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FORTY YEARS OF TROPICAL MAIZE PHYSIOLOGY: FROM CARBON PARTITIONING TO SYSTEMS BIOLOGY IN THE INTEGRATION BETWEEN GENE, METABOLISM, AND AGRONOMIC RESILIENCE

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ABSTRACT – Over the past four decades, the Magalhães–Durães group has reshaped the eco-physiology of tropical maize by establishing an integrated conceptual framework that links morphological, metabolic, structural, and molecular processes. Early studies defined the functional basis of productivity by demonstrating how carbon partitioning, harvest index, and stem reserves coordinate yield under tropical conditions. Subsequent advances revealed pioneering mechanisms of metabolic plasticity, consolidating the view of source–sink regulation and the integration of carbon and nitrogen metabolism as central determinants of physiological efficiency. Research on flooding tolerance, which culminated in the Saracura variety, showed that resilience arises from coordinated responses involving structural reinforcement, redox homeostasis, and calcium-mediated signaling, marking a scientific milestone for tropical cereals. In acidic, phosphorus-deficient soils, the group demonstrated that the root is the functional core of adaptation, integrating architecture, aluminum tolerance, and maintenance of water flux under drought. The incorporation of microbial and chemical biostimulants further enhanced resilience by modulating photosynthesis, antioxidant metabolism, and plant water status. Most recently, the group unified precision phenotyping into a systems-biology model, positioning tropical maize as a global reference for understanding physiological resilience under multiple environmental stresses.

Keywords: Eco-physiology; Flooding stress; Harvest index; Drought stress; Hypoxia tolerance; Root architecture; Physiological resilience; Photosynthetic efficiency; *Zea mays* L.

Between the late 1970s and the mid-2020s, the physiology of tropical maize underwent a profound transformation, driven mainly by the scientific trajectory of the group led by Paulo César Magalhães, Frederico Durães, and collaborators at Embrapa Maize and Sorghum. Their pioneering efforts and collaborative spirit have made this program one of the most influential in the country, inspiring confidence in the group's leadership and innovation.

Over four decades, this group has built a continuous line of knowledge that has united morphology, metabolism, root architecture, mineral nutrition, drought and flooding, chemical and microbial stimulation, and, more recently, molecular regulation, always supported by experimental rigor and agronomic applicability.

The initial phase (1987–1999) established the foundations of the functional physiology of tropical maize. Concepts that are now central were consolidated, such as source-sink control, the harvest index as a metric of productive efficiency, and the physiological function of the stalk as an organ for carbon storage and redistribution. This stage allowed maize to be interpreted not only as a crop with high photosynthetic conversion, but also as a physiological system sensitive to environmental fluctuations (Magalhães et al. 1998).

Starting in the 2000s, the group initiated a more integrative phase that redefined tropical maize as a metabolically plastic organism. Studies on hypoxia and flooding led to the development of the Saracura variety, a milestone demonstrating that physiological tolerance to stress depends on coordinated responses involving structure, carbon and nitrogen metabolism, redox homeostasis, and calcium-mediated signaling. This stage expanded the conceptual scope of ecophysiology by showing that resilience arises from the integration of energetic and structural processes. This physiological characterization was made possible by the excellent work of the plant breeding team that selected 18 selection cycles of Saracura maize (Parentoni et al. 1997).

Between 2011 and 2020, research advanced towards an applied ecophysiology model, focusing on the root as the functional epicenter of tropical maize. Root architecture, phosphorus acquisition, aluminum tolerance, antioxidant metabolism, and hormonal modulation were articulated within a unified framework, demonstrating that productive efficiency and drought tolerance depend on a physiological network linking absorption, transport, photosynthesis, and grain quality. The incorporation of growth-promoting microorganisms and chemical biostimulants consolidated the view that resilience can be induced and managed (Magalhães et al. 2011; de Souza et al. 2014; Marques et al. 2021).

In the recent period (2021–2025), the group transitioned definitively to biological systems applied to tropical maize.

The integration of classical ecophysiology, physiological bioengineering, and precision phenotyping has enabled multiscale mapping of the mechanisms underlying drought tolerance and nutritional efficiency in tropical environments. The development of composite resilience metrics and the gene-root-plant-field framework marks the consolidation of a modern, comprehensive model that can guide genetic improvement and adaptive management strategies (Paiva et al. 2021; da Siva et al. 2025; Rafael et al. 2026).

Thus, Magalhães-Durães group constitutes one of the most comprehensive scientific frameworks ever developed for tropical maize, with extensive scientific outreach in the country, such as lectures, courses, books, scientific articles, and participation in congresses and other events. This work revisits this historical trajectory, systematizing the conceptual, experimental, and applied advances that have transformed the understanding of maize physiology in Brazil, and establishing the basis for an integrated view of productivity and resilience in tropical environments under multiple stresses. This effort underscores the practical importance of the research for improving crop resilience and productivity, resonating with the audience's goals.

Objective

This review synthesizes four decades of research by the Magalhães–Durães group to elucidate the physiological principles governing tropical maize productivity and resilience under multiple stresses. We aim to demonstrate how carbon partitioning, root architecture, redox regulation, nutritional efficiency, flood tolerance, and drought resilience integrate into a comprehensive functional model. By combining ecophysiology, recurrent selection, biochemical responses, microbial and chemical bioactivation, and precision phenotyping, this work positions tropical maize as a key model for understanding physiological adaptation in tropical environments.

Methodology

The Magalhães–Durães group, combining historical, physiological, and molecular analysis, developed this work from an integrative synthesis of four decades of scientific production. Initially, all studies published by the group were organized chronologically and classified into the following thematic axes: carbon partitioning, root ecophysiology, flood tolerance, drought, mineral nutrition, redox metabolism, recurrent selection, biostimulation, and biology systems. Subsequently, each set of work was examined with respect to the experimental models used, the physiological variables evaluated, and the mechanisms identified.

The next step involved comparing the results over time to identify evolutionary patterns, conceptual convergences, and paradigm shifts. Studies from different periods were integrated through a functional approach, connecting morphological, biochemical, anatomical, nutritional, and molecular processes into a single interpretative framework. The final synthesis was built from the overlapping of this evidence, allowing the reconstruction of the physiological logic that emerged over the years and the formulation of a unified model to explain the productivity, resilience, and adaptation of tropical maize under multiple stresses.

1. The Physiological Bases of Tropical Maize: From the Formation of the Magalhães-Durães Group to the Consolidation of the Concepts of Carbon Partitioning and Productive Efficiency (1977–1999).

1.1. Formation of the group and initial scientific context (1989-1992).

The scientific career of Paulo César Magalhães and his collaborators at Embrapa Maize and Sorghum dates to the end of the 1980s, when the first experiments on the growth, development, and biomass accumulation of tropical maize under different water conditions were conducted (Magalhães and Jones 1990b; Magalhães et al. 1995). In these pioneering studies, leaf area, relative growth rate (RGR), and dry matter distribution among leaves, stalks, and ears were measured, establishing the empirical basis for understanding the impact of environmental fluctuations on photosynthetic conversion efficiency.

During the first half of the 1980s, the group consolidated the view that environmental factors, such as water availability, population density, and light intensity, strongly influence the physiology of tropical plants. This ecophysiological approach, then unprecedented at Embrapa, sought to integrate morphophysiological data with production parameters, establishing the methodological basis for the controlled experiments that would define the following decade.

1.2. First experimental evidence of source-sink control (1988–1990).

In the late 1980s, Magalhães and Jones (1990a, 1990b) introduced a quantitative experimental approach to study the regulation of carbon and nitrogen partitioning in maize. The hypothesis was that adjustments in the source/sink ratio, through changes in plant density and reproductive load, directly modulate the assimilate flow and grain yield.

In the first study (Magalhães & Jones, 1990a), there authors reduced population density by 50% at two distinct phenological stages: flowering (R1) and the beginning of grain filling (R2). This reduction decreased intraspecific competition for light, water, and nutrients, increased net photosynthesis per plant and, therefore, the supply of available photoassimilates. Analysis of grain dry mass and sub-ear internode (stem below the ear) showed that thinning performed at R1 promoted an increase in grain growth rate (g plant^{-1} day^{-1}) and greater final grain weight, while thinning at R2 did not produce a significant effect.

In a subsequent study, Magalhães and Jones (1990b) further analyzed the biochemical aspects of carbon and nitrogen partitioning under different source-sink balances. They quantified total soluble sugars, total nitrogen (Kjeldahl), and starch in the sub spike internodes, upper leaves, and developing grains, identifying the stem as a temporary storage organ.

1.3. Ecophysiological expansion and harvest index modeling (1990–1995).

From 1990 onwards, the Magalhães–Durães group advanced towards the physiological quantification of productive efficiency, analyzing the behavior of the harvest index (HI) under different environmental and genetic conditions. In experiments conducted in Sete Lagoas with three hybrids of distinct cycles and varying population densities, the genetic (GI) and observed (OI) harvest indices were evaluated (Durães et al. 2002).The results showed that the high-performance of tropical hybrids at the time had a GI of 0.50–0.55, while the OI could drop to 0.35–0.43 under drought or light competition, representing physiological losses of up to 25% in carbon partitioning. The group then introduced the concept of compensatory physiological efficiency, which describes the ability of hybrids to maintain high yields under limited resource availability by prioritizing the translocation of assimilates to the grains.

In this context, the work "Physiology of the Corn Plant" (Magalhães et al.1995) was published, systematizing the acquired knowledge and consolidating the theoretical structure of tropical corn physiology by integrating photosynthesis, carbon partitioning, root morphology, and mineral nutrition into a unified physiological model. This work has received a total of 74 citations on Google Scholar.

1.4. Structural physiology and harvest stability (1998–1999).

In Magalhães et al. (1998), the group used the concept of structural physiology, demonstrating that genotypes with a higher proportion of structural carbohydrates (cellulose and lignin) exhibited less stalk lodging and greater productive stability, although with a slight reduction in the harvest index. This relationship indicated that the anatomical architecture and biochemical composition of the stalk define an adaptive balance between mechanical rigidity and metabolic reserve, directly associated with productive sustainability in tropical environments.

Physiological overview of the 1987–1999 period.

Between 1987 and 1999, the Magalhães–Durães group laid the foundations for the functional physiology of tropical maize, linking morphology, metabolism, and yield in a dynamic model of physiological efficiency. The harvest index became established as a central metric of productivity; the stalk of the ear was recognized as a key organ in assimilate partitioning; and post-anthesis leaf longevity came to be considered determinant for grain filling. These principles structured the conceptual basis that, in the following decades, would support research on responses to water stress, antioxidant metabolism, and anatomical plasticity, expanding the scope of physiology applied to tropical conditions (Durães et al. (2002).

2. Physiology of Abiotic Stresses and Metabolic Plasticity in Tropical Maize.

2.1. From carbon partitioning to metabolic integration in drought and flooding.

2.1.1. Conceptual transition and physiological maturation.

The beginning of the 2000s marked a turning point in the scientific trajectory of the Magalhães–Durães group, consolidating a new approach to understanding the physiology of tropical maize (*Zea mays* L.). The classic view, centered on carbon partitioning and harvest index, gave way to a more integrative model, in which the plant was interpreted as a system of coordinated responses among energy, and nitrogen metabolism (Ferreira et al. 2000, Ferreira et al. 2002).

This transition represented the maturation of applied physiology: tropical maize ceased to be treated merely as an object for biomass quantification and began to be analyzed as a dynamic biochemical organism, capable of reorganizing metabolic pathways in response to environmental fluctuations. The group identified that productivity is intrinsically linked to the plant's ability to maintain a balance between carbon and nitrogen metabolism, sustaining the synthesis of reducing compounds and energy flow even under water or thermal limitations. This view gave rise to a phase in which the experimental focus shifted from simple biomass measurement to understanding the physiological mechanisms that sustain productive stability—a conceptual advance that prepared the way for subsequent studies on metabolic tolerance and adaptation.

2.1.2. Carbon Metabolism and Eco-efficiency Under Water Deficit.

The first experiments in this phase evaluated the metabolic responses of tropical maize to control water deficit at different developmental stages. Irrigation interruption ten days before flowering reduced grain yield by 92–98%, while suspensions fifteen and thirty days after flowering caused drops of 53% and 16%, respectively. These results demonstrated that water stress acts directly on carbon metabolism, interfering with both CO_2 assimilation and the translocation and remobilization of photoassimilates (Magalhães et al. 2009).

Under severe drought, maize leaves showed a marked reduction in net CO_2 assimilation, accompanied by an accumulation of soluble sugars—indicative of uncoupling between sucrose synthesis and transport. The decrease in stomatal conductance and sucrose-phosphate synthase (SPS) activity limited drain loading and reduced the harvest index (HI) from 0.52 (irrigated) to 0.10 (severe drought) (Durães et al. (2002).

Conversely, an increase in the activity of glycolytic enzymes, such as phosphofructokinase (PFK) and pyruvate kinase (PK), was observed, suggesting a redirection of carbon towards short-term survival pathways. The integration of carbon and nitrogen metabolism proved essential (Magalhães et al.2009).

Maize plants with higher nitrogen use efficiency (NUE) maintained 20% more biomass and photosynthetic activity by conserving ammonium assimilation via glutamine synthetase (GS) and glutamate synthetase (GOGAT). These mechanisms demonstrated that water stress compromises not only the photosynthetic apparatus but also the carbon-nitrogen flow that sustains metabolism and yield (Ferreira et al. 2002).

2.1.3. Metabolic integration under hypoxia: the Saracura model.

In parallel, the group turned its attention to flooding, another recurring stress in tropical and subtropical zones. The challenge of understanding how tropical maize tolerates hypoxic and anoxic conditions led to the development of the Saracura variety, derived from recurrent selection, as part of one of the most ambitious physiological selection programs conducted by Embrapa Maize and Sorghum. From 2001 to 2010, this experimental variety became a world reference for demonstrating that flood tolerance in maize results from the integration of anatomical, metabolic, and energetic processes, rather than superficial morphological modifications.

2.1.3.1. Initial metabolic adjustments and the role of calcium.

The 2000s began with a conceptual milestone: calcium as a key element in the set of mechanisms of physiological tolerance to flooding in Saracura maize. The studies conducted by Vitorino et al. (2001) and Ferrer et al. (2003) demonstrated that supplying Ca^{2+} (20 mM) to maize seedlings subjected to 14 days of hypoxia reduced mesocotyl cell collapse by 47%, increased its mechanical resistance by 38%, and increased net photosynthesis by 32%.

Lipid peroxidation was substantially lower, while superoxide dismutase (SOD) activity increased by 41%. These responses showed that Ca^{2+} acts in an integrated manner: reinforcing cell walls and middle lamellae, while modulating signaling processes mediated by abscisic acid (ABA) and the cellular redox system (Lopes et al. 2005). Later, Ferrer et al. (2005), Souza et al. (2009) expanded this understanding by studying adult Saracura maize plants, already undergoing recurrent selection for flood tolerance. This opportunity marked the beginning of a very fruitful partnership with the physiology group at UFLA (Federal University of Lavras), coordinated by Professor José Donizeti Alves.

After 25 days of water saturation, an 83% increase in root aerenchyma volume, a 21% thickening of epidermal walls, and a 27% accumulation of calcium pectates were observed, modifications that increased gas diffusion and reinforced tissue stability. From a physiological point of view, Ca^{2+} supplemented plants maintained a photochemical efficiency (Fv/Fm) of 0.75. In contrast, untreated plants dropped to 0.61, demonstrating the preservation of photosystem II and the functional stability of the photosynthetic apparatus (Pereira et al. 2010).

These studies, conducted with Saracura maize, demonstrated that calcium is a key physiological component of the mosaic of adaptive mechanisms, contributing synergistically to the maintenance of cellular integrity and energy flow under hypoxia. In the context of the Saracura variety, calcium was shown to be a relevant functional factor in survival in flooded environments, reinforcing the importance of integrating structure, metabolism, and signaling in the adaptive physiology of tropical maize.

2.1.3.2. Metabolic reconfiguration in recurrent selection.

After establishing the anatomical-metabolic mechanisms mediated by calcium, the group began to investigate how these responses could be genetically fixed during generations of Saracura maize. The hypothesis guiding this new stage was that physiological tolerance to flooding was not limited to momentary adjustments but could be improved and inherited through recurrent selection under controlled hypoxia. In this context, Pereira et al. (2010) demonstrated that recurrent selection of Saracura maize under prolonged flooding promoted a remarkable physiological leap. Generations G_0 to G_4 revealed not only anatomical gains, but a coordinated metabolic reprogramming. Souza et al. (2010b), Souza et al. (2011) further complemented the same experiment by Pereira, however under field conditions, experiments which required a large research structure for development (Table 1).

The increase in alcohol dehydrogenase (ADH) ensured NAD^+ regeneration and maintained glycolytic flux under low-oxygen

Table 1. Gains from recurrent selection in Saracura maize

PARAMETERS	G_0	G_4	VARIATION
VOLUME OF ROOT AERENCHYMA	18 %	33 %	+83 %
ADH ACTIVITY	100 %	165 %	+65 %
SOD	100 %	146 %	+46 %
CAT	100 %	139 %	+39 %
POD	100 %	152 %	+52 %

conditions. In contrast, increased antioxidant enzymes (SOD, CAT, and POD) strengthened the redox system (Pereira et al. 2010) as shown in Table 1. Saracura maize has therefore evolved into a new stable metabolic state, in which fermentative, antioxidant, and structural pathways intertwine to sustain physiological activity an emblematic example of adaptive plasticity observed experimentally in tropical cereals. This work was conducted in partnership with UFLA, led by researcher Kamila R. Dázio de Souza, who was a student of Professor Donizeti at the time (Souza et al. 2010a, Porto et al. 2012).

2.1.3.3. C–N–Redox Integration and Physiological Stability (2008–2010).

With the advancement of recurrent selection and the accumulation of biochemical evidence, the group directed its efforts to understand how carbon and nitrogen metabolism and the redox system interact at the basis of flood tolerance. This systemic approach represented the conceptual maturation of the research: the plant came to be seen as an integrated energy regulation system, in which the maintenance of redox homeostasis is inseparable from carbon and nitrogen assimilation.

In this context, Souza et al. (2010a), Porto et al. (2012) worked with contrasting G_0 (sensitive) and G_4 (tolerant) populations of the Saracura series, subjected to controlled flooding for 14 days. The results confirmed the integration of C–N–Redox metabolism in tropical maize under hypoxia.

The G_4 population maintained 41% higher photosynthetic activity, $Fv/Fm \approx 0.78$, and higher nitrate reductase (NR) and glutamine synthetase (GS) activity than the sensitive variety. These responses demonstrated that maize tolerance is not limited to anatomical survival but depends on maintaining the coupling between carbon assimilation, nitrogen metabolism, and redox balance (Souza et al. 2010a).

The 37% reduction in ethanol and acetaldehyde levels and the 24% increase in malate dehydrogenase (MDH) demonstrated more efficient respiration and less carbon loss. Tolerant plants produced 6,800 kg ha^{-1} under flooding, compared to 4,900 kg ha^{-1} for sensitive plants, with 15% more foliar carbohydrates and 18% less starch in the roots, indicating better mobilization of photoassimilates. These results confirmed that the physiological behavior performance from Saracura maize comes from the coordinated integration of primary energy and structural metabolism (Souza et al. 2010a, Souza et al. 2010b).

3. The consolidation of the integrated ecophysiology of tropical maize (2011–2020).

The period from 2011 to 2020 marks a turning point in the physiological work of the group led by Paulo César Magalhães at Embrapa Maize and Sorghum. After establishing, in previous decades, the fundamentals of growth, carbon partitioning, and harvest index in tropical maize, this phase integrates three principal axes: nutritional ecophysiology in acidic and phosphorus-poor soils, maize tolerance to drought in different phenological stages, and the incorporation of biostimulation, both chemical and microbial, as a physiological tool for stress mitigation.

Maize is no longer seen merely as a model of productive response, but it is treated as a complex biological system, in which root, shoot, antioxidant metabolism, hormonal signaling, anatomy, grain quality, and interactions with microorganisms form an integrated network of adaptation to tropical conditions.

3.1. Advances in the nutritional ecophysiology of tropical maize (2011–2013): from phosphorus acquisition to ionic tolerance.

The 2010s marked a turning point in ecophysiological research on tropical maize by clearly demonstrating that the root is the functional center of nutritional efficiency in tropical soils. Between 2011 and 2013, Magalhães' group developed experiments that connected root architecture, phosphorus absorption, tolerance to aluminum toxicity, and maize yield performance in nutrient-poor environments.

Magalhães et al. (2011) published a study evaluating 10 contrasting maize genotypes under phosphorus (P) deficiency in nutrient solution and in low-availability soil. The genotypes efficient in phosphorus use showed longer fine roots, higher lateral branch density, and more acute root angles, which increased the volume of soil explored. This structural pattern resulted in greater phosphorus accumulation in young tissues and superior shoot growth, even under substantial P limitation. The central contribution of the work was methodological: it demonstrated that it is possible to select, at early stages, phosphorus-efficient maize genotypes, with a high correlation between initial root performance and P accumulation in advanced stages.

Magalhães et al. (2012) broadened the focus to aluminum toxicity. In acidic soil, three increasing levels of Al^{3+} were applied to contrasting tropical lines. The tolerant lines maintained higher root elongation rates, preserved lateral root formation, and sustained greater total maize biomass even at the highest aluminum concentrations. In contrast, the sensitive lines showed potent inhibition of root growth. These results indicated that tolerance to Al^{3+} toxicity is mediated by morphological and anatomical plasticity in roots, allowing maize to maintain phosphorus, nitrogen, and basic cation absorption under conditions of high acidity (Table 2).

At the close of this sub-period, the group integrated the results into a coherent vision: the nutritional efficiency of tropical maize depends on the root's ability to grow in environments with low phosphorus availability and high aluminum activity, adjusting its architecture and preserving functionality. This physiological basis would prove fundamental for the drought studies that followed.

Table 2. Root parameters associated with nutritional efficiency in tropical maize.

Maize genotype group	Length of fine roots	Lateral branching	Average root angle	P-use efficiency	Al^{3+} tolerance
P-efficient and al^{3+} tolerant	High	High	More acute	Elevated	Elevated
P-efficient and al^{3+} sensitive	High	Moderate	Intermediate	Moderate	Low
P-inefficient and al^{3+} sensitive	Low	Low	More obtuse	Low	Low

3.2. Nutrition, antioxidant metabolism, and drought: the root as a physiological epicenter (2013–2016)

From 2013 onwards, the group began integrating mineral nutrition and drought into a single experimental matrix, while maintaining maize as the target species. The focus shifted from how much nutrients the maize absorbs to how it uses these nutrients to sustain photosynthesis, water status, and membrane integrity under water restriction.

In studies conducted between 2012 and 2015, Magalhães, Souza, and colleagues evaluated tropical maize genotypes subjected to different nitrogen and phosphorus doses, with or without associated water deficit. Under drought conditions, maize genotypes with greater phosphorus use efficiency and better root architecture maintained higher photosynthetic rates, more stable stomatal conductance, and lower lipid peroxidation levels, indicating more effective membrane protection. The positive interaction between adequate nutrition and root function allowed these genotypes to preserve growth and dry matter production even when soil water potential was reduced (Magalhães et al. 2012; Magalhães et al. 2015, Magalhães et al. 2016).

Also, during this period, ecophysiological studies showed that nitrogen availability modulates maize antioxidant metabolism under drought. In efficient genotypes, adequate N supply was associated with higher enzyme activity, including superoxide dismutase, catalase, and peroxidases, resulting in lower reactive oxygen species accumulation in maize leaves under moderate deficit conditions. Sensitive maize, on the other hand, accumulated higher levels of MDA, evidencing greater oxidative damage (de Souza et al. 2014).

In 2015, Lavinsky, Souza, and Magalhães advanced to the anatomical analysis. In experiments with water deficit applied at different phenological stages (e.g., V5, VT, and R3), tolerant maize genotypes showed reorganization of root anatomy, including the formation of cortical aerenchyma and adjustments in vascular tissue distribution, which favored water transport. These anatomical adjustments occurred in parallel with the depth and spatial distribution of the roots and helped maintain the flow of water from the roots to the aerial parts, thereby directly impacting productivity (Lavinsky et al. 2015a; Lavinsky et al. 2015b; Lavinsky et al. 2015c).

Thus, between 2013 and 2016, the idea that the corn root is the epicenter of physiological adaptation in tropical soils was consolidated, integrating nutrition, anatomy, antioxidant metabolism, and hormonal regulation to sustain the plant under drought (Souza et al. 2013a; Souza et al. 2013b).

3.3. Integrated advances under drought conditions: hormonal modulation, root architecture, and grain quality.

Continuing the ecophysiological axis developed in the previous topic, in which nutrition began to be treated as a determining factor of functional efficiency in limiting environments, the period from 2014 to 2020 represents the consolidation of the research line on water stress in tropical maize conducted by Magalhães' group. In this stage, the focus turned to understanding why specific maize genotypes maintain productivity and physiological integrity under water deficit and how these mechanisms are organized, involving everything from hormonal signaling and antioxidant metabolism to root plasticity, carbon partitioning, and final grain quality.

Three pillars support this advance: hormonal modulation via abscisic acid and the role of this hormone in maintaining water status and photophysiology, root architecture and anatomy, which ensure absorption and sink strength during stress, and the impact of water deficit on yield and grain composition, revealing the genetic and physiological bases of maize's productive resilience.

3.3.1. Hormonal modulation with ABA: water preservation, photosynthesis, and antioxidant activity.

The study by de Souza et al. (2014) evaluated the effects of foliar application of abscisic acid in maize hybrids with contrasting drought tolerance, under irrigated conditions and under controlled water deficit. The variables included leaf water potential, CO_2 assimilation rate, stomatal conductance, PSII photochemical efficiency, antioxidant enzyme activity, and malondialdehyde as a marker of membrane damage.

The results showed that, under drought, the application of ABA in drought-tolerant maize-maintained water status, moderately reduced stomatal conductance, preserved the photosynthetic rate, increased antioxidant activity, and decreased MDA accumulation. In sensitive genotypes, the response was partial. This work consolidated the understanding that ABA acts as a chemical signal of resilience in tropical maize, coordinating water conservation, photophysiology, and antioxidant defense (de Souza et al. (2014).

3.3.2. Root architecture and anatomy: carbon economy and phenological window of stress.

In Lavinsky et al. (2015a), four contrasting tropical maize genotypes were evaluated under moderate drought to understand how root morphological characteristics influence physiological and productive performance. The tolerant genotypes showed longer fine roots, higher branching density, and more acute root angles, which increased the volume of soil explored. These genotypes maintained higher photosynthetic rates, more stable stomatal conductance, and higher grain yield than the sensitive ones.

In subsequent work, the group distinguished the fate of carbon allocated to the root during drought, separating primary metabolism, associated with growth and osmolyte synthesis, from secondary metabolism, related to the production of defense compounds. In tolerant maize, primary metabolism and root expansion were prioritized, whereas in sensitive maize, carbon was diverted to secondary compounds, penalizing growth and productivity (Lavinsky et al. 2015c).

In Souza et al. (2016), they showed that the timing of drought occurrence throughout the maize cycle is crucial. Deficits at V5 and VT induced profound anatomical changes, such as aerenchyma formation and xylem reorganization, in tolerant genotypes, thereby improving water transport and increasing yield stability. The combination of architecture, anatomy, and the phenological window has come to be seen as a determinant of water-use efficiency in tropical maize.

3.3.3. Root investment, harvest index, and grain quality under drought.

The series of experiments conducted by Ávila et al. (2017a) reinforced the interdependence between the corn root system, carbon partitioning, and the quality of the final product. Under pre-flowering drought conditions, tolerant genotypes increased the proportion of root biomass and maintained the harvest index, indicating preservation of reproductive sink strength. Sensitive genotypes, on the other hand, reduced ear assimilate allocation and experienced a sharp drop in productivity.

In the complementary study, pre-flowering drought reduced corn productivity by up to 60% and significantly altered the organic and mineral composition of the grains. There was a reduction in starch and calcium content, with a relative increase in protein, phosphorus, iron, and zinc. Tolerant genotypes showed less compositional deviation and greater productive integrity. The study introduced a groundbreaking perspective to the group: drought not only limits growth but also redefines the reproductive metabolism and nutritional quality of the corn grain (Ávila et al. 2017b).

3.4. Microbial and chemical biostimulation in tropical maize under water deficit.

Between 2018 and 2020, biostimulation emerged as a central focus in the applied ecophysiology of tropical maize. The group expanded the focus from the individual plant to the plant-microorganism system, exploring how rhizosphere bacteria and bioactive molecules can modulate, in an integrated way, root growth, photosynthesis, antioxidant metabolism, and yield under drought.

Marques et al. (2020) investigated the inoculation of *Azospirillum brasilense* in two contrasting maize hybrids under moderate drought in acidic tropical soil. Inoculation significantly increased the total length of fine roots, the density of lateral branches, the photosynthetic rate, and the activity of antioxidant enzymes. In parallel, it reduced the accumulation of malondialdehyde and hydrogen peroxide in maize leaves. Grain yield increased by an average of 15%. These results showed that *Azospirillum* acts as a bioinducer of redox homeostasis and root expansion in maize, thereby reinforcing carbon source-sink flow and absorption capacity under drought.

During the same period, Rabelo et al. (2019), Veroneze Jr. et al. (2019), and Ambrósio et al. (2020) focused on chemical biostimulation in maize. Foliar applications of chitosan derivatives and osmoprotective mixtures containing trehalose promoted an increase in the photosynthetic rate, greater photochemical efficiency, a reduction in the formation of reactive oxygen species, and productivity increases under moderate water deficit. In the work of Ambrósio et al. (2020), gains in maize grain yield exceeded 20% compared with the control under drought, reinforcing the potential of these molecules as complementary physiological tools, in synergism with the intrinsic mechanisms of tolerance.

3.5. Physiological synthesis of the period (2011–2020).

Between 2011 and 2020, the work of Paulo César Magalhães' group on tropical maize shifted ecophysiology from a descriptive approach to an integrated functional view. In acidic, phosphorus-poor soils, the maize root was recognized as a central organ of nutritional efficiency, integrating architecture, plasticity, and tolerance to aluminum toxicity. Under drought, tolerance came to be understood as the result of a network that incorporates hormonal signaling, antioxidant metabolism, anatomy, carbon partitioning, and grain quality. Inoculation with growth-promoting microorganisms and the application of chemical biostimulants showed that maize resilience can be reinforced by strategies that operate in conjunction with the genetic and physiological mechanisms already present in tropical genotypes (Siqueira et al. 2020, Almeida et al. 2020, Paiva et al. 2021 and Marques et al. 2021).

This set of contributions concludes the decade with a coherent model: tropical maize tolerant to drought and limiting soils is one whose roots efficiently explore the soil, maintain growth and absorption under aluminum and water deficit, organize carbon partitioning to protect the harvest index, sustain the nutritional quality of the grain, and interact advantageously with microorganisms and bioactive molecules. From this point that the period from 2021 to 2025 advances towards molecular and biology systems, deepening the genomic and metabolomic basis of these mechanisms.

4. From Ecophysiology to Biology Systems: Molecular, Metabolic, and Microbial Integration in Tropical Maize's Drought Resilience.

The scientific progress achieved by 2020 established a solid ecophysiological basis for interpreting the structural and functional mechanisms underlying drought tolerance in tropical maize. Between 2021 and 2025, the group coordinated by Magalhães deepened this trajectory by connecting gene regulation, root metabolomics, nutritional interaction, physiological bioengineering, and precision phenotyping. This set of studies represents the definitive transition from classical ecophysiology to a biology systems model, in which tolerance emerges from the integration between levels of organization—molecular, metabolic, anatomical, and agronomic in tropical environments under multiple stresses.

4.1. Metabolomic and nutritional integration in multiple stress environments.

Tolerant genotypes exhibited a higher sucrose/hexose ratio and enrichment in metabolites associated with maintaining membrane integrity, P flux, and Al^{3+} sequestration in the rhizosphere. These results showed that tolerance depends on a root metabolic economy, in which carbon is strategically reallocated among detoxification, osmoprotection, and root-structure pathways.

In Siqueira et al. (2020) expanded this view by relating the absorption of P, Ca, and Al^{3+} to metabolic composition: tolerant genotypes accumulated mannitol, trehalose, and organic acids, which stabilize absorption under acidic pH. Thus, root metabolism serves as a functional link between nutrition, redox, and hormonal signaling, thereby structuring an integrated model of physiological adaptation.

4.2. Physiological bioengineering and symbiotic modulation under drought.

As a result of advances in molecular and metabolic research, the group deepened its use of bioactive molecules as resilience signalers. In de Novais Portugal et al. (2021), Rabelo et al. (2019) and Reis et al. (2019) the exogenous application of trehalose, and chitosan to plants under moderate drought increased grain yield by 22%. It increased photochemical efficiency (Fv/Fm) while simultaneously reducing ROS accumulation and MDA.

This performance resulted from the integrated reinforcement of antioxidant activity and stomatal regulation, indicating that these molecules function as complementary metabolic modulators of the endogenous mechanisms in tolerant genotypes. In parallel, the group's work on *Azospirillum* and *Bacillus* reinforced the idea that the microbial symbiotic association also affects water stability and hormonal signaling, expanding the capacity for plant physiological adjustment under water deficit. These studies have consolidated physiological bioengineering as a field of direct application of molecular biology (Reis et al. 2019, Rafael et al. 2026).

4.3. Final synthesis: consolidation of biology systems applied to tropical maize.

Between 2021 and 2025, the Magalhães group unified the multiple scales of drought tolerance into a coherent systems biology model, in which gene regulation defines molecular readiness for stress; root metabolism maintains nutrition, ionic flows, and carbon economy; bioactive molecules and microbial symbionts enhance responsiveness; and precision phenotyping translates invisible mechanisms into agronomic selection. This period represents the culmination of forty years of research, consolidating tropical maize as a model system for understanding the integration between molecules, tissues, microorganisms, and the environment under stress (da Silva et al. 2025, de Oliveira et al. 2025, Rafael et al. 2026 and de Oliveira et al. 2026).

Final Considerations

The scientific trajectory of the Magalhães–Durães group teaches that understanding tropical maize requires abandoning fragmented explanations and adopting a truly integrative vision. Four decades of research reveal that productivity and resilience arise from the convergence of carbon partitioning, root architecture, nutritional efficiency, redox metabolism, hormonal signaling, and anatomical mechanisms, organized as a continuous functional system. By demonstrating how these processes are articulated under multiple stresses, the group showed that tropical maize responds through interdependent networks rather than isolated components. This integrated, systems-based perspective has been crucial in advancing plant science, enabling reinterpretation of approaches from recurrent selection to molecular techniques. The key contribution of this work is to clearly show that plant adaptation in tropical environments can only be understood when the plant is viewed as a dynamic, coherent system capable of reorganizing in response to adversity.

References

ALMEIDA, L. G.; MAGALHÃES, P. C.; KARAM, D.; SILVA, E. M. da; ALVARENGA, A. A. Chitosan application in the induction of water deficit tolerance in maize plants. **Acta Scientiarum-Agronomy,** v. 42, e42463, 2020. DOI: https://doi.org/10.4025/actasciagron.v42i1.42463.

AMBRÓSIO, A. S.; PORTUGAL, J. A. N.; SOUZA, K. R. D.; SILVA, L. C.; DIAS, D. F.; MANTOVANI, J. R.; MAGALHÃES, P. C.; SOUZA, T. B.; SOUZA, T. C. A mixture of trehalose derivatives mitigates the adverse effects of water deficits in maize: an analysis of photosynthetic efficiency. **Photosynthetica,** v. 58, n. 3, p. 808-818, 2020. DOI: http://doi.org/10.32615/ps.2020.031.

ÁVILA, R. G.; MAGALHÃES, P. C.; ALVARENGA, A. A. de; LAVINSKY, A. de O.; CAMPOS, C. N.; SOUZA, T. C. de; GOMES JÚNIOR, C. C. Drought-tolerant maize genotypes invest in root system and maintain high harvest index during water stress. **Revista Brasileira de Milho e Sorgo**, v. 15, n. 3, p. 450-460, 2016. DOI: https://doi.org/10.18512/1980-6477/rbms.v15n3p450-460.

ÁVILA, R. G.; SILVA, E. M. da; MAGALHÃES, P. C.; ALVARENGA, A. A.; LAVINSKY, A. O. Drought changes yield and organic and mineral composition of grains of four maize genotypes. **Academia Journal of Agricultural Research**, v. 5, n. 9, p. 243-250, 2017.

DURÃES, F. O. M.; MAGALHÃES, P. C.; OLIVEIRA, A. C. Índice de colheita genético e as possibilidades da genética fisiológica para melhoramento do rendimento de milho. **Revista Brasileira de Milho e Sorgo**, v. 1, n. 1, p. 33-40, 2002. Available at: https://www.alice.cnptia.embrapa.br/alice/bitstream/doc/480563/1/Indicecolheita.pdf. Accessed on: 13 May 2026.

FERREIRA, V. M.; MAGALHÃES, P. C.; DURÃES, F. O. M. Produtividade de genótipos de milho (Zea mays) sob manejo diferenciado de irrigação e adubação. **Ciência e Agrotecnologia,** v. 24, n. 3, p. 663-670, 2000. Available at: https://www.alice.cnptia.embrapa.br/alice/bitstream/doc/484475/1/Produtividadegenotipos.pdf. Accessed on: 13 May 2026.

FERREIRA, V. M.; MAGALHÃES, P. C.; DURÃES, F. O. M.; OLIVEIRA, L. E. M. de; PURCINO, A. A. C. Metabolismo do nitrogênio associado à deficiência hídrica e sua recuperação em genótipos de milho. **Ciência Rura**l, v. 32, n. 1, p. 13-17, 2002. Available at: https://www.alice.cnptia.embrapa.br/alice/bitstream/doc/485227/1/Metabolismonitrogenio.pdf. Accessed on: 11 May 2026.

FERRER, J. L. R.; MAGALHÃES, P. C.; ALVES, J. D.; VASCONCELLOS, C. A.; DELU FILHO, N.; FRIES, D. D.; MAGALHÃES, M. M.; PURCINO, A. A. C. Calcium partially relieves the deleterius effects of hypoxia on a maize cultivar selected for waterlogging tolerance. **Revista Brasileira de Milho e Sorgo**, v. 4, n. 3, p. 381-389, 2005. Available at: https://www.alice.cnptia.embrapa.br/alice/bitstream/doc/489518/1/Calciumpartially.pdf. Accessed on: 13 May 2026.

LAVINSKY, A. O.; MAGALHÃES, P. C.; GOMES, M. M. D.; GOMES JÚNIOR, C. C.; CASTRO, E. M.; AVILA, R. Root system traits and its relationship with photosynthesis and productivity in four maize genotypes under drought. **Cereal Research Communications**, v. 44, p. 89-97, 2015a. DOI: https://doi.org/10.1556/0806.43.2015.029.

LAVINSKY, A. O.; MAGALHÃES, P. C.; AVILA, R. G.; GOMES JÚNIOR, C. C.; CARNEIRO, N. P. Analysis of maize photosynthesis parameters and whole plant oxidative damage under long-term drought. **Advances in Crop Science and Technology**, v. S1, p. 1-6, 2015b. DOI: https://doi.org/10.4172/2329-8863.1000S1-007.

LAVINSKY, A. O.; MAGALHÃES, P. C.; ÁVILA, R. G.; DINIZ, M. M.; SOUZA, T. C. de. Partitioning between primary and secondary metabolism of carbon allocated to roots in four maize genotypes under water deficit and its effects on productivity. **The Crop Journal**, v. 3, n. 5, p. 379-386, 2015c. DOI: https://doi.org/10.1016/j.cj.2015.04.008.

LOPES, M. J. C.; SOUZA, I. R. P. de; MAGALHÃES, P. C.; GAMA, E. E. G. e; ALVES, J. D.; MAGALHÃES, M. M. Oxidação proteica e peroxidação lipídica em plantas de diferentes ciclos de seleção do milho 'Saracura', sob encharcamento contínuo. **Revista Brasileira de Milho e Sorgo**, v. 4, n. 3, p. 362-373, 2005. Available at: https://www.alice.cnptia.embrapa.br/alice/bitstream/doc/489532/1/Oxidacaoproteica.pdf. Accessed on: 11 May 2026.

MAGALHÃES, P. C.; JONES, R. Aumento de fotoassimilados sobre os teores de carboidratos e nitrogênio em milho. **Pesquisa Agropecuária Brasileira**, v. 25, n. 12, p. 1755-1761, 1990a. DOI: https://doi.org/10.1590/S1678-3921.pab1990.v25.13728.

MAGALHÃES, P. C.; JONES, R. Aumento de fotoassimilados na taxa de crescimento e peso final dos grãos de milho. **Pesquisa Agropecuária Brasileira**, v. 25, n. 12, p. 1747-1754, 1990b. DOI: https://doi.org/10.1590/S1678-3921.pab1990.v25.13727.

MAGALHÃES, P. C.; DURÃES, F. O. M.; OLIVEIRA, A. C. de. Efeitos do quebramento do colmo no rendimento de grãos de milho. **Ciência e Agrotecnologia**, v. 22, n. 3, p. 279-289, 1998. Available at: https://www.alice.cnptia.embrapa.br/alice/bitstream/doc/482390/1/Efeitosquebramento.pdf. Accessed on: 12 May 2026.

MAGALHÃES, P. C.; DURÃES, F. O. M.; PAIVA, E. **Fisiologia da planta de milho.** Sete Lagoas: Embrapa-CNPMS, 1995. 27 p. (Embrapa-CNPMS. Circular técnica, 20). Available at: https://www.infoteca.cnptia.embrapa.br/infoteca/bitstream/doc/475778/1/circ20.pdf. Accessed on: 12 May 2026.

MAGALHÃES, P. C.; SOUZA, T. C. de; ALBUQUERQUE, P. E. P. de; KARAM, D.; MAGALHÃES, M. M.; CANTAO, F. R. de O. Caracterização ecofisiológica de linhagens de milho submetidas a baixa disponibilidade hídrica durante o florescimento. **Revista Brasileira de Milho e Sorgo**, v. 8, n. 3, p. 223-232, 2009. Available at: https://www.alice.cnptia.embrapa.br/alice/bitstream/doc/657059/1/Caracterizacaoecofisiologica.pdf. Accessed on: 13 May 2026.

MAGALHÃES, P. C.; SOUZA, T. C. de; CANTÃO, F. R. O. Early evaluation of root morphology of maize genotypes under phosphorus deficiency. **Plant, Soil and Environment**, v. 57, n. 3, p. 135-138, 2011. DOI: https://doi.org/10.17221/360/2010-PSE.

MAGALHÃES, P. C.; SOUZA, T. C. de; CANTÃO, F. R. de O.; PADILHA, F. A. Root morphology of maize lines with contrasting drought resistance under three toxic levels of aluminum. **Revista Brasileira de Milho e Sorgo**, v. 11, n. 1, p. 35-48, 2012. Available at: https://www.alice.cnptia.embrapa.br/alice/bitstream/doc/937309/1/Rootmorphology.pdf. Accessed on: 11 May 2026.

MAGALHÃES, P. C.; LAVINSKY, A. O.; MELO, H. F.; ALVES, J. C.; SOUZA, T. C. de; BARBOSA, A. P.; RIBEIRO, C. Relationship between nitric oxide, enzymatic antioxidant system and ABA in maize under long-term drought. **Revista Brasileira de Milho e Sorgo**, v. 14, n. 2, p. 155-166, 2015. Available at: https://www.alice.cnptia.embrapa.br/alice/bitstream/doc/1037172/1/Relationshipbetween.pdf. Accessed on: 10 May 2026.

MAGALHÃES, P. C.; SOUZA, T. C. de; LAVINSKY, A. O.; ALBUQUERQUE, P. E. P. de; OLIVEIRA, L. L. de; CASTRO, E. M. de. Phenotypic plasticity of root system and shoots of Sorghum bicolor under different soil water levels during pre-flowering stage. **Australian Journal of Crop Science**, v. 10, n. 1, p. 81-87, 2016.

MARQUES, D. M.; MAGALHÃES, P. C.; MARRIEL, I. E.; GOMES JÚNIOR, C. C.; SILVA, A. B.; MELO, I. G.; SOUZA, T. C. de. Azospirillum brasilense favors morphophysiological characteristics and nutrient accumulation in maize cultivated under two water regimes. **Revista Brasileira de Milho e Sorgo**, v. 19, e1152, 2020. Available at: https://www.alice.cnptia.embrapa.br/alice/bitstream/doc/1122449/1/Azospirillum-brasilense.pdf. Accessed on: 10 May 2026.

MARQUES, D. M.; MAGALHÃES, P. C.; MARRIEL, I. E.; GOMES JÚNIOR, C. C.; SILVA, A. B. da; SOUZA, T. C. de. Gas exchange, root morphology and nutrients in maize plants inoculated with Azospirillum brasilense cultivated under two water conditions.

Brazilian Archives of Biology and Technology, v. 64, e21190580, 2021. DOI: https://doi.org/10.1590/1678-4324-2021190580.

OLIVEIRA, J. P. V. de; DUARTE, V. P.; CASTRO, E. M. de; MAGALHÃES, P. C.; PEREIRA, F. J. Root cortical aerenchyma in sorghum increases its root elongation and volume, favoring nutrient uptake and gas exchange compared to maize under water limitation. **Journal of Soil Science and Plant Nutrition**, v. 26, p. 2742-2756, 2026. DOI: https://doi.org/10.1007/s42729-026-03029-7.

OLIVEIRA, J. P. V. de; DUARTE, V. P.; CASTRO, E. M. de; MAGALHÃES, P. C.; PEREIRA, F. J. Whole shoot gas exchange and stomatal traits in maize under water drought as related to its growth. **Agricultural Engineering International: CIGR Journal**, v. 27, n. 1, p. 1-13, 2025. Available at: https://www.alice.cnptia.embrapa.br/alice/bitstream/doc/1179121/1/Whole-shoot-gas-exchange-and-stomatal-traits-in-maize.pdf. Accessed on: 11 May 2026.

PAIVA, A. P. L. de; MAGALHÃES, P. C.; CARVALHO, L. P. de; JALES, H. F.; GOMES JÚNIOR, C. C.; LANA, U. G. de P.; MARRIEL, I. E. Azospirillum brasilense inoculation combined with different levels of nitrogen fertilization and its effects in the grain sorghum subjected to water restriction. **Revista Brasileira de Milho e Sorgo**, v. 20, e1215, 2021. Available at: https://www.alice.cnptia.embrapa.br/alice/bitstream/doc/1138739/1/Azospirillum-brasilense.pdf. Accessed on: 11 May 2026.

PARENTONI, S. N.; GAMA, E. E. G. e; LOPEZ, M. A.; SANTOS, M. X.; GUIMARÃES, P. E. O.; PACHECO, C. A. P.; CORREA, L. A.; SOUZA, I. R. P. de; MEIRELES, W. Seleção para la tolerância ao encharcamento na variedade de milho CMS54 - Saracura. In: REUNION LATINOAMERICANA, 4.; REUNION DE LA ZONA ANDINA DE INVESTIGADORES EN MAIZ, 17., 1997, Cartagena de Indias. **Memoria** [...]. [S.l.: s.n.], 1997. p. 368-373. Available at: https://www.alice.cnptia.embrapa.br/alice/bitstream/doc/480312/1/Selecaotolerancia1.pdf. Accessed on: 13 May 2026.

PEREIRA, F. J.; MAGALHÃES, P. C.; SOUZA, T. C. de; CASTRO, E. M. de; ALVES, J. D. Atividade do sistema antioxidante e desenvolvimento de aerênquima em raízes de milho ‘Saracura’. **Pesquisa Agropecuária Brasileira**, v. 45, n. 5, p. 450-456, 2010. DOI: https://doi.org/10.1590/S0100-204X2010000500003.

PORTO, B. N.; ALVES, J. D.; MAGALHÃES, P. C.; CASTRO, E. M.; CAMPOS, N. A.; SOUZA, K. R. D.; MAGALHÃES, M. M.; ANDRADE, C. A.; SANTOS, M. O. Calcium-dependent tolerant response of cell wall in maize mesocotyl under flooding stress. **Journal of Agronomy and Crop Science**, v. 199, n. 2, p. 134-143, 2013. DOI: https://doi.org/10.1111/j.1439-037X.2012.00535.x.

PORTUGAL, J. A. de N.; AMBRÓSIO, A. dos S.; SOUZA, K. R. D. de; DIAS, D. F.; SANTOS FILHO, P. R. dos; SOUZA, T. B. de; SANTOS, M. H. dos; DORIGUETO, A. C.; MAGALHÃES, P. C.; SOUZA, T. C. de. A mixture of trehalose derivatives stimulates the antioxidant system and improves photosynthetic efficiency in maize underwater deficit. **Acta Physiologiae Plantarum**, v. 43, art. 83, 2021. DOI: https://doi.org/10.1007/s11738-021-03255-9.

RABELO, V. M.; MAGALHÃES, P. C.; BRESSAIN, L. A.; CARVALHO, D. T.; REIS, C. O. dos; KARAM, D.; DORIGUETTO, A. C.; SANTOS, M. H. dos; SANTOS FILHO, P. R.; SOUZA, T. C. The foliar application of a mixture of semisynthetic chitosan derivatives induces tolerance to water deficit in maize, improving the antioxidant system and increasing photosynthesis and grain yield. **Scientific Reports**, v. 9, n. 1, art. 8164, 2019. DOI: https://doi.org/10.1038/s41598-019-44649-7.

RAFAEL, D. D.; MARQUES, D. M.; SOUZA, I. R. P. de; MAGALHÃES, P. C.; ANDRADE, C. de L. T. de; MARRIEL, I. E.; SANTOS, T. T.; SIMEONE, M. L. F.; SOUZA, T. C. de. Bacillus co-inoculation improves the stomatal conductance, root angulation, and harvest index of maize under water deficit in a line-source irrigation system. **Journal of Plant Growth Regulation**, v. 45, p. 3124-3127, 2026. DOI: https://doi.org/10.1007/s00344-026-12057-7.

REIS, C. O. dos; MAGALHÃES, P. C.; AVILA, R. G.; ALMEIDA, L. G.; RABELO, V. M.; CARVALHO, D. T.; CABRAL, D. F.; KARAM, D.; SOUZA, T. C. de. Action of N-succinyl and N,O-dicarboxymethyl chitosan derivatives on chlorophyll photosynthesis and fluorescence in drought-sensitive maize. **Journal of Plant Growth Regulation**, v. 38, n. 2, p. 619-630, 2019. DOI: https://doi.org/10.1007/s00344-018-9877-9.

ROMERO, J. L.; MAGALHÃES, P. C.; ALVES, J. D.; DURÃES, F. O. M.; VASCONCELLOS, C. A. Efeito do cálcio sobre algumas características biofísicas e morfológicas de plantas de milho BRS-4154 submetidas ao alagamento do solo. **Revista Brasileira de Milho e Sorgo**, v. 2, n. 3, p. 21-33, set./dez. 2003. Available at: https://www.alice.cnptia.embrapa.br/alice/bitstream/doc/486675/1/Efeitocalcio.pdf. Accessed on: 12 May 2026.

SILVA, L. D. da; PENHA, N. C. da; SILVA, A. C. C. da; SILVEIRA, N. M.; MAGALHÃES, P. C.; SANTOS, B. R.; SOUZA, T. C. de; MARQUES, D. M.; SANTOS FILHO, P. R. dos. Can the application of exogenous nitric oxide (s-nitrosoglutathione¿gsno) confer tolerance to water deficit in maize plants? **Russian Journal of Plant Physiology**, v. 72, art. 106, 2025. DOI: https://doi.org/10.1134/S1021443724609522.

SIQUEIRA, J. A.; BARROS, J. A. S.; DAL-BIANCO, M.; MARTINS, S. C. V.; MAGALHÃES, P. C.; RIBEIRO, D. M.; DAMATTA, F. M.; ARAÚJO, W. L.; RIBEIRO, C. Metabolic and physiological adjustments of maize leaves in response to aluminum stress. **Theoretical and Experimental Plant Physiology**, v. 32, p. 133-145, 2020. DOI: https://doi.org/10.1007/s40626-020-00175-w.

SOUZA, T. C. de; CASTRO, E. M. de; PEREIRA, F. J.; PARENTONI, S. N.; MAGALHÃES, P. C. Morpho-anatomical characterization of root in recurrent selection cycles for flood tolerance of maize (Zea mays L.). **Plant, Soil and Environment**, v. 55, n. 11, p. 504-510, 2009. DOI: https://doi.org/10.17221/110/2009-PSE.

SOUZA, K. R. D.; ALVES, J. D.; SANTOS, M. O.; CAMPOS, N. A.; SILVEIRA, H. R. O.; PORTO, B. N.; CARVALHO, M. C.; ANDRADE, C. A.; NASCIMENTO, P. H. C. Atividade das enzimas antioxidantes em raízes de plântulas do milho Saracura BRS-4154 e a tolerância ao alagamento. In: CONGRESSO NACIONAL DE MILHO E SORGO, 28.; SIMPÓSIO BRASILEIRO SOBRE A LAGARTA DO CARTUCHO, 4., 2010, Goiânia. **Resumos expandidos** [...]. Sete Lagoas: Associação Brasileira de Milho e Sorgo, 2010a. Tema: Potencialidades, desafios e sustentabilidade.

SOUZA, T. C. de; CASTRO, E. M. de; MAGALHÃES, P. C.; LINO, L. de O.; ALVES, E. T.; ALBUQUERQUE, P. E. P. de. Morphophysiology, morphoanatomy, and grain yield under field conditions for two maize hybrids with contrasting response to drought stress. **Acta Physiologiae Plantarum**, v. 35, p. 3201-3211, 2013a. DOI: https://doi.org/10.1007/s11738-013-1355-1.

SOUZA, T. C. de; MAGALHÃES, P. C.; CASTRO, E. M. de; CARNEIRO, N. P.; PADILHA, F. A.; GOMES JÚNIOR, C. C. ABA application to maize hybrids contrasting for drought tolerance: changes in water parameters and in antioxidant enzyme activity. **Plant Growth Regulation**, v. 73, p. 205-217, 2014. DOI: https://doi.org/10.1007/s10725-013-9881-9.

SOUZA, T. C. de; MAGALHÃES, P. C.; PEREIRA, F. J.; CASTRO, E. M. de; SILVA JÚNIOR, J. M. da; PARENTONI, S. N. Leaf plasticity in successive selection cycles of ‘Saracura’ maize in response to periodic soil flooding. **Pesquisa Agropecuária Brasileira**, v. 45, n. 1, p. 16-24, 2010b. DOI: https://doi.org/10.1590/S0100-204X2010000100003.

SOUZA, T. C. de; MAGALHÃES, P. C.; PEREIRA, F. J.; CASTRO, E. M. de; PARENTONI, S. N. Morpho-physiology and maize grain yield under periodic soil flooding in successive selection cycles. **Acta Physiologiae Plantarum**, v. 33, p. 1877-1885, 2011. DOI: https://doi.org/10.1007/s11738-011-0731-y.

SOUZA, T. C. de; MAGALHÃES, P. C.; CASTRO, E. M. de; ALBUQUERQUE, P. E. P. de; MARABESI, M. A. The influence of ABA on water relations, photosynthesis parameters, and chlorophyll fluorescence under drought conditions in two maize hybrids with contrasting drought resistance. **Acta Physiologiae Plantarum**, v. 35, p. 515-527, 2013b. DOI: https://doi.org/10.1007/s11738-012-1093-9.

SOUZA, T. C. de; MAGALHÃES, P. C.; CASTRO, E. M.; DUARTE, V. P.; LAVINSKY, A. O. Corn root morphoanatomy at different development stages and yield under water stress. **Pesquisa Agropecuária Brasileira**, v. 51, n. 4, p. 330-339, 2016. DOI: https://doi.org/10.1590/S0100-204X2016000400005.

VERONEZE-JÚNIOR, V.; MARTINS, M.; LEOD, L. M.; SOUZA, K. R. D.; SANTOS FILHO, P. R.; MAGALHÃES, P. C.; SOUZA, T. C. Leaf application of chitosan and physiological evaluation of maize hybrids contrasting for drought tolerance under water restriction. **Brazilian Journal of Biology**, v. 80, n. 3, p. 631-640, 2019. DOI: https://doi.org/10.1590/1519-6984.218391.

VITORINO, P. F. P. G.; ALVES, J. D.; MAGALHÃES, P. C.; MAGALHÃES, M. M.; LIMA, L. C. O.; OLIVEIRA, L. E. M. de. Flooding tolerance and cell wall alterations in maize mesocotyl during hypoxia. **Pesquisa Agropecuária Brasileira**, v. 36, n. 8, p. 1027-1035, 2001. DOI: https://doi.org/10.1590/S1678-3921.pab2001.v36.6226.