



## Characterization of quaternary ammonium compounds in *Flourensia* xerophytic communities and response to UV-B radiation



L.A. Piazza<sup>a,\*</sup>, D. López<sup>a</sup>, M.P. Silva<sup>a</sup>, M.J. López Rivilli<sup>a</sup>, J.J. Cantero<sup>b,c</sup>, G.M. Tourn<sup>a,d</sup>, A.L. Scopel<sup>a,e,\*\*</sup>

<sup>a</sup> Estación de Biología Sierras, Facultad de Agronomía-Sede Punilla, Universidad de Buenos Aires, Casilda S/N, Huerta Grande, 5174, Córdoba, Argentina

<sup>b</sup> Departamento Biología Agrícola, Facultad de Agronomía y Veterinaria, Universidad de Río Cuarto, Río Cuarto, 5800 Córdoba, Argentina

<sup>c</sup> Instituto Multidisciplinario de Biología Vegetal (CONICET-UNC), 5000, Córdoba, Argentina

<sup>d</sup> Cátedra de Botánica Agrícola, Facultad de Agronomía, Universidad de Buenos Aires, Argentina

<sup>e</sup> Investigaciones en Biociencias Agrícolas y Ambientales (INBA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina

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### ABSTRACT

As part of ongoing studies aimed at characterizing molecular components involved in the ecophysiological adaptations of native xerophytic plants from central Argentina, we demonstrated the presence of compatible solutes in *Flourensia campestris* (FC) and *Flourensia oolepis* (FO), specifically glycine betaine (GB) through TLC, LC, <sup>1</sup>H NMR and <sup>13</sup>C-NMR. GB content (leaves:  $38 \pm 7 \mu\text{mol g}^{-1}$  DW; adult plants > seedlings), and distribution (capitula > vegetative leaves > reproductive leaves > shoots > roots) were similar to other quaternary ammonium compound (QAC) accumulators. *Flourensia* seedlings from both species protected from UV-B exposure – a major abiotic stress in these natural environments – showed a significant increase of GB in the leaves ( $p < 0.01$ ) and a significant decrease in the roots ( $p < 0.05$ ). In FC and FO xerophytic shrub-dominated communities QACs were detected for the first time in 41% of co-occurring species ( $N = 39$ ), 14 of 28 natives (50%) and 2 of 11 exotics (18%), being GB in natives only (57% of QAC accumulators). GB may be considered as a chemotaxonomical character for the genus *Flourensia*, since it was also detected in *Flourensia hirta*, *Flourensia niederleinii*, *Flourensia riparia*, *Flourensia fiebrigii*, *Flourensia macroligulata* and *Flourensia heterolepis*. Our controlled UV-B experiments, set up in the same natural environment where these species grow, clearly show that solar UV-B – and therefore oxidative stress – is involved in regulating GB contents and within-plant distribution in FC and FO seedlings. The findings in *Flourensia* co-occurring native species suggest that QACs accumulation may be considered as a community-specific ecophysiological trait in these xerophytic environments.

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### 1. Introduction

The genus *Flourensia* (Asteraceae) belongs to the subtribe Ecliptinae, tribe Heliantheae (Robinson, 1981), and comprises about 25 species of resinous shrubs that grow from southern United States to Argentina and Chile, twelve of which are present in Argentina (Funk et al., 2009). Two endemic species of the genus live in Central Argentina: *Flourensia campestris* Griseb (FC) and *Flourensia oolepis* S.F. Blake (FO) (Dillon, 1984). They are commonly known as “chilcas”, and have been traditionally used as aromatic, tinctorial and – specially their roots – as firewood (Barboza et al., 2009). FO and FC show distinct spatial distribution and are frequently found growing at high densities in almost

pure stands known as “chilcales” (Luti et al., 1979), in natural environments characterized by abiotic stress conditions (e.g., elevated UV-B, droughts, skeletal soils, low and high temperatures). We recently isolated a phytotoxic compound (–)-hamanasic acid A from FC and FO (Silva et al., 2012; López et al., 2013) that accumulates at high concentration on plant surfaces, which suggests its allelochemical potential in the adaptive strategies displayed by these species; the same compound was also characterized in other two from five South American *Flourensia* species (López et al., 2013).

The effects of stressful conditions on plants such as drought, salinity, high radiances, and high and low temperatures can have a major impact on plant growth and survival. In order to cope with these stresses plants have evolved an array of defense mechanisms which involve dynamic, complex cross-talk between different regulatory levels, including adjustment of metabolism and gene expression for physiological and morphological adaptations (Krasensky and Jonak, 2012). In response to osmotic and oxidative stress, many plant species accumulate significant amounts of small molecules (compatible solutes) including sugars, polyols, amino acids and quaternary ammonium compounds (QACs) such as glycine betaine, alanine betaine, proline betaine, choline

Abbreviations: FC, *Flourensia campestris*; FO, *Flourensia oolepis*; GB, glycine betaine; QAC, quaternary ammonium compound.

\* Corresponding author. Tel.: +54 3548 426421.

\*\* Correspondence to: A.L. Scopel, Estación de Biología Sierras, Facultad de Agronomía-Sede Punilla, Universidad de Buenos Aires, Casilda S/N, Huerta Grande, 5174 Córdoba, Argentina. Tel.: +54 3548 426421.

E-mail addresses: [leonardoalbertopiazza@yahoo.com.ar](mailto:leonardoalbertopiazza@yahoo.com.ar) (L.A. Piazza), [scopel@agro.uba.ar](mailto:scopel@agro.uba.ar) (A.L. Scopel).

O-sulfate, hydroxyproline betaine and pipercolate betaine (Hanson and Wyse, 1982; Rhodes and Hanson, 1993; Carillo et al., 2008; Chen and Murata, 2011).

Glycine betaine (N,N,N-trimethylglycine), one of the best-studied QACs is synthesized through two steps from Cho oxidation by specific enzymes in plants, mammals, marine invertebrates, bacteria and hemophilic archaeobacteria (Rhodes and Hanson, 1993; Takabe et al., 2006; Chen and Murata, 2008). In plants, levels of GB vary considerably among species and organs, and they increase, translocate and/or show intracellular distributions when subjected to abiotic stress (Storey et al., 1977; Chen and Murata, 2011; Zhang et al., 2012). Results obtained from studies in natural GB-accumulating and transgenic plants (Robinson and Jones, 1986; Chen and Murata, 2002) show that GB enhances tolerance to abiotic stress mainly through stabilization of complex proteins and induction of ROS-scavenging enzyme genes. The protective effects exerted by GB on the photosynthetic machinery has been extensively investigated under the combined effects of light stress and other kinds of abiotic stresses, such as osmotic stress and chilling and freezing stress (Carillo et al., 2011; Chen and Murata, 2011). However, no studies have investigated the specific effect of UV-B radiation on GB levels and distribution within plants. As a major abiotic stress, UV-B (280–315 nm) has several effects on the physiology of terrestrial plants as a result of direct photochemical damage to key macromolecules such as proteins and nucleic acids, or as an indirect consequence of the increased production of ROS (Piri et al., 2011). The degree of damage caused by UV-B depends strongly on the efficiency of constitutive and UV-induced mechanisms of protection and repair, such as the accumulation of UV-absorbing sunscreens and the activation of antioxidant defenses (Mazza et al., 2000). Mohammed and Tarpley (2013) recently found that exogenous application of GB ameliorated the effects of UV-B irradiation resulting in increased rice yield. Based on these facts, it is reasonable to speculate that GB-accumulating plants growing under elevated UV-B radiation would have an additional strategy to tolerate this abiotic stress. At present there is no information regarding the presence of QACs as compatible solutes in the genus *Flourensia*, or their potential involvement in the tolerance to UV-B, a main abiotic stress in its natural environment. It could be hypothesized that plants coexisting in xerophytic environments may have evolved common traits that would allow them to endure and reproduce in these harsh conditions. In this sense, a generalized occurrence of QACs within a plant community would emphasize its ecophysiological role in the tolerance of plant species to abiotic stresses.

The present study was aimed at: 1) Assessing the presence, distribution and molecular characterization of QACs in *FC* and *FO* species; 2) Evaluating the effects of solar UV-B radiation on QACs content and within-plant distribution in *FC* and *FO* plants; 3) Exploring whether the accumulation of QACs may be a widespread adaptive strategy within *FC*- and *FO*-dominated communities; and 4) Assessing the presence of QACs in other species of the genus *Flourensia*.

QACs in general, and specifically GB and its precursor Cho were determined through a screening technique we devised, that involves a fast tissue extraction and TLC analysis. The methodology was conveniently validated for linearity, limits of detection and quantitation, precision, selectivity and accuracy. Molecular forms of detected QACs were studied through chromatographic isolation and spectroscopic identification (LC,  $^1\text{H}$  NMR,  $^{13}\text{C}$ -NMR). Evidence of the accumulation of QACs in the plant material from UV-B experiments, was further studied through a combination of TLC and  $^1\text{H}$  NMR studies.

## 2. Materials and methods

### 2.1. Plant material and study sites

Plant materials were collected in natural areas corresponding mainly to the Punilla Valley, Córdoba province, Argentina, and air dried plant organs were used for subsequent analysis. This hilly area (altitudes

between 700 and 1800 MASL) belongs to the northern outcrops of the Sierras Pampeanas. Soils are predominantly of litosolic characteristics (INTA Manfredi, 2006). Mean annual rainfall in the area is 550 mm, more than 90% of which fall between October and April, resulting in a pronounced dry season from May to September. Mean monthly temperature ranges between 16 and 17 °C with an annual amplitude of 14 to 15 °C. High and low temperatures, low relative humidity and high irradiances are prominent in the area. The study areas were located in shrub communities (total plant cover ~70–90%), dominated by the evergreen shrubs *F. campestris* Griseb. (*FC*) and *F. oolepis* S.F. Blake (*FO*), and plant material from these communities was collected in late spring (Nov) of 2009, 2010 and 2011.

For the initial assessment of QACs we used pooled samples of plant material collected at 2 different sites for each species: Pintos and El Dragón (*FC*), and Los Terrones and Los Cocos (*FO*), all four located in the Punilla Valley.

Plant material of co-dominant and conspicuous native species (Luti et al., 1979; Giorgis et al., 2011), as well as of the main exotic species invading these natural areas was also collected and analyzed.

#### 2.1.1. *FC* and *FO* cohabiting species

2.1.1.1. *Native species.* Anacardiaceae: *Lithraea molleoides* (Vell.) Engl. “Molle”; Asteraceae: *Acanthostyles buniifolius* (Hook and Arn.) R.M. King and H. Rob. “Chilca”, *Achyrocline satureioides* (Lam.) DC. “Marcela”, *Ambrosia tenuifolia* Spreng., *Baccharis articulata* (Lam.) Pers. “Carquejilla”, *Bidens pilosa* L. “Amor seco”, *Eupatorium viscidum* Hook. et Arn., *Grindelia cabreræ* Ariza, *Grindelia pulchella* Dunal, *Heterothalamus alienus* (Spreng.) Kuntze “Romerillo”, *Parthenium hysterophorus* L., *Viguiera tucumanensis* (Hook. et Arn.) Griseb. “Girasolillo”, *Vernonanthura nudiflora* (Less.) H. Rob. f. *nudiflora* “Falso alecrín”, *Thelesperma megapotamicum* (Spreng.) Kuntze “Te pampa”, *Xanthium spinosum* L. var. *spinosum* “cepa caballo”, *Zinnia peruviana* (L.) L. “Chinita del campo”; Euphorbiaceae: *Croton* Baill.; Fabaceae: *Acacia caven* (Mol.) Molina “Espinillo”, *Apurimacia dolichocarpa* (Gris.) Burkart, *Collaea argentina* Griseb. “Primavera”, *Sophora linearifolia* Griseb. “Sofora”; Rhamnaceae: *Colletia spinosissima* J. F. Gmel. “Barba del tigre”, *Condalia microphylla* Cav. “Piquillín”; Rosaceae: *Kageneckia lanceolata* Ruiz and Pav. “Durazno del campo”; Solanaceae: *Cestrum parqui* L' Hér. “Duraznillo negro”; Ulmaceae: *Celtis ehrenbergiana* (Klotzsch) Liebm. “Tala”; Verbenaceae: *Aloysia gratissima* (Gillies and Hook. ex Hook.) Tronc. “Palo amarillo”; Zygophyllaceae: *Larrea divaricata* Cav. “Jarilla”.

2.1.1.2. *Exotic species.* Asteraceae: *Carduus acanthoides* L. “cardo”, *Xanthium cavanillesii* Schouw. “abrojo grande”; Fabaceae: *Robinia pseudoacacia* L. “acacia blanca” and *Gleditsia triacanthos* L. “acacia negra”; Meliaceae: *Melia azedarach* L. “paraíso”; Moraceae: *Morus alba* L.; Oleaceae: *Ligustrum lucidum* W.T. Aiton “ligustro” and *Ligustrum sinense* Lour. “ligustrina”; Pinaceae: *Pinus taeda* L.; Rosaceae: *Cotoneaster franchetii* Bois. “cotoneaster”; *Pyracantha atalantioides* (Hance) Stapf “crataegus”; Ulmaceae: *Ulmus pumila* L. “olmo”.

#### 2.1.2. Other species of the genus *Flourensia*

Six additional South American *Flourensia* species were investigated and collected in their native habitats. *Flourensia hirta* S.F. Blake (*FH*, endemic), was collected in La Rioja province (1640 MASL), where it grows as a companion species in different bush-dominated communities (ca. 400 km northwest from Punilla Valley). *Flourensia niederleinii* S.F. Blake (*FN*, endemic) was also collected in La Rioja, on the slopes of Sierras de Velazco (1543 MASL), from almost pure stands. *Flourensia riparia* Griseb. (*FR*, endemic) and *Flourensia fiebrigii* S.F. Blake (*FF*) were collected in the province of Salta (ca. 900 km north from Punilla Valley), (1000 MASL and 3000 MASL, respectively), *Flourensia macroligulata* Seelgm. (*FM*) was collected in the province of Jujuy (ca. 1000 km north from Punilla Valley), and *Flourensia heterolepis* S.F. Blake (*FHe*) was

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