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Senescence in field-grown maize: From flowering to harvest

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ABSTRACT

The objective of this work was to describe the dynamics of senescence of field-grown maize from silking to harvest, at both leaf and plant level. At the leaf level, the dynamics of symptoms of senescence were considered on each leaf taken individually and described according to zones from the tip to the base of the leaf lamina. At the whole plant level, foliar ranks were each considered as an entity to describe the time course of senescence. To this end, we use a database built-up from field trials conducted during three consecutive years (1994–1996) and thus undergoing variable meteorological and soil water conditions. Leaf chlorophyll content was estimated using two different methods based on the optical properties of the leaves. In Trial I, chlorophyll estimates were based on leaf optical density measured with a MacBeth TR-924 densitometer. In Trial II and Trial III, chlorophyll estimations were based on measurement using a hand-held Minolta SPAD-502 device. In Trial II and Trial III, chlorophyll fluorescence analyses under filed conditions were performed. These analyses focused on the photosystem II (PSII) maximum efficiency (Fv'/Fm') parameter in the light-adapted state. Measurements were done with a Waltz PAM-2000 portable fluorometer. We report detailed descriptions of the spatio-temporal dynamics of these indicators of senescence. We found that, after silking, a strong relationship exists between available water and leaf chlorophyll content. Further, the maximum efficiency of PSII decreased faster in maize plants undergoing low available soil water than in irrigated plants. The rank of a leaf is determinant of the time for the beginning of the decline in both chlorophyll content and maximum efficiency of PSII. At plant and leaf level, the onset of senescence was marked by a decrease in chlorophyll content that was not concomitant with a dramatic decrease in the maximum efficiency of PSII. Our analyses suggest that a non-linear functional relationship could exist between these two parameters during monocarpic senescence. In the mean time, the results presented in this paper could be used to refine the senescence related modules in plant and crop models.

1. Introduction

Maize (*Zea mays* L.) is grown worldwide for grain and forage. Statistics by the Food and Agriculture Organization (FAO) of the United Nations show that maize, together with rice (*Oryza sativa* L.) and wheat (*Triticum* spp L.), is one of the three most important cereals for human and animal consumption in the world (FAOSTAT, 2011). Maize contributes by one third to world's cereals production. Trend analysis suggests that cereal production would have to increase from ca. 2.5 billion tonnes in 2009 to some three billion tonnes by 2050. This challenge should prompt renewed research efforts in, for example, genetics, crop physiology and agronomy that allow improving crop productivity with more efficient and sustainable production methods adapted to climate change (FAO, 2009).

From an agronomic perspective, the structure of a crop canopy and the spatial positioning of leaf surfaces strongly affect the amount of intercepted solar radiation and thus crop's production of biomass by photosynthesis (Sinoquet and Bonhomme, 1989). In a similar way, leaf senescence can dramatically affect crop production by its effects on carbon assimilation and dry matter transfer from senescing leaves to harvestable organs (Rajcan et al., 1999; Rajcan and Tollenaar, 1999a,b; Gregersen et al., 2008).

The contribution of individual leaves to biomass production and grain yield in maize has for long time interested plant physiologists and agronomists (Tanaka and Yamaguchi, 1972). It is well documented that in conventional maize genotypes, as well as in leafy (Subedi and Ma, 2005a) and stay-green (He et al., 2003; Pommel et al., 2006) genotypes, the principal source of photosynthates for grain filling is largely from upper leaves surrounding the ear-node. Lower leaves export relatively less to the ear and more to the roots (Yan et al., 2011). It is also well known that photosynthetic

Abbreviations: DAS, days after sowing; Fv', variable fluorescence from light-adapted leaves; Fm', maximal fluorescence from light-adapted leaves; GDD, growing degree-day; PSII, photosystem II; WHC, water holding capacity.

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functioning of leaves after silking is a major determinant of grain yield in maize (Tollenaar and Daynard, 1978; Tollenaar, 1999).

In monocarpic species such as maize, senescence of leaves is coordinated with the senescence of the whole plant and influenced by the reproductive function and the environment (Smart, 1994; Combe and Escobar-Gutiérrez, 2009). Maize leaf senescence has been the object of much research from cellular to crop levels. At the leaf and plant level, research on senescence has aimed, for example, to: (i) analyse its effects on quality and yield of grain and forage (Ottman and Welch, 1988; Subedi and Ma, 2005a,b; Pommel et al., 2006); (ii) analyse its role in genetic improvement for grain yield (Valentinuz and Tollenaar, 2004; Ding et al., 2005; Tollenaar and Lee, 2006; Echarte et al., 2008); and (iii) improve the predictive capacity of yield by tools such as remote sensing (Strachan et al., 2002; Viña et al., 2004) and crop modelling (Birch et al., 1998, 2003; Heng et al., 2009; Hsiao et al., 2009; Steduto et al., 2009).

The objective of the work reported in this paper was to describe the dynamics of senescence of field-grown maize from silking to harvest, at both leaf and plant level. At the leaf level, the dynamics of symptoms of senescence were considered on each leaf taken individually and described according to zones from the tip to the base of the leaf lamina. At the whole plant level, foliar ranks were each considered as an entity to describe the time course of senescence. To this end, we use a database built-up from field trials conducted during three consecutive years (1994–1996) and thus undergoing variable meteorological and soil water conditions.

2. Materials and methods

2.1. Field conditions and crop management

This study exploits a database built-up from three field trials conducted during the years 1994–1996 on a deep silt loam soil (Tardieu et al., 1990) in INRA's Research Centre at Thiverval-Grignon, France (48°50′22″ N, 1°57′10″ E, 130 m elevation). Hereafter, these three trials are named "Trial I", for 1994; "Trial II", for 1995; and "Trial III" for 1996. Maize hybrid 'Déa' was sown at a density of 10 plants m^{-2} in 0.80 m rows. Sowing dates are presented in Table 1. The plow layer (0–30 cm) contained in average 2.5% organic matter and has a pH value of 8.0. From seedbed preparation to harvest, local agronomic recommendations were followed and weeds were chemically controlled. No manure was added. However, in order to ensure plants were well-nurtured, 25 g m^{-2} of N, 7.5 g m^{-2} of P and 7.5 g m^{-2} of K were applied just before sowing each trial. Due to the crop rotation scheme followed for managing the experimental station, each year the trial was established in different plots within the same paddock. In Trial III, natural rainfall was supplemented with low-flow drip irrigation in one-half of the experimental plot. Meteorological conditions were automatically recorded by a standard agro-meteorological station located in the Research Centre, close to the experimental field. Daily mean temperature, precipitation and reference evapotranspiration (ET_0) during the three growing seasons are presented in Fig. 1. Growing degree-day (GDD) was calculated as the sum of daily mean temperature −6 °C that was considered the base temperature (Combe and Escobar-Gutiérrez, 2009).

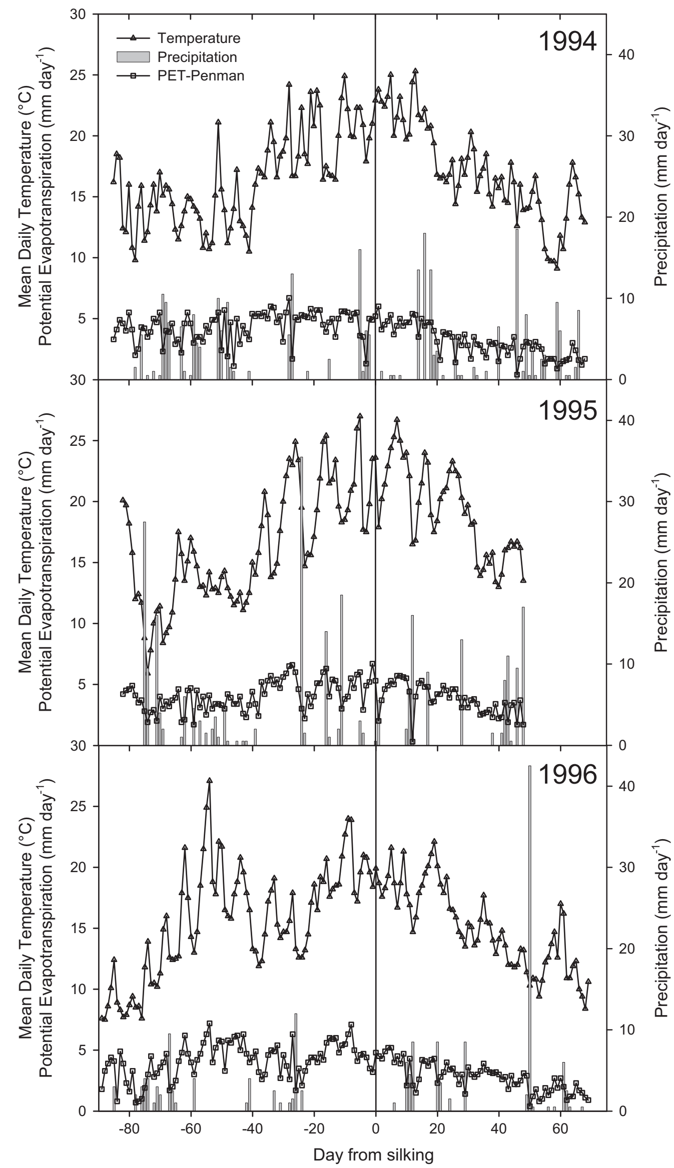

Fig. 1. Daily mean air temperature, potential evaporation and precipitation during the maize growing seasons in 1994, 1995 and 1996 at INRA's Research Centre at Thiverval-Grignon, France.

Table 1
Summary of key dates, cumulative growing degree-day, cumulative rainfall and cumulative irrigation (in italics) of a 'Déa' maize crop grown at INRA's Research Centre at Thiverval-Grignon, France.

Year	1994	1995	1996	1996
Irrigation	No	No	No	Yes
Sowing date	28 Apr	05 May	03 May	03 May
Silking date (50% of the plants)	22 July	26 July	31 July	31 July
Harvest date	28 Sept	19 Sept	25 Sept	8 Oct
Growing degree-days from sowing to silking (°C d^{-1})	852	843	868	868
Growing degree-days from silking to harvest (°C d^{-1})	796	664	535	622
Cumulative water supply from sowing to silking (mm)	140	167	65	65 + *232*
Cumulative water supply from silking to harvest (mm)	134	76	87[a]	98[a] + *43*

[a] It includes a 43 mm rain four days before harvesting the non-irrigated plot (control).