Impact of air drought on photosynthesis efficiency of the Siberian crabapple (Malus baccata L. Borkh.) in the forest-steppe zone of Transbaikalia, Russia (Postprint)

Authors: Alexandr RUDIKOVSKII

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Abstract

The adaption of photosynthesis, being a key metabolic process, plays an important role in plant resistance to air drought. In this study, the Siberian crabapple (Malus baccata L. Borkh.) in the forest-steppe zone of Transbaikalia region, Russia, was subjected to air drought stress and its photosynthesis characteristics were analyzed. The results show that air drought and sufficient soil moisture supply lead to the decrease in the total chlorophyll (Chl) content, while the ratio of Chls to carotenoids is constant in the Siberian crabapple tree. The function of photosystem II (PS-II) in the crabapple trees is characterized by a decrease in the fraction of absorbed light energy spent on the photochemical work and an increase in the proportion of non-photosynthetic thermal quenching. These changes indicate the photosynthetic down-regulation that acts as a universal photoprotective mechanism. During the midday hours, the combination of high air temperature and low air humidity leads to the decrease in the maximum photochemical quantum yield of photosystem II (Fv/Fm) and the efficiency of photosynthesis (PABS). The parameters of leaf gas exchange show the significant differences in these values between the control and experimental variants. During the morning hours, the Siberian crabapple, growing in the Irkutsk City, assimilates carbon dioxide more intensively. Due to the higher air humidity, the stomata are kept open and the necessary amount of carbon dioxide entries the sites of carboxylation. The low air humidity combined with wind in the experimental variants leads to the unreasonably high water loss in the crabapple leaves by more than 27% as compared to the control variant (Irkutsk City). However, water use efficiency in the morning hours increases during plant photosynthetic processes, i.e., 42% higher than that of control. This, apparently, is a reflection of the adaptation processes of the Siberian crabapple to the air drought and parching wind.

Full Text

Preamble

Impact of Air Drought on Photosynthetic Efficiency of the Siberian Crabapple (Malus baccata L. Borkh.) in the Forest-Steppe Zone of Transbaikalia, Russia

Alexandr RUDIKOVSKII, Elena RUDIKOVSKAYA*, Lyubov DUDAREVA
Siberian Institute of Plant Physiology and Biochemistry, Siberian Branch, Russian Academy of Sciences, Irkutsk 664033, Russia

Abstract: Adaptation of photosynthesis, being a key metabolic process, plays an important role in plant resistance to air drought. In this study, the Siberian crabapple (Malus baccata L. Borkh.) in the forest-steppe zone of the Transbaikalia region, Russia, was subjected to air drought stress and its photosynthetic characteristics were analyzed. The results show that air drought combined with sufficient soil moisture supply leads to a decrease in total chlorophyll (Chl) content, while the ratio of Chls to carotenoids remains constant in Siberian crabapple trees. The function of photosystem II (PS-II) in these trees is characterized by a decrease in the fraction of absorbed light energy spent on photochemical work and an increase in the proportion of non-photosynthetic thermal quenching. These changes indicate photosynthetic down-regulation that acts as a universal photoprotective mechanism. During midday hours, the combination of high air temperature and low air humidity leads to a decrease in the maximum photochemical quantum yield of photosystem II (Fv/Fm) and the efficiency of photosynthesis (PABS). The parameters of leaf gas exchange show significant differences between control and experimental variants. During morning hours, Siberian crabapple growing in Irkutsk City assimilates carbon dioxide more intensively. Due to higher air humidity, stomata remain open and the necessary amount of carbon dioxide enters the carboxylation sites. Low air humidity combined with wind in the experimental variants leads to unreasonably high water loss in crabapple leaves—more than 27% compared to the control variant (Irkutsk City). However, water use efficiency during morning hours increases during photosynthetic processes, i.e., 42% higher than that of the control. This apparently reflects the adaptation processes of Siberian crabapple to air drought and parching wind.

Keywords: air drought; chlorophyll fluorescence; leaf gas exchange; pigments; water use efficiency

Abbreviations: ABS, absorbed energy flux; Chl, chlorophyll; ET, electron transport flux; ETR, electron transport rate; F0, minimum fluorescence yield in dark-adapted state; Fm, maximum fluorescence yield in dark-adapted state; Fm', maximum fluorescence yield in light-adapted state; F0' , minimum fluorescence yield in light-adapted state; Fv/Fm, quantum yield of photosystem II; PAR, photosynthetically active radiation; PS-II, photosystem II; RC, reaction center; TR, trapping flux; VPD, vapour pressure deficit; WUE, water use efficiency;

Y(II), effective quantum yield of photosystem II; Y(NPQ), quantum yield of non-photochemical quenching; Ψ0, probability that a photon trapped by the PS-II reaction center enters the electron transport chain beyond QA (the primary electron acceptor quinone in PS-II) (at t=0); Po, the maximum quantum yield of primary photochemistry at t=0.

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*Corresponding author: Elena RUDIKOVSKAYA (E-mail: rudal69@mail.ru)

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1 Introduction

Climate change estimates show that the presently observed increase in average global temperature will continue in the future (Bodner et al., 2015; Borland et al., 2015). Rising temperatures and vapour pressure deficit (VPD) in the air enhance soil evaporation and leaf transpiration, leading to water stress in plants. Soil and air drought are among the most significant abiotic stress factors limiting plant growth and ecosystem productivity globally (Bodner et al., 2015).

The ability of plants to adapt to changing conditions is directly or indirectly connected with the plasticity of photosynthesis, which—combined with other processes—determines plant growth and development and ultimately their successful propagation. Since photosynthesis is highly sensitive to external environmental factors, the dependence of plant growth and development on these factors can be estimated by measuring the photosynthetic response to ecological stressors (Lang et al., 2018).

The factors limiting plant photosynthesis under drought conditions can be of stomatal or non-stomatal nature. The degree of influence of each factor can be estimated by studying net photosynthetic rate (Pn), intercellular CO2 concentration (Ci), and stomatal limitation (Lang et al., 2018). Research shows that the decrease in Pn after a certain degree of drought may result from the joint influence of stomatal and non-stomatal factors (Zhang et al., 2010).

Increasing drought intensity or duration reduces net photosynthetic productivity due to non-stomatal limitation—structural and functional alterations of the leaf photosystem connected with damage to the photosynthetic apparatus as well as reduced electron transport activity and light energy conversion efficiency (Lang et al., 2018). Additionally, drought causes noticeable destruction of membrane systems and ultrastructural damage to chloroplasts (Ghotbi-Ravandi et al., 2014).

Persistence of photosynthetic light reactions under drought conditions and reduced Ci leads to accumulation of reduced components of the electron transport chain, which may cause severe damage to the photosynthetic apparatus. Protective mechanisms such as thermal dissipation of light energy, the xanthophyll cycle, the Mehler reaction, and dissociation of light-harvesting complexes from photosystem II (PS-II) reaction centers (Basu et al., 2016) function in plant cells to reduce such damage. Some authors consider the decrease in pigment content under drought as a special photoprotective mechanism that reduces light absorption (Liu et al., 2011). As drought intensifies, a higher Chla/Chlb ratio leads to decreased amounts of peripheral light-harvesting complexes, reducing light absorption by PS-II.

The mechanism limiting photosynthetic rate becomes especially complex when drought reaches a certain severity. In such cases, simple analysis of leaf gas exchange parameters cannot accurately represent the degree of damage to the photosynthetic apparatus. Chlorophyll fluorescence can be considered an integrated probe for studying the interrelation between plant photosynthesis and environment and is now widely used in studies devoted to mechanisms underlying responses of different vegetation types to ecological stress (Lang et al., 2018).

The effects of high air temperature and drought on plants are fairly well studied. However, experiments combining water stress and high temperature are rare, although these factors together often adversely affect plant growth and productivity in nature (Sehgal et al., 2018). The combination of soil and air drought with high temperature is expected to increase in the near future, making the study of this stressor combination—and the contribution of each stressor —highly topical for understanding the mechanisms of influence and possibly for improving tolerance in economically valuable crops (Zandalinas et al., 2018). Generally, photosynthetic activity is repressed via destabilization of Rubisco and PS-II damage under abiotic stresses. However, the influence of drought, thermal stress, or their combination on photosynthesis can differ depending on plant species and habitat.

In arid and semi-arid forest ecosystems, changes in forest structure and increased tree mortality rates have been observed recently, deemed to be connected with climate warming and severe droughts (Borland et al., 2015; Liang et al., 2016). Climate change consequences are most pronounced in semi-arid regions. To understand adaptation potential and estimate species vulnerability under drought and high temperature, we must study these processes in forest ecosystems at a regional level.

Although soil moisture plays a crucial role in local differentiation of forests and steppes due to differing plant water demand (Liu et al., 2015), air drought and attendant VPD also greatly influence leaf gas exchange and consequently reduce stomatal conductance (Perez-Martin et al., 2009). VPD is especially important for woody plants, being the main driver influencing transpiration and stomatal conductance within 24 hours. There is high probability that rising air temperature, closely connected with global warming, will increase VPD and enhance stress load in plants against the background of soil drought in forest biomes (Borland et al., 2015). This necessitates individual estimation of air drought contribution to the overall influence of moisture deficiency.

The Transbaikalia region in Russia includes forest-steppe ecotones in southern and eastern Baikal Lake areas and is currently under the influence of both air and soil drought. The Transbaikalia forest-steppe ecotone is an area with low precipitation, which decreased by almost 25% during the first decade of the 21st century (Kharuk et al., 2013). The locally estimated warming trend for this region amounts to 0.05°C–0.08°C per annum, with accelerated warming shown to occur in the second half of the 20th century (Anenkhonov et al., 2015).

In this region, we found small populations of Siberian crabapple (Malus baccata L. Borkh.) growing in the underbrush of sparse pine forests and steppe areas (Rudikovsky et al., 2008). The Siberian crabapple grows directly next to mountain streams. These plants are not endemic species and have sufficient soil moisture. However, during the spring/summer season, the trees are subject to unfavorable influences of dry air and high air temperature. Comparing trees growing near mountain streams with control ones will allow individual estimation of air drought influence and sufficient soil water supply on photosynthetic apparatus efficiency. It should be noted that control plants grow under conditions close to optimal and are, by origin, clones of trees growing under natural conditions described above. In addition to information about photosynthetic apparatus functioning under these unusual conditions, we obtain a model of artificial irrigation of apple trees, a practice that can be improved based on gained knowledge.

In light of this, the aim of our study is to analyze the influence of air drought on adaptation processes of the photosynthetic apparatus of Siberian crabapple (Malus baccata L. Borkh.) growing in the contact zone of forest and steppe. To achieve this aim, we measured gas exchange parameters in leaves, pigment content, and chlorophyll fluorescence of Siberian crabapple growing naturally and under control conditions.

2.1 Study Area and Materials

The Transbaikalia region has a continental climate characterized by a short vegetation period of 100-130 days, abrupt oscillations of daily and monthly average air temperatures, May–June drought that decreases plant crops, high intensity of solar radiation, and insufficient, uneven precipitation. Annual precipitation in the middle Selenga River current is 210–250 mm, while 80%–90% falls in July–August. Currently, vegetation of the sub-taiga belt is presented by steppificated pine forests interspersed with steppe areas, suggesting fluctuation of forest ecosystems in the contact zone and their probable transformation to steppe.

In this study, we evaluated Siberian crabapple plants growing near Yagodnoye Village (1st site; 51°24 05 N, 106°30 30 E), 12.5 km from Gusinoozersk Town

(Selenga Province, Buryat Republic) in the contact zone between forest and dry steppe. The trees were growing close to a flowing mountain stream (about 2 m). Siberian crabapple trees growing at the experimental site of the Siberian Institute of Plant Physiology and Biochemistry within Irkutsk City (2nd site) served as control plants. These trees represented clones from the natural experimental population propagated from root suckers.

Climate in Irkutsk City is less continental compared to the Transbaikalia region due to functioning of hydroelectric power stations and other water reservoirs along the Angara River. Mean annual precipitation is 472 mm, with more than half occurring in summer. Table 1 presents values of air humidity, precipitation, temperature, and maximum wind speed for June–July of 2010–2012 in Yagodnoye Village and Irkutsk City. Data were taken from http://www.rp5.ru.

2.2 Pigment Measurement

The quantitative composition of pigments was determined by spectrophotometric method using a standard approach (von Wettstein, 1957). Leaf tissue (50 mg) frozen with liquid nitrogen was homogenized using 3 mL of 80% acetone with a small amount of CaCO3. The homogenate volume was increased to 10 mL and centrifuged at 2000 g (Allegra 64 R, Germany) for 10 min at 4°C. Acetone extract (3 mL) was placed in a cuvette and optical density was determined at 440.5, 644.0, and 662.0 nm using spectrophotometer SF-46 (LOMO, Russia). Concentrations of chlorophyll a (Chla), chlorophyll b (Chlb), total Chla+b, and carotenoids (Car) were calculated using the following formulas (Osipova et al., 2016):

Chla = 9.78A662 -0.990A644
Chlb = 21.43A644 -4.65A662
Chla+b = 5.134A662 + 20.44A644
Car = 4.695A440.5 -0.268(Chla+b)

where A662 is absorbance at 662 nm; A644 is absorbance at 644 nm; and A440.5 is absorbance at 440.5 nm.

2.3 Chlorophyll Fluorescence

Chlorophyll a fluorescence of apple leaves was measured in the morning, at noon, and in the evening. Photosynthetic efficiency was estimated by chlorophyll a fluorescence values determined using a portable pulse fluorimeter PAM-2500 (Walz, Effelrich, Germany). Dark adaptation of leaves was carried out for 30 min. Red actinic light (677 mol/($m^2 \cdot s$)) was used to support photosynthesis. For analysis, we used well-lit leaves from the middle part of plants that were fully developed, dark green, of the same size, and without signs of damage. Measurements were conducted in the morning (09:00–11:00 LST), at noon (12:00–14:00), and in the evening (17:00–20:00).

In Yagodnoye Village, chlorophyll fluorescence measurements were carried out during a week in June (9-16 June in 2010, 2011 and 2012) or July (9-16 July in 2010, 2011 and 2012). In Irkutsk City, the same measurements were also conducted for a week in June (18-24 June in 2010, 2011 and 2012) or July (18-24 July in 2010, 2011, and 2012). Fluorescence results were considered separately: those obtained on sunny, hot days when temperature and lighting were highest, and those obtained on days when midday temperature did not rise above 25°C.

Quantitative analysis of primary photosynthesis process characteristics was conducted based on fluorescence kinetic curve parameters using the OJIP-test, which is based on energy pathway theory (Strasser et al., 2004). For calculations, we used the following curve parameters: minimal fluorescence yield in dark-adapted state (F0 or O); fluorescence intensity at 300 s; fluorescence intensity at 2 ms (F2ms, J-peak); fluorescence intensity at 30 ms (F30ms, I-peak); and maximal fluorescence yield in dark-adapted state (Fm or P). OJIP-test parameters and calculation formulas (Kalaji et al., 2014) are given in Table 2 .

2.4 Stomatal Conductance, Transpiration, and Photosynthetic Rate

To evaluate carbon dioxide assimilation rate, we determined stomatal conductance, transpiration rate, carbon dioxide assimilation rate, and carbon dioxide concentration in fully developed leaves from the middle part of plants without signs of damage. Measurements were conducted using a portable gas analyzer (LCi Photosynthesis System, ADC BioScientific Ltd., Hoddesdon, England). Water use efficiency (WUE) was calculated as the ratio of net photosynthesis to transpiration. Data on air temperature and light intensity were also measured.

Field soil humidity and full field water capacity (FFWC) were determined according to Vadyunina and Korchagina (1986). Air vapour pressure deficit was calculated using Murray’ s formula (1967) with temperature and air humidity taken into account.

Each experiment to determine chlorophyll fluorescence and photosynthesis parameters was performed with five biological replicates. Chlorophyll concentration studies were performed with 5-9 biological replicates. Statistical analyses were conducted using Excel software (MS Office 2007) and StatSoft STATISTICA 12. Normality of distribution was assessed using the Shapiro-Wilk criterion. Significance of differences between variants was determined using Student’ s t-criterion (P 0.05).

3 Results

Soil physical properties showed that in the underbrush of pine forest near Yagodnoye Village, on sites where apple trees grew next to the mountain stream, soil moisture was 71.0% (±4.2%) of FFWC in June, varying only slightly in July. Soil humidity at the Irkutsk City site was 79.6% (±9.1%) of FFWC in June and

July. During hot weather in June in Irkutsk City, soil humidity was sustained at an optimal level (75%-80% of FFWC).

There was no significant difference between photosynthetically active radiation values obtained at the Yagodnoye and Irkutsk sites (Fig. 1 [Figure 1: see original paper]).

Total chlorophyll content in leaves increased in July compared to June. For trees growing under natural conditions in Yagodnoye Village, total chlorophyll content was lower in both June and July compared to trees growing in Irkutsk City (Fig. 2a [Figure 2: see original paper]).

No significant differences were found in the ratio of chlorophylls to carotenoids between trees at control and experimental sites, including both June and July periods (Fig. 2b).

Plants from both study sites maintained a functional photosynthetic mechanism in June and July according to main chlorophyll fluorescence parameters (Tables 3 and 4). This was confirmed by low F0 values and high potential maximum chlorophyll fluorescence levels (Fv/Fm) in the morning.

However, drought in the forest-steppe zone in June adversely affected photosynthetic efficiency of Siberian crabapple (Table 3). In June, evaluated groups differed only slightly in basic chlorophyll a fluorescence parameters during morning hours, but this difference increased during midday. Plants growing in Irkutsk City showed higher Fv/F0 values, suggesting greater probability of capturing excited energy by PS-II antenna systems in these apple leaves (Table 3), which in turn influenced PABS values.

The main differences observed between plants growing under natural conditions and those in Irkutsk City were in Y(II) parameters (real quantum efficiency of PSII). This value was approximately 1.5 times higher in Irkutsk City than in Yagodnoye Village (see Table 3), reflecting differences in the degree of photochemical usage of absorbed PS-II light energy in the studied apple trees. Additionally, apple plants growing under natural conditions showed higher quantum yield of Y(NPQ) (non-photochemical fluorescence quenching). Values of Fv/Fm, Y(II), and Y(NPQ) indicated that leaves reduced negative drought effects on the photosynthetic apparatus through down-regulation.

OJIP-test data also indicated intensified negative impact of adverse conditions in the contact area on PS-II of apple leaves in June at midday, when sunny day temperatures exceeded 25°C. This was accompanied by decreased Fv/Fm and PABS index values (Table 3). In this case, relative variable fluorescence at 2 ms (VJ) increased in experimental trees compared to control plants, indicating a higher proportion of closed reaction centers relative to their total number. Siberian crabapple trees in Irkutsk City showed higher Fv/F0 rates, which characterize the ability of antenna systems to capture energy. Treated trees in Irkutsk City also had greater Ψ0 values, reflecting higher probability of electron transfer from the primary electron acceptor quinone in PS-II (QA) to the quinone pool.

In July, spring-summer drought is somewhat mitigated by increased air humidity and rainfall in the Transbaikalia region (Table 1). Increasing moisture content improved PS-II condition in plant leaves in both experimental variants. Nevertheless, real quantum efficiency of PS-II values indicated that the proportion of absorbed light energy directed to photochemical work was greater in trees growing in Irkutsk City (Table 4). Apparently, this is because despite slight increases in air humidity, water vapour pressure deficit values remained high due to high air temperature in the Transbaikalia region (Fig. 3 [Figure 3: see original paper]).

Due to higher temperature and lower humidity, VPD values were higher at the control site in both July and June (Fig. 3). High VPD values were accompanied by higher wind speed, a trend typical for both months (Fig. 4 [Figure 4: see original paper]). Correlation coefficients in Irkutsk City were 0.988 in June and 0.955 in July, while in Yagodnoye Village they were 0.970 in June and 0.955 in July.

Carbon dioxide assimilation rate findings showed significant differences between control and experimental variants (Table 5), caused by environmental conditions. In the morning, leaves of apples growing in Irkutsk City assimilated carbon dioxide more intensively due to available soil moisture and higher air humidity, which allowed plants to keep stomata open, providing necessary carbon dioxide access to carboxylation sites. Lower air humidity in Yagodnoye Village resulted in stomatal conductance for vapour and transpiration decreasing by more than twofold to reduce unreasonably high water loss in crabapple leaves. This eventually reduced carbon dioxide assimilation speed in experimental trees in Yagodnoye Village by more than 27% compared to control trees in Irkutsk City. Activation of mechanisms contributing to water consumption optimization (stomatal closure and consequent conductance decrease) resulted in WUE increase during photosynthesis in naturally growing plants—42% higher than in control plants.

4 Discussion

It is generally believed that changes in the ratio of chlorophylls to carotenoids against a background of decreased total chlorophyll indicate plant stress status (Lichtenthaler and Babani, 2004). Since chlorophyll reduction in apple was not accompanied by changes in the Chls/carotenoids ratio in our case, the reduction in total chlorophyll content may be assumed to be adaptive in nature (reduction in ability to capture radiant energy). Under drought conditions, excessive light absorption by the photosynthetic apparatus is accompanied by formation of reactive oxygen species that adversely affect cells. Reducing their amount can be achieved by degradation of a certain portion of photosynthetic pigments (Liu et al., 2011).

Dissipation of excess light energy via the xanthophyll cycle acts as a photoprotective mechanism, converting light energy into heat (Jahns et al., 2012). At high light levels, when stomatal conductance is reduced against a background of available carbon dioxide, leaves generate more energy than consumed by the Calvin cycle. Under such circumstances, down-regulation of photosynthesis can be a powerful mechanism protecting C3 plants against photodamage (Cruces et al., 2017).

Since all studied trees were sufficiently supplied with soil moisture, the decrease in real quantum yield of PS-II and increase in non-photochemical quenching share may be due to adverse temperature and low air humidity influences. High VPD values, which depend on these parameters, intensify physiological stress in plants during drought and increase water loss in anisohydric plants or reduce carbon absorption in isohydric types (McDowell et al., 2008). Increased wind speed at the experimental site contributes additional adverse effects that strengthen drought action (Huang et al., 2016).

Our results confirm information about drought effects on chlorophyll fluorescence obtained for Siberian crabapple trees growing in Hunshandak sandland in Inner Mongolia, China—a region with desertification symptoms. That work shows significant damage to the photosynthetic apparatus of Siberian crabapple can be caused by temperatures exceeding 25°C or photosynthetically active radiation (PAR) greater than 1500 photons per meter per second (Li et al., 2003). According to our data, PAR in Yagodnoye Village and Irkutsk City did not exceed this level and was the same for study areas on sunny, cloudless days in June. Therefore, in our experiment, natural apple plants were subjected only to thermal stress accompanied by increased VPD. In contrast to plants growing under natural conditions, leaves of Siberian crabapple in Irkutsk City showed no evidence of PS-II down-regulation at midday, most likely resulting from the cooling effect of transpiration, which was twice as high in Irkutsk City as in Yagodnoye Village.

There are two stages of stomatal conductance reaction to VPD changes. At the first stage, conductance is close to maximum at low or moderate VPD, but shows strong decrease after a certain threshold, found in apple trees (Kullaj et al., 2017) and wheat (Schoppach et al., 2017). At low VPD, stomatal conductance is assumed to be adjusted according to feedback from photosynthesis products. Stomatal restriction becomes a limiting factor for photosynthesis at higher VPD. VPD values of about 1.5 kPa are considered close to the threshold for domestic apple (Massonnet et al., 2007). In our case, this threshold was certainly exceeded.

Plants use essentially different mechanisms to adapt to drought of varying intensity. When sufficient ground water is available, apple plants can successfully employ an isohydric adaptation strategy, allowing them to keep stomata open for extended periods while maintaining gas exchange, photosynthesis, and biomass accumulation. In our opinion, open stomata combined with leaf cooling needs explain increased transpiration by apple leaves at midday, causing WUE to decrease during photosynthesis at this time.

5 Conclusions

Our experiments revealed changes in the photosynthetic apparatus of Siberian crabapple under air drought influence accompanied by normal soil moisture supply. Under these conditions, total chlorophyll content decreased in leaves, likely because high illumination and forced stomatal closure make lower chlorophyll content sufficient for photosynthesis. Siberian crabapple trees growing in the forest-steppe zone maintain efficient photosynthetic apparatus during morning hours regardless of spring-summer air drought influence, confirmed by unchanged F0 values, sufficiently high Fv/Fm levels, and non-significant differences in PABS. Air drought influence on PS-II leads to decreased fraction of absorbed light energy spent on photochemical work while increasing quantum yield of non-photochemical fluorescence quenching—Y(NPQ). High temperature (above 25°C) and low air humidity at midday and early afternoon adversely affect PS-II of Siberian crabapple, inducing slight decreases in the Fv/Fm coefficient and PABS values. Spring-summer drought and windy weather negatively influence carbon dioxide assimilation in Siberian crabapple. Increased vapour pressure deficit decreases stomatal conductance for water vapour by more than twofold with corresponding transpiration reduction in crabapple leaves, ultimately reducing carbon dioxide assimilation rate by more than 27% compared to the control variant (Irkutsk City). Due to transpiration decrease, water use efficiency of crabapples growing under more intense drought conditions increases during photosynthetic processes, which can be considered an adaptation to such conditions.

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Note: Figure translations are in progress. See original paper for figures.