

Comparison of Growth and Grain Yield of Spring Wheat in Lhasa, the Tibetan Plateau, with those in Sapporo, Japan

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Abstract : The Tibetan Plateau is one of the highest cultivated regions in the world. The objective of the present study was to compare wheat growth and grain yield in the high altitude region with those in a low altitude region. Two spring wheat cultivars were grown for two years at an experimental field in Lhasa (29°N, 3688 m above sea level) in the Tibetan Plateau in 2001 and 2003, and in Sapporo (43°N, 15 m above sea level), Japan in 2002 and 2003. In Lhasa, temperature throughout the growth period was lower and photoperiod before heading was shorter than in Sapporo. There was no significant difference in grain yield between Lhasa and Sapporo. Dry matter production was higher in Lhasa than in Sapporo. The crop growth rate before heading was similar in both locations, but the time to heading was 15 days longer in Lhasa than in Sapporo. Leaf senescence was more decelerated in Lhasa than in Sapporo. These results suggested that high dry matter production in Lhasa was mainly due to the longer growth period.

Key words : Dry matter production, Grain yield, Temperature, Tibetan Plateau, *Triticum aestivum* L., Wheat.

The Tibetan Plateau is one of the highest cultivated regions in the world. Cereals are cultivated mainly in the valley along the Yarlung Zangbo River, where the altitude is relatively low and irrigation systems are available (Lin et al., 2001; Luo et al., 2002). Although barley (*Hordeum vulgare* L.) is traditionally the most widely cultivated cereal in this region, wheat (*Triticum aestivum* L.) has been cultivated widely since the 1950s (Lin et al., 2001) and is the second important cereal today; its sown area and production in the Tibet Province, China, from 1996 to 2000 averages 53600 ha and 291000 t, respectively (Tibet Statistics Bureau, 2002).

The climate in high altitude regions differs greatly from that in low altitude regions at the same latitude. In Lhasa (29°N, 91°E, capital of Tibet Province), the total yearly solar radiation and yearly average air temperature are 7000-7800 MJ m⁻² and 7.9°C, respectively (Lin et al., 2001; National Astronomical Observatory, 2004). The corresponding values for total solar radiation and air temperature in low altitude regions at the same latitude are about 4198 MJ m⁻² (average of six locations) and 17.6°C (average of seven locations), respectively (Lin et al., 2001; National Astronomical Observatory, 2004).

Hokkaido, which is located in a lower altitude and higher latitude region compared with the Tibetan

Plateau, is the main cultivating area of wheat in Japan. Wheat sown area and production in Hokkaido from 1996 to 2000 averages 94500 ha and 332400 t, respectively (Statistics and Information Department, Ministry of Agriculture, Forestry and Fisheries, 2002). Climate condition especially solar radiation is different from that in the Tibetan Plateau. For example, in Sapporo (43°N, 141°E, capital of Hokkaido prefecture) the total yearly solar radiation and yearly average air temperature are 4376 MJ m⁻² (obtained from National Agricultural Research Center for Hokkaido Region) and 8.5°C (National Astronomical Observatory, 2004), respectively.

Higher solar radiation and lower air temperature in high altitude regions are favorable environmental conditions for crop production. High solar radiation generally increases the crop growth rate and results in high grain yields (Monteith, 1981). Low temperature is also a factor for high yields through prolonging growth duration and inhibiting the respiration rate (Wardlaw et al., 1980; Wardlaw and Wrigley, 1994). However, low CO₂ partial pressure at a high altitude, at about 65% in Lhasa relative to sea level, decreases the CO₂ concentration in mesophyll cells, resulting in a low leaf photosynthetic rate (Terashima et al., 1995). In rice, Ying et al. (1998) compared crop production at two altitudes (International Rice Research Institute (IRRI),

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Abbreviations : DAS, days after sowing; LAI, leaf area index; PPFD, photosynthetic photon flux density.

Table 1. Sowing date, sowing rate, fertilizer rate and number of replications for each experiment.

Location	Year	Sowing date	Sowing rate (seeds m ⁻²) [†]		Fertilizer rate (kg ha ⁻¹)						Number of replications
					At sowing [‡]			At heading			
					3u90	Haruyutaka	N	P ₂ O ₅	K ₂ O	N	
Lhasa	2001	4 May									2
	2003	20 Apr	550	600	40	18	11	35	6	4	3
Sapporo	2002	23 Apr									4
	2003	28 Apr	450	350	54	90	45	0	0	0	3

[†] Seeds were sown in rows 0.25 m apart in all experiments.

[‡] Sheep manure (10 t ha⁻¹) was applied at sowing in addition to chemical fertilizers in Lhasa.

Los Baños, 14°N, 21 m above sea level, Philippines and Taoyuan Township of Yunnan Province, 27°N, 1170 m above sea level, China). Total dry weight was significantly higher at the high altitude than at the low altitude because of longer growth duration and higher crop growth rate at the high altitude. They concluded that longer growth duration in Yunnan was due to lower temperature and longer photoperiod, and that greater leaf area index (LAI) rather than solar radiation in Yunnan was responsible for the higher crop growth rate. In wheat, there are few reports comparing crop production at high and low altitudes.

The present study aimed to compare growth and grain yields of wheat in Lhasa with those in Sapporo. Spring wheat was cultivated at an experimental field in Lhasa and Sapporo. One cultivar from each region was used as a representative of the major cultivars in each region.

Materials and Method

1. Plant materials and growth conditions

Spring wheat cultivars 3u90 and Haruyutaka were used. 3u90 was bred in Xingjiang Province, China, and is cultivated widely in the Tibetan Plateau. Haruyutaka was bred in Hokkaido, and is the main cultivar of spring wheat. Experiments were conducted in the fields at Lhasa Plateau Ecological Research Station (29°N, 91°E, 3688 m above sea level) of the Chinese Academy of Sciences in Lhasa in 2001 and 2003 and at the Experimental Farms of Field Science Center for Northern Biosphere, Hokkaido University (43°N, 141°E, 15 m above sea level) in Sapporo, Hokkaido in 2002 and 2003. Except for Lhasa in 2003 where only 3u90 was used, the two cultivars were examined each year. The soil was Fluvent with pH 7.4 and total nitrogen concentration of 0.05% at Lhasa (Smith et al., 1999), and Fluvent with pH 5.5 and total nitrogen concentration of 0.24% at Sapporo. Sowing dates, sowing rates and fertilizer rates followed the conventional practices in each experimental region (Table 1). Sowing rate was based on seed weight per unit area in Lhasa while it was based on seed number

per unit area and germination rate in Sapporo. Fertilizer was applied at sowing: 40, 18 and 11 kg ha⁻¹ of N, P₂O₅ and K₂O, respectively, and at heading: 35, 6 and 4 kg ha⁻¹ of N, P₂O₅ and K₂O, respectively, in Lhasa. Sheep manure was also applied at the rate of 10 t ha⁻¹ at sowing in Lhasa. In Sapporo, fertilizer was applied at sowing: 54, 90 and 45 kg ha⁻¹ of N, P₂O₅ and K₂O, respectively. Topdressing was not applied in Sapporo because it is not effective (Hokkaido Branch, Japanese Society of Soil Science and Plant Nutrition, 1987). The crops before heading were irrigated when needed in Lhasa. The experimental design in each location was a randomized complete block design with two to four replications. Each plot size varied with the location and year from 10.5 to 11.4 m² (11–13 rows × 3.5–4.2 m long).

2. Measurements

Meteorological data of temperature, precipitation and sunshine hours were obtained from each experimental institute, except for sunshine hours in Sapporo that were obtained from the Japan Meteorological Agency. Radiation was measured by using a radiation sensor IKS-37 (Koito, Japan) in Lhasa in 2003 and an MS-601 (EKO, Japan) in Sapporo in 2002 and 2003. The average temperature and precipitation for the last 20 years in Lhasa and for the last 30 years in Sapporo were obtained from “Chronological Scientific Tables 2005” (National Astronomical Observatory, 2004).

Heading was defined as the date when 70% of stems headed, except for 3u90 in Lhasa in 2003 where it was not recorded and was defined as the date when the accumulated thermal time with a base temperature of 0°C from sowing was 1050°C d, which was the accumulated thermal time from sowing to heading for 3u90 in 2001 in Lhasa. Chlorophyll concentration (SPAD value) of eight flag leaves for each plot was measured using a SPAD-502 (Konica Minolta Sensing, Japan) once a week from heading stage until SPAD values were not detected.

Plants from an area of 0.3 m² in each plot were

harvested to measure the leaf area and total above ground dry weight. The plants were harvested near the spikelet initiation stage, heading stage and one month after the heading stage in Lhasa in 2001, three times at two-week intervals after heading in Lhasa in 2003, and six to seven times at two-wk intervals after sowing in Sapporo in 2002 and 2003. Green leaf blades were separated and leaf area was measured using a leaf area

meter AM200 (ADC BioScientific, UK) in Lhasa in 2003 and AAM-7 (Hayashi Denko, Japan) in Sapporo in both years. In Lhasa in 2001, 200–500 samples were taken from green leaf blades with a leaf punch (8 or 10 mm in diameter) to determine the specific leaf area, and leaf area was calculated from specific leaf area and dry weight of leaf blade. Leaf blade and other parts were oven-dried at 80°C for 48 hours and weighed in all experiments and the total above ground dry weight was determined.

Plants from 1 m² in each plot were harvested for the final harvest at the ripening stage of each cultivar, except for 3u90 in Lhasa in 2003 where plants were harvested at the yellow ripe stage when the grain dry weight usually reaches its maximum. The grain dry weight was measured for 100 g fresh weight grain for each plot. The ratio of dry to fresh grain weight of the sample was used to calculate the grain yield. The total above-ground dry weight, and the numbers of ears and grains per unit area were also determined.

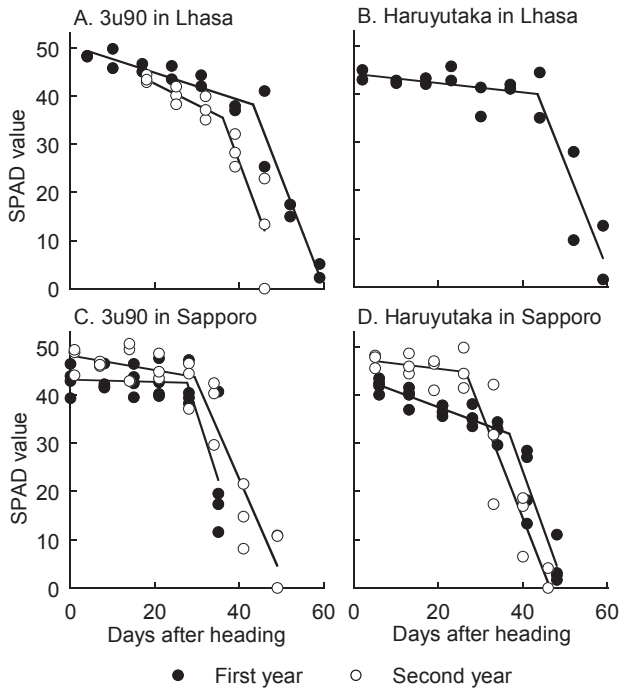


Fig. 1. Changes in chlorophyll contents (SPAD values) of flag leaves after heading in (A) 3u90 and (B) Haruyutaka in Lhasa, and (C) 3u90 and (D) Haruyutaka in Sapporo. Data of all replicates are shown. Two regression lines were fitted for each set of data.

3. Statistical analysis

The daily radiation in August in Lhasa and Sapporo was determined by using regression analysis for the daily sunshine hours, the location being treated as a dummy variable. The SPAD values showed a steady phase that was distinct from a rapid decline phase (Fig. 1), and so an analytical process based on bilinear regression analysis was used to identify the duration of the steady phase of SPAD values (Wilkinson et al., 1995). The SPAD values were fitted with two regression lines, and then the end of the steady phase was identified as the intersection of two lines. To test the differences between locations, we pooled data from all replicates and analyzed them using the independent two-sample *t*-test.

Table 2. Mean values (\pm standard error) of grain yield, total dry weight, harvest index and other yield components in Lhasa and Sapporo.

Location	Year	Cultivar	Grain yield (g m ⁻²)	Total dry weight (g m ⁻²)	Harvest index (%)	Ears per m ²	Grains per m ² ($\times 10^3$)	Grains per ear	Grain weight (mg)
Lhasa	2001	3u90	534 \pm 82	1932 \pm 180	28.3 \pm 6.9	536 \pm 93	15.5 \pm 0.8	30.2 \pm 6.8	34.4 \pm 3.6
		Haruyutaka	417 \pm 21	1368 \pm 357	33.2 \pm 10.2	808 \pm 27	14.4 \pm 0.1	18.2 \pm 1.0	28.9 \pm 1.3
	2003	3u90	360 \pm 63	1390 \pm 62	25.7 \pm 3.4	536 \pm 26	12.0 \pm 1.3	22.4 \pm 1.5	29.5 \pm 1.8
		Haruyutaka	406 \pm 8	1183 \pm 34	34.4 \pm 0.7	380 \pm 12	11.0 \pm 0.2	28.9 \pm 0.4	37.0 \pm 0.5
Sapporo	2002	3u90	411 \pm 11	991 \pm 27	41.5 \pm 0.1	472 \pm 15	12.2 \pm 0.4	26.0 \pm 0.4	33.6 \pm 0.2
		Haruyutaka	450 \pm 30	1192 \pm 82	37.8 \pm 0.3	346 \pm 16	12.1 \pm 0.8	34.9 \pm 0.7	37.2 \pm 0.3
	2003	3u90	432 \pm 10	1001 \pm 24	43.2 \pm 0.1	481 \pm 6	11.9 \pm 0.2	24.7 \pm 0.5	36.4 \pm 0.8
		Haruyutaka	411 \pm 11	991 \pm 27	41.5 \pm 0.1	472 \pm 15	12.2 \pm 0.4	26.0 \pm 0.4	33.6 \pm 0.2
Statistical effect									
Location	3u90	NS	**	**	***	NS	NS	**	
	Haruyutaka	NS	*	NS	***	**	***	**	

Statistical significance of location-effect for each cultivar is indicated as * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$) or NS (not significant).

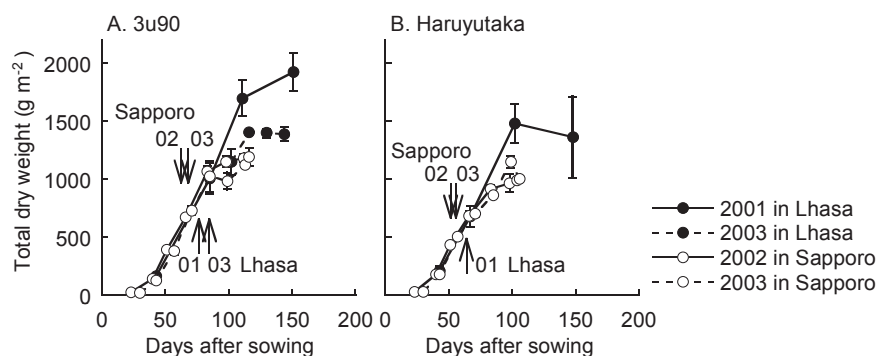


Fig. 2. Change in total dry weight during the cropping period in (A) 3u90 and (B) Haruyutaka. Bars indicate standard errors ($n=2-4$). Arrows indicate the heading date. 01, 02 and 03 in the figure mean 2001, 2002 and 2003, respectively.

Results

1. Growth and yield

There was no significant difference in grain yield between Lhasa and Sapporo in both cultivars (Table 2). The average grain yield in Lhasa and Sapporo was 437 and 425 g m^{-2} , respectively. Harvest index was lower in Lhasa than in Sapporo and the difference was significant for 3u90. The numbers of ears and grains per unit area were significantly higher in Lhasa than in Sapporo with the exception for grain number in 3u90. The number of grains per ear was significantly lower in Lhasa than in Sapporo in Haruyutaka but there was no significant difference in 3u90. Grain weight of both cultivars was significantly lower in Lhasa (30.9 mg on the average) than in Sapporo (36.1 mg on the average).

Total dry weight at harvest was significantly heavier in Lhasa than in Sapporo in both cultivars (Table 2). The average total dry weight at harvest was 1563 g m^{-2} in Lhasa and 1092 g m^{-2} in Sapporo. Fig. 2 shows the change of total dry weight during crop period. The difference in total dry weight between locations was small before 85 days after sowing (DAS) for 3u90 and before 70 DAS for Haruyutaka. Thereafter, the difference increased as the crops matured.

The maximum value of LAI during the crop period was around four for both cultivars in Lhasa and Sapporo (Fig. 3). LAI was higher than one at 110 DAS in Lhasa, but it was almost zero in Sapporo. SPAD values measured to identify leaf senescence were in the range of 40 to 50 at heading in all experiments (Fig. 1). After heading, two phases were characterized by distinct changes in SPAD value, i.e., a steady phase and a rapid decline phase. The duration of the steady phase, in average, was 41 days in Lhasa and 30 days in Sapporo. It was seven days longer in 2001 than in 2003 for 3u90 in Lhasa and was 10 days longer in 2002 than in 2003 for Haruyutaka in Sapporo.

The duration from sowing to heading and from

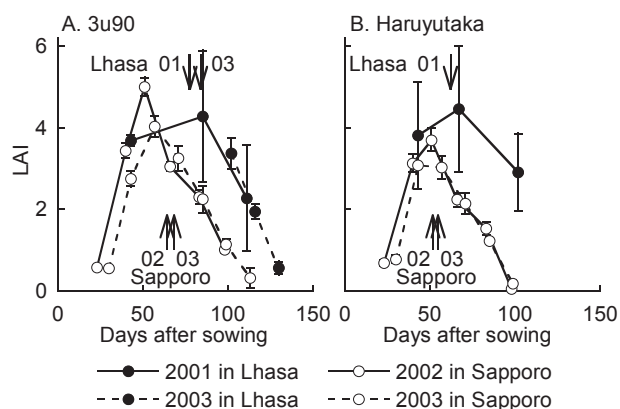


Fig. 3. Change in leaf area index (LAI) during the cropping period in (A) 3u90 and (B) Haruyutaka. Bars indicate standard errors ($n=2-4$). Arrows indicate the heading date. 01, 02 and 03 in the figure mean 2001, 2002 and 2003, respectively.

heading to maturity in Lhasa was 75 and 73 days in average, respectively (Table 3). These values were 15 and 23 days longer, respectively, compared with those in Sapporo. The growth duration from emergence to maturity was 148 days in Lhasa and that was 110 days in Sapporo. The growth duration differed between 2001 and 2003 by 7 days in Lhasa for 3u90 and the yearly difference was 2–4 days in Sapporo for both cultivars. The growth duration in Lhasa was 34 and 43 days longer on the average, than in Sapporo for 3u90 and Haruyutaka, respectively.

2. Climatic patterns

Fig. 4 shows temperature profiles in all experiments. On the average of the two years, the mean temperature during the cropping season (May to September in Lhasa and May to August in Sapporo) was 3.0°C lower in Lhasa (14.1°C) than in Sapporo (17.1°C). In Lhasa, the temperature increased during one month after sowing and then was stable toward harvest. In Sapporo, it continued to increase from sowing to

Table 3. Mean value (\pm standard error) of phenological characters in Lhasa and Sapporo.

Location	Year	Cultivar	Duration (days)		
			Sowing to heading	Heading to maturity	Sowing to maturity
Lhasa	2001	3u90	77 \pm 3.5	74	151
		Haruyutaka	64 \pm 2.0	84	148
	2003	3u90	84 [†]	60 [†]	144
Sapporo	2002	3u90	65 \pm 1.1	47	112
		Haruyutaka	52 \pm 0.3	52	104
	2003	3u90	67 \pm 0.3	49	116
		Haruyutaka	55 \pm 0.6	51	106
Statistical effect					
	Location	3u90	**	-	-
		Haruyutaka	***	-	-

Statistical significance of location-effect for each cultivar is indicated as ** ($P < 0.01$) or *** ($P < 0.001$).

[†] Heading was calculated using thermal time with a base temperature of 0°C from sowing.

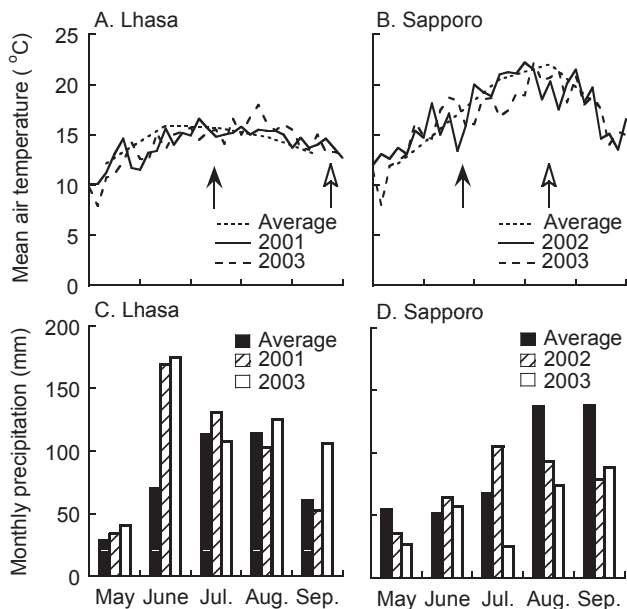


Fig. 4. Mean air temperature in (A) Lhasa and (B) Sapporo, and monthly precipitation in (C) Lhasa and (D) Sapporo from May to September. Mean air temperatures are shown as 5 d averages for this study and one-month average for the average values. Black and white arrows indicate heading date and maturity date, respectively, as the average for all experiments at each location.

harvest. The difference between locations was small during one month after sowing, and then increased as the crops matured. The monthly average temperature through the cropping season in Lhasa was less variable 11.4–15.7°C, and it was 12.8–20.2°C in Sapporo. In comparison with the average values, the temperature in Lhasa were 1.8–1.9°C lower during June in 2001 and 2003 and were 1.4°C higher in August in 2003; temperatures in Sapporo was 2.9°C lower in July in 2003 and were 1.4–2.1°C lower during August in 2002

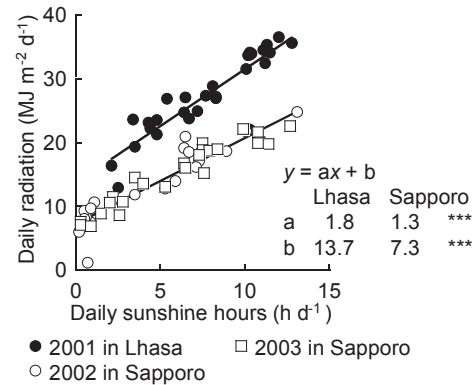


Fig. 5. Relationship between daily radiation and daily sunshine hours in August in Lhasa and Sapporo. Regression lines were fitted to all the data location being treated as a dummy variable. The overall R^2 of the regression was 0.93 ($P < 0.05$). Statistical significance of location-effect is indicated as *** ($P < 0.01$).

and 2003.

Total precipitation during the cropping season was about twice as high in Lhasa (522 mm, two-year average) than in Sapporo (241 mm). The precipitation was almost the same during one month after sowing in both locations. After that, it was higher in Lhasa than in Sapporo until harvest. The difference between locations was extremely large around heading stage i.e. during June and July. Comparison with the average values, the monthly total precipitation in Lhasa was about 100 mm higher during June (before heading) in 2001 and 2003 and was 46 mm higher during September (after heading) in 2003; in Sapporo it was 38 mm higher during July (after heading) in 2002, 42 mm lower during July in 2003 and 44–63 mm lower during August in 2002 and 2003.

Daily solar radiation in August at both locations was plotted against daily sunshine hours to find the

Table 4. Mean daily sunshine hours and radiation in Lhasa and Sapporo during the spring wheat growth season.

	Location	Year	May	June	July	August	September
Mean radiation (MJ m ⁻² d ⁻¹) †	Lhasa	2003	—	—	—	27.9	23.4
	Sapporo	2002	19.5	18.3	13.3	11.1	12.4
		2003	17.9	17.8	17.1	13.3	11.2
Sunshine hours (h d ⁻¹)	Lhasa	2001	7.9	8.4	7.6	5.7	7.2
		2003	7.8	6.5	5.9	7.5	6.8
	Sapporo	2002	7.7	7.1	5.0	4.8	5.7
		2003	7.9	9.5	6.4	6.0	5.7

† Radiation in Lhasa was measured from 1 August to 12 September in 2003.

difference in the effect of sunshine hours between the two locations at different altitudes and latitudes (Fig. 5). Regression equations showed that both slopes and intercepts were higher for Lhasa than for Sapporo, resulting in higher radiation in Lhasa for a given number of sunshine hours, i.e., 53–73% higher radiation at 2.5 to 13.0 sunshine hours a day. Daily sunshine hours were almost the same during May, and were about one hour shorter on average in Lhasa than in Sapporo during June (Table 4); thereafter, they were about one hour longer in Lhasa than in Sapporo until September. Thus, the average solar radiation each month throughout the cropping season was estimated to be 50–80% higher in Lhasa than in Sapporo.

Discussion

Little is known about spring wheat growth and grain yield in the Tibetan Plateau. Bao and Zuo (1982) investigated spring wheat growth in the Qaidam Basin in northern Tibetan Plateau. Total dry weight and grain yield were in the ranges of 1239–3075 g m⁻² and 602–1520 g m⁻², respectively. Yu et al. (1998) cultivated two cultivars of winter wheat in the same experimental field as in the present study. They reported that total dry weight and grain yield were 2460 g m⁻² and 930 g m⁻², respectively. In the present study, total dry weight and grain yield in Lhasa were 1563 g m⁻² and 437 g m⁻², respectively, as the average of all experiments. Compared with the results obtained by Bao and Zuo (1982), total dry weight of spring wheat was in the same range, but grain yield was much lower, indicating a lower harvest index in the present study. Harvest index in Lhasa of the present study was also lower than that of winter wheat in Lhasa of Yu et al. (1998).

The total dry weight and grain yield of spring wheat in Hokkaido were reported to be in the ranges of 979–1265 g m⁻² and 288–502 g m⁻², respectively (Takahashi et al., 1988; Sawaguchi and Sato, 2001; Sato and Tsuchiya, 2002). In the present study, total dry weight and grain yield in Sapporo were 1092 g m⁻² and 425 g m⁻², respectively, as the average of all experiments. Both total dry weight and grain yield were in the same range as in the previous studies.

In the present study, total dry weight in Lhasa was significantly heavier than that in Sapporo while grain yield was similar in two locations. Lower harvest index might be responsible for similar level of grain yield in Lhasa and Sapporo. It is possible that a high sowing rate results in a low harvest index in Lhasa in the present study. In general, total dry weight is increased while harvest index is decreased by a high sowing rate (Ellen, 1990; Stapper and Fischer, 1990). The reduction of harvest index was caused by a lighter grain weight and fewer grains per ear (Ellen, 1990). Compared with the results in Sapporo, grain weight was significantly lower in Lhasa in both cultivars and grain number per ear was significantly lower in Lhasa in one of two cultivars. This suggested that a high sowing rate in Lhasa decreased harvest index in the present study. Bao and Zuo (1982) and Yu et al. (1998) did not mention the sowing rates. Yu et al. (1998) reported that the number of ears at harvest was 450 per square meter in winter wheat, which was lower than that in Lhasa of the present study (536–808 per square meter).

The total dry weight in Lhasa was significantly heavier than that in Sapporo in both cultivars in the present study. Ying et al. (1998) compared rice production between two altitudes, Los Baños (21 m above sea level), Philippines with that in Yunnan Province (1170 m above sea level), China. They concluded that longer growth duration and higher crop growth rate at high altitudes increased total dry weight compared to low altitudes. Temperature and photoperiod was responsible for the difference in growth duration, and LAI was responsible for the difference in crop growth rate. In the present study, growth duration was longer in Lhasa than in Sapporo while crop growth rate was similar in both locations in both cultivars. This indicated that growth duration rather than crop growth rate was responsible for heavier total dry weight in Lhasa.

The low temperature and short photoperiod in Lhasa may delay heading and maturity. Heading is hastened (Butterfield and Morison, 1992) and the phenology of spring wheat, semi-winter wheat and

winter wheat is enhanced (Slafer and Rawson 1995) by the increase in temperature. The duration from heading to maturity was also shortened by a high temperature. Marcellos and Single (1972), Wiegand and Cuellar, (1981) and Sayed and Ghandorah (1984) indicated that the duration from anthesis to maturity was shortened by 1.6 to 6 days for each one degree centigrade increase. Air temperature was lower in Lhasa than in Sapporo throughout the cropping period in the present study. The lower temperature in Lhasa may delay heading and prolong the duration from heading to maturity.

A short photoperiod also delays heading in wheat. A decrease in photoperiod from 15 to 12 hours increases the time to heading in wheat by average of 8.6 days on the average (Slafer and Rawson, 1995). Theoretically, the photoperiod from the end of March to the end of September is shorter in Lhasa than in Sapporo because of the lower latitude in Lhasa. The photoperiod in Lhasa from May to June (i.e., from sowing to heading) was 13.1–13.9 hours, about one hour shorter than in Sapporo (13.9–15.2 hours). The short photoperiod in Lhasa may have contributed to the later heading in Lhasa.

The crop growth rate is generally proportional to intercepted radiation (Monteith, 1981). In this study, although the maximum value of LAI did not differ between the two locations, the intercepted radiation was assumed to be higher in Lhasa than in Sapporo because of much higher solar radiation in Lhasa. However, the crop growth rate was similar in both locations. One possible reason is that solar radiation was not a limiting factor for canopy photosynthetic rate in the present environment in Lhasa. The leaf photosynthetic rate and canopy photosynthetic rate of wheat are light-saturated at a photosynthetic photon flux density (PPFD) of 1000–1500 and 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively (Burkart et al., 2000; Shangguan et al., 2000). At the locations of the present study, solar radiation generally exceeds a PPFD of 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ on a clear day (data not shown). Another possible reason is the low CO_2 partial pressure in Lhasa because of its high altitude. The decrease in CO_2 partial pressure in the air results in the low concentration of CO_2 in mesophyll cells, and leads to low photosynthetic rate (Terashima et al., 1995). The differences in these two factors, solar radiation and CO_2 partial pressure, may have caused no difference in crop growth rate between the two locations.

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References

- Bao, X. and Zuo, K. 1982. On mineral nutrition and its relationship to the production of high-yielding spring wheat in Qaidam Basin. *Acta Biologica Plateau Sinica* 1 : 247-265.
- Burkart, S., Manderscheid, R. and Weigel, H.-J. 2000. Interacting effects of photosynthetic photon flux density and temperature on canopy CO_2 exchange rate of spring wheat under different CO_2 -concentrations. *J. Plant Physiol.* 157 : 31-39.
- Butterfield, R.E. and Morison, J.I.L. 1992. Modelling the impact of climatic warming on winter cereal development. *Agric. For. Meteorol.* 62 : 241-261.
- Ellen, J. 1990. Effects of nitrogen and plant density on growth, yield and chemical composition of two winter wheat (*Triticum aestivum* L.) cultivars. *J. Agron. Crop Sci.* 164 : 174-183.
- Hokkaido Branch, Japanese Society of Soil Science and Plant Nutrition. 1987. Soil science and plant nutrition in Hokkaido agriculture, 1987. Hokunoukai, Sapporo.
- Lin, R., Li, C., Zhang, Y. and Xie, Y. 2001. Xizang Lhasashi Nongye Qihou Ziyuan. China Meteorological Press, Beijing, China*.
- Luo, T., Li, W. and Zhu, H. 2002. Estimated biomass and productivity of natural vegetation on the Tibetan Plateau. *Ecol. Appl.* 12 : 980-997.
- Marcellos, H. and Single, W.V. 1972. The influence of cultivar, temperature, and photoperiod on post-flowering development of wheat. *Aust. J. Agric. Res.* 23 : 533-540.
- Monteith, J.L. 1981. Climate variation and the growth of crops. *Quart. J. R. Met. Soc.* 107 : 749-774.
- National Astronomical Observatory. 2004. Chronological Scientific Tables 2005. Maruzen, Tokyo, Japan**.
- Sato, M. and Tsuchiya, T. 2002. Studies on the cultivation of spring wheat seeded in early winter in central Hokkaido. *Jpn. J. Crop Sci.* 71 : 455-462***.
- Sawaguchi, A. and Sato, M. 2001. Cultivation by early winter seeding of spring wheat in central Hokkaido. *Jpn. J. Crop Sci.* 70 : 505-509***.
- Sayed, H.I. and Ghandorah, M.O. 1984. Association of grain-filling characteristics with grain weight and senescence in wheat under warm dry conditions. *Field Crops Res.* 9 : 323-332.
- Shangguan, Z., Shao, M. and Dyckmans, J. 2000. Effects of nitrogen nutrition and water deficit on net photosynthetic rate and chlorophyll fluorescence in winter wheat. *J. Plant Physiol.* 156 : 46-51.
- Slafer, G.A. and Rawson, H.M. 1995. Photoperiod \times temperature interactions in contrasting wheat genotypes: Time to heading and final leaf number. *Field Crops Res.* 44 : 73-83.
- Smith, C.A.S., Clark, M., Broll, G., Ping, C.L., Kimble, J.M. and Luo, G. 1999. Characterization of selected soils from the Lhasa region of Qinghai-Xizang Plateau, SW China. *Permafrost Periglac. Process.* 10 : 211-222.
- Stapper, M. and Fischer, R.A. 1990. Genotype, sowing date and plant spacing influence on high-yielding irrigated wheat in southern New South Wales. II Growth, yield and nitrogen use. *Aust. J. Agric. Res.* 41 : 1021-1041.
- Statistics and Information Department, Ministry of Agriculture,

- Forestry and Fisheries 2002. Crops on Statistics 2000. Association of Agriculture and Forestry Statistics, Tokyo.
- Takahashi, T., Nakaseko, K. and Gotoh, K. 1988. Differences in productivity between short-and long-culm varieties and their relationships with cell wall and cellular components of culm in spring wheat. *Jpn. J. Crop Sci.* 57 : 53-58 ***.
- Terashima, I., Masuzawa, T., Ohba, H. and Yokoi, Y. 1995. Is photosynthesis suppressed at higher elevations due to low CO₂ pressure? *Ecology* 76 : 2663-2668.
- Tibet Statistics Bureau. 2002. Tibet Statistical Yearbook 2001. China Statistics Press, Beijing, China.
- Ying, J., Peng, S., He, Q., Yang, H., Yang, C., Visperas, R.M. and Cassman, K.G. 1998. Comparison of high-yield rice in tropical and subtropical environments I. Determinants of grain and dry matter yields. *Field Crops Res.* 57 : 71-84.
- Yu, C., Zhang, Y., Zhou, Y., Lin, Z. and Liu, Y. 1998. Analysis of agro-ecological environmental factors on the causes for high-yield wheat in Qinghai-Xizang plateau. *J. Natural Resour.* 13 : 97-103****.
- Wardlaw, I.F., Sofield, I. and Cartwright, P.M. 1980. Factors limiting the rate of dry matter accumulation in the grain of wheat grown at high temperature. *Aust. J. Plant Physiol.* 7 : 387-400.
- Wardlaw, I.F. and Wrigley, C.W. 1994. Heat tolerance in temperate cereals: an overview. *Aust. J. Plant Physiol.* 21 : 695-703.
- Wiegand, C.L. and Cuellar, J.A. 1981. Duration of grain filling and kernel weight of wheat as affected by temperature. *Crop Sci.* 21 : 95-101.
- Wilkinson, M.H., Cranage, S., Berger, P.J., Blanch, N. and Adamson, T.M. 1995. Changes in the temporal structure of periodic breathing with postnatal development in preterm infants. *Pediatr. Res.* 38 : 533-538.

* In Chinese.

** In Japanese.

*** In Japanese with English abstract.

**** In Chinese with English abstract.