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Short communication

Leaf physico-chemical and physiological properties of maize (*Zea mays* L.) populations from different origins

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ABSTRACT

In this study we evaluated the leaf surface properties of maize populations native to different water availability environments. Leaf surface topography, wettability and gas exchange performance of five maize populations from the Sahara desert, dry (south) and humid (north-western) areas of Spain were analysed. Differences in wettability, stomatal and trichome densities, surface free energy and solubility parameter values were recorded between populations and leaf sides. Leaves from the humid Spanish population with special regard to the abaxial side, were less wettable and less susceptible to polar interactions. The higher wettability and hydrophilicity of Sahara populations with emphasis on the abaxial leaf surfaces, may favour dew deposition and foliar water absorption, hence improving water use efficiency under extremely dry conditions. Compared to the other Saharan populations, the dwarf one had a higher photosynthesis rate suggesting that dwarfism may be a strategy for improving plant tolerance to arid conditions. The results obtained for different maize populations suggest that leaf surfaces may vary in response to drought, but further studies will be required to examine the potential relationship between leaf surface properties and plant stress tolerance.

1. Introduction

Drought is the main limiting factor for crop production (Boyer, 1982; Farooq et al., 2009) since it may limit plant survival, development and geographic distribution (Grace, 1997; Liu et al., 2014). Water shortage is expected to occur more frequently with climate change (Intergovernmental Panel on Climate Change, IPCC, 2013), and this may compromise food production to cover societal demands. Understanding the basis of drought tolerance is of paramount importance for releasing varieties with enhanced drought resistance (Takeda and Matsuoka, 2008), and the identification of the variability of characters related to the response to water stress is necessary as a preliminary step.

Maize originated in a tropical environment in Central America more than 8000 years ago, subsequently spreading throughout America and to the rest of the World after the XV Century (Revilla et al., 2003). The dispersion of maize was possible because of the large adaptive ability of this species; maize is currently cultivated from the Equator to the 50° latitude, from 0 to 4000 m above sea level, and from the rainy tropics to the desert. Although this species was introduced in northern Africa less than 500 years ago, maize grown in the oasis of Sahara desert has produced large morphological and genetic variability (Aci et al., 2013). Due to the extremely arid conditions of Sahara desert, maize populations from temperate areas cannot be successfully cultivated there, while maize populations from the desert are tolerant to such harsh environment.

Plant surfaces are important for protecting organs against multiple biotic and abiotic stress factors including the uncontrolled loss of water (Mamrutha et al., 2010; Wu et al., 2014). On the other hand, plant surface water permeability may be a phenomenon of ecophysiological relevance since it may impede or facilitate the absorption of water in the form of, for example, liquid drops deposited on to the surfaces (Oliveira et al., 2005; Fernández et al., 2014a), fog (Limm and Dawson, 2010; Eller et al., 2013; Berry et al., 2014) or dew (Konrad et al., 2012). The surface of organs with primary growth such as leaves, fruits, stems or flowers, is covered with epidermal cells (including structures such as stomata and/or

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trichomes), the outermost epidermal cell wall layer being the cuticle (Guzmán et al., 2014). The epicuticular wax layer is the most external part of the cuticle and is in direct contact with the surrounding atmosphere (Mamrutha et al., 2010). Epidermal micro- and nano-surface features (Koch and Barthlott, 2009) together with surface chemical composition (Khayet and Fernández, 2012) will determine the degree of surface wettability and drop adhesion or repellence (Fernández and Khayet, 2015). While the mechanisms of foliar uptake of water and solutes by plant surfaces are still not fully characterised (Fernández and Eichert, 2009; Fernández and Brown, 2013), several studies analysed the interactions of plant surfaces with water (e.g., Brewer et al., 1991; Hanba et al., 2004; Roth-Nebelsick et al., 2012; Rosado and Holder, 2013; Urrego-Pereira et al., 2013a, 2013b; Wang et al., 2014; Koukos et al., 2015). Recent studies (Fernández et al., 2011, 2014a, 2014b; Fernández and Khayet, 2015) measured contact angles of three liquids with different degrees of polarity and apolarity as tool for characterising the surface free energy and solubility parameter of a few organs (mostly leaves) and species.

Under humid climates or in sprinkler irrigated areas, water drop repellence of, for example, rainfall or irrigation water, may favour plant water use efficiency, principally by increasing the amount of water that goes into the soil (Holder, 2012; Rosado and Holder, 2013). For species with wettable leaves, water deposited on to the surfaces may decrease photosynthetic rates (Hanba et al., 2004). Working with sprinkler irrigated maize, Urrego-Pereira et al. (2013a) found that photosynthetic rates decreased during the irrigation period. This was associated with its high leaf wettability which ultimately led to a reduction of maize yield (Cavero et al., 2008; Urrego-Pereira et al., 2013b). Consequently, maize cultivars with less wettable leaves may be cultivated for increasing water use efficiency under humid climates and sprinkler-irrigated areas. Under dry conditions (arid and semiarid climates), dew deposited on to plant surfaces can be a substantial water source for plants. The amount of dew water in arid and semiarid climates may range between 10 and 30 mm yr^{-1} (Duvdevani, 1964; Zangvil, 1996; Malek et al., 1999; Zhang et al., 2015). Moreover, dew may increase plant water use efficiency in the early morning (Ben-Asher et al., 2010). Several studies showed that dew should be taken into account when calculating crop irrigation requirements in arid and semi-arid climates (Moratiel et al., 2013, 2016; Yasutake et al., 2015). Dew formation on to aerial plant organs depends on the wettability of the surfaces (Agam and Berliner, 2006; Fernández et al., 2014a). For maize, values of dew have been reported to range from 0.01 to 0.6 mm per night (Atzema et al., 1990; Kabela et al., 2009; Yasutake et al., 2015). Thus, under dry conditions maize cultivars with increased leaf wettability may be advantageous for improving plant water economy. The potential adaxial and abaxial surface variations between leaves from various cultivars of a crop developed under different eco-physiological conditions have never been analysed so far, either alone or in relation to water drop interactions. In this preliminary study, we examined for the first time the wettability and physico-chemical features of abaxial and adaxial maize leaf surfaces of cultivars from different climates, ranging from the humid temperate northwest of Spain to three different Sahara desert areas.

2. Materials and methods

2.1. Plant material

Three maize open-pollinated populations representing the geographic diversity of the Saharan desert were included in this characterization, namely PI542687 from the south, PI527470 from the west, and the dwarf population PI527464 from the north of the Algerian Sahara (Table 1). These three populations have similar plant size and growth cycle under the conditions of Pontevedra (northwest of Spain). Two Spanish populations were used for comparison: Cee from Corunna (a province in the northwest of Spain with humid climate), and EPS14(FR)C3 which is an improved synthetic population made from the combination of four populations coming from the dry regions of eastern Spain. The five populations were sown in Pontevedra (northwest of Spain) the 13th of May 2015. Pontevedra has a mild humid climate with an average annual rainfall of 1600 mm with a mild summer drought.

2.2. Leaf surface traits and physico-chemical properties

For assessing the relationship between leaf surface features and water interactions, several aspects have been measured using maize populations originated in areas of differential aridity (Table 1). For the development of trials, the leaf below the main ear of ten plants per population was cut after female flowering (mid July of 2015). The topography of gold sputtered adaxial (upper) and abaxial (lower) leaf surfaces of the different maize populations was observed by scanning electron microscopy (SEM; Hitachi S-3400 N, Tokyo, Japan). The average number of trichomes and stomata were assessed by image analysis of adaxial and abaxial SEM micrographs (ImageJ 1.45s, W.R., National Institutes of Health, Bethesda, Maryland, USA). For characterizing the physico-chemical properties of adaxial and abaxial maize leaves, advancing contact angles of drops of double-distilled water, glycerol and diiodomethane (both 99% purity, Sigma-Aldrich) were measured at 20 °C with a Drop Shape Analysis System (DSA 100, Krüss, Germany). Approximately 2 µl drops of each liquid were deposited on the adaxial and abaxial surface of 10 maize leaves (40 repetitions per leaf surface) with a manual dosing system holding a 1 ml syringe with a 0.5 mm diameter needle. Side view images of the drops were captured at a rate of 10 frames s^{-1}. Contact angles were automatically calculated by fitting the captured drop shape to the one calculated from the Young–Laplace equation. For adaxial and abaxial leaf surfaces the total surface free energy (γ), its components (i.e., the Lifshitz-van der Waals (γ_s^{LW}) and acid-base (γ_s^{AB}; γ^+ and γ_s^-)), and surface polarity were calculated considering the surface tension components of water ($\gamma_l = 72.80$ mJ m^{-2}, $\gamma_l^{LW} = 21.80$ mJ m^{-2}, $\gamma_l^+ = \gamma_l^- = 25.50$ mJ m^{-2}), glycerol ($\gamma_l = 63.70$ mJ m^{-2}, $\gamma_l^{LW} = 33.63$ mJ m^{-2}, $\gamma_l^+ = 8.41$ mJ m^{-2}, $\gamma_l^- = 31.16$ mJ m^{-2}) and diiodomethane ($\gamma_l = \gamma_l^{LW} = 50.80$ mJ m^{-2}, $\gamma_l^+ = 0.56$ mJ m^{-2}, $\gamma_l^- = 0$ mJ m^{-2} (Fernández and Khayet, 2015).

2.3. Leaf photosynthetic traits

The net photosynthetic, stomatal conductance, and transpiration rates of the leaf below the uppermost ear of ten plants per population were determined with a portable photosynthesis system Li-6400XT (Li-Cor Inc., Lincoln, NE, USA). The relative leaf chlorophyll content (SPAD) was assessed with a hand-held CCM-200 Chlorophyll Content Meter (Opti-Sciences, Tyngsboro, Massachusetts, USA). The quantum efficiency of photosystem II (ΦPSII) was recorded using an OS-30p Chlorophyll Fluorometer (Opti-Sciences, Tyngsboro, Massachusetts, USA) in the leaf below the main ear of ten plants per population.

3. Results and discussion

3.1. Leaf surface traits and physico-chemical properties

Stomata were present on both sides, but trichomes were restricted to the upper leaf side (Fig. 1, Table 2). The density of trichomes on upper leaf sides slightly varied between populations