeding low-tillering cultivars which would not produce excessively large biomass with low reserves of WSC when grown at high N status. A fine balance would need to be maintained so that yield potential is not sacrificed when water supply is adequate.

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