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# Trade-off between leaf turnover and biochemical responses related to drought tolerance in desert woody plants

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ABSTRACT

We describe differences in leaf photo-protection mechanisms in a group of arid adapted $C_3$ and $C_4$ shrubs that differ in their leaf life-span and compared these mechanisms to known differences in drought tolerance. The experiments were carried out in the field with fourteen woody species native to the Hexi Corridor region, northwestern China. We assessed water status, chlorophyll content, antioxidant enzymes activity, and solute content. We found that differences in photo-protection mechanism among species were not a consequence of differences in photosynthetic pathway, but they were related to leaf life-span. Further, we found evidence that supports the concept of a trade-off between leaf turnover and photo-protective mechanism: species with a longer leaf life-span (leaves with low turnover rate) had higher values of enzymatic (POD and CAT) and no-enzymatic (Chl a, Chl b, Car, and soluble sugars-SS) compounds, than species with a shorter life-span (high turnover rate). These different photoprotective strategies are in accordance with known differences in morphological and physiological leaf attributes that allow for rapid acquisition resources (i.e. acquisitive type) or permit conservation of resources within well protected tissues (i.e. conservative type).

## 1. Introduction

Plants native to arid environments have developed an array of adaptations to drought, resulting in a high diversity of growth forms, from deep-rooted evergreen sclerophyllous, to deciduous shrubs and geophytes and winter annual herbs, which escape drought by finishing their annual cycle before the onset of drought (Ehleringer and Mooney, 1983). In desert shrubs, differences in the physiology of water, nutrients and carbon acquisition provide different strategies of resource use and partition to cope with water stress (Sala et al., 2012).

Shrubs with $C_4$ photosynthetic pathway tend to have high radiation, nitrogen, and water use efficiencies, and are thus, able to tolerate higher levels of stresses than shrubs with $C_3$ photosynthetic pathway (Ghannoum, 2009). It is well-established that the physiological advantages, conferred by the higher photosynthetic efficiency under high light and temperature of $C_4$ relative to $C_3$, are crucial for the ecological dominance of $C_4$ plants in open, hot and arid environments (Long, 1999; Osmond et al., 1982). Still, terrestrial vegetation is composed of about 95% $C_3$ plants and 5% $C_4$ and CAM plants, but primary productivity of $C_4$ plants is high and accounts for 20% of the total primary productivity (Ward et al., 1999). Predictions of global warming and changes in precipitation patterns are likely to expose plants to increase water stress (IPCC, 2007). The consequences of this change are likely to be on the form of lower water availability and higher water demand from the atmosphere, leading to an increase in the proportion of land area covered by $C_4$ plants (Henderson et al., 1994). In particular, in the desert of the central Hexi Corridor, $C_4$ woody plants tend to be dominant (Moore, 1994) and environmental change has the potential to increase this dominance. The understanding of how physiological and biochemical traits differ between $C_3$ and $C_4$ plants and how variable within these two groups these traits are, could help us predict potential changes in species composition and ecosystem carbon cycling under global warming scenarios.

Low water availability and/or high salt concentration typical in the soils of arid environments are manifested primarily as osmotic stress, resulting in the disruption of homeostasis and ion distribution in the cells of plants growing in dry environments (Serrano et al., 1999). Oxidative stress, which frequently accompanies

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**Abbreviations**

| | |
|---|---|
| Car | carotenoid |
| CAT | catalase |
| Chl a | chlorophyll a |
| Chl b | chlorophyll b |
| Chl a/Chl b | chlorophyll a/chlorophyll b |
| LWP | leaf water potential |
| MDA | monodehydroascorbate |
| NR | nitrate reductase |
| POD | peroxidase |
| Pro | proline |
| RWC | relative water content |
| SOD | superoxide dismutase |
| SP | soluble protein |
| SS | soluble sugar |
| TFA | total free amino acid |
| $\delta^{13}$C | stable carbon isotope ratio (‰). |

drought and temperature stress, may cause denaturation of functional and structural proteins. As a consequence, these diverse environmental stresses often activate similar cell signaling pathways or cellular responses, such as the production of stress proteins, up-regulation of anti-oxidants and accumulation of compatible solutes (Knight and Knight, 2001). Plant tissue dehydration induces reactive oxygen species (ROS) synthesis, which could disrupt normal metabolism of plants through oxidative damage to lipids, proteins, nucleic acids and photosynthetic pigments (Ozkur et al., 2009). In order to overcome oxidative stress, plants have developed enzymatic (such as superoxide dismutase-SOD, catalase-CAT, and peroxidase-POD; Smirnoff, 1993; Reddy et al., 2004) and non-enzymatic (such as carotenoids; Adams et al., 1999; Munné-Bosch and Peñuelas, 2003) antioxidant defense mechanisms to quench ROS and stabilize photosynthetic complexes. Reduction in the content of pigments (such as chlorophyll a and b, and carotenoid) as a result of either slow synthesis or fast breakdown has been considered as a protective mechanism to avoid oxidative stress (Smirnoff, 1993). Another energy dissipative mechanism, distinguished by its faster kinetics, is related to the energy-dependent chlorophyll fluorescence quenching (Krause and Weis, 1991). All these photo-protective mechanisms help to maintain the high oxidative state of the primary electron acceptors of PSII, reducing the probability of photo-damage and photo-oxidative stress in chloroplasts.

In $C_3$ plants exposed to water stress, photorespiration may act as an alternative electron sink, protecting them from over reduction of the photosynthetic electron transport chain (Cornic and Fresneau, 2002; Osmond and Grace, 1995). In $C_4$ plants, the scope for photorespiration acting as a protective electron sink is minimal, and it is expected that the activity of antioxidant enzymes should be greater than in $C_3$ plants, contributing to their greater drought tolerance (Osmond and Grace, 1995). The multiple roles of metabolic mechanisms to tolerate drought in plants with different photosynthetic pathways is not completely understood and raises the question if $C_4$ plants are better adapted to severe drought than $C_3$ plants (Ripley et al., 2007).

While $C_3$ and $C_4$ shrubs are expected to adjust differently to low water availability, it is also expected that shrubs with leaves that differ in life span have different photo-protective mechanisms (Ishida et al., 2006). Leaf longevity modifies photosynthetic capacity, foliage nitrogen concentration and specific leaf area (SLA), and thus, structural and functional adaptation to cope with the stress factors should also differ for leaves of different life span. Long-lived leaves tend to have low SLA and a prolonged nutrient retention (Wright et al., 2002), that allow the plant to buffer the cost of construction of low-productivity leaves, over a longer period (Kikuzawa, 1991). However, structural and chemical protection is necessary for leaves with a long life span to enhance their tolerance to physical hazards (Coley, 1988). In contrast, short-lived leaves have high SLA and traits that allow for a greater carbon acquisition capacity (high nitrogen and chlorophyll content; Poorter et al., 2009; González-Paleo and Ravetta, 2011).

These functional differences related to leaf-longevity (i.e. inverse of leaf turnover) should be also reflected in differences in their photo-protective mechanisms (Ain-Lhout et al., 2004; Hamerlynck and Huxman, 2009). The dissipation of excess absorbed radiation by photorespiration and/or antioxidant enzymes when $CO_2$ uptake is reduced by stomata closure is essential for avoiding chronic photo-inhibition. It is expected that this response should be better developed in leaves with a longer life span. Ishida et al. (2006) proposed that in deciduous trees, due to the low leaf construction cost, the dissipation of excess-absorbed light energy is mainly achieved by photorespiration. By contrast, long-lived leaves in trees exhibit down-regulation of photochemical capacity through the synthesis of non-enzymatic (i.e. carotenoids) and enzymatic compounds.

Our objective was to evaluate, in a group of $C_4$ and $C_3$ shrubs differing in leaf-span, whether the biochemical photoprotective strategy fits the world-wide leaf economics spectrum described by Wright et al. (2002). A general empirical quantification of the differences in energy dissipation and the links to photosynthetic pathway and leaf-type is lacking.

Thus, in this study, we hypothesized that: 1) $C_4$ shrubs have a higher capacity for antioxidant production (enzymatic and non-enzymatic) than $C_3$ shrubs and this capacity should be positively associated with drought tolerance (relative water content and leaf water potential) and water use efficiency (higher $\delta^{13}$C) under drought stress; 2) the tolerance to photo-inhibition during drought-stress is more conspicuous in leaves with long leaf-span than in leaves with a short leaf-span (i.e. there is a trade-off between leaf turnover and photo-protective mechanism).

## 2. Materials and methods

### 2.1. Study site and plant material

This study was conducted in the Hexi Corridor region, Gansu province, northwestern China (38°42′–39°25′ N, 100°03′–100°24′ E). The area is characterized by a temperate arid desert climate with an average temperature of 7.6 °C, while the absolute maximum and minimum may reach 39.1 °C and −27 °C, respectively with a mean annual precipitation of 116.8 mm (Su et al., 2004). We studied fourteen native shrubs that were chosen because they are the most abundant in this ecosystem (Table 1). Species were classified according to two criteria: 1) photosynthetic pathway, $C_3$ or $C_4$; and 2) leaf type. Although leaves have traditionally been categorized as corresponding to evergreen or deciduous plants, we defined three categories based on longevity: short-lived leaves, long-lived leaves and intermediate-lived leaves (Table 1). For each species, we collected and pooled three samples of leaves for 10 to 20 individuals (mixed samples), in mid-July 2011. In July, the midday photosynthetic photon flux density can exceed 2000 $\mu$mol $m^{-2}$ $s^{-1}$, and the air temperature can exceed 40 °C. Leaves were immediately frozen in liquid nitrogen and stored at −70 °C until analyzed.