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# Field Crops Research

# Analysis of source and sink dynamics involved in oil and protein accumulation in sunflower achenes using a bi-linear model

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## ARTICLE INFO

## ABSTRACT

Most recent mechanistic crop models are based on source-sink relationships. To build a conceptual framework for achene quality traits in sunflower (*Helianthus annuus* L.), source-sink relationships were investigated in contrasting environments. Two experiments were performed under field conditions in 2011 and 2012. Oil, protein, hull (sink), leaves, receptacles and stems (source) were measured weekly under contrasting nitrogen (N−: no fertilization; N+: 150 kg N per ha), plant density (3 and 4.5 plants per m$^2$) and genotype (cv. Kerbel, cv. LG5451 HO and cv. Olledy) treatments. A bi-linear model was fitted to source and sink component dry weight (DW) dynamics per m$^2$. Nitrogen and plant density influenced rates and duration of all source and sink dynamics, while genotype had a significant influence on timing parameters. More significant factor interactions were found in 2011 than in 2012, probably because of other factors that occurred or interacted during grain filling (water stress and/or thermal stress). We constructed a robust source-sink framework for oil and protein accumulation in relation to remobilization processes. The observed "source" chronology was receptacles, stems and green leaves, and we confirmed the "sink" chronology of receptacles, hulls, protein and oil. Chronologies were influenced mostly by genotype. Such a framework is highly useful for dynamic modeling of sunflower. We also discuss the relevance and adaptability of the bi-linear model.

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## 1. Introduction

With the emergence of new food and non-food markets over the last ten years (Pilorgé, 2010), oil and protein concentrations are of growing interest among oilseed crops. Combining high oil and high protein concentrations could provide significant added value for sunflower (*Helianthus annuus* L.) in particular, given its high oil potential (Berger et al., 2010) and its market-competitive protein concentration for meals obtained from new dehulling methods (Peyronnet et al., 2014). Providing advice about the best variety to grow relies on knowledge about its performances under

potential conditions as well as under stressed conditions, since sunflower genotypes have displayed diverse responses under different management practices (Champolivier et al., 2011) and water availability conditions (Casadebaig et al., 2008, 2011). Knowing only a genotype's oil or protein potential is not reliable enough to predict its performance under various environmental conditions (Champolivier et al., 2011; Andrianasolo et al., 2014, 2016a). It is necessary to understand how physiological processes at the plant level occur during oil and protein development and how they are influenced by crop management and environmental factors.

In a companion paper (Andrianasolo et al., 2016b), the influences of genotype (G), nitrogen (N) and plant density (D) were quantified in a two-year field experiment. Based on the analysis of selected "sink" and "source" processes and compartment indicators, the authors demonstrated that differences in final oil and protein concentrations could be explained by varying intensities of G, N and D factors on sink and source components. The sink and source concepts consider that not only is either component affected but that

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both sink and source could be influenced at different intensities during different sensitive periods. Recommendations for maximizing oil concentration depended greatly on the genotype, nitrogen and plant density treatments, while those for maximizing protein concentration were fairly constant among nitrogen and plant density treatments. However, interaction effects were detected on sink and source components that deserve further investigation. Significant effects found at harvest were only partly linked to differences at flowering, suggesting that new factors or interactions of factors have influence during grain filling.

To better understand such genotype × environment × management (G × E × M) interactions, Connor and Hall (1997) suggested analyzing the dynamics of oil and protein accumulation after flowering. We investigated these interactions by analyzing the influence of G, N and D factors during grain filling, assuming that they are determining factors for oil and protein accumulation. Interactions occur because factors (1) have influence at different periods of grain filling, leading to differential sensitivity windows; (2) influence different growth parameters (rate, duration, or both); or, (3) influence remobilization processes (via rates and durations) from source organs, leading to different final results.

Dynamics of sink organs in sunflower are well documented in the literature, whether in response to variations in available carbohydrates (Andrade and Ferreiro, 1996; Aguirrezábal et al., 2003; Izquierdo et al., 2008; Echarte et al., 2012) or in genotypes (Mantese et al., 2006) differing in initial pericarp weight and duration of oil accumulation. However, little is known about the influence of nitrogen on oil- and protein accumulation dynamics. Additionally, interactions between determining factors have never been analyzed. The framework for achene components in sunflower – hulls, proteins, and oil (Champolivier and Merrien, 1996; Connor and Hall, 1997; Mantese et al., 2006) – is well established, but the validity of such a framework under contrasting nitrogen, plant density and genotype conditions should be explored.

Since carbon components required for the oil and nitrogen components that are necessary for protein production originate from source organs – stems, receptacles, and leaves (Bauchot and Merrien, 1988; Connor and Hall, 1997; López-Pereira et al., 2000, 2008) – the influence of one or more of these source organs could affect sink organs. At the source level, Agüera et al. (2012) demonstrated that the sunflower green canopy was highly sensitive to plant nitrogen status, while De la Vega et al. (2011) reported genotypic differences in leaf area index (LAI) dynamics. Andrade and Ferreiro (1996) demonstrated the influence of plant density on stem growth. These factors could influence both assimilation (leaves) and remobilization (leaves, stems, and receptacles) processes. Dosio et al. (2000) observed that remobilization occurred first from the closest source organs, then from those more distant. The framework and chronology for "source" remobilization has not yet been established for sunflower. We developed such a framework and tested it under contrasting nitrogen, genotype and plant density treatments.

Understanding the priority order among source and sink components could help design a conceptual framework for their relationships in sunflower, as established for other species such as soybean (Sinclair et al., 2003) or sorghum (Van Oosterom et al., 2010). Such frameworks are helpful in building dynamic models. Models that accurately predict oil and protein concentrations in oilseed crops are rare, and most are statistical (Chapman et al., 1993; Villalobos et al., 1996; Pereyra-Irujo and Aguirrezábal, 2007; Casadebaig et al., 2011; Andrianasolo et al., 2014). Since little is known about the influence of major factors on dynamics, no models consider their effects. It seems essential to include such physiological processes to understand G × E × M effects, better predict final oil and protein concentrations and provide reliable advices to farmers.

The objectives of this study were (1) to analyze the influence of nitrogen, density and genotype on oil, protein, and related source-organ dynamics in sunflower; and (2) to establish a source-sink framework for sunflower that can be used in future dynamic crop modeling of grain quality.

## 2. Materials and methods

### 2.1. Site and experimental design

#### 2.1.1. Site characteristics

Two field experiments were conducted in 2011 and 2012 at the INRA station in Auzeville, south-west France (43°31′41.8″ N, 1°29′58.6″ E). Sunflower was grown in a deep loamy soil (accessible root depth > 100 cm) with a potential available water reserve of 180 mm and little or no stoniness. The crop was preceded by maize in 2010 and sorghum in 2011; residual N before sowing amounted to 48 and 33 kg N ha$^{-1}$ in 2011 and 2012, respectively. Three commercial hybrids were used: cv. Kerbel (in both years), cv. LG5451 HO (2011) and cv. Olledy (2012). According to Terres Inovia (2015), cultivars had contrasting achene oil concentrations (cv. Kerbel: high-oil; cv. Olledy: medium-oil; cv. LG5451 HO: low-oil) and hull/kernel ratios (highest for cv. Kerbel). Daily weather data (i.e. global radiation, rainfall, minimum and maximum temperature, potential evapotranspiration) were collected locally at a height of 2 m.

#### 2.1.2. Experimental design and crop management

The crops were sown on 8 and 6 April and harvested on 30 August and 11 September in 2011 and 2012, respectively. In both years, the experiment consisted of a split-plot design with the nitrogen factor as the main plot (N+: non-limiting; N−: deficiency) and genotype and plant density (D1: 3 plants m$^{-2}$; D2: 4.5 plants m$^{-2}$) as subplots; these were randomly distributed with 3 replicates. The size of each microplot was 30 m$^2$ (6 rows), and row width was 50 cm. For N+, 150 kg N ha$^{-1}$ was divided and applied in two applications during vegetative growth: 75 kg N ha$^{-1}$ each on 19 May and 6 June in 2011 (15 May and 1 June in 2012). Plots were over-sown at 9 plants m$^{-2}$, then thinned to desired densities at the 8-leaf stage. To avoid severe water stress, the crop was irrigated on 13 April (28 mm) and 26 May (43 mm) in 2011 and on 29 June (25 mm) and 17 July (29 mm) in 2012. Weeds, pests and diseases were adequately controlled with chemicals. Half of the plots were dedicated to non-destructive measurements throughout the grain-filling period. Destructive measurements were performed on adjacent paired plots.

### 2.2. Dynamic measurements

#### 2.2.1. Phenology

Sunflower phenological stages were recorded weekly at the whole-plot scale from visible bud stage until late after physiological maturity (noted as R9, when capitulum bracts turned from yellow to brown, Schneiter and Miller, 1981). Flowering was scored when 95% of plants in a plot displayed stamens in all florets from the outer ring of the capitulum (stage R5.1, Schneiter and Miller, 1981).

#### 2.2.2. Sink dynamics

Beginning at flowering, 40 random plants in the four middle rows of each plot were tagged for weekly destructive measurements. At each sampling date, three heads per unit plot were randomly cut (i.e 9 heads for each treatment); receptacles and grains were separated and oven-dried at 80 °C for 48 h. Capitula and grain parts were weighed. Eight harvest dates occurred from early flowering to maturity for both years. Achene number and