



Water content dynamics of achene, pericarp and embryo in sunflower: Associations with achene potential size and dry-down

Déborah P. Rondanini^{a,*}, Anita I. Mantese^b, Roxana Savin^c, Antonio J. Hall^a

^a IFEVA, CONICET/Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, C1417DSE Buenos Aires, Argentina

^b Cátedra de Botánica Agrícola, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, C1417DSE Buenos Aires, Argentina

^c Department of Crop and Forest Sciences, University of Lleida, Centre UdL-IRTA, Av. Rovira Roure 191, 25198 Lleida, Spain

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ABSTRACT

The post-anthesis dynamics of the water content of whole sunflower achene and its major parts (pericarp, embryo) were examined for seven genotypes that spanned a broad range of final achene size (30–100 mg achene⁻¹). Objectives were: (i) to establish the relative contributions of pericarp and embryo to whole-achene water content dynamics, (ii) to determine the relationship between maximum water content of the pericarp and final achene size, and (iii) to examine the effect of final achene size (as affected by genotype and environment) on achene dry-down dynamics after physiological maturity (=maximum achene weight). Four experiments were conducted over 2 years under field and glasshouse conditions. Across genotypes and growth conditions, whole-achene and pericarp water contents peaked earlier and more sharply during grain filling (ca. 35% of grain filling duration, or 30% of final achene weight), maximum embryo water content was achieved somewhat later and declined less sharply. Although the pericarp was a minor (17–35%) component of final achene dry weight, it contained 65–70% of achene maximum water content. Absolute pericarp water content did not fall to values close to those of the embryo until after physiological maturity. Final achene and embryo dry weights were closely (r^2 0.90 and 0.85, respectively) associated with maximum pericarp water content. After maximum achene water content, rates of whole-achene dry-down were linear (ca. 1.35% d⁻¹), and absolute rates of water loss per achene (range = 1.1–3.7 mg H₂O achene⁻¹ d⁻¹) were strongly associated with achene maximum water content and final achene dry weight (r^2 0.86 and 0.75, respectively). Excluding the inbred line HA89, the remaining genotypes achieved harvest (17%) and storage (11%) achene water concentrations at about 15 and 20 d, respectively, after physiological maturity, largely because absolute rates of achene water loss increased with achene size. We conclude that the pericarp is the dominant component of whole-achene water content dynamics, and that pericarp and achene maximum water contents are good indicators of potential final achene and embryo sizes and achene dry-down rates. Present results also provide a first approximation to the quantification of post-physiological maturity dry-down in this crop.

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1. Introduction

The dynamics of grain water content during grain filling (Adams and Rinne, 1980; Egli, 1998) has been studied in several grain crops (e.g., soybean [Fraser et al., 1982]; maize [Egli and TeKrony, 1997; Borrás and Westgate, 2006]; wheat [Dodds et al., 1979; Schnyder and Baum, 1992; Calderini et al., 2000; Pepler et al., 2006]; and sunflower [Rondanini et al., 2007]), often with a view to determine the value of grain water concentration (WC, %) that coincides with achievement of maximum grain dry weight (i.e., physiological

maturity). The relationship between relative (to maximum) achene dry weight and decreasing achene water concentration (%) during grain filling has been described using bi-linear functions for wheat, maize and soybean (Fraser et al., 1982; Brooking, 1990; Egli and TeKrony, 1997; Calderini et al., 2000) and, more recently, using trilinear functions for maize (Borrás and Westgate, 2006) and sunflower (Rondanini et al., 2007). For maize, the first section of the trilinear model (associated with the lag phase of kernel growth) had a lower slope than the second (Borrás and Westgate, 2006). This is in direct contrast to the greater slope of the first section of the same relationship in sunflower (Rondanini et al., 2007). It is possible that the distinctive pattern for sunflower may relate to the dominant role of the pericarp (a quantitatively much less important component of the maize grain) in determining achene water dynamics during early grain-filling in this species. An examination

* Corresponding author at: CRILAR-CONICET, Entre Ríos y Mendoza s/n, 5301 Anillaco, La Rioja, Argentina. Tel.: +54 3827 494251; fax: +54 3827 494231.

E-mail address: drondanini@crilar-conicet.com.ar (D.P. Rondanini).

of the relative contributions of the pericarp and the embryo of sunflower to achene water content dynamics should throw light on this issue.

Cereal grains (fruits with relatively little pericarp) achieve their maximum water content earlier during the grain filling process than true seeds such as soybean (Egli, 1998; Borrás et al., 2004; Borrás and Westgate, 2006). It has been suggested that maximum grain water content may be used as surrogate for maximum grain volume (e.g., Ray et al., 1972; Sofield et al., 1977; Ney et al., 1993; Egli, 1998) and that maximum grain volume may limit maximum final grain dry weight (Millet and Pinthus, 1984; Egli, 1990; Schnyder and Baum, 1992; Borrás et al., 2004; Bingham et al., 2006). The relationship between maximum achene water content and achene final dry weight has not been explored for sunflower. Because pericarp maximum dry weight in sunflower is achieved well before maximum embryo dry weight during grain filling (Mantese et al., 2006), and if maximum pericarp water content can be used as a surrogate for maximum pericarp size, it may also serve as an indicator of the maximum size of the embryo contained within the pericarp. Sunflower is a good model system to study these issues given the ease (relative to cereal grains) with which pericarp of the growing achene can be separated from its contents.

Achene water concentration dynamics after physiological maturity conditions the timing of harvest maturity and the achievement of the achene water concentration suitable for grain storage. There have been some recent attempts to describe post-physiological maturity dry-down in cereals (Pepler et al., 2006; Gambín and Borrás, 2007; Gambín et al., 2007). It is usually assumed that grain dry-down is strongly dependent on environmental conditions, especially temperature and atmospheric water concentration (Paulsen et al., 1983; De Lucía and Assennato, 1993; Thomison et al., 2001; Bragachini and Casini, 2005), and on the effects of diseases (Dimmock and Gooding, 2002a,b). However, crop and grain characteristics (e.g. spike position, spike structure and endosperm composition) have also been shown to affect grain dry-down in maize (Kang et al., 1986; Brooking, 1990; Córdova-Tellez and Burris, 2002). There is very little information in the literature relating to sunflower dry-down (Farizo et al., 1982; Bragachini and Casini, 2005; Giner and Gelly, 2005), in spite of the susceptibility of this crop to yield and quality losses through stem and root lodging, and through bird and fungal damage, during the interval between physiological maturity and harvest; and no attempt has yet been made to examine dry-down in sunflower genotypes of different grain size or to relate dry-down to achene water content dynamics.

Work presented here aimed at documenting – in a set of seven genotypes of contrasting final grain size – whole-achene, pericarp and embryo water content dynamics from just after anthesis until achievement of a grain water content which would allow the grain to be harvested. Particular objectives were: (i) to determine the relative contributions of pericarp and embryo to whole-achene water content dynamics; (ii) to establish the relationships between final achene weight and maximum achene and pericarp water contents; and (iii) to establish the relationships between achene size and achene water concentration dynamics and post-physiological maturity dry-down.

2. Materials and methods

2.1. Plant material and cultural details

Four experiments were conducted at the Facultad de Agronomía, Universidad de Buenos Aires (34°35'S) during the 2002–2003 and 2004–2005 growing seasons. Sunflower genotypes (seven in total) used in these experiments covered a broad range of final achene

size (30–100 mg achene⁻¹) and pericarp proportion (17–35%), and included an inbred line (HA89), white-striped hybrids (P30, M734 sown in spring and in autumn [M734i], CF19) and black-striped hybrids (P20, VDH, Aguara) (for further details see Rondanini et al., 2007). Experiments were sown during the normal spring season (Exps. 1 and 4), in the summer (Exp. 2) or late in the autumn (Exp. 3). Plants in Exps. 1, 3 and 4 were grown in 7 m × 6 m plots (population density 8 plants m⁻², rows separated by 0.7 m) fertilised at sowing with 80 kg ha⁻¹ Ca(NO₃)₂. Soil was a reconstituted profile consisting of a 180-cm deep layer of Typic Argiudoll plough layer resting on native loess. Plants used in Exp. 2 were grown in 50-L pots filled with a mixture of earth, sand and peat (4:2:1, v/v/v), and fertilised at sowing with 5 g pot⁻¹ Ca(NO₃)₂. The pots were arranged as a crop (rows separated by 0.7 m) with one plant pot⁻¹. Genotypes in Exp. 1 were arranged in randomised complete blocks with three replications. Genotypes sampled in Exps. 2–4 formed part of larger experiments (see details in Rondanini et al., 2007) and three plants were sampled for each genotype. All experiments were irrigated as needed and weeds, pests and diseases controlled when necessary. Environmental conditions during grain-filling and during post-physiological maturity dry-down are shown in Table 1.

2.2. Measurements

Sampling began at anthesis (defined by the appearance of stamens in all flowers of the outer ring of the capitulum [stage R5.1, Schneiter and Miller, 1981]), when individual plants were tagged to register the start of flowering, and continued until 30 d after physiological maturity (PM = maximum achene dry weight). Three achenes per replicate were harvested at 2- or 3-d intervals from the peripheral achenes (derived from florets in the third to fifth [counted from the rim of the capitulum] floral circles) of the capitulum in all genotypes. Achenes from intermediate positions (derived from florets in seventh to ninth floral circles) on the capitulum were also harvested from all genotypes except HA89. Harvested achenes were immediately sealed into Eppendorf tubes or, when achene grew larger, into aluminium foil envelopes. Achenes were weighed within 3–5 min after harvest to determine fresh weight, and immediately separated into pericarp and embryo and each component weighed (peripheral achene only). In early phases of achene development the embryo component included the aqueous endosperm (present at the early stages of embryo development and consumed during embryo growth). Material was dried for 48 h at 60 °C to determine component dry weight. Achene, pericarp and embryo absolute water content (WC, in mg) was calculated as the difference between the respective fresh and dry weights, while water concentration (%WC, on a fresh weight basis) was calculated as the ratio, expressed as percentage, between absolute water content and fresh weight.

2.3. Data analysis

The non-linear routine of TBL curve (Jandel TBLCURVE, 1992) was used to fit bi-linear broken-stick functions ($r^2 = 0.80–0.98$) with an unknown break point to unit achene, pericarp and embryo mass/time after anthesis relationships (Ploschuk and Hall, 1995). The conditional model fitted was $y = b(x - a)$ for $x < c$ and $y = bc$ for $x > c$; where y was achene, pericarp or embryo dry weight, x was days from anthesis, a was the intercept and b the slope of the non-plateau section of the broken-stick, and c was the unknown break point (i.e., the timing of maximum achene, pericarp or embryo weight). Bi-linear broken-stick functions were chosen to model the growth of grain, pericarp and embryo instead of sigmoidal functions because they are simpler (three parameters instead of five for sigmoidal functions), and all parameters have biological

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