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# Nitrogen supply and sink demand modulate the patterns of leaf senescence in maize

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ABSTRACT

Senescence is a key physiological process that can regulate crop grain yield. Patterns of leaf senescence and its association with grain yield for a short maturity maize hybrid were investigated in a factorial combination of two tillage treatments (conventional and no-till), three amounts of stubble (0, 3 and 5 t ha$^{-1}$) and three N rates (0, 80 and 120 kg N ha$^{-1}$) over three seasons in 2015 long rains, 2015/2016 short rains and 2016 long rains. Leaf senescence from flowering to harvest was assessed at (a) the whole-plant scale by the visual scoring of dry leaves and (b) the canopy-layer scale by measuring leaf greenness with a SPAD 502 chlorophyll meter. A bilinear model was used to quantify the patterns of senescence at the whole-plant scale. A logistic function was fitted to estimate the traits of senescence at three canopy layers (top, mid, bottom), including minimum and maximum SPAD, onset of senescence (EC90), time to loss of 50% maximum SPAD (EC50) and the rate of senescence in each layer. Nitrogen rate effect on patterns and traits of senescence were large and its interactions with stubble were more frequent than interactions between other treatments. Tillage and stubble amount had marginal effects. EC50 was delayed in the unfertilized controls compared with fertilized crops and was negatively correlated with grain yield. Rate of senescence was faster in fertilised crops compared with unfertilized controls at both whole-plant and canopy-layer scales. Grain yield, grain number and nitrogen remobilization efficiency were associated with faster rates of senescence in the top and mid leaves but with slower rates of senescence in the bottom layer leaves. We advance a sink-driven leaf senescence ideotype for high yield and efficient use of nitrogen for short maturity maize.

## 1. Introduction

No-till (NT) management and stubble retention protects the soil from water and soil erosion, improves soil water capture and storage, and promotes soil chemical and physical properties, which leads to higher yields (FAO, 2015). Previous studies on the impact of these practices on crops and cropping systems are restricted to crop growth and yield, water and nutrient economy, with little emphasis on physiological processes (Verhulst et al., 2011; Brouder and Gomez-Macpherson, 2014). Kitonyo et al. (2018) concluded that nitrogen (N) modifies crop response to NT and stubble retention in a sub-humid tropical environment, by altering N nutrition index (NNI), which explained most of the variation in crop growth rate in the critical window of yield determination. Crop growth rate in turn accounted for most of the variation in kernel number and yield while grain yield was linearly correlated with N remobilization efficiency (NRE), which is defined as the difference in shoot N at flowering and harvesting (Kitonyo et al., 2018). The manipulation of patterns of leaf senescence that impact photosynthesis, harvest index and N remobilization, and potentially N use efficiency has received little attention in cropping systems (Masclaux-Daubresse et al., 2010; Wu et al., 2012).

In monocarpic plants such as maize, leaf senescence is a developmental process that involves the gradual loss of green leaf area in the older leaves and finally the whole plant (Gregersen et al., 2013). High yield potential in maize has been achieved through the extension of photosynthetic duration and increased harvest index, two traits that are related with leaf senescence (Bänziger et al., 2002; Wu et al., 2012). Genetic and environmental factors trigger and regulate senescence

*Abbreviations:* NT, no-till; CT, conventional tillage; N, nitrogen; NNI, N nutrition index; NRE, N remobilization efficiency; NUE, N use efficiency; °C, degree celsius; °C d, growing degree day; t, tonnes; ha, hectare; P, phosphorus; kg, kilogram; g, grams; L, litre; DK, DeKalb; DM, dry mass; SPAD, chlorophyll unit; $SPAD_{min}$, minimum SPAD unit before harvesting; $SPAD_{max}$, maximum SPAD unit before the onset of senescence; EC90, onset of senescence; EC50, time to loss of 50% $SPAD_{max}$

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(Gregersen et al., 2013; Thomas and Ougham, 2015). There is considerable genetic variation in the patterns of senescence in maize (Gregersen et al., 2013). Broadly, senescent hybrids senesce earlier irrespective of growing conditions while the "stay-green" phenotypes show prolonged green leaf area duration (Gregersen et al., 2013).

The genetic control of senescence is complex and involves both programmed cell death and hormonal regulation (Wilkinson and Davies, 2002; van Doorn and Woltering, 2004; Liu et al., 2005; Lim et al., 2007). Hormonal signals such as abscisic acid, ethylene, cytokinins and jasmonic acid regulate senescence in response to stress and source-sink ratios (Harding et al., 1990; Staswick, 1992; Schippers et al., 2007; Davies and Gan, 2012). Environmental factors like water, nutrient stress and temperature modulate senescence (Gregersen, 2011). Both leaf area duration and green leaf area proportionally impact grain yield (Gregersen et al., 2013). The ratio of assimilate supply (i.e., source) to demand (i.e., sink) during grain filling also regulates senescence, and impacts nutrient fluxes from the senescing leaves to the grain (Feller et al., 2007; Wei et al., 2018). In some species, such as tomato, low source:sink ratios favour senescence but in maize the response of senescence to source:sink ratios varies with hybrid (Crafts-Brandner and Poneleit, 1987; Sadras et al., 2000).

The translocation of N from senescing tissues to the grain indirectly impacts N use efficiency (NUE) (Masclaux-Daubresse et al., 2008; Gregersen, 2011). At the crop level, NUE, the ratio between grain yield and fertilizer supplied (Dobermann, 2007) depends on N uptake from the soil, internal utilization and the subsequent partitioning and remobilization of N to the grain (Masclaux-Daubresse et al., 2010). Nitrogen remobilisation is fundamental for crop N economy since it controls a large part of N fluxes from sources to sinks (Masclaux-Daubresse et al., 2008). N remobilization efficiency (NRE) accounted for 85% variation in grain yield in both maize (Kitonyo et al., 2018) and wheat (Barraclough et al., 2014). Despite the fundamental role played by N remobilization in crop N economy (Yang and Udvardi, 2017), patterns of leaf senescence are least explored for the improvement of NUE in NT and stubble retention systems.

In the model advanced by Christopher et al. (2014), the key traits of senescence are quantified: the minimum leaf greenness before harvesting, maximum greenness before the onset of senescence, the timing of onset of senescence, and the progression and rate of senescence. Profiles of leaf senescence vary within the spatial arrangement of leaves, which affects light interception and attenuation, thus shaded leaves often senesce earlier than unshaded ones (Maddonni et al., 2001). In addition, carbon assimilation and N transfer from senescing leaves to the grain varies with leaf position (Feller et al., 2007). The middle leaves and top leaves provide N for grain filling in maize, while the bottom leaves export more N to the roots than to the grain (Feller et al., 2007).

This study investigated the patterns of leaf senescence in maize and their association with yield in a context of NT and stubble retention. Our aims were to (i) characterize the time-course of post-flowering leaf senescence under conventional tillage and NT, and with three stubble and three N rates, and (ii) establish relationships between senescence and grain yield, yield components, crop N status quantified as NNI, and traits related to nitrogen use efficiency.

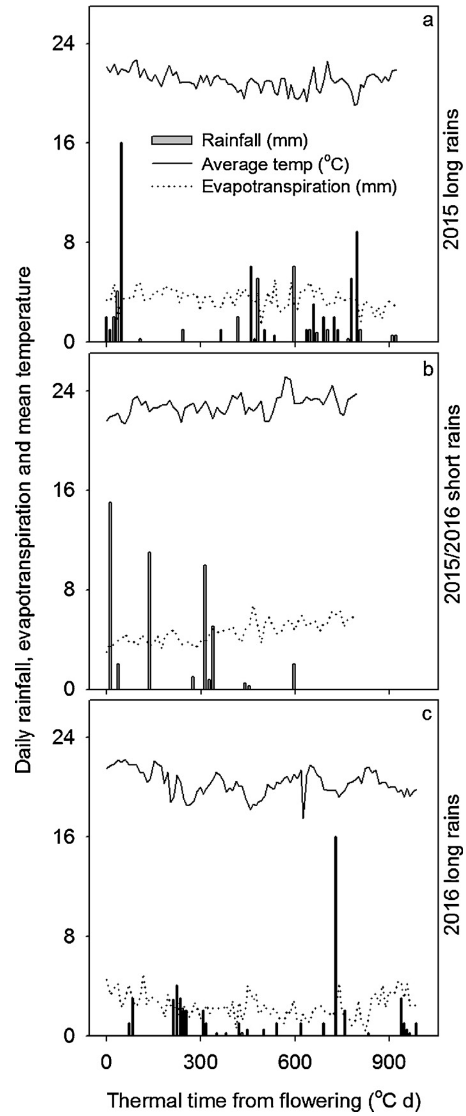


**Fig. 1.** Growing conditions from flowering (50% pollen shedding) to harvesting of maize during 2015 long rains (a), 2015/2016 short rains (b) and 2016 long rains (c) at the Kenya Agricultural and Livestock Research Organisation, Embu research station.

## 2. Materials and methods

The experiments are fully described in Kitonyo et al. (2018). Here we briefly summarise treatments and experimental design, and focus on measurements and analysis of senescence.

### 2.1. Site

A field study was conducted at the Kenya Agricultural and Livestock Research Organisation, Embu research station (0.515 °S, 37.273 °E, 1425 masl), for three consecutive seasons during the 2015 long rains, 2015/2016 short rains and 2016 long rains. Embu is in the upper midland zone three (UM3) and has a sub-humid climate with mean annual temperature of 22 °C (Jaetzold et al., 2006). In this environment, there are two five-month rainy seasons; the long rains that occur between April and August, and the short rains season from October to February. Soils are deep (> 2.5 m) well-weathered humic nitisols with low exchangeable bases and relatively high P-sorption, and of medium to low fertility (Jaetzold et al., 2006).

### 2.2. Treatments and experiment design

Effects of conventional tillage (CT) and no-till (NT), three amounts of maize stubble (0, 3 and 5 t $ha^{-1}$) and three fertilizer N rates (0, 80 and 120 kg N $ha^{-1}$) were evaluated under continuous maize cropping over three seasons during 2015 long rains, 2015/2016 short rains and 2016 long rains. Tillage and stubble treatments were applied two weeks before sowing in the same plot in all seasons. Prescribed amounts of stubble were supplied in the first season while in the next two seasons, additional stubble allowed for undecomposed material. In CT plots stubble was chopped to small pieces and incorporated into the soil by digging to 15 cm depth while the NT treatments were not disturbed and