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RESEARCH ARTICLE

PHYSIOLOGICAL RESPONSES OF SPRING WHEAT CULTIVARS GROWN IN WARM AND COOL ECOTOPES

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ABSTRACT

Rising levels of atmospheric temperatures in growing ecotopes are thought to affect physiological functioning of plants. Four wheat cultivars, UNZA II (heat tolerance), Loerie II (check), Nduna and Pungwa were tested in both warm and cool ecotopes for their acclimation capacity to subsequently enhance production. Using five replications, a randomised complete block design was used and data on canopy temperature (CT), stay green duration (SGD) and dry matter production and accumulation (DM) was collected and analysed using GENSTAT software version 18. Results revealed that all cultivars had 3oC low CT than their temperatures in cool ecotope in 2014 and 3oC to 6oC high CT than their cool ecotope in 2015. Cultivars terminated their DM production and accumulation in the warm ecotope 7 days earlier than in cool ecotope. DM production and accumulation was quick in 2014 and slows in 2015 in the warm compared to the cool ecotope. Pungwa showed superiority with 52.8% SGD and 39.8% SGD remaining at 28 days after anthesis in 2014 and 14 days after anthesis in 2015 in the warm ecotope, respectively when other cultivars had lost over 65% and 76% of the SGD and maintained its DM at physiological maturity in both seasons. Pungwa with longer SGD, low CT and more DM accumulation suggests the ability to support plant growth and could enhance wheat production in warm ecotope.

Keywords: Biomass, Canopy temperature, Dry matter, Ecotope, Stay green duration, Temperature stress, Wheat cultivar

INTRODUCTION

Rising mean ambient temperatures, causing high temperature stress, has drawn the attention of researchers in the field of agriculture. For wheat crops, mean temperatures of 18 to 25^{o}C are considered optimum (Dhanda and Munjal 2012). However, in some growing ecotopes, high ambient mean temperatures of above 30^{o}C for long periods could prevail and cause high temperature stress, which affects plant development, growth, photosynthesis and its yield (Kumar *et al*. 2012; Chandra *et al*. 2014). High temperatures, above the optimum temperatures, are known to shorten stay green duration (SGD) after anthesis, cause high canopy temperature (CT), lowers production and increase accumulation of dry matter (DM). Thus plant height is affected and the grain filling period accelerated, consequently reducing crop yield (Sanghera and Thind 2014; Thomas and Ougham 2014). The reduction in crop yield is the result of lighter, poorly filled grains.

In Zambia, wheat is grown in the winter season in cooler ecotopes and yields could exceed 10tha^{-1}, whereas in the warm ecotopes yields below 5tha^{-1} are common (Nxumalo 2002; ACF 2011). Yet, Zambia's warm ecotopes have natural and artificial water

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bodies inducing wheat growers to plant wheat, but experience mean temperatures of 19 to 32°C most of the year (Bunyolo *et al*. 1997). Thus, the low production reported in the warm ecotope is linked, but not limited to, high temperature stress, use of unsuitable cultivars, and also limited knowledge and understanding of physiological responses, which can be manipulated to produce normal growth and yield.

Physiological traits such as low CT and long SGD are used as indirect selection indicators for development of high temperature tolerant wheat cultivars by breeders (Cossain and Reynolds 2012; Deery *et al*. 2019; Anderegg *et al*. 2021). Cultivars that maintain a low CT dissipates the heat through transpiration, depend on stimulated subcellular and biochemical substances synthesized in response to heat stress such as phytohormones, various osmoprotectants, heat shock proteins, and reactive oxygen species suppressing and scavenging enzymatic and non-enzymatic defense mechanisms (Sharma *et al*. 2012; Wang *et al*. 2014; Deery *et al*. 2019).

Studies have concluded that wheat cultivars with low CT will also lengthen their SGD and support the process of photosynthesis during the grain filling period (Bazzaz *et al*. 2015; Neukam *et al*. 2016; Deery *et al*. 2019; Anderegg *et al*. 2021). Thus, any wheat cultivar exhibiting SGD or/and low CT after anthesis is an option for cultivation in heat prone environments (Cossain and Reynolds 2012; Yang *et al*. 2016; Deery *et al*. 2019). According to Christopher *et al* (2016), SGD could either be functional or non-functional. When SGD is functional, the process of photosynthesis results in net photosynthesis, while in a non-functional SGD, plant leaves appear green, but the plant does not benefit due to lesions occurring in chlorophyll, as well as a disrupted transfer of nitrogen from the leaf to the grain (Christopher *et al*. 2016; Anderegg *et al*. 2021). Net photosynthesis (the difference between produced photo-assimilates and consumption by respiration) promotes production and accumulation of more FM and DM, which could be used for plant growth and grain development (Cossain and Reynolds 2012; Sanghera and Thind 2014). However, high temperatures in warm ecotopes increase the rate of photorespiration and night respiration, thereby affecting net photosynthesis and limiting DM accumulation in wheat (Kheirandish *et al*. 2015; Urban *et al*. 2017).

Prolonged SGD during the grain filling period is, however, counterproductive as it promotes vegetative growth. Low CT is seen as a huge expense for plants, because the roots need to increase water absorption for transpiration, cooling the plant rather than translocating assimilates for grain filling (Deery *et al*. 2019; Anderegg *et al*. 2021). It is clear from these different studies that the scientific community is not convinced that the choice of cultivars, showing long SGD after anthesis and low CT could produce more FM (fresh matter) and DM and grow normally under heat stress. It is also unclear whether the cultivars could improve wheat production or lead to the development of new improved cultivars for a warm ecotope. Possible answers to the argument could be that the cultivars possess specific genes for certain adaptations (Moshatati *et al*. 2012).

Extending SGD after anthesis could be an option for increasing FM and DM production, growth and ultimately the yield. Cultivar choice, based on the physiological traits of SGD, CT, FM and DM accumulation, remains crucial to promote wheat production in both cool and warm ecotopes. This choice has to meet the expectation of the wheat growers, focusing primarily on resistance to high temperature stress and a more stable yield with high grain nitrogen content rather than tolerance to heat stress adaptation mechanisms advocated by scientists (Distelfeld *et al*. 2014; Anderegg *et al*. 2021).

Most agronomic heat management strategies can encourage wheat production, even in Zambia’s warm ecotopes, if supported by the knowledge and understanding of physiological processes of plant growth, development, photosynthesis, respiration, transpiration and duration of grain filling period. Thus, growers could manipulate these physiological processes through external application of stimulants or enhancers, leading to normal growth and yield, or aid wheat breeders in developing appropriate cultivars. The objective of this study was to evaluate the physiological responses of four spring wheat cultivars grown under cool and warm ecotope conditions.

MATERIALS AND METHODS

Experimental sites

The trial was conducted at Chiawa (latitude 15°53'S, longitude 28°52'E and altitude of 369 meters above sea level) and Zambia – China Demonstration Centre (latitude 15°21'S, longitude 28°27' E and altitude 1417.32 meters above sea level) all in the Lusaka Province of Zambia. Chiawa and Lusaka were used as warm and cool ecotopes respectively, for two seasons. Temperatures during the growing seasons were obtained using a data logger (Onset HOBO U12 – 012, Tempcon Instrumentation Ltd, UK) for each site. Chiawa soils were classified as loamy sand and the Lusaka as sandy loam using the USDA texture classification (Soil Survey Division Staff 1993). Chiawa soils had a pH by 0.01M $CaCl_2$ of 6.73, 7.05, and 0.72 and 1.28% organic matter, potassium of 0.06mgkg^{-1} and 0.23mgkg^{-1}, phosphorus of 18.09 cmol kg^{-1} and 31.76 cmol kg^{-1}, respectively for the 2014 and 2015 season and a nitrogen content of 0.07% for each season. Lusaka soils had a pH by 0.01M $CaCl_2$ of 5.24 and 5.28, organic matter of 0.8 and 1.6.%, nitrogen of 0.07% and 0.1%, potassium of 0.04mgkg^{-1} and 0.15mgkg^{-1}and phosphorus of 29.64 cmolkg^{-1} and 21.95 cmolkg^{-1} for the 2014 and 2015 seasons, respectively.

Agronomic management

Four irrigated spring wheat cultivars; UNZA II (heat tolerant), Pungwa and Nduna commonly grown by farmers, and Loerie II (susceptible to heat stress) were planted in both warm and cool ecotopes during the 2014 and 2015 growing seasons. Field trials were laid out as a Randomized Complete Block Design with five replications. Treatment plots contained thirteen rows 5m in length with an inter-row spacing of 0.20m. The thirteen rows were comprised of four rows for above ground fresh biomass and dry matter determination (inner two rows used), five rows for canopy temperature and stay green duration (inner three rows used), and four rows to separate the two areas. A border area of 50cm was left on both sides of each plot to diminish border effects.

Planting rows were ripped and wheat basal applied at a rate of 300 kgha^{-1} to supply 35.29 kg N, 80.56 kg P_2O_5, 61.38 kg K_20, 46.04 kg S, 30.69 kg Mg, 7.67 kg Cu, 11.51 kg Fe, 19.18 kg Zn and 7.67 kg B and lightly covered with soil. Thereafter a seed rate of 120 kgha^{-1} was used to plant all cultivars. Trials were established on 3rd and 8th May 2014 in the Chiawa and Lusaka site respectively, for season I and similarly on 7th and 14th May 2015 for season II. Prior to planting, all cultivar seeds were treated and dressed with insecticides for protection against soil borne pests and diseases and to boost germination.

Nitrogen fertilizer, using urea (46% N), was split applied amounting to 305 kg ha^{-1} and using ammonium sulphate (26%) to supply 145 kg ha^{-1} for the whole season. The doses were 46 kg N for 6 and 12 days after sowing (DAS) each and 48.3 kg N at 40 DAS in the form of urea and 37.7 kg N at 53 DAS in the form of ammonium sulphate per season. The total applied nitrogen in each season including nitrogen in the basal fertilizer was 213.29 kg ha^{-1}.

Water application started a day after planting in all seasons. In the warm ecotope, 520 mm water was applied in the 2014 season and 548 mm in the 2015 season. In the cool ecotope, totals of 574 mm and 511 mm were applied in the 2014 and 2015 growing seasons, respectively. Emerging weeds in the cool ecotope were removed by hand, while herbicides (glyphosate at 1, 250 g ha^{-1} a day after sowing, endimethalin at 910 g ha^{-1} and paraquat at 625 g ha^{-1} were applied on 3 DAS, bromoxynil at 425 g ha^{-1} and fenoxaprop-p-ethyl at 60 g ha^{-1} were applied on 17 DAS), insecticides (fipronil at 2.5 g ha^{-1} , at 25 DAS, methomyl at 270,000 g ha^{-1} and fipronil at 100 g ha^{-1}, emamectin benzoate at 5,000 g ha^{-1}

and lufenuron at 20,000 g ha^{-1} were applied at 34 and 46 DAS, chlorpyrifos at 450 g ha^{-1} and cypermetrin at 50 g ha^{-1} were applied at 52 DAS and for 2014 season alone emamectin benzoate at 7.5 g ha^{-1} and acetamiplid at 18.75 g ha^{-1} were applied at 102 DAS) and fungicides (tebuconazole at 100 g ha^{-1} and trifoxystrobin at 50 g ha^{-1} were applied at 48 DAS and 34 DAS for 2014 and 2015 season, respectively, were applied in the warm ecotope.

Ten plants were tagged and for each treatment plot and stay green duration was assessed, following the scoring method of Pask and Pietragalla (2012). The scoring started when all the plants in each plot had reached 100% flowering and was reported based on days after complete anthesis (DAAS). Ten randomly picked plants were cut at ground level, packed in black plastic bags in the field, and weighed the same day in the laboratory, using a digital scale, to obtain the FM accumulation. After taking the FM, the plants were oven dried to a constant mass for four days at a constant temperature of 65^{o}C. In both seasons, oven dried plants were weighed to obtain the DM accumulation. Both FM and DM accumulation were determined at 40, 60, 76, 90 104, 111, 118 and 125 DAS as well as physiological maturity. During 2015 season, Nduna attained maturity at 97 DAS, thus both FM and DM were calculated. The average of ten plants was reported for each treatment plot.

Canopy temperatures were measured using an infra-red thermometer (Model MT6, India) during the day at two points on the three middle rows of the non-destructive area. Readings were taken between 12:00 and 14:00 hours on a clear sky day according to the procedure of Pietragalla (2012). Readings were taken from the side of each plot at an angle of approximately 450 in a range of directions to cover different regions of the plot and integrate many leaves. The averages of two readings were taken as CT at seedling, booting, early milk and the dough growth stage of the crop.

Data was analyzed using the GENSTAT statistical package; Eighteenth Edition (Payne *et al.* 2015). Means were separated using Tukey's LSD test at 5% probability level.

RESULTS AND DISCUSSION

Weather conditions

The ambient temperatures in the warm ecotope were higher than in the cool ecotope in both seasons (Table 1). The average maximum temperatures were consistently above 30^{o}C and the mean temperatures were above 23^{o}C in warm ecotope while the in the cool ecotope, the highest average maximum temperature of 31^{o}C was only recorded in September of 2015 and mean temperatures were consistently below 20^{o}C. However, during the 2015 season water could not always be pumped owing to a national power load shedding problem, which indirectly induce drought. In the warm ecotope, water stress occurred at the start of the flowering stage to soft dough development stage, while in the cool ecotope it was at the start of the kernel and milk stage. The high temperatures and the indirect drought in the second season altered the physiological responses in the wheat cultivars.

Canopy temperature

Plants had cool CT (CT ranged from 17.1^{o}C to 22.8^{o}C) during 2014 and hot CT (above 25^{o}C) from early milk to dough stage in 2015 in the warm ecotope (Table 2). In both seasons the ecotope significantly (P = < 0.05) affected CT from seedling to dough stage, the interaction between ecotope and cultivar at dough stage, but not the cultivar. However, during the 2015 season the three factors (ecotope, cultivar and interaction between them) showed no significant effect on plant CT at booting stage. During the 2014 season, CT was lower in the warm than in the cool ecotope, except at booting stage when it increased by 2.89^{o}C and even at lower temperatures than the optimum 25^{o}C for wheat. A decrease of 3.79^{o}C and 5.03^{o}C in CT was found in plants grown in the warm ecotope at seedling and early milk growth stage, respectively. The temperatures ranged from 3.04^{o}C (UNZA II) to 3.94^{o}C (Pungwa) at dough stage despite cultivars showing

Table 1: Agro thermal data of experimental sites for the 2014 season and the 2015 season

Month	Ecotope	2014 Season				2015 Season			
		T_{MIN} (°C)	T_{MAX} (°C)	T_{MEAN} (°C)	RH (%)	T_{MIN} (°C)	T_{MAX} (°C)	T_{MEAN} (°C)	RH (%)
May	Warm	18.1	32.6	25.4	53.0	17.8	31.2	24.5	44.5
	Cool	12.4	27.1	19.8	63.5	10.7	26.0	18.3	68.1
June	Warm	15.7	31.3	23.5	49.5	16.2	29.5	22.9	51.1
	Cool	10.9	25.3	18.1	60.2	9.6	24.6	17.1	66.0
July	Warm	14.8	31.4	23.1	46.5	15.7	31.0	23.4	47.3
	Cool	10.1	25.4	17.7	55.7	9.4	25.8	17.6	61.1
August	Warm	17.0	34.5	25.8	39.3	16.9	33.3	25.1	39.0
	Cool	12.6	28.5	20.6	45.0	10.7	27.7	19.2	48.0
September	Warm	16.8	33.4	25.1	39.8	20.9	35.9	28.4	38.9
	Cool	15.1	29.7	22.4	41.8	14.8	31.3	23.1	41.3

RH = Relative humidity, Min = Minimum, Max = Maximum and T = Temperature

similar CT at dough stage in warm ecotope, during the 2014 season. During the 2015 season, CT was higher in warm than the cool ecotope, recording 2°C and 4.68°C at seedling and early milk stage, respectively and ranging from 3.54°C (Loerie II) to 6.88°C (Nduna) at dough stage. From early milk to dough stage, the CT in the warm ecotope was higher than the optimum 25°C with Nduna (4.74°C) recording the highest and Loerie II (2.33°C) the lowest increase.

The low CT of below 25°C in the 2014 season suggested cooling mechanisms, which could have been triggered in the warm ecotope to support physiological processes, ultimately supporting plant growth, as was reported by Bahar *et al*. (2011) and Deery *et al*. (2019). Contrary to results obtained in this study, significant differences were reported in CT among wheat cultivars at booting, heading and milk stages within and between different temperatures environments by Bazzaz *et al*. (2015), Deery *et al*. (2019) and Anderegg *et al*. (2021). In this study, even the heat tolerant cultivar (UNZA II), could not show complete superiority to other cultivars in both seasons, though Nduna showed sensitivity in the 2015 season, when CT was increased by 6.88°C at dough stage in the warm ecotope. The non-significant differences observed among cultivars in ecotopes from seedling to early milk stage could be ascribed to the equal effect of ecotopes on the cultivar plant CTs.

Stay green duration

During both seasons the main factors (ecotope and cultivar) and the interaction between them had a significant (P = < 0.001) effect on SGD (Table 3). However, loss of SGD was not affected by the ecotope at 14 DAAS during the 2014 season. Surprisingly, during the 2014 season, the loss of SGD was initiated early in the cool Lusaka area and differed significantly with Loerie II (5.60%) and Nduna (10.60%) recording the highest decrease observed at 0 DAAS and 7 DAAS, respectively while the other two cultivars did not show differences. The heat tolerant cultivar UNZA II maintained SGD in both ecotopes at 7, 14 and 28 DAAS, whereas Loerie II and Pungwa maintained their SGD at 7 and 21 DAAS, and Nduna only once at 14 DAAS.

During the 2015 season, loss of SGD was significantly ($P \leq 0.05$) higher for all cultivars in the warm ecotope up to 28 DAAS and lower in the cool ecotope from 0 to 14 DAAS. All cultivars were similar from 28 to 35 DAAS, but significantly differed in the cool ecotope. Pungwa showed the lowest decrease followed by UNZA II at 35 DAAS, while Nduna showed the highest decrease but not different from Loerie II in the cool ecotope. In the warm ecotope, the plants of Nduna generally showed the highest decrease in SGD, while those for Loerie II were the

Table 2: Canopy temperatures (°C) during seedling, booting, early milk and dough developmental stage as affected by ecotope and cultivar

Cultivar (C)	Ecotope (E)	2014 Season				2015 Season			
		SD	BT	EM	Dough	SD	BT	EM	Dough
Loerie II	Warm	19.75	22.84	17.78	22.40 c	23.00	22.48	26.21	27.33 c
	Cool	23.05	19.51	22.58	25.47 ab	21.15	21.75	21.50	23.79 d
Nduna	Warm	19.39	22.84	17.78	22.27 c	23.05	22.31	26.78	29.79 a
	Cool	23.59	19.76	22.86	25.80 ab	21.11	22.27	22.25	22.86 d
Pungwa	Warm	19.40	22.26	17.66	21.96 c	23.43	22.49	25.97	27.98 a
	Cool	23.64	20.26	22.89	25.90 a	21.25	22.59	21.82	23.82 d
UNZA II	Warm	19.69	22.82	17.09	22.33 c	23.13	22.68	26.63	28.46 b
	Cool	23.13	19.68	22.20	25.37 b	21.08	22.27	21.29	23.35 d
LSD $_{T(0.05)}$	**C x E**	**ns**	**ns**	**ns**	**0.497**	**ns**	**ns**	**ns**	**1.082**
Cultivar means	Loerie II	21.17	21.17	20.18	23.94	22.08	22.11	23.86	25.56
	Nduna	21.30	21.30	20.37	24.04	22.08	22.29	24.52	26.30
	Pungwa	21.26	21.26	20.28	23.93	22.34	22.54	23.89	25.90
	UNZA II	21.25	21.25	19.65	23.85	22.10	22.47	23.96	25.91
LSD $_{T(0.05)}$	**C**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
Ecotope means	Warm	19.56 b	22.69 a	17.60 b	22.24	23.15 a	22.49	26.40 a	28.46
	Cool	23.35 a	19.80 b	22.63 a	25.64	21.15 b	22.22	21.72 b	23.35
LSD $_{T(0.05)}$	**E**	**0.558**	**0.430**	**0.699**	**0.249**	**0.347**	**ns**	**0.479**	**0.541**

SD = Seedling, BT = Booting, EM = Early milky, Warm = Chiawa, Cool = Lusaka and ns = not significant at 5% probability level (P< 0.05). Means followed by the same letter at same developmental phase are not significantly different at 5% probability level (P< 0.05) using Tukey's LSD test.

lowest at 0 and 21 DAAS and Pungwa at 7 to 14 DAAS.

In both ecotopes, during the 2014 season, plants of Loerie II and Pungwa required 35 DAAS of functional SGD, while Nduna needed 28 DAAS in both ecotopes, respectively to reach physiological maturity (Table 3). Heat tolerant UNZA II was inconsistent, recording 7 days shorter in the warm ecotope compared to 35 DAAS in the cool ecotope. UNZA II (65.40%) showed a longer SGD, while Loerie II and Nduna were the same with shorter SGD with flag leaf senescence of 95.20% and 95.60%, respectively under the warmer Chiawa ecotope. Under the cooler Lusaka ecotope, Nduna (72.60%) had longer SGD, while Pungwa (98.60%) and UNZA II (97.40%) were the same and showed the highest loss in SGD.

However, in the 2015 season, the warm ecotope conditions accelerated the loss of SGD, recording 100% SGD at physiological maturity for all cultivars. It is also apparent from Table 3 that SGD was lost earlier, at 21 DAAS for Nduna, 28 DAAS for Pungwa and UNZA II, while Loerie II between 28 and 35 DAAS before completing grain filling. In the cool ecotope, Pungwa (89.60%) showed the longest SGD, while Nduna (99.60%) and Loerie II (98.70%) were similar and the shortest. This early loss of SGD during the 2015 season explains the low DM production and accumulation. The early loss of SGD can potentially reduce assimilate availability for grain filling in the warm ecotope. Thus, grains could be shrivelled and light, due to limited assimilates, consequently compromising grain yield and quality (Balla *et al*. 2014). It also explains the observed high CT, since transpirational cooling is only supported by green leaves. Therefore, the completion of grain filling during the 2015 season could have been supported by photosynthesis from the spikes and assimilate remobilization, which is stimulated by leaf senescence (Cossain and Reynolds 2012).

Significant (P = < 0.05) differences observed in SGD among cultivars implied different timings in their flag leaf senescence (onset, initiation, and rate of the process), and that long SGD under high temperature stress could sustain grain filling and increase grain yield

Table 3. Stay green duration (percentage of flag leaves dead) of wheat as affected by ecotope and cultivar after complete anthesis

Cultivar (C)	Ecotope (E)	2014 Season							2015 Season						
		0 DAAS	7 DAAS	14 DAAS	21 DAAS	28 DAAS	35 DAAS	PM	0 DAAS	7 DAAS	14 DAAS	21 DAAS	28 DAAS	35 DAAS	PM
Loerie II	Warm	0.00 c	7.60 c	17.20 b	44.40 a	72.20 b	95.20 b	95.20 ab	2.80 c	29.80 b	76.20 c	89.00 b	95.40 a	100.00 a	100.00 a
	Cool	5.60 a	8.40 bc	19.20 a	41.40 ab	61.60 d	94.16 b	94.16 b	0.00 d	5.40 e	13.60 e	31.80 c	89.40 b	97.40 a	97.40 ab
Nduna	Warm	0.00 c	8.60 bc	11.60 d	39.60 b	95.60 a	99.80 a	95.60 ab	13.40 a	71.20 a	99.40 a	99.80 a	100.00 a	100.00 a	100.00 a
	Cool	2.60 b	10.60 a	11.80 d	26.60 d	72.60 b	99.00 a	72.60 d	0.00 d	3.20 e	10.80 e	56.80 c	95.80 a	99.60 a	99.60 a
Pungwa	Warm	0.00 c	7.40 c	17.40 b	34.80 c	47.20 e	85.60 c	85.60 c	3.20 c	13.40 d	60.20 d	94.80 a	99.00 a	100.00 a	100.00 a
	Cool	2.40 b	7.80 bc	13.20 c	32.20 c	61.40 d	98.60 a	98.60 a	0.00 d	3.60 e	8.20 e	40.60 d	70.40 c	89.60 c	89.60 c
UNZA II	Warm	0.00 c	8.40 bc	12.00 cd	34.40 c	65.40 c	85.00 c	65.40 c	6.40 b	23.20 c	86.00 b	95.80 a	99.80 a	100.00 a	100.00 a
	Cool	2.40 b	8.00 bc	11.80 d	22.20 d	64.00 cd	97.40 a	97.40 ab	0.00 d	6.20 e	12.00 e	42.80 d	72.40 c	95.00 b	95.00 b
LSD $_T$ (0.05)	**C x E**	**0.522**	**1.165**	**1.273**	**3.554**	**3.500**	**3.045**	**3.484**	**1.092**	**4.294**	**5.559**	**5.301**	**5.076**	**3.106**	**3.106**
Cultivar means	Loerie II	2.80	8.00	18.20	42.90	66.90	94.68	94.68	1.40	17.60	44.90	60.40	92.40	98.70	98.70
	Nduna	1.30	9.60	11.70	33.10	84.10	99.40	84.10	6.70	37.20	55.10	78.30	97.90	99.80	99.80
	Pungwa	1.20	7.60	15.30	33.50	54.30	92.10	92.10	1.60	8.50	34.20	67.70	84.70	94.80	94.80
	UNZA II	1.20	8.20	11.90	28.30	64.70	91.20	81.40	3.20	14.70	49.00	69.30	86.10	97.50	97.50
LSD $_T$ (0.05)	**C**	**0.369**	**1.165**	**0.900**	**2.513**	**2.475**	**2.153**	**2.463**	**0.772**	**3.036**	**3.930**	**3.749**	**3.589**	**2.196**	**2.196**
Ecotope means	Warm	0.00	8.00	14.55	38.30	71.10	91.40	85.45	6.45	34.40	80.45	94.85	98.55	100.00	100.00
	Cool	3.25	14.00	14.00	30.60	64.90	97.29	90.69	4.60	4.60	11.15	43.00	82.00	95.40	95.40
LSD $_T$ (0.05)	**E**	**0.261**	**0.430**	**ns**	**1.777**	**1.750**	**1.523**	**1.742**	**0.546**	**2.147**	**2.779**	**2.651**	**2.538**	**1.553**	**1.553**

Warm = Chiawa, Cool = Lusaka, DAAS = Days after complete anthesis, PM = Physiological maturity and ns = not significant at 5% probability level ($P < 0.05$).

Means followed by the same letter at same developmental phase are not significantly different at 5% probability level ($P < 0.05$) using Tukey's LSD test.

as was earlier reported by other studies in wheat (Kamal *et al*. 2019; Anderegg *et al*. 2021). The benefit of long SGD is derived from transpiration, promoting heat dissipation and protecting soluble proteins (especially of photosystem II and Rubisco) and the destruction of membranes by lipid degradation (Latif *et al*. 2020). Therefore cultivars showing longer SGD with photosynthetic competencies (having green leaves with chlorophyll with capacity to carry photosynthesis optimally), provided there is an unlimited sink capacity accompanied by production and accumulation of assimilates, could be desirable for wheat production in warm ecotopes.

Dry matter accumulation

Interaction between ecotope and cultivar significantly (P =< 0.05) affected the DM production and accumulation. More DM was produced and accumulated in the warm Chiawa ecotope than in the cool Lusaka ecotope throughout the 2014 season (Table 4). DM increased in the range of 12.6% (Pungwa) to 45.6% (Loerie II) compared to the cooler ecotope at 40 DAS, 26.8% (Nduna) and 27.0% (Pungwa) at 60 DAS, 7.2% (UNZA II) at 76 DAS, 27.4% (Loerie II) to 27.6% (Nduna) at 90 DAS and 8.7% (Loerie II) to 18.1% (Pungwa) at physiological maturity.

However, at physiological maturity, the plants of Pungwa and UNZA II maintained DM in both ecotopes, though Pungwa was higher than UNZA II. In the warm ecotope, Loerie II increased by 12.68%, while Nduna decreased by 18.62%, compared to the cool ecotope.

Under warm ecotope conditions, Loerie II (4.780 g plant-1) recorded the highest accumulated DM, while Nduna (4.170 g plant -1) and UNZA II (4.164 g plant-1) which were similar and lowest. In the cool ecotope, Nduna with 5.124 g plant-1 had more DM, while Loerie II and UNZA II were similar, but lower. UNZA II and Nduna accumulated excess DM at physiological maturity during the 2014 season, suggesting un-disrupted physiological processes especially photosynthesis. This was supported by longer flag leaf SGD of 34.6% (UNZA II) and 4.4% (Nduna), which remained at physiological maturity and could have been functional (Table 3). Cultivar Pungwa showed an early peaking and a high DM accumulation, which could imply an adaptive mechanism to high temperature stress. Short, gradual and/or continuous rise in temperatures have been reported to switched on escape adaptive mechanism through early establishment and attaining of physiological maturity, or avoidance, or resistance and/or tolerance (through relatively longer duration) (Gursoy *et al*., 2012; Wang *et al*., 2014; Poudel and Poudel, 2020).

During 2015, the interaction effect between ecotope and cultivar was not significant (P = < 0.05) from 40 to 76 DAS (Table 4). However, the main effects of ecotope and cultivar were highly significant (P = < 0.001) in the accumulation of DM. High temperatures in the warm ecotope increased DM by 18.85% at 40 DAS, but decreased by 12.20% and 14.12% at 60 and 76 DAS, respectively. Plants of Loerie II tended to accumulate less DM in the range of 9.2% (1.32 g plant-1) to 15.8% (0.28 g plant-1) compared to those of Pungwa from 40 to 76 DAS The accelerated senescence of flag leaves during this season could have reduced the photosynthetic capacities of all cultivars, causing low DM accumulation from 60 DAS until physiological maturity in the warm ecotope, compared to the cool ecotope. At a later stage, Loerie II and Pungwa maintained DM in both ecotopes, though Pungwa was higher than Loerie II, UNZA II increased DM by 15.91% in the warm ecotope, while Nduna decreased by 49.57%. Thus, the decreased DM in the warm ecotope showed limitations in photosynthesis, photoassimilate partitioning, canopy cooling which depends on availability assimilates for root water absorption, which could make DM unavailable for growth and grain formation.

The significant (P = < 0.05) differences observed in this study are supported by previous research, where genetic constitution is the main factor for responses of wheat to high temperature stress (Moshatati *et al*.

Table 4. Dry matter production and accumulation (g plant^{-1}) of wheat as affected by ecotope and cultivar

Cultivar (C)	Ecotope (E)	2014 Season 40 DAS	60 DAS	76 DAS	90 DAS	104 DAS	111 DAS	118 DAS	125 DAS	PM	2015 Season 40 DAS	60 DAS	76 DAS	90 DAS	104 DAS	111 DAS	118 DAS	PM
Loerie II	Warm	0.364 b	1.222 b	2.194 ab	2.874 c	4.386 b	4.780 b	4.780 bc	4.780 b	4.780 b	0.2836	1.266	2.095	2.849 e	4.127 d	4.127 d	4.127 b	4.127 bc
	Cool	0.250 d	1.136 b	1.994 b	2.256 f	3.776 d	4.332 d	4.384 d	4.242 d	4.242 d	0.279	1.385	2.271	3.316 c	4.651 c	5.183 c	3.981 b	3.981 c
Nduna	Warm	0.412 a	1.522 a	2.242 a	3.596 a	4.170 c	4.940 a	4.940 b	4.940 a	4.170 d	0.4052	1.326	2.124	3.101 d	3.119 e	3.119 e	3.119 d	3.109 d
	Cool	0.296 c	1.200 b	2.276 a	2.614 d	3.838 d	4.606 c	5.124 a	4.544 c	5.124 a	0.301	1.489	2.406	3.582 b	5.172 b	6.165 a	4.085 b	6.165 a
Pungwa	Warm	0.358 b	1.588 a	2.220 a	3.366 b	4.812 a	4.402 d	4.402 d	4.402 cd	4.402 c	0.3506	1.302	2.267	3.289 cd	4.357 d	4.357 d	4.357 a	4.357 b
	Cool	0.318 c	1.250 b	2.194 ab	2.570 de	4.074 c	5.008 a	4.650 c	4.400 cd	4.400 c	0.301	1.594	2.775	3.840 a	5.504 a	6.071 a	4.267 ab	4.267 bc
UNZA II	Warm	0.414 a	1.176 b	2.242 a	3.252 b	4.164 c	4.340 d	4.340 d	4.340 d	4.164 d	0.3654	1.257	2.203	3.132 d	4.342 d	4.342 d	4.342 ab	4.342 b
	Cool	0.314 c	1.238 b	2.092 b	2.460 e	3.898 d	4.920 ab	4.714 c	4.260 d	4.260 d	0.301	1.399	2.663	3.051 de	5.118 b	5.659 b	3.746 c	3.746 c
LSD $_{T (0.05)}$	**C x E**	**0.03**	**0.119**	**0.124**	**0.144**	**0.018**	**0.151**	**0.167**	**0.155**	**0.13**	**ns**	**ns**	**ns**	**0.169**	**0.252**	**0.266**	**0.229**	**0.248**
Cultivar means	Loerie II	0.307	1.179	2.094	2.565	4.081	4.556	4.582	4.511	4.511	0.2813 b	1.326 b	2.183 b	3.082	4.389	4.655	4.054	4.054
	Nduna	0.354	1.361	2.259	3.105	4.004	4.773	5.032	4.742	4.647	0.3531 a	1.407 ab	2.265 b	3.341	4.146	4.642	3.602	4.637
	Pungwa	0.338	1.419	2.207	2.968	4.443	4.705	4.526	4.401	4.401	0.3258 a	1.448 a	2.521 a	3.564	4.931	5.124	4.312	4.312
	UNZA II	0.364	1.207	2.167	2.856	4.031	4.63	4.527	4.3	4.212	0.3332 a	1.328 b	2.433 a	3.091	4.73	5	4.044	4.044
LSD $_{T (0.05)}$	**C**	**0.021**	**0.084**	**0.087**	**0.102**	**0.091**	**0.107**	**0.1177**	**0.109**	**0.092**	**0.039**	**0.088**	**0.16**	**0.12**	**0.178**	**0.188**	**0.1616**	**0.175**
Ecotope means	warm	0.387	1.377	2.224	3.272	4.383	4.615	4.615	4.615	4.379	0.3512 a	1.288 b	2.172 b	3.093	3.986	3.986	3.986	3.984
	Cool	0.295	1.206	2.139	2.475	3.897	4.716	4.718	4.361	4.506	0.2955 b	1.467 a	2.529 a	3.447	5.111	5.769	4.02	4.54
LSD $_{T(0.05)}$	**E**	**0.015**	**0.059**	**0.062**	**0.072**	**0.064**	**0.075**	**0.083**	**0.0773**	**0.065**	**0.028**	**0.062**	**0.113**	**0.085**	**0.126**	**0.133**	**ns**	**0.124**

DAS = days after sowing and ns = nonsignificant at 5% probability level (P<0.05). Means followed by the same letter at the same days after sowing are not significantly different at 5% probability level (P< 0.05) using Tukey's LSD. Samples in the warm ecotope and cool ecotope during 2015 season stopped at 104 and 118 DAS, respectively.

2012; Deery *et al*. 2019; Anderegg *et al*. 2021). However, the high temperatures in the warm Chiawa ecotope led to two different responses, depending on the season. During 2014, the high temperature stress reaction in the seedling development stage could have triggered heat tolerance in all cultivar plants. Thus the entire crop life was acclimatized to higher ambient temperatures, which enabled normal functioning, more DM production than in the cool ecotope, as found by Gursoy *et al*. (2012) and Wang *et al*. (2014). The decline in DM accumulation observed after 40 DAS during 2015, suggests failure of plants to maintain the induced acclimation and disrupted physiological processes functionality due to the increase in hours of exposure to high temperatures. Poudel and Poudel (2020) attributes disrupted photosynthesis to breakdown of the enzyme rubisco activase and rubisco, vacuolar collapse, loss in membrane integrity, disturbance of cellular homeostasis leading to accelerated leaf senescence. Thus, any induced acclimation or adaptation could therefore have been reversed in the warm ecotope (Moshatati *et al*. 2012).

CONCLUSION

It is evident that wheat cultivars with inherent or acquired adaptive physiological mechanisms to high temperature stress can be grown in a warm ecotope and produce well filled in grains and produce wheat yields. All cultivars showed 3oC low CT than their temperatures in cool ecotope in 2014 and 3oC to 6oC high CT than their cool ecotope in 2015. Cultivars terminated their DM production and accumulation in the warm ecotope 7 days earlier than in cool ecotope. DM accumulation was quick in 2014 and slows in 2015 in the warm compared to the cool ecotope. Loerie II and Pungwa produced and accumulated more DM for longer durations during the seasons and maintained high DM in both ecotopes at physiological maturity. The heat tolerant cultivar (UNZA II) generally, did not perform better than the other cultivars in both ecotopes. Nduna had fast accumulation of DM in both ecotopes during the seasons. Pungwa showed superiority with 52.8% SGD and 39.8% SGD remaining at 28 days after anthesis in 2014 and 14 days after anthesis in 2015 in the warm ecotope, respectively when other cultivars had lost over 65% and 76% of the SGD and maintained its DM at physiological maturity in both seasons. Pungwa with longer SGD, low CT and more DM accumulation suggests the ability to support plant growth and could enhance wheat production in warm ecotope. Based on these results, Pungwa and Nduna could offer better options for cultivation under cool ecotope while Pungwa could be suitable for the warm ecotope. The responses of Nduna and Pungwa in the warm ecotope suggest induced acclimation with potential to support plant growth and wheat production.

AUTHOR CONTRIBUTION

MS performed the experiments, analyzed and interpreted data. MS and AJ conceptualized and designed the study. MS, AJ and EW contributed in drafting the manuscript. AJ critically revised the manuscript.

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