J Plant Res (2011) 124:147–154
DOI 10.1007/s10265-010-0340-7

REGULAR PAPER

Genotypic variation in drought stress response and subsequent recovery of wheat (*Triticum aestivum* L.)

Valya Vassileva · Constant Signarbieux · Iwona Anders · Urs Feller

Received: 22 December 2009 / Accepted: 8 March 2010 / Published online: 26 May 2010

Abstract Three wheat (*Triticum aestivum* L.) genotypes, Sadovo, Katya and Prelom, with different tolerance to drought were comparatively evaluated in terms of leaf respiratory responses to progressing dehydration and consecutive rewatering. Under drought stress, the respiration of all varieties gradually decreased, as the drought-tolerant Katya showed the most pronounced decline at earlier stages of dehydration. When water stress intensified, this genotype gave relatively stable respiration rates compared with the drought-sensitive varieties. Additionally, dehydrated Katya leaves displayed lower stomatal conductance and higher photosynthesis values, which resulted in greater water use efficiency during the dehydration period. Combination of drought stress and short-term changes in leaf temperature also induced genotype-specific response that differed from the response to drought only. Over the whole temperature range, the leaves of Katya exposed to dehydration for 14 days, showed higher respiration rates compared to the drought-sensitive varieties. The sensitive varieties maintained higher respiration rates under control conditions and mild dehydration, and very low rates under severe drought. In Katya, respiration and photosynthesis were fully restored from the stress within the first day of rewatering. The drought-sensitive genotypes displayed a considerably slower recovering capacity. The results are discussed in terms of possible physiological mechanisms underlying plant tolerance to drought.

Keywords Drought tolerance · Leaf respiration · Stomatal conductance · Wheat variety

Abbreviations

Q_{10}	Change in respiration during a 10°C increase in temperature
WUE	Water use efficiency

Introduction

Around the world, plant performance and yield are often limited by soil and atmospheric drought. Reduced plant growth under water deficit conditions is mainly attributed to the negative carbon balance, determined by an unfavorable relationship between photosynthesis and respiration (Flexas et al. 2007). The photosynthetic efficiency of higher plants exposed to drought is dynamically changing in a spatio-temporal manner, whereas the respiration capacity is less sensitive. Percentage of respired carbon is likely to be greater under dehydration due to the fact that the inhibitory effect of drought on photosynthesis is typically higher than that on plant respiration. Drought-dependent responses of photosynthesis have been studied at different organizational levels (Flexas and Medrano 2002; Lawlor and Cornic 2002; Flexas et al. 2004), however only few reports focuse on leaf respiration under reduced water supply (Flexas et al. 2005; Ribas-Carbo et al. 2005; Galmes et al. 2007). Taking into consideration the greater reduction of photosynthesis under drought conditions, the rate of

V. Vassileva (✉)
Acad. M. Popov Institute of Plant Physiology,
Bulgarian Academy of Sciences, Academik Georgi Bonchev,
Str., Block 21, 1113 Sofia, Bulgaria
e-mail: valyavassileva@mail.bg

C. Signarbieux · I. Anders · U. Feller
Institute of Plant Sciences and Oeschger Centre for Climate
Change Research (OCCR), University of Bern, Altenbergrain 21,
3013 Bern, Switzerland

respiration appears to be an important determinant, controlling plant survival during periods of water scarcity (Flexas et al. 2005; Galmes et al. 2007). The effect of dehydration on leaf respiratory metabolism depends basically on the duration and severity of drought periods. In general, leaf respiration slightly decreases or is unaffected during an early phase of dehydration stress. In some cases, it shows increased rates or a biphasic response consisting of successive inhibition and stimulation. Recovery of leaf respiration after rewatering does not also support a uniform response, showing either increased or unaffected respiratory rates (reviewed in Atkin and Macherel 2009).

Plants are often exposed to large temperature variations, which have important consequences for the respiratory metabolism in leaves (Bunce 2007). Temperature response of respiration is commonly described using Q_{10} values (change in respiration during a 10°C increase in temperature) as indicator of temperature sensitivity (Bruhn et al. 2008). Although Q_{10} values of respiration are assumed to be around 2.0 meaning that respiration rates double for each 10°C temperature rise, in most plant tissues they differ from this number. Generally, Q_{10} values are higher in tissues with high levels of soluble carbohydrates (Whitehead et al. 2004) and in tissues with higher energy demands associated with environmental stress (Atkin et al. 2000). In addition, temperature sensitivity of leaf respiration differs considerably among species (Galmes et al. 2007).

One of the approaches to improving plant performance under drought is development and cultivation of plants with high intrinsic water use efficiency (WUE). In agronomic terms, WUE is defined as the ratio between total dry matter produced and water used. At leaf level, it is defined as the ratio of net carbon assimilation to transpiration from stomata (Condon et al. 2002). There is evidence for genetic variation of WUE among cultivars and populations (Pou et al. 2008). According to Hubick et al. (1986), WUE might not be used as a criterion for determining the advantage of one particular species over others but can give an idea about the variation amongst genotypes under limited water supply.

Plant drought tolerance is a highly complex trait that involves multiple genetic, physiological and biochemical mechanisms (Cushman and Bohnert 2000; Erdei et al. 2002; Mattana et al. 2005). The degree of plant drought tolerance differs not only among various species but also among different varieties of the same species. A recent report on the performance of three genotypes of winter wheat with different drought tolerance displayed a variety-specific respiratory response under drought stress and during the subsequent recovery at tissue and organelle levels (Vassileva et al. 2009). Phosphorylation efficiency of leaf mitochondria in the drought-sensitive genotypes was significantly reduced under dehydration due to the decreased cytochrome pathway activity and an increased contribution of the alternative pathway. Additionally, these mitochondria exhibited a reduced presence in leaf tissue under drought conditions. On the contrary, mitochondria from the drought-tolerant variety showed higher phosphorylation rates and better structural performance. This report raised a number of questions concerning the relation of respiration to other physiological processes and its role in plant drought tolerance.

In the present study, the same three wheat varieties as those tested for drought-induced responses of leaf mitochondria were used to compare effects of dehydration on leaf gas exchange parameters, focusing particularly on respiration characteristics. Plants were subjected to moderate and severe drought stress conditions, followed by a 3-day period of rehydration. Additionally, the effect of drought and short-term changes of leaf temperature in the range 20–45°C on leaf respiratory parameters was studied. A combination of drought and high temperature stress is often encountered by many plants in the field. Moreover, stomatal closure in response to water stress can lead to an increased temperature in the leaves and affects their respiration properties.

Materials and methods

Plant material and growth conditions

Experiments were performed with three varieties of winter wheat (*Triticum aestivum* L.) differing in their field drought resistance: Sadovo considered as drought-sensitive, Katya classified as drought-tolerant, and Prelom considered as drought-sensitive (Simova-Stoilova et al. 2006; Demirevska et al. 2008; Vassileva et al. 2009). Plants were grown in pots containing an enriched soil mixture (9 plants per pot, 3 plants per variety in the same pot) under controlled conditions in a growth chamber with a light intensity of 150 μmol m^{-2} s^{-1}, day/night temperatures 25/21°C, and a 14-h photoperiod. Drought was induced on 22-day-old plants by withholding watering for 14 days, followed by a 3-day rehydration period. Control plants were watered every 2 days. Throughout the experiments, the first (lowest) leaf was used for respiration and gas exchange measurements.

Leaf water potential

Leaf water potential was measured every day during the experimental period using a Scholander pressure chamber (SKPM, Skye Instruments Ltd, Powys, UK). Three replicates per treatment were obtained from three different plants.

Respiration measurements

Respiration rates of the three wheat varieties grown under progressive drought stress and subsequent 3-day recovery period were measured as net rates of CO_2 efflux in darkness by an open gas analyzer system (CIRAS-1, PP Systems, Amesbury, Hitchin, UK) equipped with a PLC4 (B) Broad Leaf Cuvette. A single leaf was measured in the cuvette, partially covering the cuvette window. Upon completion of respiration assays, the length and diameter of each measured leaf section were defined, and the leaf area was calculated geometrically. The recorded respiration rates were adjusted for the actual leaf area. The response of respiration to short-term temperature changes within the range 20–45°C was determined by placing a single leaf in the PLC4 cuvette and rapidly changing the cuvette temperature. This system provided accurate automatic control of cuvette temperature. Measurements were done after the temperature and respiration rates were stable for about 5 min at each temperature. These measurements were conducted within 2 h of the beginning of the dark period, to avoid substrate deficiency affecting respiration. Q_{10} values were calculated across the temperature range of 20–45°C, using the data in Fig. 4, according to the equation $Q_{10} = (R2/R1)^{[10/(T2 - T1)]}$, where $T2$ is the higher measurement temperature, $T1$ is the lower measurement temperature, $R2$ is the respiration rate at temperature $T2$, and $R1$ is the respiration rate at temperature $T1$.

Gas exchange measurements

Stomatal conductance, transpiration and photosynthetic capacity were determined at saturating light (400 μmol m^{-2} s^{-1}), 25°C and 380 μmol mol^{-1} CO_2 with a portable photosynthesis measuring device (CIRAS-2, PP Systems, Hitchin, UK) connected to a PLC6 (U) Automatic Universal Leaf Cuvette and a LED-light unit. The leaf gas exchange parameters were monitored every day. WUE at leaf level was calculated as the ratio of carbon assimilation to transpiration efficiency of the stomata.

Statistical analyses

The results presented are the mean with standard errors of three to eight replicates from two independent experiments. Data are presented as mean ± SE (standard error). One-way analysis of variance (ANOVA) followed by post hoc multiple comparison using Tukey test (Sokal and Rohlf 1981) was performed to estimate the significance of the results. The minimum accepted P value for significance is 0.05.

Results

Leaf water potential

Water stress was imposed on the wheat varieties Sadovo, Katya and Prelom by withholding water supply for a 14-day period. Leaf water potential values were measured in the first leaf and varied between −0.3 and −0.4 MPa in well-watered plants (Fig. 1). Upon dehydration, these values gradually decreased, and after 7 days of water cessation, the leaves of the drought-tolerant Katya genotype maintained higher water potential than the drought-sensitive Sadovo and Prelom varieties. In the end of the drought period (14th day), all varieties showed values around −2.0 MPa. During the recovery period however the leaf water potential of Katya increased faster reaching −0.7 MPa at the first day after rewatering, whereas the drought-sensitive varieties returned to values close to controls only at the third day after the beginning of the recovery period.

Leaf respiration

Figure 2 shows the response of leaf respiration to progressive drought stress. In well-watered plants, the rate of respiration per unit leaf area averaged between 1.00 and 1.25 μmol m^{-2} s^{-1} and did not differ significantly among the wheat varieties studied. Under dehydration, these rates gradually decreased, as the drought-tolerant Katya showed

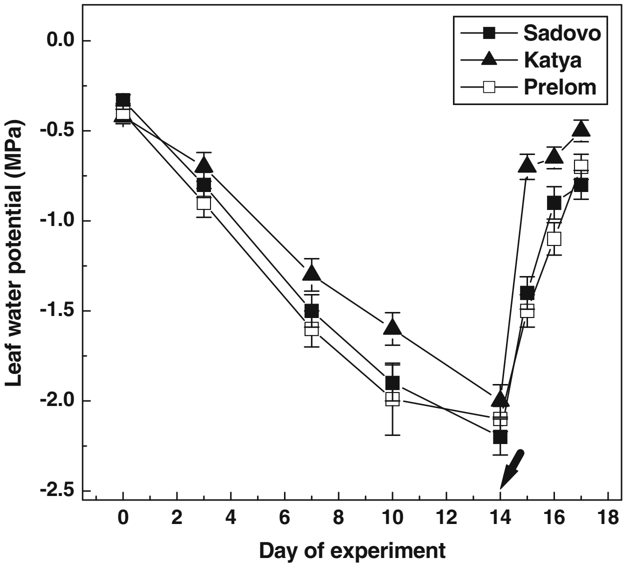

Fig. 1 Leaf water potential of three wheat genotypes exposed to gradual drought stress and subsequent rewatering. The *arrow* indicates the beginning of the recovery period. *Vertical bars* represent standard errors of the mean ($n = 3$). *Some bars* are not shown when masked by the *symbol*

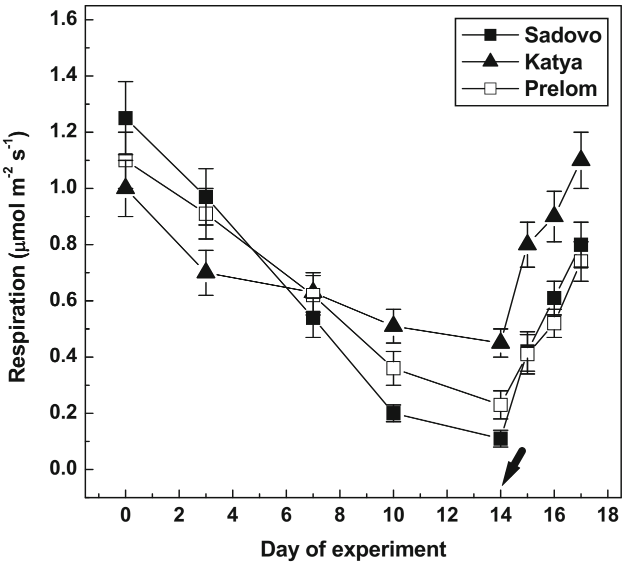

Fig. 2 Leaf respiration of three wheat genotypes exposed to gradual drought stress and subsequent rewatering. The *arrow* indicates the beginning of the recovery period. *Vertical bars* represent standard errors of the mean ($n = 8$)

the most pronounced respiration decrease at earlier stages of water cessation. As dehydration intensified, this genotype gave higher values than those of the drought-sensitive varieties. Under severe drought stress conditions (on 10th and 14th day after withholding irrigation), respiration rates in Katya leaves were significantly higher than those in drought-sensitive varieties. The effect of rewatering was also variety-dependent and varied from rapid recovery in Katya to slow and only partial recovery in the drought-sensitive Sadovo and Prelom genotypes.

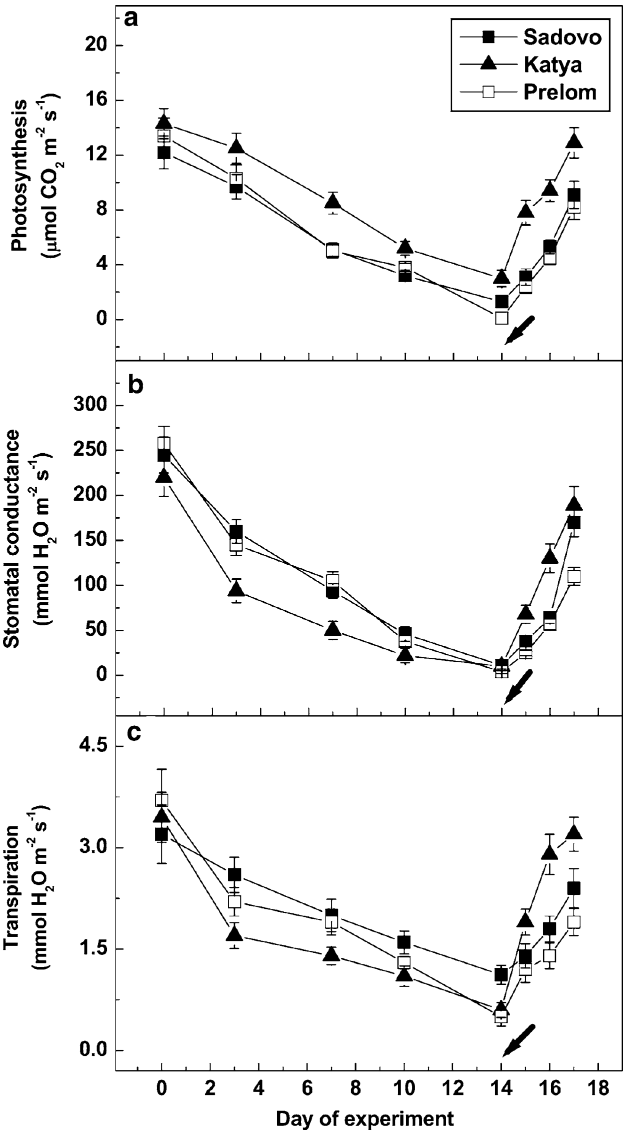

Fig. 3 Leaf gas exchange parameters of three wheat genotypes exposed to gradual drought stress and subsequent rewatering. The *arrow* indicates the beginning of the recovery period. *Vertical bars* represent standard errors of the mean ($n = 5$). *Some bars* are not shown when masked by the *symbol*

Leaf gas exchange parameters

Measurements of leaf gas exchange parameters under control, drought and recovery conditions showed very similar response patterns for all varieties studied (Fig. 3). In general, progressive dehydration caused a gradual decline of leaf gas exchange rates. However, during the water stress progression, the photosynthetic capacity of the drought-sensitive Sadovo and Prelom varieties was approximately 40% lower than that of the drought-tolerant Katya variety (Fig. 3a). At the 14th day of water withholding (severe dehydration), the variety Prelom was identified as the most sensitive genotype in terms of photosynthetic capacity. Interestingly, after 4 and 7 days of drought, the stomatal conductance in Katya leaves (Fig. 3b) was lower than that of Sadovo. Another interesting aspect was that stomata of Katya showed greater dynamics compared with the drought-sensitive varieties. The average time for the decrease of stomatal conductance under dehydration and for its increase under rewatering was much shorter for Katya than for Sadovo and Prelom. Leaf transpiration followed closely the pattern of stomatal opening (Fig. 3c). In addition, the drought-induced stomatal closure in Katya led to an increase in the leaf WUE, which persisted during the whole period of dehydration (Table 1). In the leaves of drought-susceptible genotypes, the level of WUE was kept below the control values almost during the entire drought experiment, and could reach values close to controls only after rewatering.

Table 1 Water use efficiency of three varieties of winter wheat exposed to normal watering, drought stress and rewatering

	Sadovo	Katya	Prelom
Days after beginning of drought stress			
0	3.81 a	4.14 a	3.62 a
3	3.83 a	7.35 b	4.68 b
7	2.55 b	6.07 b	2.63 a
10	2.00 b	4.72 a	2.92 a
14	1.16 c	5.00 ab	0.80 c
Beginning of rewatering			
15	2.21 b	4.11 a	2.00 ac
16	2.94 ab	3.24 a	3.21 a
17	3.79 a	4.03 a	4.32 ab

The values were calculated as the ratio of photosynthesis to transpiration, using the data in Fig. 3

Different letters in the same column indicate significant difference by multiple comparison Tukey's test ($P < 0.05$)

Temperature dependence of leaf respiration under drought treatment

In well-watered plants, leaf respiration responded to short-term variations in temperature with a gradual increase of respiration rates that were not significantly different among varieties in the range 20–35°C (Fig. 4a). However, with a temperature rise to 40 and 45°C, Katya leaves showed approximately 35% lower respiration increase as compared to the drought-sensitive Sadovo and Prelom. A similar tendency was observed in plants subjected to drought stress for 7 days (Fig. 4b). At the 14th day of exposure to water cessation, Katya leaves demonstrated higher respiration rates almost over the whole temperature range (Fig. 4c). At the maximum point of 45°C, these rates were twofold greater than those of Sadovo and Prelom. In addition, 1 day rewatering resulted in almost complete recovery of leaf respiration at all measurement temperatures in Katya, whereas in the drought-sensitive varieties it could reach only about one-third of the control values. Calculation of Q_{10} values showed that the drought-stressed Katya leaves were less temperature sensitive across the whole measurement temperature range, displaying lower Q_{10} values than the drought-sensitive varieties (Table 2).

Discussion

Three wheat genotypes Sadovo, Katya and Prelom were subjected to a progressive water stress and their water status was assessed by measuring leaf water potential and stomatal conductance. The leaf water potential significantly decreased in a variety-dependent manner. The drought-sensitive Sadovo and Prelom genotypes displayed a sharper water potential decline in comparison to the drought-tolerant Katya that maintained slightly higher values. Flexas et al. (2004) have shown that stomatal conductance is a more sensitive indicator of the severity and pattern of water stress development. According to the three measured intervals, the stomatal conductance values higher than 0.2 mol H_2O m^{-2} s^{-1} are considered as

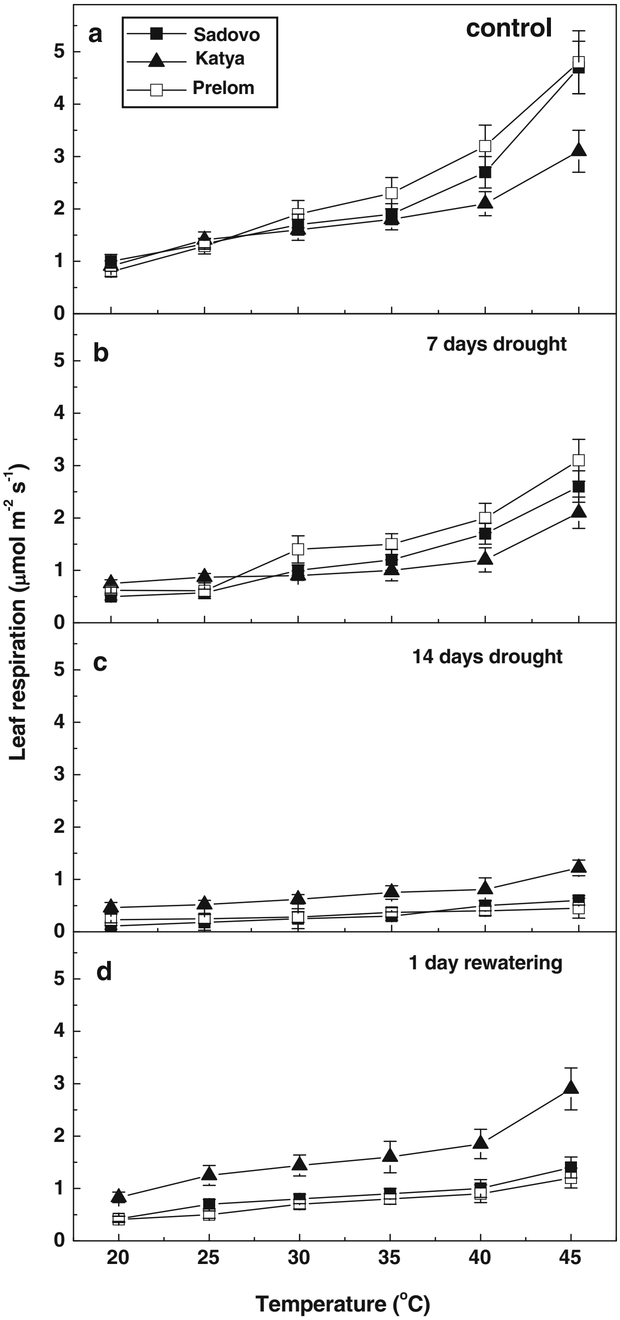

Fig. 4 Dependence of leaf respiration on short-term changes of temperature of three wheat genotypes exposed to gradual drought stress and subsequent rewatering. The *arrow* indicates the beginning of the recovery period. *Vertical bars* represent standard errors of the mean ($n = 3$). *Some bars* are not shown when masked by the *symbol*

Table 2 Q_{10} values for three varieties of winter wheat exposed to normal watering, 7 and 14 days drought stress and 1 day recovery

Variety	Control	7 days drought	14 days drought	1 day rewatering
Sadovo	1.87 ± 0.13 b	2.06 ± 0.12 b	2.16 ± 0.13 b	1.58 ± 0.18 a
Katya	1.47 ± 0.15 a	1.56 ± 0.16 a	1.62 ± 0.09 a	1.43 ± 0.16 a
Prelom	1.97 ± 0.15 b	2.11 ± 0.21 b	1.34 ± 0.08 a	1.49 ± 0.10 a

Q_{10} values were calculated across the temperature range of 20–45°C, using the data in Fig. 4, according to the equation $Q_{10} = (R2/R1)^{[10/(T2 - T1)]}$, where $T2$ is the higher measurement temperature, $T1$ is the lower measurement temperature, $R2$ is the respiration rate at temperature $T2$, and $R1$ is the respiration rate at temperature $T1$

Different letters indicate significant differences ($P < 0.05$) between treatments, evaluated by a multiple comparison Tukey's test

control rates, values between 0.1 and 0.2 mol H_2O m^{-2} s^{-1}—as mild water stress, and lower than 0.1 mol H_2O m^{-2} s^{-1}—as severe water stress. By these criteria, the drought-sensitive Sadovo and Prelom varieties reached level of mild water stress between second and seventh days of the drought period. Interestingly, in the drought-tolerant Katya variety, the stomatal conductance dropped faster and at the third day of drought treatment reached threshold values indicative of severe water stress. It seems that under low water supply, Katya genotype has the ability to maintain higher leaf water potential by keeping stomata less open. It is thought that rapid stomatal response may act as a drought resistance mechanism, which permits to keep water for later use and thus to maintain higher leaf water potentials (Teare et al. 1973; Jones 1974). Generally, stomatal closure protects plants against excessive water loss, but also restricts the diffusion of CO_2 into the photosynthetic parenchyma. In Katya genotype however, despite the lower stomatal conductance, photosynthesis values were kept higher during the whole drought period. In general, stomatal closure causes a greater decrease in transpiration than in photosynthesis rates, thereby increasing the relative leaf WUE (Pou et al. 2008). The quicker decrease in the transpiration rates of Katya leaves and lower decrease in photosynthesis efficiency resulted in much higher intrinsic leaf WUE. The higher value of WUE at leaf level in Katya has been already reported by Van den Boogaard et al. (1996). Thus, more dynamic stomata of Katya genotype could be one of the prerequisites for a better performance during drought stress.

On the other hand, the respiration of mature leaves in the drought-tolerant Katya variety was significantly reduced at earlier stages of water limitation when stomatal conductance values decreased bellow 0.2 mol H_2O m^{-2} s^{-1}, whereas respiration in the drought-sensitive genotypes basically decreased when stomatal conductance dropped below 0.1 mol H_2O m^{-2} s^{-1}. Generally, the respiration rate of plant tissues is affected by supply of substrates and demand for ATP (Williams and Farrar 1990). It is regulated at several levels ranging from metabolite control to gene expression (Atkin and Macherel 2009). Leaves show very diverse character of respiratory responses to dehydration and rewatering (Flexas et al. 2005), and some of these responses give implications for plant stress tolerance. Our recently published work with mitochondria isolated from leaves of wheat plants grown under dehydration and subsequent recovery clearly demonstrated variety-specific differences in leaf respiration (Vassileva et al. 2009). Mitochondria from the drought-tolerant Katya genotype had a relatively stable oxidative phosphorylation efficiency, whereas mitochondria from the drought-sensitive Sadovo and Prelom showed very low phosphorylation rates due to decreased cytochrome pathway activity. Comparing differences in leaf respiration due to short-term temperature increase demonstrated similar respiration responses for all the genotypes studied. The temperature increase was accompanied by an increase in leaf respiration rates, which was most clearly seen at the highest temperatures; Q_{10} of respiration also showed a tendency of increase. Hence, simultaneous application of drought stress and high temperature affected metabolism of the wheat varieties in different manner, compared with the application of drought stress only. However, over the whole temperature range, the leaves of Katya, exposed to dehydration for 14 days, showed higher respiration rates compared to drought-sensitive genotypes. This is just opposite to what was found for Sadovo and Prelom that kept higher respiration rates under control and mild drought stress conditions, and very low rates under severe water stress. Mitochondria may play a crucial role when water stress and high temperature occur simultaneously, due to the fact that photosynthesis is greatly suppressed, whereas respiration is increased in order to meet demands for ATP (Rizhsky et al. 2002; Atkin and Macherel 2009). The functional capacity and structural stability of mitochondria isolated from leaves of Katya exposed to severe drought was much higher than that of the drought-sensitive varieties (Vassileva et al. 2009). It appears that Katya can adjust mitochondrial respiration rates according to the increased demands for ATP under a combination of drought and high temperature, as well. Its ability to recover quickly from co-occurring stress damages, returning back to the control respiration values at the first day after rewatering, contributes additionally to its stress tolerance. Capacity of plants to recover after severe stress is a very crucial element of plant drought resistance in the field. Selection and introduction of cultivars and varieties with a high recovering capacity is especially important, as the severity of stress injury could be reduced. The drought-tolerant Katya variety showed a remarkably rapid restoration speed after severe drought treatment for all other leaf gas exchange parameters tested, being able to reach values similar to controls at the first day after rewatering. Leaf respiration showed a faster recovery speed at the first day and proportional to the photosynthesis restoration in the next 2 days of rewatering. It seems that the increased respiration is necessary for the recovery of photosynthesis after a period of dehydration (Kirschbaum 1988). Mitochondrial respiration may play an important role in supplying chloroplasts with ATP, thus supporting chloroplast functions, and ultimately plant survival (Reinhold et al. 2007). Generally, plant carbon balance during recovery phase depends on the rates and extent of photosynthesis and respiration recovery (Flexas et al. 2006). However, the photosynthesis of the drought-sensitive varieties could recover only partially. One of the reasons for this incomplete recovery could be the drought-induced damages of chloroplasts and mitochondria. Transmission electron microscopy study of Sadovo and Prelom leaf samples displayed an enhanced mitochondrial degradation and pronounced morphological changes in the mitochondria provoked by exposure to severe drought (Vassileva et al. 2009). After the 3-day rehydration period, mitochondrial structure and leaf cell occupancy by mitochondria could not recover completely and some visible damages still occurred. At the same conditions, the organelles of the drought-tolerant Katya variety undergo complete recovery (Vassileva et al. 2009).

In conclusion, evaluation of the leaf gas exchange parameters in three wheat genotypes with different drought tolerance displayed the importance of leaf respiration for overcoming the periods of water deficit and successful recovery. Understanding the physiological mechanisms associated with genetic variation of plant stress tolerance and recovering capacity is crucial for the development and introduction of more drought-tolerant genotypes of crop species.

Acknowledgments This study was supported by grants from the Swiss National Science Foundation, SCOPES (project IZ73AO-111142, DILPA) and from the Ministry of Education and Science of Republic Bulgaria (project CC 1503). We apologize to all colleagues whose relevant work could not be cited due to space limitations.

References

Atkin OK, Macherel D (2009) The crucial role of plant mitochondria in orchestrating drought tolerance. Ann Bot 103:581–597

Atkin OK, Holly C, Ball MC (2000) Acclimation of snow gum (*Eucalyptus pauciflora*) leaf respiration to seasonal and diurnal variations in temperature: the importance of changes in the capacity and temperature sensitivity of respiration. Plant Cell Environ 23:15–26

Bruhn D, Schortemeyer M, Edwards EJ, Egerton JJG, Hocart CH, Evans JR, Ball MC (2008) The apparent temperature response of leaf respiration depends on the timescale of measurements: a study of two cold climate species. Plant Biol 10:185–193

Bunce JA (2007) Direct and acclimatory responses of dark respiration and translocation to temperature. Ann Bot 100:67–73

Condon AG, Richards RA, Rebetzke GJ, Farquhar GD (2002) Improving intrinsic water-use efficiency and crop yield. Crop Sci 42:122–131

Cushman JC, Bohnert HJ (2000) Genomic approaches to plant stress tolerance. Plant Biol 3:117–124

Demirevska K, Simova-Stoilova L, Vassileva V, Feller U (2008) Rubisco and some chaperone protein responses to water stress and rewatering at early seedling growth of drought sensitive and tolerant wheat varieties. Plant Growth Regul 56:97–106

Erdei L, Tari I, Csiszár J, Pécsváradi A, Horváth F, Szabó M, Ördög M, Cseuz L, Zhiponova M, Szilák L, Györgyey J (2002) Osmotic stress responses of wheat species and cultivars differing in drought tolerance: some interesting genes (advices for gene hunting). Acta Biol Szeged 46:63–65

Flexas J, Medrano H (2002) Drought-inhibition of photosynthesis in C_3 plant: stomatal and non-stomatal limitation revisited. Ann Bot 89:183–189

Flexas J, Bota J, Loreto F, Cornic G, Sharkey TD (2004) Diffusive and metabolic limitations to photosynthesis under drought and salinity in C3 plants. Plant Biol 6:269–279

Flexas J, Galmes J, Ribas-Carbo M, Medrano H (2005) The effects of water stress on plant respiration. In: Lambers H, Ribas-Carbo M (eds) Plant respiration: from cell to ecosystem. Advances in photosynthesis and respiration series, vol 18/6. Springer, Dordrecht, pp 85–94

Flexas J, Bota J, Galmes J, Medrano H, Ribas-Carbo M (2006) Keeping a positive carbon balance under adverse conditions: responses of photosynthesis and respiration to water stress. Physiol Plant 127:343–352

Flexas J, Diaz-Espejo A, Galmes J, Kaldenhoff R, Medrano H, Ribas-Carbo M (2007) Rapid variations of mesophyll conductance in response to changes in CO_2 concentration around leaves. Plant Cell Environ 30:1284–1298

Galmes J, Ribas-Carbo M, Medrano H, Flexas J (2007) Response of leaf respiration to water stress in Mediterranean species with different growth forms. J Arid Environ 68:206–222

Hubick KT, Farquhar GD, Shorter R (1986) Correlation between water-use efficiency and carbon isotope discrimination in diverse peanut (*Arachis*) germplasm. Aust J Plant Physiol 13:803–816

Jones HG (1974) Assessment of stomata control of plant water status. New Phytol 73:851–859

Kirschbaum MUF (1988) Recovery of photosynthesis from water stress in *Eucalyptus pauciflora*—a process in two stages. Plant Cell Environ 11:685–694

Lawlor DW, Cornic G (2002) Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. Plant Cell Environ 25:275–294

Mattana M, Biazzi E, Consonni R, Locatelli F, Vannini C, Provera S, Coraggio I (2005) Overexpression of *Osmyb4* enhances compatible solute accumulation and increases stress tolerance of *Arabidopsis thaliana*. Physiol Plant 125:212–223

Pou A, Flexas J, Alsina Mdel M, Bota J, Carambula C, de Herralde F, Galmés J, Lovisolo C, Jiménez M, Ribas-Carbó M, Rusjan D, Secchi F, Tomàs M, Zsófi Z, Medrano H (2008) Adjustments of water use efficiency by stomatal regulation during drought and recovery in the drought-adapted *Vitis* hybrid Richter-110 (*V. berlandieri* × *V. rupestris*). Physiol Plant 134:313–323

Reinhold T, Alawady A, Grimm B, Beran KC, Jahns P, Conrath U, Bauer J, Reiser J, Melzer M, Jeblick W, Neuhaus HE (2007) Nocturnal ATP import into chloroplasts as a novel control element in chlorophyll biosynthesis is critical to prevent photooxidative damage in Arabidopsis. Plant J 50:795–809

Ribas-Carbo M, Taylor NL, Giles L, Busquets S, Finnegan PM, Day DA, Lambers H, Medrano H, Berry JA, Flexas J (2005) Effects of water stress on respiration in soybean leaves. Plant Physiol 139:466–473

Rizhsky L, Liang H, Mittler R (2002) The combined effect of drought stress and heat shock on gene expression in tobacco. Plant Physiol 130:1143–1151

Simova-Stoilova L, Vassileva V, Petrova T, Tsenov N, Demirevska K, Feller U (2006) Proteolytic activity in wheat leaves during drought stress and recovery. Gen Appl Plant Physiol Spec Issue 91–100

Sokal RR, Rohlf FJ (1981) Biometry: the principles and practice of statistics in biological research, 2nd edn. Freeman, San Francisco

Teare ID, Kanemasu ET, Powers WL, Jacobs HS (1973) Water-use efficiency and its relation to crop canopy area, stomatal regulation, and root distribution. Agron J 65:207–211

Van den Boogaard R, de Boer M, Veneklaas EJ, Lambers H (1996) Relative growth rate, biomass allocation pattern and water use efficiency of three wheat cultivars during early ontogeny as dependent on water availability. Physiol Plant 98:493–504

Vassileva V, Simova-Stoilova L, Demirevska K, Feller U (2009) Variety-specific response of wheat (*Triticum aestivum* L.) leaf mitochondria to drought stress. J Plant Res 122:445–454

Whitehead D, Griffin KL, Turnbull MH, Tissue DT, Engel VC, Schuster WSF, Brown KJ, Walcroft AS (2004) Response of total night-time respiration to differences in total daily photosynthesis for leaves in a *Quercus rubra* L. canopy: implications for modeling canopy CO_2 exchange. Glob Chang Biol 10:925–938

Williams JHH, Farrar JF (1990) Control of barley root respiration. Physiol Plant 79:259–266