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Rapid drought-recovery of gas exchange in *Caragana* species adapted to low mean annual precipitation

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Abstract

While variation in mean annual precipitation (MAP) of the native habitat of a species has been shown to determine the ability of a species to resist a hydraulic decrease during drought, it remains unknown whether these variations in MAP also influence the ability of a species to recover and survive drought. Leaf hydraulic and gas exchange recovery following drought and the underlying mechanisms of these responses in six *Caragana* species from habitats along a large precipitation gradient were investigated during rehydration in a common garden. The gas exchange of species from arid habitats recovered more rapidly during rehydration after mild, moderate and severe drought stress treatments than species from humid habitats. The recovery of gas exchange was not associated with foliar abscisic acid concentration, but tightly related to the recovery of leaf hydraulic conductance (K_{leaf}). The recovery of K_{leaf} was associated with the loss of K_{leaf} during dehydration under mild and moderate drought stress, and to leaf xylem embolism formation under severe drought stress. Results pointed to the different ability to recover in gas exchange in six *Caragana* species post-drought is associated with the MAP of the species in its native habitat.

KEYWORDS

biogeography, foliar abscisic acid, gas exchange, leaf hydraulics, mean annual precipitation

1 | INTRODUCTION

The predicted increase in severity and frequency of droughts in many parts of the globe with climate change suggest a significant impact on plant growth (Adams et al., 2017; Allen et al., 2010; Anderegg et al., 2016; Carnicer et al., 2011; Choat et al., 2012, 2018; Engelbrecht et al., 2007). To grow and survive in this increasingly more extreme climate, species depend not only on their ability to cope with drought (Blackman et al., 2012, 2014; Choat et al., 2012; Yao et al., 2021), but also the degree and speed of recovery from drought before the next drought event occurs. Research over the last decade has shown that species adapted to low precipitation environments have a slow loss of stem/leaf hydraulic conductance during dehydration relative to species adapted to high precipitation environments (Blackman et al., 2012, 2014; Choat et al., 2012; Engelbrecht, 2012; Gleason et al., 2016; Nardini & Luglio, 2014; Yao et al., 2021). However, a rapid recovery in gas exchange parameters post drought stress would also allow species to accumulate more assimilates to withstand a subsequent water shortage; such a feature would be particularly advantageous in arid environments experiencing long and/or frequent droughts. The time for recovery of gas exchange from drought stress has important implications for how

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species perform in drought-prone environments (Blackman et al., 2009; Creek et al., 2018; Lovisolo et al., 2008; Scoffoni & Sack 2017; Skelton et al., 2017; Turner & Burch, 1983), but surprisingly few studies have investigated the role of post-drought responses to recovery in hydraulics and gas exchange among species growing along gradients of mean annual precipitation (MAP).

Leaf hydraulic conductance (K_{leaf}), the ratio of flow rate or rate of transpiration to the water potential gradient (driving force), is likely an important contributor to the recovery of gas exchange as the ability of stomata to reopen for photosynthesis during recovery depends on the plant's capacity to replace the water loss to the atmosphere through diffusion from the stomata (Blackman et al., 2009). Indeed, studies have shown that the maximum stomatal conductance ($g_{s\text{-}max}$) and maximum photosynthetic rate (A_{max}) increase linearly with the maximum K_{leaf} ($K_{leaf\text{-}max}$) in angiosperms (Brodribb & Feild, 2000; Choat et al., 2012; Nardini and Salleo, 2003) and in gymnosperms (Brodribb & Feild, 2000; Hubbard et al., 2001), and K_{leaf} recovery following rehydration enables recovery of leaf gas exchange (Blackman et al., 2009; Brodribb & Cochard, 2009; Creek et al., 2018; Lovisolo et al., 2008; Martorell et al., 2013; Skelton et al., 2017). Therefore, it is important for plants growing in arid environments with intermittent drought cycles to recover K_{leaf} quickly from drought (Nardini et al., 2012; Scoffoni & Sack, 2017; Turner & Burch, 1983). Actually, the degree of recovery of hydraulics depends on the degree of drought-induced loss of K_{leaf} experienced before rehydration (Blackman et al., 2009; Brodribb & Cochard, 2009; Brodribb et al., 2010; Lovisolo et al., 2008; Skelton et al., 2017). The less drought-induced hydraulic loss, the more rapid the recovery in K_{leaf} and gas exchange, as indicated by the faster recovery in K_{leaf} observed in the progeny of species collected from habitats experiencing less severe drought stress (Blackman et al., 2009). Previous research has shown that species adapted to low-MAP environments have slow loss of stem/leaf hydraulic conductance during dehydration (Blackman et al., 2012, 2014; Choat et al., 2012; Engelbrecht, 2012; Gleason et al., 2016; Nardini & Luglio, 2014; Yao et al., 2021). We hypothesise that the smaller the loss of K_{leaf} with decreasing leaf water potential during drought should enable a faster recovery in K_{leaf} and leaf gas exchange in species from arid habitats.

K_{leaf} is affected by water movement through both the xylem of the vein (K_x) and outside-xylem pathways (K_{ox}) (Trifilò et al., 2016; Scoffoni et al., 2017a). During dehydration, some studies have suggested that the decrease in K_{leaf} could be induced by the partial or full collapse of the xylem conduits in minor veins of leaves or pine needles (Zhang et al., 2016), or by embolism in the xylem (Brodribb et al., 2016; Johnson et al., 2009; Nolf et al., 2016; Skelton et al., 2017). However, other studies have shown that the K_{ox} explained most of K_{leaf} loss (Scoffoni & Sack, 2017; Scoffoni et al., 2017a; Trifiló et al., 2016; Yao et al., 2021), and conduit embolism only occurs with severe drought (Scoffoni et al., 2017b; Yao et al., 2021). Therefore, if rehydration occurs before initial embolism formation in leaf veins, the rapid recovery in K_{leaf} is likely to be associated with a fast recovery in K_{ox}, but after embolism formation in the leaf veins recovery in K_x and K_{leaf} will be slow. Characteristics such as a more negative turgor loss point (π_{tlp}) (Scoffoni & Sack, 2017; Scoffoni et al., 2014), narrow xylem vessels (Cai & Tyree, 2010; Markesteijn et al., 2011; Negret et al., 2013; Scoffoni et al., 2017b), a high density of major veins (Scoffoni et al., 2011) that enable a species to resist K_x loss, all can contribute to a quick recovery in K_{leaf}.

Abscisic acid (ABA), which is involved in stomatal closure with soil drying, commonly accumulates during drought, and is considered an important constraint to stomatal opening after drought release (Brodribb & McAdam, 2011, 2013; Lovisolo et al., 2008; McAdam & Brodribb, 2014; Nolan et al., 2017). Following soil re-watering, it has been shown that while leaf water potential (Ψ_{leaf}) tends to recover very rapidly, the recovery of gas exchange is comparatively slower (Blackman et al., 2009; Creek et al., 2018; Lovisolo et al., 2008; Martorell et al., 2013). Additionally, stomatal responses to seasonal rainfall across a range of plant types was reported to be strongly influenced by ABA (McAdam & Brodribb, 2015). However, other research has shown that ABA concentrations increased with the initial decrease in Ψ_{leaf}, but under sustained drought decreased to the concentrations in the adequately-watered control plants in some conifers and angiosperm species (Brodribb et al., 2014; Nolan et al., 2017). Furthermore, ABA reached similar concentrations to those in the unstressed plants within 24 h after rehydration (Davies et al., 2002; Skelton et al., 2017). Therefore, we tested whether foliar ABA concentrations are related to the differences with the recovery of gas exchange across species growing along a MAP gradient in their native habitat.

Caragana species are woody perennial shrubs or small trees that occur over a wide range of habitats, from deserts to deciduous woodland along a MAP gradient from less than 200 mm to more than 1400 mm (Fang et al., 2017; Yao et al., 2021). In a recent study, we showed that high hydraulic safety and efficiency combined with greater stomatal sensitivity triggered by ABA production and leading to greater water use efficiency provided drought tolerance in *Caragana* species from arid habitats (Yao et al., 2021). Here, we compare the degree and speed of recovery in K_{leaf} and leaf gas exchange after induced mild, moderate and severe drought stress. We hypothesise that: (1) the gas exchange recovery responses after rehydration are associated with the MAP of their native habitat, with *Caragana* species from arid habitats exhibiting rapid recovery of gas exchange during rehydration, while *Caragana* species from humid habitats exhibit slow recovery of gas exchange; (2) the ability of species to recover in gas exchange after drought is associated with their ability to recover in K_{leaf} and not of ABA degradation, while the speed of recovery of K_{leaf} is related to its vulnerability to drought-induced dehydration.

2 | MATERIALS AND METHODS

2.1 | Plant materials

The plant material used in the study is described in Fang et al. (2017) and Yao et al. (2021). In this study, we selected six *Caragana* species, the seeds or stem tissue (*C. sinica*) of which were collected from regions varying strongly in MAP (110–1400 mm) and the aridity index (AI = potential evapotranspiration/MAP and varied from 0.68 to 32.2). Mean annual temperature (MAT) varied less than rainfall throughout these regions, ranging from 2.6°C to 8.5°C with seasonal minimum temperatures (January) varying from −26°C to −5°C and seasonal maximum temperatures (July) varying from 14°C to 30°C across the regions (data from the China Meteorological Data Sharing Service system, http://data.cma.cn/). More than 70% of the total annual precipitation occurs during the growing season from May to October in the areas of collection of the species. Hereafter for convenience, we classified the six *Caragana* species into two groups: (i) three species from arid habitats with a MAP of less than 400 mm and a MAT of 4.7°C, and (ii) three species from humid habitats with a MAP of more than 400 mm and a MAT of 7.6°C.

In June to August 2012, seeds of *Caragana korshinskii*, *C. intermedia*, *C. microphylla*, *C. boisi and C. stipitata* were collected from wild populations at physiological maturity, when the pods change colour from green to brown. After collection, ripe fruit was spread out in the laboratory at 20°C until the fruits opened and the seeds were removed. The seeds were stored at 4.0°C until the start of the experiment. Seeds of the five species were placed in Petri dishes lined with wet filter paper to germinate at 20°C in February 2013. After germination, three seedlings per pot were transferred into plastic pots, 270 mm high and 170 mm in diameter, containing 3.6 kg of a 1:1 (v:v) mixture of sieved peat soil and Perlite with a dry bulk density of 0.63 g cm^{-3} and a pot capacity (PC) of 35% after being saturated with water and allowed to drain for 48 h (Turner, 2019). *C. sinica* is triploid, has no seeds and tissue was cultured from more than 100 individuals as described by Song et al. (2007). Thirty-one days after sowing, the seedlings were thinned to one per pot and the tissue-cultured seedlings of *C. sinica* were moved to the pots (one individual per pot). All pots were irrigated every 2 days to maintain the soil above 80% PC by weighing the pots and replacing the water lost. The plants were grown in a naturally-lit glasshouse at the Yuzhong campus (35° 51′ N, 104° 07′ E, altitude 1620 m) of Lanzhou University, Lanzhou, Gansu Province, China. The pots were covered with ca. 20 mm of Perlite to minimise soil evaporation.

2.2 | Drought stress and re-watering

On 1 June 2014, 16-month-old plants ($n = 40$) of each species with a height of 0.5–1.0 m and with >120 compound leaves were selected, and two experimental treatments were randomly imposed: (i) well-watered (WW) and (ii) re-watered after three drought stress treatments differing in intensity (RW) (Figure S1). In the WW treatment (10 pots per species), plants were watered every day to maintain the soil water content near 80% (PC) by replacing the water lost through transpiration. Five pots of each species were used to measure predawn Ψ_{leaf}, leaf gas exchange and leaf ABA concentration every 2–3 days during the entire length of the experiment, and the remaining 5 pots of each species were used to measure the K_{leaf}.

In the RW treatment (30 pots per species), plants were re-watered daily after receiving a different intensity of drought. First, water was withheld such that every day over the period of 10 days, individuals were re-watered with one-half of the volume of water transpired during the preceding day (Brodribb & McAdam, 2013). After 10 days, water was withheld completely and plants were divided into three groups of 10 pots, each receiving a different intensity of drought before rehydration; 10 pots were re-watered when the predawn Ψ_{leaf} reached about −2 MPa (mild drought stress), 10 pots were re-watered when predawn Ψ_{leaf} reached about −4 MPa (moderate drought stress), and 10 pots were re-watered when predawn Ψ_{leaf} reached about −6 MPa (severe drought stress). Rehydration was achieved by re-watering each pot to 100% PC in the morning (07:30 h Beijing Standard Time [BST]), and maintaining pots at 80% PC by watering daily until the gas exchange of the RW plants reached that in the WW controls (1–20 days after re-watering). In each of the three rehydration treatments, 5 pots were used to measure the recovery of Ψ_{leaf} and K_{leaf}, and the remaining 5 pots were used to measure Ψ_{leaf}, the recovery of gas exchange and leaf ABA concentration.

2.3 | Leaf water potential (Ψ_{leaf}) measurements

The predawn Ψ_{leaf} of four upper fully-expanded leaves from different individuals was measured every 2–3 days, between 04:30 and 05:30 h BST using a pressure chamber (Model 1000, PMS Instrument Company) in the WW treatments and during dehydration in the RW treatments by the method and precautions described by Turner (1988). After re-watering at 7.30 h BST, the leaves were wrapped in moist paper towel and double bagged for 0.5 h to allow water potentials to equilibrate throughout the leaf, then Ψ_{leaf} was measured in four upper fully-expanded leaves from four individuals every 0.5 to 1 h until 16:00 h BST. On subsequent days, predawn Ψ_{leaf} was measured between 04:30 and 05:30 h BST until values in the RW treatments were similar to those in the WW controls.

2.4 | Leaf hydraulic conductance (K_{leaf}) measurement

K_{leaf} was measured in both WW and RW treatments at 07:30, 12:00 and 16:00 h BST on the first day after re-watering and then in the morning (between 04:30 and 06:30 h BST after the measurement of predawn Ψ_{leaf} that doubled as the initial leaf water potential (Ψ_o) for K_{leaf} measurements from the first day after re-watering) each day for 1–19 days until K_{leaf} in the RW plants recovered to that observed in the WW controls. K_{leaf} was measured using the evaporative flux method (Sack et al., 2002; Scoffoni et al., 2011; Sack & Scoffoni, 2012). Two leaves adjacent to the leaf used for measure Ψ_{leaf} were excised at each sampling time to measure Ψ_o using the pressure chamber and methodology described above. A third leaf (typically the middle leaf) was excised, under double-distilled water, connected to silicone tubing to determine K_{leaf} under a light source

(1000 µmol m^2 s^{-1} photosynthetically active radiation). The leaf transpiration was measured under the light source for 0.5–1 h. After stable flow was achieved, the leaves were removed from the tubing and placed in a sealable bag for equilibration for at least 0.5 h, and then the final leaf water potential (Ψ_f) was measured. K_{leaf} was calculated as the light-acclimated, steady-state transpiration rate of the excised leaf divided by Ψ_f (driving force). Notably, Ψ_o measured from the two leaves were within 0.2 MPa before each measurement throughout the experiment. Percentage loss of K_{leaf} was determined as $(1 - K_{leaf}/K_{leaf\text{-}control}) \times 100$, where K_{leaf} is the leaf hydraulic conductance at −2 and −4 MPa and $K_{leaf\text{-}control}$ is K_{leaf} of well-watered plants at the time that K_{leaf} was measured. The number of days it took for K_{leaf} to recover (RK_{days}) was recorded, and the percentage recovery of K_{leaf} 24 h after re-watering (%RK_{24h}) was determined as $(K_{leaf\ re\text{-}watered} - K_{leaf\ stressed})/K_{leaf\ control} \times 100$, where $K_{leaf\ re\text{-}watered}$ is K_{leaf} 24 h after re-watering, $K_{leaf\ stressed}$ is the K_{leaf} before re-watering, and $K_{leaf\ control}$ is the K_{leaf} of well-watered plants at the time that $K_{leaf\ re\text{-}watered}$ was measured.

2.5 | Gas exchange measurement

In the WW treatments, the rate of leaf photosynthesis (A) and stomatal conductance (g_s) of one upper fully-expanded leaf from four individuals were measured in the morning (07:00 and 09:30 h BST), when gas exchange is usually at its highest (data not shown), using a portable open gas-exchange system (LI-6400, LiCor) supplied with a photosynthetic photon flux density of 1200 µmol m^{-2} s^{-1} provided by a LED source, and maintained at a leaf temperature of 22°C, CO_2 at 400 ppm and VPD about 1.5 kPa.

In the RW treatments, A and g_s were measured every 0.5–1 h until 16:00 h BST for the first day after re-watering and then in the morning between 07:00 and 09:30 h BST on subsequent days for 1–19 days until the rate of A and g_s recovered to that of the WW controls. The leaflet used for the measurement of gas exchange was an upper fully-expanded leaflet adjacent to the leaflet used for K_{leaf}. The number of days it took for A (RA_{days}) and g_s (Rg_{days}) to recover to values of the WW controls was recorded. The percentage recovery of A and g_s 24 h after re-watering (%RA_{24h} and %Rg_{24h}) were determined as $(X_{re\text{-}watered} - X_{stressed})/X_{control} \times 100\%$, where $X_{re\text{-}watered}$ is the A or g_s 24 h after re-watering, $X_{stressed}$ is the A or g_s before re-watering, and $X_{control}$ is the A or g_s of well-watered plants at the time that $X_{re\text{-}watered}$ was measured. After each gas exchange measurement, the leaflets used to measure gas exchange were cut off and scanned to calculate the stomatal conductance and rate of photosynthesis per unit area.

2.6 | ABA determination

Leaf ABA concentration in six species during dehydration has already been determined by Yao et al. (2021). In this study, leaf ABA concentration was only determined during rehydration. In brief, after each gas exchange measurement, leaflets in close proximity to the leaflet used for measuring gas exchange were divided into two groups, one group was weighed immediately and then dried to constant mass to determine the dry mass/fresh mass ratio, while the other group was also weighed immediately and placed in liquid nitrogen and stored in a freezer at −80°C for the measurement of the abscisic acid (ABA) content. The leaf tissue then was removed from the freezer, immediately ground into powder in a small volume of liquid nitrogen, and kept in 10 mL 80% (vol/vol) methanol in water (with 0.02 mol/L butylated hydroxytoluene [BHT]) after stored at 4°C for 12 h. Samples were centrifuged (10 min at 10 000*g*) at 4°C, the supernatant liquid was dried with nitrogen gas. The dried samples were dissolved in 1 mL methanol (chromatographically pure) for quantification by high-performance liquid chromatography using an OrbiTrap Fusion LUMOS system (Thermo Fisher) according to the methods of McAdam (2015). The ABA concentration (ng g^{-1} dry weight) was calculated as the ABA concentration per leaf fresh mass × (leaf dry mass/leaf fresh mass of adjacent leaflets to the leaflet sampled for ABA).

2.7 | Leaf anatomical traits

The anatomical dimensions of the xylem in the leaf, including the minor and major vein density and leaf xylem area per leaflet area, were previously determined by Yao et al. (2021). In this study, only the xylem conduit diameter and the number of major and minor veins were measured. In brief, six compound leaves from different individuals of each species were cut. Then leaf sections were cut using a freeze-microtome, stained with 5% toluidine blue, and mounted on glass microscope slides in phenol glycerine jelly to measure the xylem conduit diameter of the midrib and minor veins in cross sections across the middle of the leaf using ImageJ software (https://imagej.nih.gov/ij/), and to count the number of xylem conduits of the midrib.

2.8 | Statistical analyses

Differences between means were evaluated by one-way analysis of variance with *Caragana* species as the factor with four replicates (Duncan's multiple range test) performed with SPSS 15.0 (SPSS Inc.), and considered significant at $p < 0.05$. The linear relationships and the correlation coefficients were calculated using SigmaPlot 10.0 (Systat Software, Inc.).

3 | RESULTS

After re-watering, plants subjected to mild drought stress (−2 MPa) rehydrated to Ψ_{leaf} levels observed in the WW treatments within a few hours, while plants subjected to greater drought stress (−4 and −6 MPa) required 24–48 h to recover (Figure 1). However, K_{leaf}

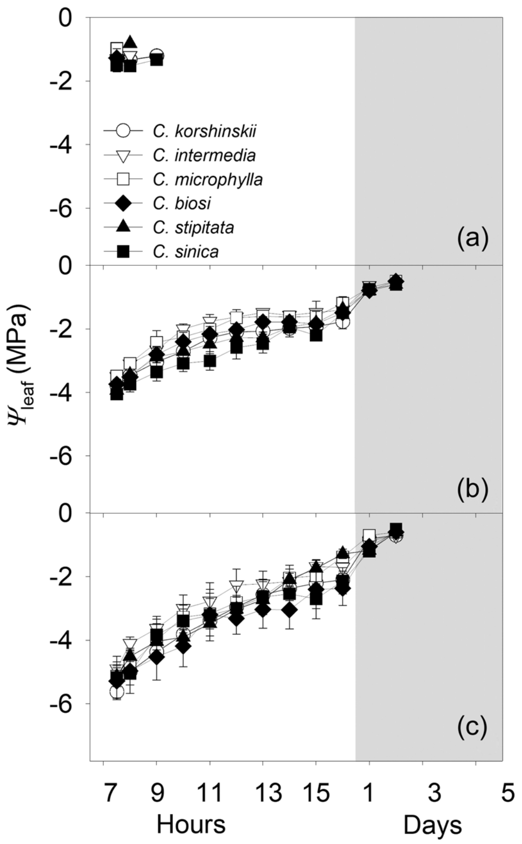

FIGURE 1 Recovery of leaf water potential (Ψ_{leaf}) with time after re-watering in six *Caragana* species. The recovery of leaf water potential (Ψ_{leaf}) from mild (−2 MPa) (a), moderate (−4 MPa) (b), and severe (−6 MPa) (c) drought stress in *Caragana* species from arid (open symbols) and humid (closed symbols) habitats. The white background covers the recovery on the first day after re-watering which started at 7:30 h (BST), and the grey background covers the recovery on subsequent days [measurements were taken at predawn (04:30–06:30 h BST) on those days]. Symbols are not shown when Ψ_{leaf} recovered to that in the well-watered controls (Control). The bars are ± one standard error of the mean ($n = 4$) when larger than the symbol. BST, Beijing Standard Time

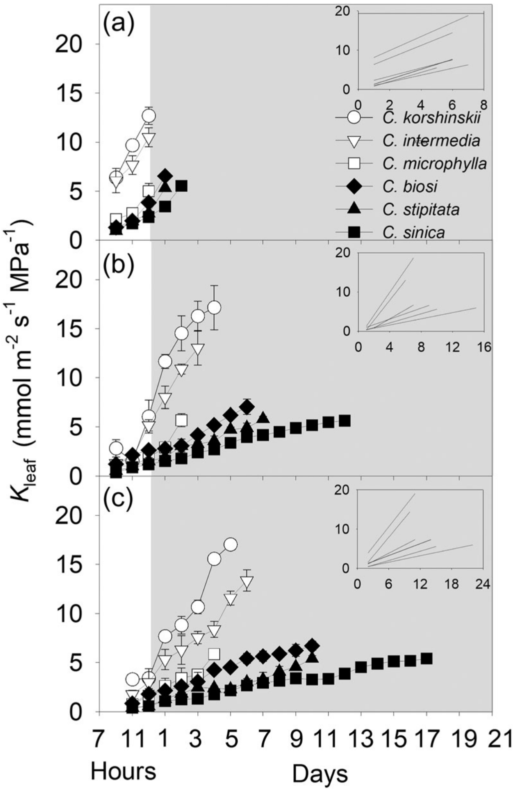

FIGURE 2 Recovery of leaf hydraulic conductance (K_{leaf}) with time after re-watering in six *Caragana* species. The recovery of leaf hydraulic conductance (K_{leaf}) from mild (−2 MPa) (a), moderate (−4 MPa) (b), and severe (−6 MPa) (c) drought stress in *Caragana* species from arid (open symbols) and humid (closed symbols) habitats. The white background covers the recovery on the first day after re-watering which started at 7:30 h (BST), and the grey background covers the recovery on subsequent days (measurements were taken at 04:30–06:30 h BST). Symbols are not shown when K_{leaf} recovered to that in the well-watered controls (Control). The inserted panels indicated that K_{leaf} increased linearly with the time of recovery from mild, moderate and severe drought stress ($r^2 = 0.78–0.92$, $p < 0.05$). The K_{leaf} in plants re-watered at −6 MPa was not measured at 7:30 h BST. The bars are ± one standard error of the mean ($n = 4$) when larger than the symbol. BST, Beijing Standard Time

recovered slower than Ψ_{leaf} in all treatments and species (Figure 2). After re-watering from the mild drought stress treatment, K_{leaf} of species from arid habitats showed a more rapid recovery than species from humid habitats. It took 11 h to recover to WW levels in species from arid habitats and 1–2 days in species from humid habitats (Figure 2a). After exposure to moderate and severe drought stress (that induced a larger decrease in K_{leaf}), K_{leaf} required up to 8.5-fold longer to recover: 2–4 days and 4–6 days, respectively, were required for K_{leaf} recovery after exposure to moderate and severe drought stress in species from arid habitats, and 6–12 days and 10–17 days, respectively, in species from humid habitats (Figure 2b,c). Across species, K_{leaf} recovered linearly with the time after rehydration (Figure 2). Even though the conditions in the chamber were maintained constant, A and g_s were affected by the external light and humidity environment in the naturally-lit glasshouse, so that both *A* and g_s decreased during the first afternoon after rehydration in all treatments and species (Figures 3 and 4). With re-watering after mild drought stress, both *A* and g_s recovered to the WW treatment in 1 to 2 h in species from arid habitats and 24 h in species from humid habitats (Figures 3 and 4). From 24 h after re-watering, the recovery pattern of *A* and g_s across species and treatments was similar to that of K_{leaf} (Figures 3 and 4).

With increasing MAP, RK_{days}, Rg_{days}, and RA_{days} of the species increased linearly in all three drought treatments (Figure 5). Across species, a significant linear relationship was exhibited between RA_{days} and Rg_{days}, Rg_{days} and RK_{days} (Figure 6) and RA_{days} and RK_{days} ($p < 0.05$, data not shown) in all three drought treatments. The species from arid habitats had less percentage loss of K_{leaf} than species from humid habitats at values of predawn Ψ_{leaf} of −2 and −4 MPa (Table 1). The RK_{days} was negatively associated with the

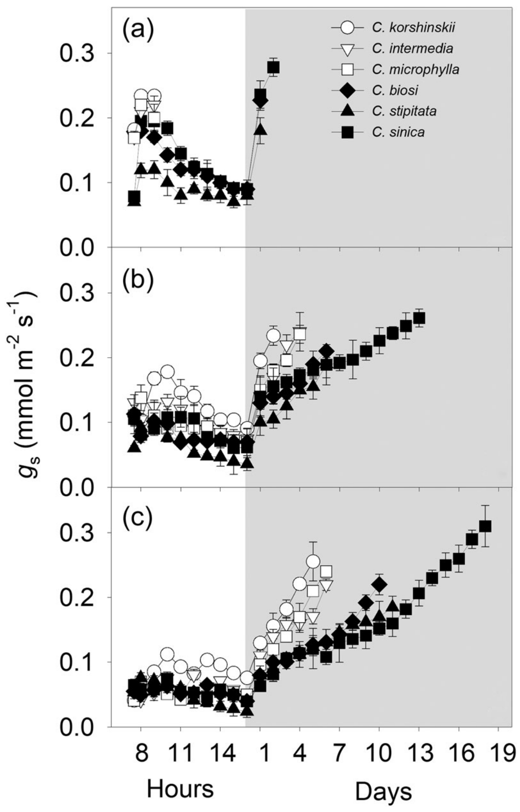

FIGURE 3 Recovery of stomatal conductance (g_s) with time after re-watering in six *Caragana* species. The recovery of stomatal conductance (g_s) from mild (−2 MPa) (a), moderate (−4 MPa) (b), and severe (−6 MPa) (c) drought stress in *Caragana* species from arid (open symbols) and humid (closed symbols) habitats. The white background covers the recovery on the first day after re-watering which started at 07:30 h BST, and the grey background covers the recovery on subsequent days (where measurements were taken at 07:30–10:00 h BST). Symbols are not shown when g_s recovered to that in the well-watered controls (Control). The bars are ± one standard error of the mean ($n = 4$) when larger than the symbol. BST, Beijing Standard Time

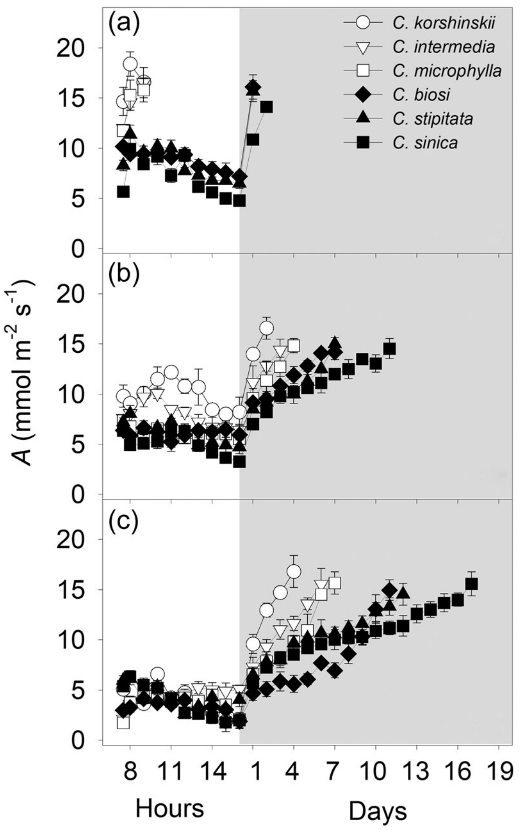

FIGURE 4 Recovery of leaf photosynthesis (A) with time after re-watering in six *Caragana* species. The recovery of leaf photosynthesis (A) from mild (−2 MPa) (a), moderate (−4 MPa) (b) and severe (−6 MPa) (c) drought stress in *Caragana* species from arid (open symbols) and humid (closed symbols) habitats. The white background covers the recovery on the first day after re-watering which started at 7:30 h BST, and the grey background covers the recovery on subsequent days (measurements taken at 07:30–10:00 h BST). Symbols are not shown when A recovered to that in the well-watered controls (Control). The bars are ± one standard error of the mean ($n = 4$) when larger than the symbol. Beijing Standard Time

percentage of K_{leaf} of control (Figure 7a,b), the percentage of K_{leaf} of control was negatively associated with K_{leaf} P_{50} (Figure 7c,d), and RK_{days} of species from arid habitats decreased more negatively across species with K_{leaf} P_{50} when the plants recovered from the mild (−2 MPa) and while moderate (−4 MPa) drought stress (Figure 7a,b), while the relationship between RK_{days} and K_{leaf} P_{50} was not significant from recovery from −6 MPa ($p = 0.07$).

With recovery from severe drought stress (−6 MPa), a significant relationship was observed between RK_{days} and the leaf water potentials at which cumulative 'embolized' conduits reached 50% (PLC_{major} P_{50}) in 1° + 2° vein orders measured by Yao et al. (2021) (Figure 8). PLC_{major} P_{50}, in turn, was positively correlated with xylem conduit diameter in minor and midrib veins, negatively correlated with midrib xylem area per leaflet area, but not correlated with xylem conduit number, major vein length per area (VLA) and minor VLA (Figure S2 and Table 1).

The percentage recovery of K_{leaf} after 24 h ($\%RK_{24h}$), and similar recovery of g_s and A ($\%Rg_{24h}$ and $\%RA_{24h}$) from imposed drought stresses of −4 and −6 MPa decreased across species from arid to humid habitats (Figure S3), and the significant negative relationships between $\%RK_{24h}$, $\%Rg_{24h}$, $\%RA_{24h}$ and the MAP in the native habitat of the species were observed (Figure S4), along with significant positive relationships between $\%RA_{24h}$ and $\%Rg_{24h}$, and between $\%Rg_{24h}$ and $\%RK_{24h}$ (Figure S5). With recovery from −4 MPa, the $\%RA_{24h}$ was negatively associated with the % loss of K_{leaf} (Figure S6).

During the decrease in Ψ_{leaf}, the leaf ABA concentration increased linearly until the predawn Ψ_{leaf} reached −3 to −4 MPa across species, and then decreased (Figure 9), with the ABA reaching higher peak concentrations in species from arid habitats than humid habitats. Irrespective of the differences in peak concentration, the leaf ABA concentrations returned to those of the controls within 1 day after rehydration in all six species (Figure 9).

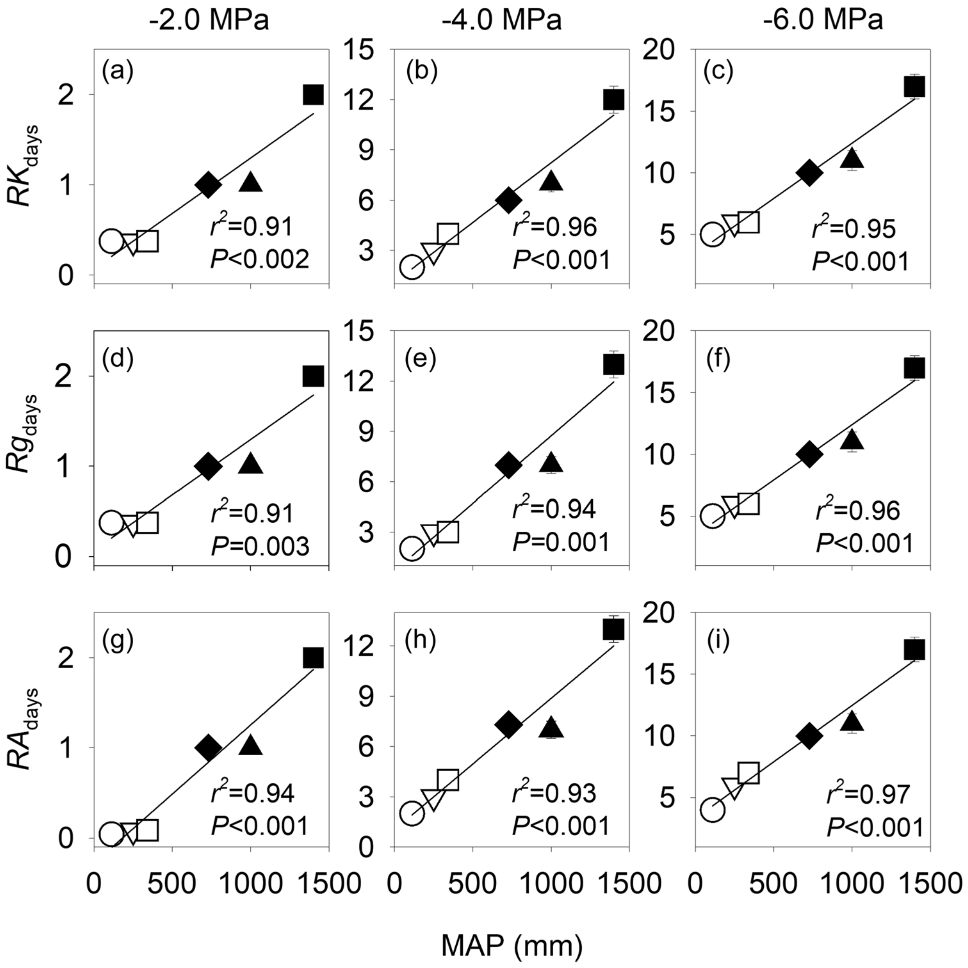

FIGURE 5 Relationships between RK_{days}, Rg_{days}, RA_{days} with MAP in six *Caragana* species exposed to different drought treatments. The number of days required to recover to control values for leaf hydraulic conductance (RK_{days}), stomatal conductance (Rg_{days}) and photosynthesis (RA_{days}) are shown for six *Caragana* species previously exposed to mild (−2 MPa) (a, d, g), moderate (−4 MPa) (b, e, h), and severe (−6 MPa) drought stress (c, f, i). Open symbols represent three species from arid habitats, closed symbols represent three species from humid habitats: *C. korshinskii*, ○; *C. intermedia*, ▿; *C. microphylla*, □; *C. boisi*, ◆; *C. stipitata*, ▲; and *C. sinica*, ■. The bars are ± one standard error of the mean (n = 4) when larger than the symbol. The correlation coefficient (r^2) and probability (P) of the fitted linear regressions are shown in each plot. Note the scale of the y-axes varies across plots

4 | DISCUSSION

Previous research on plant hydraulics has focused largely on resistance to hydraulic loss and its effect on gas exchange and growth during the development of water deficits across species from contrasting habitats along a global precipitation gradient (Blackman et al., 2014; Choat et al., 2012; Gleason et al., 2016; Maherali et al., 2004; Narfini & Luglio, 2014; Yao et al., 2021). However, far less is known about the recovery of hydraulics and gas exchange from drought across species growing along a MAP gradient in their native habitats. In the present study, six *Caragana* species that grow along a strong precipitation and aridity gradient in their native habitat were grown in a common garden. The leaf hydraulic and gas exchange recovery, and the underlying mechanisms, were followed during rehydration following different degrees of drought stress. The results showed that both Ψ_{leaf} and ABA concentration recovered rapidly after re-watering in all six Caragana species. The leaf hydraulics and gas exchange of species from arid habitats recovered more rapidly during rehydration compared to species from humid habitats. The rapid recovery of gas exchange in the species from arid habitats was associated with a faster recovery of K_{leaf}, and was not associated with the foliar ABA concentration (Figure 10). The study showed that the characteristics that enable species to resist a hydraulic decrease with imposed drought were similar to those that enabled the species to recover quickly from drought.

4.1 | The recovery of gas exchange in *Caragana* species

It is a fundamental biological process for plants to regulate the gas exchange between the biosphere and atmosphere such that the rate

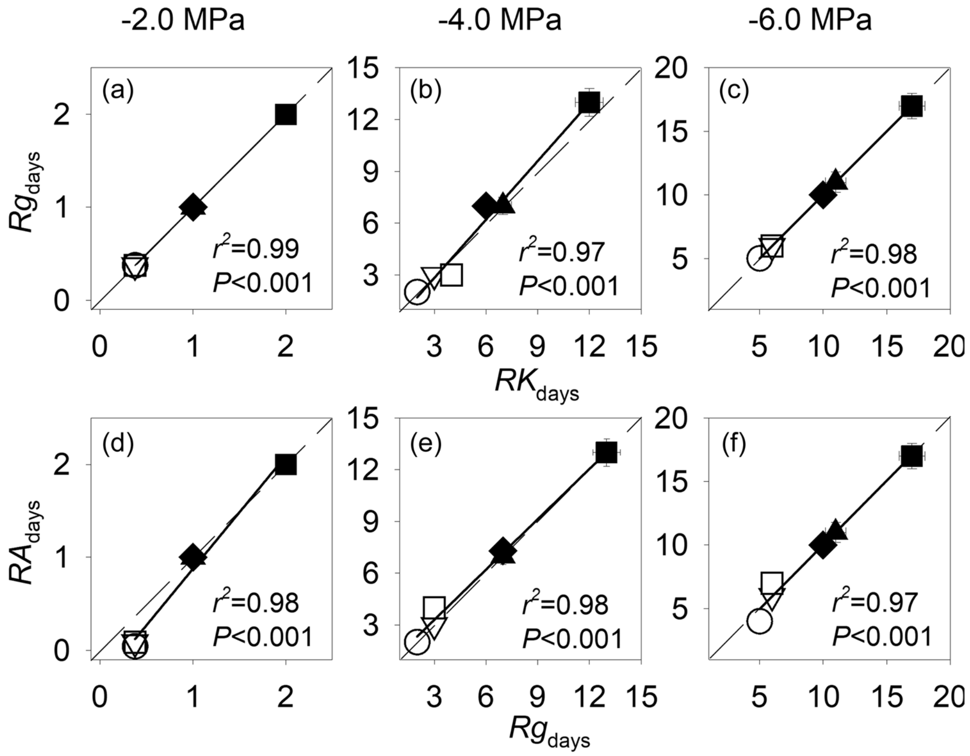

FIGURE 6 Relationships between RK_{days}, Rg_{days} and RA_{days} in six *Caragana* species. The number of days required to recover to control values of leaf hydraulic conductance (RK_{days}), stomatal conductance (Rg_{days}) and photosynthesis (RA_{days}) are shown for six *Caragana* species previously exposed to mild (−2 MPa) (a, d), moderate (−4 MPa) (b, e), and severe (−6 MPa) drought (c, f). Open symbols represent three species from arid habitats, closed symbols represent three species from humid habitats: *C. korshinskii*, ○; *C. intermedia*, ▿; *C. microphylla*, □; *C. boisi*, ◆; *C. stipitata*, ▲; and *C. sinica*, ■. The bars are ± one standard error of the mean ($n = 4$) when larger than the symbol. The correlation coefficient (r^2) and probability (P) of the fitted linear regressions are shown in each plot. The grey dashed line in all panels represents the 1:1 relationship. Note the scale of the *y*-axes varies across plots

TABLE 1 Percentage loss of leaf hydraulic conductance (K_{leaf}) during dehydration and leaf vein anatomy traits in six*Caragana species*.

	Loss of K_{leaf} (%)		Mean xylem conduit diameter (μm)		Midrib conduit number (×10^4)
Caragana species	−2 MPa	−4 MPa	Midrib vein	Minor vein	Per leaflet (cm^2)
C. korshinskii	42.5 ± 1.5**b**	84.3 ± 4.2**b**	21.9 ± 1.1**c**	6.6 ± 0.42**b**	0.41 ± 0.04**a**
C. intermedia	49.8 ± 5.1**b**	86.0 ± 1.7**b**	20.1 ± 1.1**c**	7.2 ± 0.28**b**	0.35 ± 0.02**a**
C. microphylla	45.6 ± 4.5**b**	91.6 ± 0.76**ab**	22.2 ± 1.1**c**	6.7 ± 0.28**b**	0.21 ± 0.01**b**
C. boisi	77.8 ± 1.9**a**	94.1 ± 2.4**a**	26.2 ± 1.1**b**	9.6 ± 0.44**a**	0.24 ± 0.01**b**
C. stipitata	78.1 ± 5.8**a**	94.8 ± 1.9**a**	28.9 ± 1.4**b**	8.8 ± 0.53**a**	0.16 ± 0.005**c**
C. sinica	84.0 ± 3.0**a**	98.8 ± 1.2**a**	33.1 ± 0.9**a**	9.2 ± 0.50**a**	0.07 ± 0.006**d**

Note: The loss of leaf hydraulic conductance (K_{leaf}) as a percentage of that in well-watered controls at −2 and −4 MPa was calculated from Figure S1, the area of xylem vessels in the midrib per leaflet area was from Table S1 from Yao et al., (2020), xylem conduit diameter of the midrib (1°) vein and highest-order minor vein, and number of xylem vessels of the midrib per leaflet area were measured in this study of three Caragana species from arid habitats (*C. korshinskii*, *C. intermedia* and *C. microphylla*), and three from humid habitats (*C. boisi*, *C. stipitata* and *C. sinica*). Values are the mean ± one standard error of the mean ($n = 4$); the values in each column with a different letter are significantly different at $p < 0.05$. The % loss of K_{leaf} in plants at −6 MPa was 100% and not listed.

of gas exchange is linearly related to the MAP of their habitats (Barron-Gafford et al., 2012). However, whether MAP influences the recovery of gas exchange after release from drought stress remains largely unknown. This paper extends and deepens the question on how gas exchange in closely-related species along a MAP gradient respond to rehydration after droughts of different severity. Compared with *Caragana* species from humid habitats, the *Caragana* species from arid habitats exhibited more negative K_{leaf} P_{50}, and also

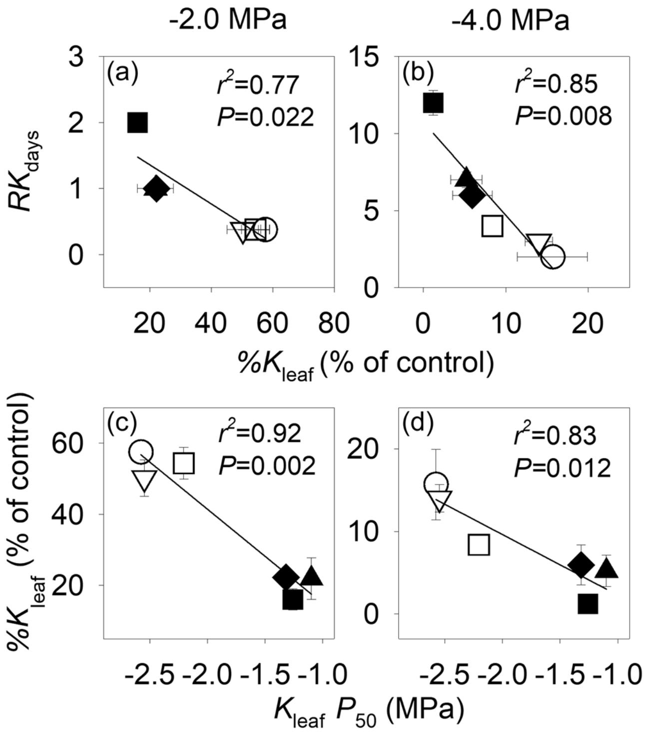

FIGURE 7 Relationships between RK_{days}, % of K_{leaf} and K_{leaf} P_{50} in six *Caragana* species. The relationship between time to full recovery of the leaf hydraulic conductance (RK_{days}) and the leaf hydraulic conductance (K_{leaf}) as a percentage of that in well-watered controls at −2 and −4 MPa (a, b), and the relationship between % loss of K_{leaf} at −2 and −4 MPa and the water potential at 50% loss of leaf hydraulic conductance (K_{leaf} P_{50}) (c, d). Open symbols represent three species from arid habitats, closed symbols represent three species from humid habitats: *C. korshinskii*, ○; *C. intermedia*, ▿; *C. microphylla*, □; *C. boisi*, ◆; *C. stipitata*, ▲; and *C. sinica*, ■. The bars are ± one standard error of the mean (n = 4) when larger than the symbol. The correlation coefficient (r^2) and probability (P) of the fitted linear regressions are shown in each plot. K_{leaf} in plants re-watered at −6 MPa could not be measured at 7:30 h BST, and % loss of K_{leaf} was not determined. Note the scale of the y-axes varies across plots. BST, Beijing Standard Time.

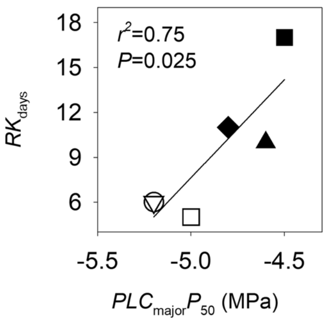

FIGURE 8 Relationship between PLC_{major} P_{50} and RK_{days} in six *Caragana* species. The relationship between the leaf water potential at which cumulative 'embolised' conduits reached 50% (PLC_{major} P_{50}) in 1° + 2° vein orders and the time to full recovery of the leaf hydraulic conductance (RK_{days}). Open symbols represent three species from arid habitats, closed symbols represent three species from humid habitats: *C. korshinskii*, ○; *C. intermedia*, ▿; *C. microphylla*, □; *C. boisi*, ◆; *C. stipitata*, ▲; and *C. sinica*, ■. The bars are ± one standard error of the mean (n = 4) when larger than the symbol. The correlation coefficient (r^2) and probability (P) of the fitted linear regressions are shown in each plot. The data of PLC_{major} P_{50} are from Yao et al. (2021).

stronger ability to resist leaf hydraulic loss during dehydration, followed by a rapid drought-recovery of gas exchange after rehydration. The recovery of gas exchange by *Caragana* species from arid habitats was only one-third of the time for recovery of *Caragana* species from humid habitats. The rate of recovery of gas exchange of all six *Caragana* species was closely associated with the recovery of K_{leaf}, but the species from arid habitats exhibited a more rapid recovery in both K_{leaf} and gas exchange than species from humid habitats. Thus, we argue that the MAP of the site of collection (habitat) influences the recovery of gas exchange among *Caragana* species.

The majority of studies have shown that there is a close association at a global scale between stem hydraulic vulnerability and MAP across environments with contrasting water availability (Choat et al., 2012; Engelbrecht et al., 2007; Maherali et al., 2004; Pockman & Sperry, 2000). Recent studies have shown that leaf hydraulic vulnerability to be equally important as stem hydraulic vulnerability in determining species distribution across precipitation gradients (Blackman et al., 2012, 2014; Nardini & Luglio, 2014; Yao et al., 2021). Both K_{stem} P_{50} and K_{leaf} P_{50} were found to be more negative with decreasing precipitation habitats across diverse species in Australian forests (Blackman et al., 2012, 2014), and also from a meta-analysis of 130 angiosperm species (Nardini & Luglio, 2014; Scoffoni & Sack, 2017). This trend was also recently confirmed in ten *Caragana* species, including the six species in this study, wherein species with more negative K_{leaf} P_{50} occurred in more arid habitats (Yao et al., 2021). After re-watering, a recent study has shown that the species that experienced the largest decreases in stem hydraulic conductance at 60% loss of soil volumetric water content were the slowest to recover in terms of stem water potential and photosynthesis (Kannenberg et al., 2019). At the leaf level, several studies have looked into the relationship between loss of K_{leaf} and the recovery in gas exchange after relief of water stress (Blackman et al., 2009; Martorell et al., 2013; Skelton et al., 2017) and similar results were observed to those in the stems, namely, recovery in K_{leaf} and gas exchange depended on the degree of water-deficit-induced K_{leaf} loss experienced before rehydration (Skelton et al., 2017). Further, species with more negative K_{leaf} P_{50} (less K_{leaf} loss) recovered faster from moderate stress and exhibited minimal drought-induced leaf death (Blackman et al., 2009).

Although more species need to be tested to confirm that MAP of the habitat affects the recovery patterns across species, the rapid gas exchange recovery of species from arid habitats would allow plants to: (i) accumulate assimilates quickly to withstand a subsequent water shortage (Blackman et al., 2009; Creek et al., 2018; Lovisolo et al., 2008; Scoffoni & Sack 2017; Skelton et al., 2017; Turner & Burch 1983); (ii) accumulate assimilates for the production of flowers

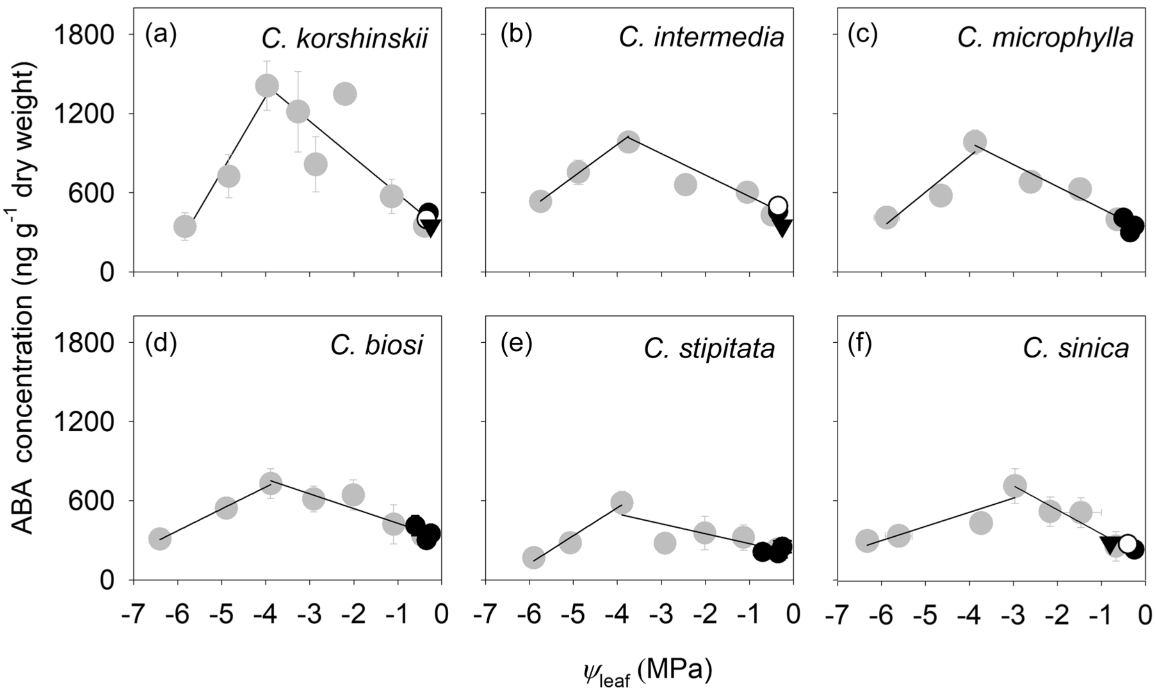

FIGURE 9 The leaf ABA concentration with dehydration and after re-watering. The leaf ABA concentration with decrease in predawn leaf water potential (ψ_{leaf}) during soil drying (grey circles; data from Yao et al., 2021) and 1 day post recovery from mild (−2 MPa; solid circles), moderate (−4 MPa; solid triangles) and severe (−6 MPa; open circles) drought stress in three *Caragana* species from arid habitats (a, b, c) and three from humid habitats (d, e, f). The bars are ± one standard error of the mean ($n = 4$) when larger than the symbol. Note the scale of the *y*-axes varies across plots. ABA, abscisic acid.

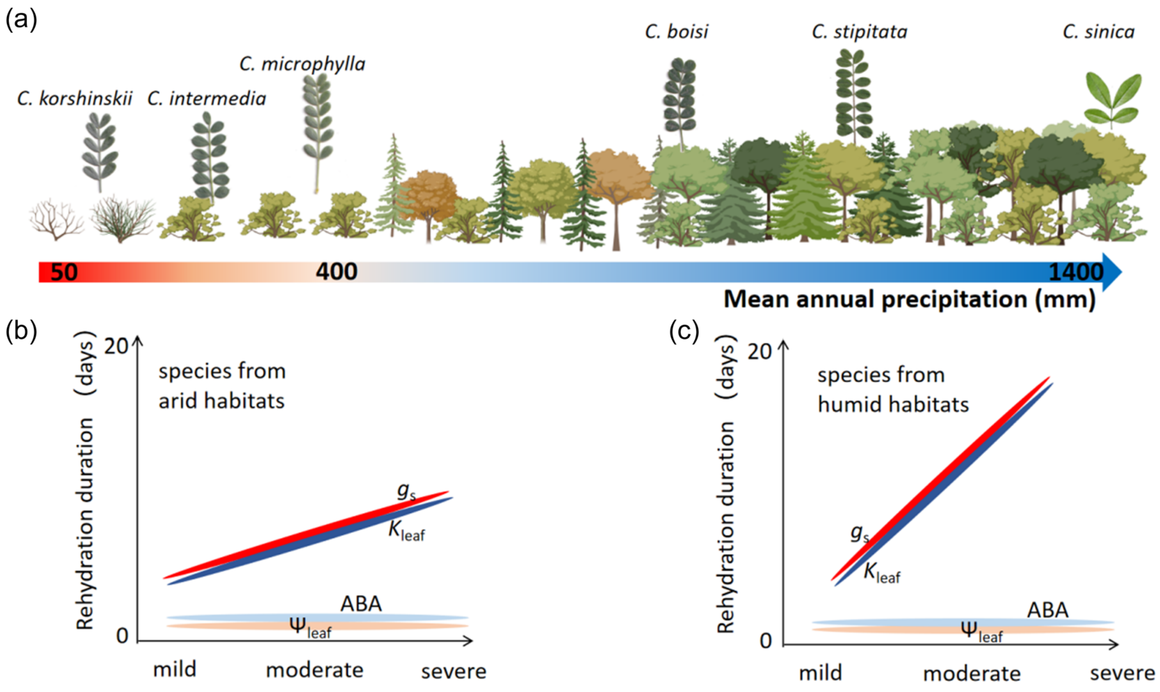

FIGURE 10 The distribution of six *Caragana* species and the recovery pattern of *Caragana* species from arid habitats and from humid habitats. Six *Caragana* species distributes along the gradient of mean annual percipitation (MAP) (a). The recovery responses in predawn leaf water potential (Ψleaf) (light orange), leaf abscisic acid (ABA) concentration (wathet blue), leaf hydraulic conductance (Kleaf) (navy blue) and stomatal conductance (gs) (red) to rehydration in Caragana species from arid habitats (b) and humid habitats (c).

and mature seeds during a short, unpredictable growing season; and (iii) use rainfall more efficiently to reduce soil evaporation as much as possible, especially during the hot and arid summer season. Thus, the results provide a functional framework for understanding how plants respond to dehydration/rehydration cycles imposed upon the majority of plants growing in the field, and point to the ability to recover in gas exchange post-drought as a strong driver shaping species' distribution along a MAP gradient.

4.2 | K_{leaf}, not ABA or Ψ_{leaf}, is associated with the recovery of gas exchange

While it has long been claimed that the stomatal conductance is closely associated with Ψ_{leaf} (Turner, 1974a, 1974b) and ABA concentration when subject to soil water deficits (Schurr et al., 1992). This study has shown that Ψ_{leaf} recovered quickly after rehydration, within 24 h, to values in the well-watered controls in all species irrespective of the MAP of their native habitat. Although we found a strong association between the recovery of K_{leaf} and the recovery of gas exchange, pointing to a potential mechanistic limitation, a possible alternative explanation for the delay in recovery of gas exchange after the recovery of Ψ_{leaf} is the persistence of ABA that builds up in the leaf and closes the stomata as water stress develops (Brodersen et al., 2013; Brodribb & McAdam, 2011, 2013; Lovisolo et al., 2008; McAdam & Brodribb, 2014). Our recent work on the same *Caragana* species showed that the leaf ABA concentration increased linearly until the predawn Ψ_{leaf} reached −3 to −4 MPa across species, and then decreased, and the peak leaf ABA concentration was higher in species from arid compared to humid habitats (Yao et al., 2021; Figure 9). With mild and moderate drought stress, Brodribb and McAdam (2013) and Skelton et al. (2017) report a possible delay in drought recovery due to the persistence of ABA-mediated stomatal closure particularly in species from humid environments as after re-watering, foliar ABA concentrations can remain unchanged or even temporarily increase (Zeevaart, 1980), inhibiting stomatal opening and transpiration (McAdam & Brodribb, 2016; Tombesi et al., 2015). However, in our study, all species showed a rapid decrease in leaf ABA concentration as Ψ_{leaf} recovered within 24 h in all treatments irrespective of the maximum ABA concentration achieved. Moreover, under severe drought stress, ABA decreased to the level in the controls before rehydration, and was not different from the control plants after rehydration, whereas the recovery of gas exchange varied from 5 days in species from arid habitats to 17 days in species from humid habitats. Therefore, there is no evidence to suggest that the ABA produced during water stress limited gas exchange recovery upon rehydration. Rather, our results point to gas exchange recovery depending strongly on the hydraulic integrity of the system.

In the present study, the recovery in K_{leaf} was closely associated with the recovery in gas exchange among closely-related species along a MAP gradient. These findings conform to a hydraulic-stomatal limitation model (Blackman et al., 2009; Brodribb & Cochard, 2009). Indeed, a positive relationship was observed between RK_{days} and Rg_{days}, suggesting that the rate of recovery of K_{leaf} was closely associated with the rate of recovery of gas exchange. Further, as the K_{leaf} measurements in this study were made on excised leaves while the measured values of K_{leaf} during recovery were closely associated with the recovery of gas exchange of leaves on whole plants. Although we did not test hydraulic conductance in other tissues, our results suggests that the hydraulic flow restriction of the leaves was sufficient to account for the recovery of gas exchange, without involving changes in hydraulic conductance in other tissues, such as stems, roots and branches.

The pathway outside the xylem has been shown to be more vulnerable to dehydration than the xylem pathway in several species (Sack et al., 2016; Scoffoni & Sack, 2017; Scoffoni et al., 2012, 2017a). In the six *Caragana* species of the present study, 80% of K_{leaf} loss occurred before the species reached their turgor loss point and 95% K_{leaf} loss occurred before initial embolism formation in the leaf mid-veins (at a Ψ_{leaf} of about −4 MPa; Yao et al., 2021). Therefore, the recovery of K_{leaf} from mild (−2 MPa) and moderate (−4 MPa) drought stress is likely to relate to the recovery of outside-xylem hydraulic conductance (K_{ox}) rather than K_{x}. Under severe drought stress when embolisms develop, the slow levels of post-drought recovery of K_{leaf} has been attributed to the slow refill of embolised xylem (Blackman et al., 2009; Brodribb et al., 2010; Choat et al., 2012; Creek et al., 2018). Refilling of embolised conduits is a slow and energetically expensive process (Creek et al., 2018; Ruehr et al., 2019; Skelton et al., 2017), while outside-xylem pathways are likely to recover in conductance faster than xylem (Ruehr et al., 2019; Scoffoni et al., 2017a; Trifiló et al., 2016). Therefore, the recovery of K_{leaf} from severe drought stress (−6 MPa) is likely to relate to the recovery of the hydraulic conductance of the xylem (K_{x}).

The question that then arises is what causes K_{ox} or K_{x} (thus K_{leaf}) to recover differently between species from humid compared to arid habitats. The evidence suggests that the leaf turgor loss point (π_{tlp}) (Yao et al., 2021) impacts K_{ox} recovery under mild and moderate drought stress as shown by: (i) a significant positive relationship observed between RK_{days} and the % loss of K_{ox} at −2 and −4 MPa, indicating that the lower % loss of K_{ox} can contribute to rapid recovery in K_{leaf} (short RK_{days}); (ii) lower % loss of K_{ox}, in turn, is tightly related to a more negative K_{leaf} P_{50} across *Caragana* species; and (iii) the more negative K_{leaf} P_{50} in species from arid habitats is driven by the more negative π_{tlp} (Yao et al., 2021). This also agrees with observations across a diverse set of species (reviewed in Scoffoni & Sack 2017). At a global scale, the π_{tlp} increases gradually from semi-desert plants with values of less than −3 MPa to forest species in the wet tropics with values of about −1.5 MPa (Bartlett et al., 2012; Lenz et al., 2006) providing potential support that species in arid habitats recover more rapidly from drought stress. Our data suggests that the recovery of K_{x} may be associated with the resistance to xylem embolism during dehydration, as RK_{days} is related to PLC_{major} P_{50}, with species from arid habitats having less conduit embolism (more negative PLC_{major} P_{50}) and more rapid recovery (less RK_{days}). During rehydration, the water needed for refilling the vessels is likely to travel in these remaining functional conduits to the proximity of the embolised xylem tissue and then flow via more localised gradients to the parenchyma cells surrounding a cavitated conduit, resulting in rapid hydraulic recovery of the xylem (Urli et al., 2013). Therefore, we argue that π_{tlp} and the characteristics that enable species to resist hydraulic decline during drought are similar to those that enable the species to recover quickly from drought.

5 | CONCLUSIONS

Plant hydraulics has focused considerable attention on the mechanisms of hydraulic loss during drought stress, while largely ignoring the ability of a species to recover following rehydration. The findings in this study highlight that the recovery of gas exchange after re-watering in six *Caragana* species was associated with the MAP of the species' habitat, with those species from arid habitats recovering their gas exchange more rapidly during rehydration than species from humid habitats as a result of a faster recovery of K_{leaf} (fig. 10). The characteristics that enable a species to resist hydraulic decline enable the species to recover quickly from drought via less drought-induced K_{leaf} loss. The results therefore represent a significant conceptual advance in our understanding of plant adaptation to dry habitats especially in a rapidly-changing climate.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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