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Argentine Research Into Crop Ecophysiology Contributing to Crop Management and Genetic Improvement of Sunflower

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Abstract

Crop ecophysiology analyzes the behavior of plant populations in interaction with their environment. This discipline integrates concepts from plant physiology, agronomy, and ecology to develop management strategies for farmers and guide the genetic improvement of crops. The inception of Argentine research in sunflower ecophysiology almost coincides with the beginning of ecophysiology research in the country. Pioneering contributions to the international literature on sunflower by Argentine authors date back to 1985. To date, Argentine researchers have authored a total of 184 papers on sunflower ecophysiology in international journals, with an average publication rate of 5.7 papers per year during the period 2021–2023. This research has addressed a wide range of topics, including phenology, the eco-physiological and numerical determinants of yield and quality, the effects of abiotic factors on these determinants, the optimization of management practices for resource-limited environments, and genotype × environment interactions, among others. Currently, sunflower is regarded by Argentine farmers as a medium- to low-yield crop, often used as an alternative to soybean and maize in situations where these crops cannot be cultivated. However, advances in ecophysiological research in Argentina have the potential to enhance sunflower's competitiveness relative to other grain crops. The knowledge accumulated through crop ecophysiology and associated disciplines (e.g., ecology, agronomy, plant breeding, molecular biology, and genomics), along with significant methodological advances in testing techniques and data interpretation, offers an encouraging outlook for addressing the challenges of sunflower production.

Keywords: Argentina ecophysiological research on sunflower; main research topics; future challenges of ecophysiological research on sunflower in Argentina.

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What is crop ecophysiology?

Crop ecophysiology analyses the behaviour of a plant population in interaction with the environment (Eastin et al., 1969; Milthorpe and Moorby, 1974; Evans, 1975). This organization level (i.e., crop) has emergent characteristic properties, and they cannot be explained by those at a lower level of organization (i.e., plant, Sadras and Calderini, 2018). For example, the first studies carried out to determine the mechanisms that regulate the transpirational flow of sunflower plants concluded that this species had a low capacity to regulate water loss during the vegetative period when exposed to water stress, due to the fact that the stomata remain open even under stress conditions. The studies that were performed later at the crop level allowed us to understand that the leaf growth rate of the crop is affected long before stomata closure. As a consequence of this, the leaf area index and the amount of water transpired per unit crop area are reduced (Sadras et al., 1993b, 1993c).

Crop ecophysiology integrates concepts from different disciplines (i.e., plant physiology, biology, agronomy, plant breeding, and ecology) at a higher level of complexity with the purpose of generating management strategies for farmers and for guiding the genetic improvement of crops. Although, traditional crop breeding and molecular biology provide tools to develop new combinations of attributes to obtain cultivars with improved productivity, crop ecophysiology is the discipline in the best position to evaluate the costs and benefits of these attributes, and their behaviour in agroecosystems (Lambers et al., 2008; Slafer et al., 2018).

Crop ecophysiology focuses on two main aspects. The first aspect is the understanding of the factors that control the size, functionality, and duration of the canopy and root system of the crop. This first aspect is crucial to understanding how the crop captures and dissipates resources from the environment (i.e., water, radiation, nutrients). The growth of a crop is a consequence of the division and elongation of its cells. These processes are the result of the production, transport and accumulation of from photosynthesis. The second aspect is concerned with the processes that regulate yield generation and the intricate functional relationships between yield and environmental variables (i.e., radiation, water, and nutrients). To explore this aspect, researchers often employ two overarching conceptual models.

The first conceptual model explains crop yield as a function of the growth factor that limits its productivity (i.e., intercepted radiation, water consumption, and nutrients uptake). There are specific reference frameworks for each of these resources; where the way in which crops capture the resource of interest, the efficiency with which they transform it into biomass and the proportion of biomass partitioned into grain are analysed (Wilson, 1967, Gallagher and Biscoe, 1978, French and Schultz, 1984, Cassman et al., 2002).

The second conceptual model elucidates crop yield by focusing on its numerical components, namely grain number per unit area and grain weight. These components are sequentially determined throughout the crop cycle, with temporal overlap that varies depending on the species under consideration. The value attained by each component depends on the crop growth rate during the generation and survival of the crop yield component under study. Moreover, different components exhibit varying sensitivity to changes in growth rate. Identifying the critical period for yield generation (i.e., the stage of the crop cycle where a decrease in growth rate significantly impacts the numerical component that most profoundly affects crop yield, usually grain number per unit area) is crucial (Carrera et al. 2023). This identification allows for pinpointing the moment(s) during which it is imperative to optimize environmental resource availability to maximize crop growth rate under the prevailing conditions (Carcova et al., 2004).

Research in crop ecophysiology in Argentina: the sunflower crop

Ecophysiology research in Argentina is estimated to have begun in 1969 because the first paper developed by Argentine researchers in this discipline was published during that time (Bermann et al, 1969), with Ing. Agr. Alberto Soriano as one of its authors. He was the first Full-time Professor of Plant Physiology and Phytogeography at FAUBA (Facultad de Agronomia, Universidad Nacional de Buenos Aires) since 1957. Also, he stood out as an advisor to new researchers and university teachers. Eleven years later, following Bermann's paper, the first international publication in this discipline was published by an Argentine research group, focusing on the effects of drought on maize crop growth (Hall et al., 1980).

During the 1980s and 1990s, there was a concerted effort to train human resources in crop ecophysiology. This period saw the establishment of the Master's Degree in Plant Production followed by the Doctorate in Agricultural Sciences at the National Universities of Buenos Aires (UBA) and Mar del Plata (UNMdP). These initiatives significantly expanded the pool of trained professionals in the field, leading to the formation of new research groups across various National Universities and experimental stations of the National Institute of Agriculture Technology (INTA) throughout the country.

Two key indicators of the growth of crop ecophysiology in Argentina from 1980 to 2015 include the increase in the number of articles published in indexed international journals and the diversification of research topics. The annual publication rate surged from 1 to 24 papers per year during the periods 1980-1990 and 2010-2015, respectively. Furthermore, there was a remarkable expansion in the range of topics covered in these publications. While a significant proportion of papers published between 1980 and 2010 focused on maize, wheat, sunflower, and soybean crops, the diversity of topics addressed in crop ecophysiology research has expanded since 2010 (Hall, 2016).

The onset of research in sunflower ecophysiology almost coincides with the beginning of research in this discipline in the country. The pioneering contributions to international literature on sunflower by Argentine authors can be traced back to the seminal works of Hernández and Orioli

(1985a, 1985b) from the National University of South (UNS). Following these initial publications, a steady growth in the volume of research contributions by Argentine authors ensued, with noteworthy contributions from the FAUBA group, as well as from research groups at the UNS and UNMdP (Hall, 2004).

To date, Argentine researchers have authored a total of 184 papers on sunflower ecophysiology in international literature, with the publication rate per year increasing from 3.4 to 5.7 papers during the periods 1985-2020 and 2021-2023, respectively. In the latter period, the increase in contributions made by researchers from the Integrated Unit of Balcarce is outstanding. The quantity and quality of these published papers, as evidenced by their inclusion in the Science Citation Index (https://access.clarivate com/login?app), highlight the global relevance of Argentina's sunflower ecophysiological research, whose originality far exceeds this crop (Hall, 2004). Tables 1 and 2 indicate the publications made during the periods 1985-2000 and 2000-2023, respectively. The works are grouped according to the topic addressed.

Table 1: Publications of Argentine authors in refereed international scientific journals published in the period 1985-2000.

Topics in sunflower ecophysiology	Bibliographic references
Phenology: photoperiod and temperature	Sadras y Hall (1988), Sadras y Villalobos, (1993a), Villalobos et al., (1996), León et al., (2000), Hall (2001)
Growth and functioning of root system	Sadras et al. (1989), Aguirrezabal et al. (1993, 1994), Aguirrezabal y Tardieu (1996), Dardanelli et al. (1997), Andriani (2000)
Biomass accumulation and its partitioning among the different structures of the plant	Hall et al. (1989, 1990a, 1990b, 1995), Whitfield et al. (1989), Trapani et al. (1992, 1994), Connor et al. (1993), Ploschuk y Hall (1995, 1997), Villalobos et al. (1994)
Nitrogen availability, leaf area index and radiation use efficiency.	Connor et al. (1993, 1995), Hall et al. (1995), Trapani y Hall (1996), Sadras et al (1993b), Trapani et al. (1999), Rousseaux et al. (1996, 1997, 1999, 2000), Sadras et al. (2000b, 2000c)
Crop water economy and responses to drought	Hernández y Orioli (1985b), Sadras y Connor (1991), Sadras et al. (1991a, 1993c, 1993d), Chimenti y Hall (1993 y 1994)
Critical period for grain number definition	Andrade y Ferreiro (1996), Cantagallo et al. (1997), Vega et al (2000)
Ecophysiological changes in sunflower hybrids released in different eras	López Pereira et al. (1999a, 1999b, 2000)
Crop simulation models	Sadras (1989), Villalobos et al., (1996)
Temporal variability of crop yield	Messina et al (1999)

The increased research in crop ecophysiology, particularly in sunflower ecophysiology over the past 53 years, has been driven by both public institutions (Universities and INTA) and public-private collaborations. The latter have emerged through direct agreements between representatives of both sectors or facilitated by non-profit civil associations like ASAGIR (Argentine Sunflower Association). Established in the 1980s, ASAGIR serves as a platform that brings together input suppliers, agricultural producers, commerce, grain storage, and industry, as well as science and technology stakeholders. In relation to this latter sector, among the actions carried out by ASAGIR stand out: i) its role in the management of public-private financing programs [i.e., nine oriented research projects funded and finished (PICTO-Asagir-2003) and the "Yield Gaps" project, recently completed] and ii) carrying out multidisciplinary research workshops and organizing National and International Sunflower Congresses.

Contributions of crop ecophysiology to crop management and the genetic improvement of sunflower.

The utilization and application of knowledge derived from crop ecophysiology aim to minimize the level of uncertainty between the expected outcome and implemented management practices. However, we will exemplify with some of the management practices that define the structure (e.g., cultivar selection, sowing date, plant density, and row spacing) of sunflower crops in environments with and without water restrictions. For readers interested in this topic, we recommend consulting three books that offer an excellent synthesis of the application of ecophysiological principles to grain crop management (e.g., wheat, corn, soybean, and sunflower) in the Pampas agroecosystems (Andrade and Sadras, 2000; Satorre et al., 2003; Miralles et al., 2010).

Table 2: Publications of Argentine authors in refereed international scientific journals published in the period 2001-2023.

Topics in sunflower ecophysiology	Bibliographic references
Morphological and anatomical development of reproductive structures	Lindström *et al.* (2006, 2007), Gutierrez et al (2010), Lindström y Hernández (2015)
Critical period to grain number definition	Cantagallo y Hall (2002), Cantagallo et al. (2004), Chimenti y Hall (2001), Cantagallo y Hall (2002), Vega et al. (2001a), Cantagallo et al. (2004), Dosio et al. (2011), Astiz al. (2013, 2014)
Source/sink relationship	Ruiz y Maddonni (2006), Gambin y Borras (2010), Echarte et al. (2012), Dosio et al. (2020)
Dynamics of grain weight, grain oil concentration, fatty acids and tocopherols in oil grain	Chimenti et al. (2001), Mantese *et al.*, (2006), González Belo et al. (2018, 2019)
Association between grain water content and physiological maturity.	Rondanini et al. (2007, 2009), Castillo et al. (2017)
Effects of abiotic stress on grain weight, oil concentration, and oil quality	Dosio *et al*. (2000), Santalla et al. (2002), Aguirrezábal et al. (2003), Cantagallo et al. (2004), Echarte et al. (2013), Rondanini et al. (2003, 2006), Velascco et al (2004), Grassini et al. (2007), Izquierdo y Aguirrezábal (2008), Izquierdo et al. (2002, 2006, 2007, 2008, 2009, 2012, 2013)
Ecophysiological determinants of "fast dry down" and "stay green" genotypes	de la Vega y Hall (2002, 2011)
Canopy and roots senescence during the grain filling period	Lisanti et al. (2012, 2013), Mangieri et al. (2017, 2020)
Canopy structure	Sadras et al. (2000), López Pereira et al. (2017, 2020, 2022), López Pereira y Hall (2019), Echarte et al. (2020)
Tolerance to root and stem lodging	Hall et al. (2010), Sposaro et al. (2008), Manzur et al. (2012), Mangieri et al. (2016)

Ecophysiological changes in sunflower hybrids released in different eras in Argentina	Chimenti y Hall (2002), Chimenti et al. (2006), Fonts et al. (2008), Lechner (2008), Pereyra-Irujo et al. (2008), de la Vega et al. (2007a, 2007b), León et al. (2003), Luquez et al. (2002), Alberio et al. (2018)
Crop simulation models	Dardanelli (2004), Pereyra-Irujo, et al. (2007), Aguirrezábal et al. (2015), Rodríguez et al. (2023)
Temporal and spatial variability of crop yield	Sadras et al. (2000a), Mercau et al. (2001), de la Vega y Hall (2002a, 2002b), Coll et al. (2012), Calviño et al. (2004), Echarte et al. (2011), Mercau et al. (2001), Calviño y Monzón (2009), Grassini et al. (2009), Angeloni et al. (2017, 2021), Diovisalvi, et al. (2018)
Effects of diseases on physiological determinants of grain yield	Creus et al. (2007), Quiros et al. (2014), Bordoy et al. (2016), Bordoy et al. (2016), Montechia et al. (2021)
Crop yield gap	Hall et al. (2013), Aramburu Merlos et al. (2015)
Genotype x environment interaction	de la Vega et al. (2000), Chapman y de la Vega (2002), de la Vega y Chapman (2001, 2006a, 2006b,2010) Bustos-Korts et al. (2022)

The determination of the critical window for the number of grains (Cantagallo and Hall, 2002, Cantagallo et al. 2004) and the positive and significant association between this component of yield and the growth rate per plant around the flowering period (Vega et al. al., 2000, 2001, 2001a) are used to decide certain management practices (e.g. sowing date) aimed at maximizing crop yield, in environments without water and nutritional limitations. Once the growing season of the crop has been defined, the sowing date is the one that allows locating the critical period with high radiation and sufficient water. These conditions, accompanied by high canopy coverage at the beginning of the critical period, obtained by regulating the density and distance between rows, ensure high growth rates during this period. Additionally, the identification of the critical windows for the definition of the weight, concentration and oil quality of the grain (Dosio et al., 2000, Aguirrezábal et al., 2003, Echarte et al., 2013) and the demonstration that crops grow under a limiting source/sink relationship after flowering (Ruiz and Maddonni, 2006; Gambin and Borras, 2010) demonstrate the importance of certain management measures (i.e., nitrogen nutrition, pest control, and crop health) that increase the duration of leaf area in post-anthesis.

The total amount of rainfall exceeds the water requirements of grain crops and, by extension, sunflower crops in the Pampas region. However, the high interannual variability often leads to water limitations for crop growth in these environments. The identification of processes regulating water transpiration under water stress conditions and the response of the harvest index to the fraction of water transpired during post-anthesis (Sadras et al., 1991; Sadras and Hall, 1989) highlighted the importance of adjusting the sowing date and/or crop density to water availability. In these environments, greater water storage in the soil profile prior to sowing and/or aligning the critical period around flowering with higher water availability help reduce yield variability between years. Additionally, canopy structures that do not fully cover the inter row during flowering (60-70%)

prevent excessive water consumption during vegetative stages and allow water use to be deferred to more advanced reproductive stages, thereby increasing yield (Sadras and Calviño, 2001).

The contribution of crop ecophysiology and, by extension, sunflower ecophysiology, to the search for secondary traits associated with yield and its stability, with the aim of supporting breeding decisions, has been minor. The reasons for this low level of contribution mainly lie on three issues of different order: i) the few links between both disciplines, ii) the difficulties in interpreting and explaining the complex interactions between secondary traits of interest and both the environment and the genetic background, and, iii) the methodological problems caused by the limited availability of rapid, accurate and cheap phenotyping methods, applicable to large populations of genotypes (Andrade, F., 2012). Despite these difficulties, local research was able to contribute to the identification and evaluation of traits associated with tolerance to water stress, e.g., root osmotic adjustment (Chimenti y Hall, 1993, 1994 and 2002) and the sensitivity of leaf growth rate (Lechner et al., 2008, Pereyra-Irujo et al., 2008). An indicator of the complexity level of this type of approach is the number of steps that must be completed until the objective is achieved. For example, the identification and study of the osmotic adjustment of roots, as an attribute of tolerance to water stress, covered the following phases: i) identification of a traits that allows maintaining a both high leaf turgor and high rate of photosynthesis under water stress conditions which is expressed throughout the ontogenic cycle, particularly important in the Pampas where water deficit can occur at any time, ii) demonstration of the existence of intraspecific variability for this attribute, iii) indirect and early identification of the degree of osmotic adjustment, which is only expressed in more advanced stages of crop development, iv) demonstration that the trait is heritable and iv) study of the ecophysiological determinants of interest (i.e. water extraction capacity, dynamics of the green leaf area index and yield) to verify if the differences in this attribute had some effect on the performance of plants of the F4 and F5 families of inbred lines with high and low osmotic adjustment potential subjected to water stress in pre- and post-anthesis.

The GxE interaction is one of the most complex aspects in the context of breeding that makes the genotype selection process difficult. These interactions have a high relative weight in the expression of the phenotype, much more than the genotype in sunflower crops. The difficulties that exist in their interpretation delay the improvement process in sunflower, but the interpretation of the ecophysiological bases of this interaction has allowed us to demonstrate: i) the selection for specific adaptation for the central and northern sunflower region of Argentina could result in a higher rate of improvement, compared to selection for broad adaptation, due to the fact that the factors that condition crop productivity differ between these two environments (de la Vega et al. 2001, 2002, Chapman and de la Vega, 2002) and, ii) the identification of traits of interest to north of country from an evaluation of the physiological determinants of yield in normal and late sowings in Venado Tuerto (de la Vega and Hall, 2002a, 2002b).

New challenges for the sunflower crop ecophysiology

The sunflower sowing area has been reduced since 2000, and it has been shifted towards more marginal areas in the Pampas region. In 2000, the sowing area was almost 3.5 million ha, whereas, in 2001, only 1.9 million ha were grown, producing 3.1 million tons (Castaño, 2018). Nowadays, sunflower crop is perceived by farmers as a crop with a low average yield, which can replace other crops such as soybean and maize, when the production of these latter crops is not possible. The reasons for this perception by farmers may have its origin in the fact that: i) the resources (e.g., fertilizers) allocated to sunflower are less than those provided to other grain crops (i.e., maize, soybean and wheat) in current agricultural systems, ii) probably, the genetic progress in recent years has been lower due to the displacement of this crop towards marginal areas. In this section, we briefly describe some contributions of crop ecophysiology to increase the competitiveness of the sunflower crop compared to other grain crops in the production systems of Argentina.

The increase in grain yield can be achieved from a rise in water limited yield potential [i.e. that obtained with the best technology and knowledge available, is restricted by radiation, temperature and water supply and also influenced by the soil type and site topography (Global Yield Gap Atlas, 2014; available at https://www.yieldgap.org/)], reducing the gap between the latter and the actual crop yield (i.e. the average crop yield achieved in a plot, area, region, country, etc.) or increasing the genotype-agronomic management interaction. Recently, and through the use of agronomic simulation models (Rodríguez et al., 2023), yield gaps were determined in different production areas for this crop in Argentina, resulting in a 30-50% reduction when yield potential is limited by water availability in the production areas. Preliminary results also suggest that the nutrient supply (i.e., nitrogen and phosphorus) would explain most of the yield gap in sunflower production environments in Argentina. However, it is necessary to make a precise quantification of the effects of fungal diseases on actual crop yield (Rodriguez, I., personal communication 2023). Then, the study and/or implementation of management practices oriented to the origin of the yield gap will allow an increase in actual crop yield.

Another alternative to increase actual crop yield is through a better understanding and exploitation of genotype x crop management interactions. The increase in the maize yield in the USA from 1t/ha in 1930 to 7t/ha in the year 2000 has been the result, at least in part, of the parallel increase in plant population densities and crop adaptation to this crop management change (Tollenaar and Lee, 2002). Different studies demonstrated that sunflower has the physiological capacity to increase its potential oil yield, in environments not limited by water, when densities are increased (14 pl m-2) well above the densities used in commercial production (3-5 pl m-2; López Pereira and Hall, 2019), but there is intraspecific genotypic variability for this response (López Pereira et al., 2022). The increase in disease tolerance (de la Vega et al., 2007, 2007a) and the identification of intraspecific variability for root lodging (Sposaro et al., 2008, Manzur et al., 2012, Mangieri et al., 2016) and stem breaking (Hall et al., 2010) offer an opportunity to increase actual crop yield by a greater tolerance to high crop density. This type of research requires an ascending and descending approach in its level of complexity. The secondary traits that are relevant to the relative performance of hybrids in response to crop density in different production environments must be identified, the variability of these traits must be discovered, and these traits must be heritable and easily monitored. The generation of new statistical analysis techniques facilitates the interpretation of triple and quadruple interactions in multi-environment experiments (i.e., density x genotype x environment and density x genotype x environment x year; Bustos-Korts et al., 2022). The advancement of molecular biology techniques (i.e., mutations, use of molecular markers, genomics, etc.) can facilitate and accelerate the last three steps of this process.

Other topics related to the increase of sunflower yields, which also deserve particular interest, are the “stay green” (de la Vega and Hall, 2002, ; de la Vega et al., 2011) and potential grain size (Castillo et al., 2017, 2018). “Stay green” hybrids maintain a higher water extraction rate for longer than “fast dry down” hybrids during the grain filling period with or without water limitations, having a positive effect on crop yield (Lisanti et al. al., 2012, 2013). The studies carried out by Mangieri et al. (2017, 2020) under field conditions, have demonstrated for the first time: i) the connection between the onset of the falling phase in leaf cytokinin levels and the onset of leaf senescence in hybrids with contrasting levels of cytokinins and, ii) that the onset of the drop in live root density occurs after the start of the decline in leaf area duration. Based on this evidence, studies of molecular markers that control leaf senescence should not only evaluate gene expression in leaves but also in roots (Mangieri, 2011).

Grain weight is an important component of sunflower oil yield but may be limited by the growth of maternal tissues (Lindstrom et al., 2006; Rondanini et al., 2009). The expansins are responsible for the greater growth of the cells that make up these structures. The research carried out by Castillo et al. (2017, 2018) suggests that the EXPN genes would be specifically involved in the expansion capacity of grain tissues, and their expression could be related to grain size in sunflower. Ecophysiological experiments are necessary to determine if the higher potential grain weight translates into a higher grain yield.

Fungal diseases are a severe limitation for the exploration of management alternatives (i.e., sowing dates, crop density, double crops, etc.) in sunflower crops, but the available information about this particular topic is scarce in relation to that reported in other grain crops (i.e., maize and soybean). The interpretation of the physiological determinants of yield in response to these management measures will generate useful information for crop management and the identification of certain attributes/characters of interest for genetic improvement.

In summary, contributions made by local research to crop management practices and genetic improvement of sunflower demonstrate the success of these disciplines in Argentina during the last 53 years. The knowledge accumulated to date by crop ecophysiology and associated disciplines (i.e., ecology, agronomy, plant breeding, molecular biology, and genomics) and the strong methodological advances of testing techniques and interpretation of information offer an encouraging panorama to solve the problems facing the grain crops production, and by extension, for sunflower. Its approach requires carrying out experiments at various levels of organization, which demand the formation of multidisciplinary teams, trained in their discipline and in the interfaces corresponding to the level of organization immediately lower and/or higher than the one in which their discipline is developed.

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