Agricultural and Forest Meteorology, 44 (1988) 151-157
Elsevier Science Publishers B.V., Amsterdam — Printed in The Netherlands

SEASONAL PATTERNS OF WINTER WHEAT PHYTOMASS AS AFFECTED BY WATER AND NITROGEN ON THE NORTH AMERICAN GREAT PLAINS*

D.J.MAJOR, B.L. BLAD, A. BAUER, J.L. HATFIELD, K.G. HUBBARD, E.T. KANEMASU and R.J. REGINATO

Research Station, P.O. Box 3000 Main, Lethbridge, Alberta T1J 4B1 (Canada)

(Received October 2, 1987; revision accepted March 10, 1988)

ABSTRACT

Major, D.J., Blad, B.L., Bauer, A., Hatfield, J.L., Hubbard, K.G., Kanemasu, E.T. and Reginato, R.J., 1988. Seasonal patterns of winter wheat phytomass as affected by water and nitrogen on the North American Great Plains. Agric. For. Meteorol., 44: 151-157.

Seasonal phytomass of winter wheat was studied at 5 locations on the North American Great Plains to assess differences in productivity at 3 soil water and 4 nitrogen levels. The average temperature at the time of rapid production of whole-plant phytomass was 11 °C and varied from 6 to 14 °C. Subsequently, temperature regimes at the 5 locations were similar, even though they occurred at different times of the year. Growth rates varied among locations and durations varied between years. At the three most southerly locations, maximum whole-plant phytomass occurred shortly after the onset of rapid grain filling, whereas at the two northern locations maximum whole-plant phytomass occurred at, or shortly before, maximum grain dry weight. The reason for this phenomenon was apparently a much greater production of vegetative tissue at the southern locations. Whole-plant and grain growth rates under rainfed conditions were 70 and 62% of the irrigated values, respectively. The daily growth rate of spikes was equal to the whole-plant growth rate in the irrigated/high N treatments. Duration of growth was reduced only by 3 days under rainfed/low N conditions for both whole-plant and head phytomass.

INTRODUCTION

The rate and duration of the vegetative and grain-filling phases of winter wheat are important to the understanding of the formation of grain yield (Gebeyehou et al., 1982a) and separation of the environmental and genetic influences on these characters is necessary before breeders can make progress in

*Funding for this study was provided by the Agricultural Research Service, U.S. Department of Agriculture, Kansas State University Agricultural Experiment Station, University of Nebraska Agricultural Experiment Station, Agriculture Canada, and the National Science Foundation, Grant Number ATM-8417995.

selecting for improved genotypes. Peterman et al. (1985) expressed spikelet initiation in terms of the product of spikelets per day, times the number of days of spikelet initiation. They found genetic variation in both characters and suggested that breeders could improve wheat spike type by breeding for these characteristics. Similarly, Nass and Reiser (1975) expressed grain filling in terms of rate of increase of grain per day and duration of grain filling. They found genetic variation in the rate of grain filling of wheat but not in the duration. Gebeyehou et al. (1982b) found variation among cultivars for both rate and duration of grain filling and a positive association of both with final yield.

Previous studies have suggested that limited nitrogen (N) and/or water, reduces the rate and possibly the duration of grain filling of wheat (Austin et al., 1977; Brocklehurst et al., 1978). Usually there is a leveling off of whole-plant phytomass after the rapid growth phase (e.g., Rickman et al., 1975) but sometimes there is a loss of whole-plant dry matter prior to the cessation of maximum grain weight (Boatwright and Haas, 1961; Daigger et al., 1976). The reasons for this drop-off and how it influences yield are not known.

The objective of this study was to compare rates and duration of whole-plant and grain growth of winter wheat, grown at different N and soil water levels, throughout the north–south limits of winter wheat production on the North American Great Plains (Reginato et al., 1988). An additional objective was to compare the dates of resumption of the rapid growth phase as affected by latitude.

MATERIALS AND METHODS

Weekly estimates of leaves, stems and heads were available for various combinations of nitrogen (N) and irrigation levels and for 2 cultivars at 5 locations (Reginato et al., 1988). Because of the labor requirement for plant sampling, locations were chosen on the basis of treatments, selecting those that were likely to produce the greatest differences. The sampling methods were identical at each location. Data were collected on the number of live tillers per plant, dry weight of green leaves, dead leaves, stems and heads, and the area of green leaves and flag leaves. In this report, only 'Colt' was considered since it was grown at all locations. Also, only two combinations of water and N were studied: rainfed, W1, combined with nitrogen level N1 or N2, depending on availability of sampling data; and irrigated, W3, combined with nitrogen level N3.

Estimates of plant population density were used to convert individual plant phytomass measurements into phytomass expressed in g m^{-2} of ground surface. Because the date of emergence varied among locations, stand counts were calibrated with the final grain-yield data reported by Major et al. (1988). The ratio of maximum head weight divided by final grain yield was used to adjust population densities for the water treatments at each location.

The date of the commencement of rapid growth was determined as the X-

intercept of the regression of the whole-plant phytomass vs. day of the year. The average temperature at this date was determined by running a regression of mean daily air temperature vs. day of the year minus the X-intercept for a 4-week period on either side of the X-intercept.

The rates of whole-plant and grain growth were calculated by regression analysis during the rapid dry-matter accumulation phase. Duration was determined by dividing maximum dry weight by the rate of growth. Differences among locations were assessed by using a general linear-regression model that allowed comparisons among year–location combinations.

RESULTS AND DISCUSSION

Good fit was obtained for whole-plant phytomass vs. date of sampling. Hence, the start-up date was subsequently subtracted from the sample dates so that location effects could be more readily detected. As expected, the date of resumption of growth was delayed as latitude increased (Table 1) except for Manhattan in 1985, where rapid growth occurred earlier than Lubbock. The intercept of temperature vs. days regression represented an estimate of average temperature on the date of the start of rapid growth. Differences were small, except for the case of Manhattan which had a very low intercept (Table 1). The mean temperature for signaling the onset of rapid growth was 11.1 °C. It must be emphasized that this temperature was not a base temperature for growth but was a temperature consistent with the end of the lag phase and the start of the rapid growth phase. The rate of increase in temperature during this 8-week period showed no latitudinal trends. This can be seen by the fact that Lethbridge in 1985 had a low rate of increase in temperature but in 1986 it had a high rate. From these values we concluded that, while the temperature regimes at these 5 locations showed considerable year-to-year variability, they were generally similar. Consequently, winter wheat would have similar thermal conditions for growth at any of these locations. The main differences, therefore, would be in soil water availability, fertility and in the photoperiod–solar radiation levels.

In most instances, leaf mass represented no more than about 10% of the total phytomass (data not shown). At all locations, leaf mass declined 40–50 days after the start of rapid growth. The peak in leaf area was generally coincident with the start of rapid grain filling. In previous studies, it has been suggested that leaf senescence may be required in order to meet the kernel requirements for N. The theory is that as seed becomes a strong sink for carbohydrates, less photosynthate is available to roots for the uptake of N. In order to meet the kernel's need for N, leaf N has to be mobilized and as a consequence leaves senesce. Van Sanford and MacKown (1987) reported that as much as 50–90% of kernel N was the result of remobilization of leaf N.

Of special interest in this study was the fact that at the southern locations

TABLE 1

Date of start of whole-plant growth, the intercept and regression coefficients for the relationship between mean daily air temperature and days 4 weeks before and 4 weeks after the start of growth, growth rates, maximum whole-plant phytomass and effective whole-plant duration of winter wheat grown under rainfed (W1) and irrigation (W3) at 5 locations on the Great Plains in 1985 and 1986

Location	Year	Start of growth (DOY)	Intercept (°C)	Daily increase (°C day^{-1})	Growth rate (g m^{-2} day^{-1})		Maximum phytomass (g m^{-2})		Duration (days)	
					W1	W3	W1	W3	W1	W3
Lubbock	1985	73	11.9bc[a]	0.123b	6.00g	10.64c-g	484	832	81	78
	1986	80	14.9a	0.107b	5.08g	10.12d-g	221	561	44	55
Manhattan	1985	70	5.7d	0.185b	13.72b-f	15.45bcd	993	1089	72	70
Tryon	1986	121	11.2bc	0.151b	15.80bcd	16.55abc	852	884	54	53
Mandan	1985	129	10.5c	0.339a	7.33fg	7.47fg	499	537	68	72
	1986	139	13.3ab	0.224ab	8.94efg	17.36ab	504	933	56	54
Lethbridge	1985	132	11.3bc	0.142b	6.83g	10.26c-g	510	783	75	76
	1986	126	9.6c	0.328a	8.74efg	15.04b-e	479	945	55	63
Mean			11.1	0.200	9.06	12.86	568	821	63	65

[a]Within temperature intercepts, temperature increase coefficients or within growth rates, values followed by the same letter did not differ at the $P = 0.05$ probability level.

stem mass declined before maximum whole-plant phytomass had been reached. This decline occurred after leaf senescence had begun. There was more leaf and stem mass at the more southerly locations than at the Lethbridge or Mandan sites. The selection of W3 at Tryon and Lethbridge in 1986 was chosen for demonstration because both had maximum whole plant phytomass of about 1000 gm^{-2} (Fig. 1). The sum of the leaves and stems at Tryon was about 600 g m^{-2} whereas it only reached about 400 g m^{-2} at Lethbridge. After grain filling began, the leaves and stems senesced at Tryon so that, by the end of grain filling, the total amount of stems and leaves was comparable with that at Lethbridge. This was also observed in both years at the other locations; Mandan was similar to Lethbridge, and Manhattan and Lubbock were similar to Tryon. The low water and N treatment was similar at both locations although the maximum phytomass was lower. As a result of this situation, maximum whole-plant phytomass occurred early in the grain-filling phase for the southern locations and at the end of the growing season at Mandan and Lethbridge.

The phytomass curves vs. time were required for determining the rate and effective duration of whole-plant growth and grain-filling. The growth rates were determined by visual selection of the rapid period of growth of whole plants and heads and then by linear regression analyses. The durations were calculated by dividing maximum whole-plant phytomass and head mass by whole-plant and head growth rates, respectively. The results were variable, no doubt owing to variable reactions to water stress vs. irrigation, but also to random variability in the data, making accurate estimates of rates and durations difficult. Also, the rate of growth, effective duration and maximum yield are

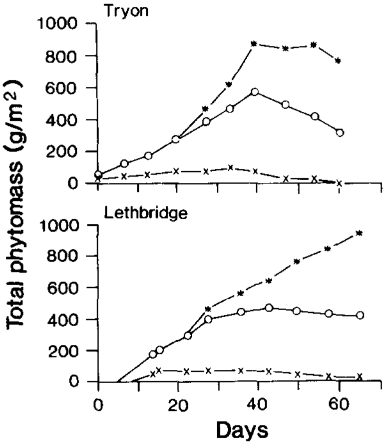

Fig. 1. Seasonal trajectory of total phytomass of 'Colt' leaves (×- -×), stems plus leaves (o- -o) and leaves plus stems plus heads (*- -*) grown under irrigation with high soil N at Tryon and Lethbridge, both in 1986, plotted against days summed from the X-intercept of a linear regression of whole-plant phytomass versus calendar days.

all related. Given a yield level, if the rate is slow then the duration will be long. In spite of these difficulties, the results indicated that the rainfed treatment, W1, had lower growth rate than the irrigation treatment, W3 (Tables 1 and 2) demonstrating that the effectiveness of irrigation with high N comes from more phytomass per unit area.

The effective duration was also longer for W3 for whole-plant phytomass and grain yield but the difference averaged over all locations was only 3 days. The rainfed effective durations averaged over locations were very similar to those reported for rainfed wheat at Lethbridge (Major and Hamman, 1981). Whole-plant growth rate of W1 was about 70% of W3 averaged over locations and 62% for grain yield. Also, the growth rates, averaged over locations, were similar for the irrigated treatment for whole-plant (12.9 g m^{-2} day^{-1}) and grain (12.3 g m^{-2} day^{-1}) growth. Major and Hamman (1981) also found that whole-plant and grain growth rates were similar and agreed with Thorne's (1965) conclusion that there was no evidence to suggest that there was retranslocation of carbohydrates from vegetative tissues to the grain in cereals. That is, all grain growth came from current photosynthesis. This conclusion means that it is critical that photosynthetic tissue be maintained in wheat, in order that photosynthates are available for grain filling. The grain growth rate for W1 was lower than that for whole-plant growth rate. This difference can be best explained by the fact that grain growth occurred at the end of the season when water stress was most severe.

The difference between years for the irrigated and rainfed treatments was mainly in the duration of grain filling. Excluding Manhattan, the average grain-

TABLE 2

Start of grain filling in days from start of whole-plant growth, rate of grain filling, final grain yield, effective filling period duration of winter wheat grown under rainfed (W1) and irrigation (W3) at 5 locations on the Great Plains in 1985 and 1986

Location	Year	Start (days)		Growth rate (g m^{-2} day^{-1})		Final grain yield (g m^{-2})		Duration (days)	
		W1	W3	W1	W3	W1	W3	W1	W3
Lubbock	1985	40	47	10.50	20.62	233	399	22	19
	1986	21	28	3.31	9.84	94	223	28	23
Manhattan	1985	37	34	5.67	5.24	242	271	43	52
Tryon	1985	13	14	7.74	10.73	276	395	36	37
	1986	19	22	11.50	14.51	164	226	14	16
Mandan	1985	38	42	7.05	7.51	145	324	21	43
	1986	22	22	8.25	12.82	186	390	23	30
Lethbridge	1985	39	41	7.91	14.63	251	500	32	34
	1986	23	28	6.10	14.46	244	506	40	35
Mean		28	31	7.56	12.26	204	359	29	32

filling duration in 1985 was 28 and 33 days for W1 and W3, respectively, a difference of 6 days. In 1986, the comparable values were both 26 days. For rate of grain filling, the 1985 values were 8.3 and 13.4 g m^{-2} day^{-1} for W1 and W3, a difference of 5 g m^2 day^{-1}. In 1986, the comparable values were 7.3 and 12.9 g m^{-2} day^{-1}, still only a difference of 5.6 g m^{-2} day^{-1} and only about1 g m^{-2} day^{-1} less than in 1985. Thus it would appear that the extra yield for W3 in 1985 came primarily from a longer duration.

In summary, winter wheat produced much more vegetative tissue at southern locations than in the northern latitudes in 1985 and 1986, but there was little difference in grain yield among the locations. Rapid growth began when mean air temperature was about 11°C. The effect of irrigation on increased yield was mainly owing to increased rate of growth, whereas the effective duration of whole-plant or grain growth was only extended slightly by irrigation. Rainfed growth rates were 60–70% of irrigated growth rates, which was sufficient to account for most of the differences in yield.

REFERENCES

Austin, R.B., Ford, M.A., Edrich, J.A. and Blackwell, R.D., 1977. The nitrogen economy of winter wheat. J. Agric. Sci. Camb., 88: 159-167.

Boatwright, G.O. and Haas, H.J., 1961. Development and composition of spring wheat as influenced by nitrogen and phosphorus fertilization. Agron. J., 53: 33-36.

Brocklehurst, P.A., Moss, J.P. and Williams, W., 1978. Effects of irradiance and water supply on grain development in wheat. Ann. Appl. Biol., 90: 265-276.

Daigger, L.A., Sander, D.H. and Peterson, G.A., 1976. Nitrogen content of winter wheat during growth and maturation. Agron. J., 68: 815-818.

Gebeyehou, G., Knott, D.R. and Baker, R.J., 1982a. Relationships among durations of vegetative and grain filling phases, yield components, and grain yield in durum wheat cultivars. Crop Sci., 22: 287-290.

Gebeyehou, G., Knott, D.R. and Baker, R.J., 1982b. Rate and duration of grain filling in durum wheat cultivars. Crop Sci., 22: 337-340.

Major, D.J. and Hamman, W.M., 1981. Comparison of sorghum with wheat and barley grown on dryland. Can. J. Plant Sci., 61: 37-43.

Major, D.J., Blad, B.L., Bauer, A., Hatfield, J.L., Hubbard, K.G., Kanemasu, E.T. and Reginato, R.J., 1988. Winter wheat grain yield response to water and nitrogen on the North American Great Plains. Agric. For. Meteorol., 44: 141-149.

Nass, H.G. and Reiser, B., 1975. Grain filling period and grain yield relationships in spring wheat. Can. J. Plant Sci., 55: 673-678.

Peterman, C.J., Sears, R.G. and Kanemasu, E.T., 1985. Rate and duration of spikelet initiation in 10 winter wheat cultivars. Crop Sci., 25: 221-225.

Reginato, R.J., Hatfield, J.L., Bauer, A., Hubbard, K.G., Blad, B.L., Verma, S.B., Kanemasu, E.T. and Major, D.J., 1988. Winter wheat response to water and nitrogen in the North American Great Plains. Agric. For. Meteorol., 44: 105-116.

Rickman, R.W., Ramig, R.E. and Allmaras, R.R., 1975. Modeling dry matter accumulation in dryland winter wheat. Agron. J., 67: 283-289.

Thorne, G.N., 1965. Photosynthesis of ears and flag leaves of wheat and barley. Ann. Bot. N.S., 29: 317-329.

Van Sanford, D.A. and MacKown, C.T., 1987. Cultivar differences in nitrogen remobilization during grain fill in soft red winter wheat. Crop Sci., 27: 295-300.