



Eco-Genomic Alchemy: The Crucial Intersections of *Brachypodium*, Agriculture, and Climate Dynamics

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Abstract

Brachypodium species, particularly *B. distachyon*, *B. hybridum*, and *B. stacei*, have rapidly become valuable models in plant research, providing important insights into the genetics, physiology, and ecology of grasses. This review examines the multifaceted importance of these species, highlighting their central role in understanding cereal crop relatives and delving into their adaptability to a range of abiotic stresses, particularly in the context of climate change mitigation. Given the increasing threat of unpredictable weather patterns and global food security, the genetic reservoir and adaptability of *Brachypodium* species offer promising opportunities for sustainable agricultural innovation. Moreover, it is emphasized that maintaining their genetic diversity is critical, not only for continuity of research, but also for the potential ecological and economic benefits they offer. As we move through the complexities of the Anthropocene, *Brachypodium* is a testament to the complex interplay of genetics, environment, and human endeavor, and calls for a collaborative approach to harness its full potential for future agricultural resilience and sustainability.

1. INTRODUCTION

In a rapidly changing world where the challenges of climate change, food security, and biodiversity loss intersect, our focus on understanding and harnessing nature's genetic reserves has increased (Muluneh, 2021; Shahzad et al., 2021). Against this backdrop, the genus *Brachypodium*, particularly *Brachypodium distachyon*, is emerging as a key player in plant research that promises insights into the future of sustainable agriculture (Mahood et al., 2023).

Brachypodium distachyon, colloquially known as purple false brome, is an annual grass native to the Mediterranean region. Its characteristics, including a sequenced and compact genome with very small number of chromosomes ($n = 5$; $2n = 10$), make it an ideal model for complicated genetic studies (Catalan et al., 2014). In addition to its genetic utility, the species also offers practical advantages such as a short life cycle and ease of transformation, underpinning its popularity in the research community (Mahood et al., 2023). Most compelling, however, is its

close genetic and physiological relationship with important temperate grasses such as wheat, barley, and oats, paving the way for breakthroughs in cereal crop biology and breeding (Catalan et al., 2014; Gordon et al., 2020).

Based on cytogenetic analyses, *B. distachyon* was divided into a series of cytotypes with diploid chromosome numbers of $2n = 10$, $2n = 20$ and $2n = 30$, forming an autopolyploid series with a basic chromosome number of $x = 5$. However, recently, the combination of phenotypic, cytogenetic and various molecular approaches, including genomic DNA and BAC-based probes in fluorescence in situ hybridization (FISH) analyses provided clear evidence that these cytotypes represent distinct species. *B. distachyon* ($2n = 10$), *B. stacei* ($2n = 20$) are two diploid species while *B. hybridum* is an allotetraploid species ($2n = 30$) deriving from their natural hybridization (Catalán et al., 2012). While *B. hybridum* is fascinating for its hybrid genetic ancestry, *B. stacei* offers evolutionary insights that reveal the rich biodiversity and

adaptive potential of the genus (López-Alvarez et al., 2015). In *B. hybridum*, Scarlett et al. (2023) suggested that evolutionary innovations are driven by relaxed selection rather than sudden genomic shocks and the similarity in the content of transposable elements between its two progenitors could explain the observed nuanced genome dominance. Taken together, this trio of *Brachypodium* not only describes a story of genetic diversity and adaptability, but also provides a glimpse of the innovative ways that modern agriculture can respond to planetary challenges (Tyler et al., 2014).

Throughout this review, we dive deeper into the multifaceted world of *Brachypodium* and understand its role in shaping the future of an agriculture that is resilient, innovative and in tune with our changing planet.

2. TAXONOMY AND GEOGRAPHICAL DISTRIBUTION

The genus *Brachypodium*, which belongs to the family of *Poaceae*, is a focal point in plant research, especially with regard to the relatives of cereal crop relatives. In fact, *Brachypodium* is characterized by its close phylogenetic relationship with the major crops in the world, such as the rice (*Oryza sativa*), wheat (*Triticum aestivum*) and barley (*Hordeum vulgare*) (Mahood et al., 2023). Within this genus, three species stand out: *B. distachyon*, *B. hybridum*, and *B. stacei*. *B. distachyon* is native to the Mediterranean region and thrives primarily in the cooler climates of the northern Mediterranean and parts of western Asia. Its habitats are diverse, ranging from forest clearings to open grasslands to disturbed areas along roadsides (Vogel, 2015). Interestingly, its adaptability to different habitats has stimulated research on its potential as a pioneer species in disturbed or changing ecosystems. *B. stacei* is rather localized and occurs predominantly in the Iberian Peninsula, representing the western Mediterranean regions. It generally prefers sandy and rocky substrates, often in drier and warmer microhabitats than *B. distachyon* (López-Alvarez et al., 2015). The history of *B. hybridum* is intriguing as it bridges the geographic ranges of its ancestors *B. distachyon* and *B. stacei*. Its occurrence in both the Iberian Peninsula and regions extending eastward is likely a testament to the hybrid's vigor and adaptability, allowing it to colonize a wider range of habitats than either parent alone (Catalan et al., 2014). While these species have historically been restricted to their native

regions, there have been isolated reports indicating potential invasive trends, particularly for *B. distachyon* (López-Alvarez et al., 2015). Some reports from North America and other non-native regions suggest that the species is capable of establishing in new ecosystems, although a comprehensive study of its spread and ecological impacts is still pending (Scholthof et al., 2018).

Future climate projections characterized by increasing temperatures, changing precipitation patterns, and increasing frequency of extreme events could lead to a shift in the range of these species (Budescu et al., 2014). *B. distachyon*, with its inherent adaptability, could take advantage of new habitats created by climate-related disturbances, potentially expanding northward or to higher elevations (Bevan et al., 2010). Similarly, the drought tolerance of *B. stacei* could give it an advantage under increasingly arid conditions and lead to its spread in areas of water scarcity (López-Alvarez et al., 2015). *B. hybridum* may have greater ecological flexibility due to its hybrid vigor and adapt to a wider range of altered habitats (Catalan et al., 2015).

3. THE EVOLVING MAP: GENETIC STRUCTURE AND FUTURE HABITATS OF KEY BRACHYPODIUM SPECIES

The *Brachypodium* genus, predominantly represented by *B. distachyon*, *B. hybridum*, and *B. stacei*, offers a unique window into the intricate world of grass genetics (Hasterok et al., 2022). Their genetic makeup, a blend of resilience and adaptability, provides insights not only into their current distribution but also into potential habitats they might colonize under changing environmental conditions (Vogel, 2015). Recent advances in genetic mapping have deepened our understanding of the genetic structures of these species. Molecular markers, from SSRs to SNPs, have revealed the nuances of genetic diversity and differentiation within and among these species, highlighting their evolutionary histories and adaptive strategies (Neji et al., 2015, 2022). This genetic blueprint, when interpreted against the backdrop of their native habitats, displays their potential adaptability to environmental gradients, both current and future. Climate change, characterized by global temperature rises and erratic precipitation patterns, presents challenges and opportunities for plant species (Pachauri et al., 2014). Given the adaptive genetic diversity observed in the *Brachypodium* species, particularly in *B. distachyon*, it is plausible to speculate potential

habitat shifts in response to climatic alterations (López-Alvarez et al., 2015). While *B. stacei* with its drought-resilient genetics might find favor in arid regions exacerbated by global warming, *B. hybridum*, due to its hybrid vigor, could emerge as a versatile colonizer across varied landscapes (Catalan et al., 2015). Predictive models, coupling genetic data with climatic scenarios, can provide more precise insights into potential range shifts. However, irrespective of the predictive model, one thing remains clear: the genetic structures of these species will play a pivotal role in shaping their response to our planet's changing tapestry.

4. ADAPTIVE ARSENAL: MORPHOLOGICAL, PHYSIOLOGICAL, AND MOLECULAR CAPABILITIES OF *BRACHYPODIUM* IN THE FACE OF CLIMATE CHANGE

As climate change continues to alter the world's ecosystems, the adaptive capacity of species is of paramount importance. In the genus *Brachypodium*, this adaptability manifests itself through an interplay of morphological, physiological, and molecular mechanisms.

4.1. Drought resistance

Brachypodium species have evolved adaptive mechanisms to combat the drought conditions prevalent in their native habitats. In response to drought stress, *Brachypodium* species exhibit a range of morphological and physiological changes to reduce water loss and maximize water uptake. Morphologically, changes in root architecture are conspicuous, with these plants developing deeper and more extensive root systems. This strategic growth allows them to access water from deeper soil layers, which is beneficial during prolonged drought (Priest et al., 2014). While *B. distachyon* tends to deepen its root system to tap underground water sources, *B. stacei* adapts by increasing its lateral root spread to optimize water uptake from the immediate subsoil (Mayer & Charron, 2021). *B. hybridum*, which exhibits a mixture of traits from its parent species, shows a mixed strategy of root deepening and lateral propagation, depending on the severity and duration of drought stress (Martínez et al., 2018). In addition to root changes, changes in leaf morphology are also observed. Reduced leaf area and increased leaf thickness serve to reduce the surface area exposed to transpiration, effectively storing water in plant tissues. Physiologically, these species increase their osmotic adaptive capabilities. By accumulating solutes, they

maintain cell tension even under conditions of water-deficit conditions, ensuring that vital metabolic processes continue unabated. This osmotic adjustment is complemented by increased synthesis of abscisic acid (ABA), a key phytohormone. In *Brachypodium*, the importance of ABA is particularly evident when drought conditions increase. As a key phytohormone, ABA serves as a sentinel that monitors water status in the plant. As water availability decreases, the level of ABA increases, triggering a cascade of physiological responses aimed at water conservation (Julkowska, 2020). One of the most immediate and important of these responses is the regulation of stomatal opening. ABA-induced stomatal closure reduces transpirational water loss, ensuring that vital moisture is retained within the plant's cellular structures. This stomatal regulation is mediated by complicated signaling pathways involving ABA receptors, ion channels, and second messengers that collectively control the stomatal response (Hsu et al., 2021). In addition to leaves, ABA also exerts its influence underground. It plays a central role in regulating root growth and root function of *Brachypodium* under drought stress. Research has shown how ABA improves root hydraulic conductivity and optimizes water uptake from the soil even under low moisture conditions (Julkowska, 2020). In addition, signals from ABA promote the development of deeper root systems that allow the plant to tap into moisture reserves in deeper soil layers (Duan et al., 2016). The synergy of these responses mediated by ABA provides *Brachypodium* species with the resilience needed to overcome the challenges of water scarcity and highlights the hormone's central role in plant adaptation to drought.

At the molecular level, the *Brachypodium* genome provides a treasure trove of adaptive mechanisms. Recent transcriptomic studies have revealed a few drought-responsive genes that are upregulated during water stress (More et al., 2023). Most notably, these include genes encoding dehydrins, which stabilize cell membranes, and aquaporins, which control cellular water transport (Neji et al., 2015). Furthermore, research has shown that certain microRNAs in *Brachypodium* play a critical role in post-transcriptional regulation during drought and ensure a rapid and efficient response to water stress (Zhang et al., 2018).

Brachypodium species activate a variety of molecular signaling pathways to address water deficits at the cellular and systemic levels. At the

forefront is the modulation of gene expression, with several drought-responsive genes being upregulated upon water stress (More et al., 2023). These genes often encode proteins that either directly mitigate the effects of drought or regulate downstream response pathways. For instance, the expression of genes encoding dehydrins, a group of hydrophilic proteins, increases under drought. Dehydrins play a pivotal role in protecting cell structures and enzymes from damage caused by dehydration (Kandhol et al., 2022). In addition, aquaporins, which are central to cellular water transport, undergo changes in their expression that allow the plant to fine-tune its internal water dynamics in response to external moisture content (Neji et al., 2015, 2021). *B. distachyon*, with its well-characterized genome, exhibits upregulation of genes encoding dehydrins, aquaporins, and several transcription factors that respond to drought (Zhang et al., 2018). Another important player in the molecular response of *Brachypodium* to drought is the synthesis and signaling of the phytohormone abscisic acid (ABA). Upon water stress, the biosynthesis of ABA is upregulated, leading to its accumulation in plant tissues. ABA then binds to its receptors, PYR/PYL/RCAR family proteins, initiating a cascade that ultimately leads to the expression of ABA-dependent genes (Yoshida et al., 2021). This intricate signaling network contributes to stomatal regulation, modulation of root growth, and activation of genes related to osmotic adjustment. In addition, post-transcriptional and post-translational modifications in *Brachypodium* provide a rapid response under drought conditions. MicroRNAs, small noncoding RNA molecules, have been found to play a role in modulating the expression of drought-responsive genes, adding another level of regulation to the plant's response to drought (More et al., 2023). According to Abdul Aziz et al., (2021), *B. stacei*, although less studied, has shown evidence of unique drought-responsive microRNAs that post-transcriptionally modulate key genes involved in drought response. On the other hand, *B. hybridum*, benefiting from the genetic input of its ancestors, displays a broad repertoire of the two molecular strategies, providing it with a versatile toolkit to cope with drought stress (Chen et al., 2020). Taken together, these molecular strategies enable *Brachypodium* species to skillfully cope with the challenges of water scarcity and offer insights into the mechanisms of drought resistance in plants.

4.2. Tolerance to salinity

Salinity poses a dual challenge to plants, inflicting osmotic stress and ion toxicity. *Brachypodium* species, hailing from diverse habitats, including coastal zones, have evolved a variety of mechanisms to tolerate high salinity levels. The three species display distinct morphological changes tailored to their unique evolutionary histories and habitats. In *B. distachyon*, there is an evident reduction in the leaf surface area under salt stress, likely a means to diminish the transpirational water loss. Additionally, the leaves tend to adopt a thicker morphology, possibly as a strategy to conserve water under high-salt conditions (Álvarez et al., 2023). Its root system, too, undergoes noticeable changes. Rather than extensive elongation, roots of *B. distachyon* become denser and more compact, likely optimizing for water absorption while evading saline soil zones (Lehman et al., 2023; Meng et al., 2022). *B. stacei*, native to habitats that might have periodic salt influxes, has developed its own set of morphological strategies. Observations suggest a more pronounced succulence in its leaves under saline conditions compared to *B. distachyon*. This succulence is not just a feature to conserve water but might also play a role in storing excess salts, preventing them from causing cellular damage (Lei et al., 2023). The root morphology in *B. stacei* is particularly adaptive; studies have noted a more branched root system, possibly enhancing its ability to tap into non-saline pockets in the soil (López-Alvarez et al., 2015). *B. hybridum*, representing the evolutionary lineage of its parental species, reveals an intriguing mix of morphological responses. Its leaf adaptation to salinity seems intermediate, with moderate reductions in size and subtle thickening, echoing the strategies of both *B. distachyon* and *B. stacei* (Catalan et al., 2015). The root system of *B. hybridum* is flexible, with its depth and density likely modulating based on the salinity gradient and duration of exposure, representing a best-of-both-worlds adaptation (Meng et al., 2022). Moreover, *Brachypodium* species have developed distinctive physiological tactics to combat salinity. *B. distachyon* has fine-tuned its internal environment to resist saline stress. It actively accumulates specific osmolytes like proline and sugars. These not only counteract the osmotic stress but also act as a shield against oxidative damage induced by salt stress; ensuring cellular metabolic activities continue seamlessly (Arif et al., 2020). Furthermore, its advanced ion regulatory system stands out. *B.*

distachyon is known to employ specialized ion transporters that masterfully regulate sodium and potassium balance, prioritizing potassium uptake, thereby sustaining vital cellular processes under salt stress (Hirayama & Shinozaki, 2010). Native habitats of *B. stacei*, subjected to periodic salinity spikes, have carved its unique salt-adaptive profile. One of its hallmarks is the accumulation of betaines. These compounds, beyond their osmoprotective roles, are crucial in defending cellular machinery, especially proteins and enzymes, from salt-induced perturbations (Waditee-Sirisattha et al., 2012). Additionally, *B. stacei* has a well-orchestrated mechanism to manage excess sodium ions, shunting them to vacuoles, which ensures optimal sodium concentrations in the cytoplasm and protects the cell from potential ionic imbalances (Garcia deblás et al., 2003). The interspecies dynamism of *B. hybridum* is evident in its salinity response. Drawing from the strengths of its progenitor species, it displays a versatile osmotic adjustment strategy, amassing both proline and betaines, equipping it to deal with diverse saline conditions (Shiposha et al., 2020).

At the molecular helm of salinity responses in *Brachypodium*, intricate gene networks and regulatory cascades orchestrate adaptations. In *B. distachyon*, genomic and transcriptomic explorations have unveiled a rich tapestry of genes tailored to counteract saline stress. These include those implicated in ion transport, like the HKT (High-affinity K⁺ transporter) family, which mediate sodium and potassium fluxes to optimize cellular ion balance under saline conditions (Abdul Aziz et al., 2021). Of particular significance is the SOS (Salt Overly Sensitive) pathway, which is integral to sodium ion homeostasis. Genes within this pathway, such as SOS1, SOS2, and SOS3, coordinate to manage sodium levels, ensuring its sequestration or expulsion and thus safeguarding cellular functions (Wu, 2018). Delving deeper into *B. distachyon*'s transcriptomic landscape, microRNAs have emerged as key players in the salinity response. These tiny RNA molecules modulate gene expression post-transcriptionally, fine-tuning the plant's reaction to salt stress, with miR169 and miR393 being notable examples in this context (Barrera-Figueroa et al., 2012). *B. stacei*, despite sharing a common lineage with *B. distachyon*, manifests a nuanced molecular repertoire in confronting salinity. Genes distinct from *B. distachyon* have been identified as salinity-responsive in this

species, suggesting unique or specialized pathways might be at play (Garcia Molina et al., 2021). Recent research has also indicated a different set of microRNAs in *B. stacei* that are differentially regulated under salt stress, suggesting that while the overarching salinity response mechanisms might be conserved, the details could vary, allowing for species-specific adaptability (Garcia Molina et al., 2021). The hybrid species, *B. hybridum*, provides a compelling narrative at the molecular level. Drawing genes from both *B. distachyon* and *B. stacei*, it harnesses a versatile molecular toolkit to tackle salinity. It not only expresses shared salt-responsive genes from its parents but also has been observed to activate specific genes that are dormant in either parent under non-stress conditions. This genetic malleability might confer *B. hybridum* an edge in responding swiftly and robustly to salinity variations (Chen et al., 2020).

4.3. Response to cold

Cold stress prompts an array of adaptations in plants, and the *Brachypodium* species, given their temperate origins, are no exception. Morphologically, in response to cold, *B. distachyon* plants have been observed to exhibit a more compact growth habit with reduced internodal lengths. This could be a strategy to minimize exposure to chilling winds and conserve energy (Ream et al., 2014). The leaves often appear thicker, perhaps to reduce transpirational loss in cold conditions and to insulate internal cellular machinery. Physiologically, *B. distachyon* shows an enhancement in antioxidant enzyme activities, like superoxide dismutase and peroxidase, which act as a defense against the oxidative stress that cold often induces (Catalán et al., 2012). Cold stress can also lead to cellular dehydration, and osmotic adjustment via the accumulation of solutes such as proline is a common adaptive response, aiding in water retention and cellular protection. At the molecular level, the cold response is quite intricate. Transcriptomic studies have revealed that hundreds of genes are differentially regulated in *B. distachyon* under cold stress. Many of these genes are associated with signal transduction, transcriptional regulation, and metabolic adjustments, underscoring the profound cellular reprogramming that occurs under cold stress (Dasgupta et al., 2020). Cold-responsive (COR) genes and certain transcription factors like CBF (C-repeat binding factors) have been identified

as pivotal players in the cold response, orchestrating a range of downstream genes to confer cold tolerance (Peng et al., 2020). For *B. stacei*, detailed investigations into cold responses are somewhat limited compared to *B. distachyon*. However, preliminary observations suggest it tends to have a slightly reduced cold tolerance relative to *B. distachyon*. This might be attributed to its habitat preference, which leans towards slightly warmer niches compared to its counterpart (Minadakis et al., 2023). *B. hybridum*, owing to its hybrid nature, is believed to harness cold-response traits from both parental species. Preliminary observations suggest that it possesses an intermediate cold tolerance between *B. distachyon* and *B. stacei*. Given its hybrid nature, it is conceivable that *B. hybridum* could leverage a broader genetic toolkit to respond to cold, but detailed studies elucidating its specific cold-response mechanisms are awaited.

4.4. Nutrient deficiency

In the evolving backdrop of climate change, nutrient dynamics in soils are anticipated to undergo significant shifts. Rising global temperatures and altered precipitation patterns could profoundly affect soil nutrient cycling and community structures (Peng et al., 2020). Such changes might exacerbate nutrient imbalances, challenging plant uptake. Concurrently, elevated carbon dioxide levels, while boosting photosynthesis, may reduce plant nutritional quality due to potential nutrient dilution, underscoring the importance of understanding plant responses to nutrient deficits (Shikha et al., 2023). *B. distachyon*, under nutrient-poor conditions, often curtails its growth, adopting a more diminutive stature with smaller leaves as a possible energy and nutrient conservation strategy (Gordon et al., 2020). Physiologically, it responds to nitrogen deficiency by diminishing its chlorophyll content and to phosphorus scarcity by increasing root hair density, aiming to optimize nutrient absorption (Martínez-Peña et al., 2023; Neji et al., 2021). On the genomic front, an upregulation of genes like NRTs for nitrogen and PHTs for phosphorus is noticeable, with molecular pathways, including those steered by microRNAs, playing pivotal roles in nutrient management (Marro et al., 2022). *B. stacei*'s responses to nutrient stress, while less documented, seem to resonate with *B. distachyon*. Morphologically, it is suggested to conserve growth under limited nutrient availability. Enhanced lateral root development

under phosphorus-deficient scenarios has been posited, drawing parallels with other *Brachypodium* species (López-Alvarez et al., 2015). The molecular intricacies of its nutrient response remain largely enigmatic but are believed to mirror patterns seen in other *Brachypodium* members. The hybrid, *B. hybridum*, is theorized to incorporate nutrient response strategies from both *B. distachyon* and *B. stacei*. Its physiological adaptations suggest a nimble resource reallocation under nutrient stress, echoing findings from studies on other *Brachypodium* species (Neji et al., 2021). Genomically, it is plausible that *B. hybridum* leverages an expansive genetic toolkit inherited from its parents', though more detailed investigations are warranted.

4.5. Response to other abiotic challenges

As climate change progresses, *Brachypodium* species are poised to confront a myriad of heightened abiotic stressors, including heat, oxidative stress, and erratic water availability. Addressing these challenges demands complex adaptive strategies that span across morphological, physiological, and molecular dimensions. In response to rising temperatures, *B. distachyon* has displayed alterations in flowering time, potentially a strategy to bypass peak heat periods (Woods et al., 2020). Accompanying these phenological changes are morphological adaptations, such as reduced leaf size, acting as a countermeasure to minimize transpirational losses during warmer periods. Concurrently, the onslaught of oxidative stress, a common companion to heat or elevated UV radiation, triggers a robust physiological defense in *B. distachyon*. Notably, there is an accentuated synthesis of antioxidant enzymes, such as catalase and superoxide dismutase, serving as cellular shields against the detrimental reactive oxygen species (ROS) (Dinakar et al., 2016). At the heart of these responses lies a complex molecular network. Genes encoding heat shock proteins (HSPs) are notably upregulated, playing a sentinel role in protein protection and repair under thermal stress conditions (Waters & Vierling, 2020). *B. stacei*, given its inclination for slightly warmer habitats compared to *B. distachyon*, might innately harbor a modicum of heat tolerance. Anticipated physiological countermeasures encompass strategies such as osmolyte accumulation and the ramped-up synthesis of antioxidant enzymes, both aiming to counteract heat-induced cellular perturbations. While comprehensive studies on *B. stacei*'s

oxidative stress response are awaited, initial assessments suggest a potent ROS-scavenging system, potentially drawing parallels with other *Brachypodium* members in its approach (López-Alvarez et al., 2015). In the realm of hybrid vigor, *B. hybridum* stands poised to meld the resilience traits of its parent species. Potentially manifesting intermediate heat responses, it might combine altered phenological cues with physiological shifts, like heightened osmolyte production. Facing oxidative challenges, *B. hybridum* is likely to bolster its antioxidant defense machinery, orchestrating a symphony of enzymes to neutralize ROS. Molecularly, there's a tantalizing prospect that *B. hybridum* leverages an expansive genetic toolkit inherited from both its progenitors, although exhaustive studies are imperative to substantiate this notion (Neji et al., 2021).

5. THE *BRACHYPODIUM* MODEL: A GENETIC GOLDMINE FOR CLIMATE RESILIENCE

Brachypodium, as a genus, stands out as an exceptional model for studying grass genetics, bearing profound implications for understanding and developing climate-resilient crops. Key species, including *B. distachyon*, *B. stacei*, and *B. hybridum*, collectively offer a wealth of genetic information that encompasses a spectrum of environmental adaptations. The genome of *B. distachyon*, sequenced in 2010, bridged many genetic gaps between significant cereal crops and model plant systems (Hasterok et al., 2022b). Native to the cooler climates of the Mediterranean and parts of Western Asia, it provides valuable genetic insights into traits like cold tolerance, drought resistance, and nutrient uptake mechanisms. In contrast, *B. stacei*, thriving in the warmer and drier parts of the Iberian Peninsula, presents genetic adaptations for heat and drought tolerance, due to its penchant for sandy and rocky substrates in these warm microhabitats (López-Alvarez et al., 2015). *B. hybridum*, a genetic melding of *B. distachyon* and *B. stacei*, is found across diverse habitats, suggesting its genetic toolkit is broad, possibly encompassing the adaptive strengths of both its parent species (Shiposha et al., 2020). As a hybrid, it stands as a testament to the potential of combining genetic assets to endure a variety of environmental conditions. Given the rapidly changing climate, the genetic resources harbored within these *Brachypodium* species are invaluable. Delving into their genomes can unravel a host of adaptive genes and pathways, which, when understood, can inform strategies

to fortify cereal crops against current and looming environmental challenges.

6. TRANSLATIONAL GENOMICS: BRIDGING *BRACHYPODIUM* INSIGHTS TO MAJOR CEREALS

The *Brachypodium* genus, notably *B. distachyon*, has positioned itself as an illuminating genomic model for grasses, casting valuable insights that resonate with the genomics of principal cereal crops. Recognizing the genetic congruence and conserved molecular mechanisms between *Brachypodium* and staple cereals such as wheat, barley, and rice is enabling a renaissance in the sphere of translational genomics. As early as the completion of the *B. distachyon* genome in 2010, its potential as a proxy for temperate cereals became evident (Hasterok et al., 2022). Its streamlined genome, bearing resemblances to those of wheat and barley, serves as a more manageable scaffold for understanding intricate traits from biotic resistance to grain morphology (Gordon et al., 2020). Comparative genomic initiatives, aligning the genomic landscapes of rice, *Brachypodium*, and wheat, have spotlighted conserved genomic regions that underpin essential agronomic traits, setting the stage for expedited trait improvement in these staple crops (Hirai et al., 2019). Insights into plant-pathogen dynamics, crucial for cereal crop protection, have been enriched by *Brachypodium* studies. Its interactions with formidable foes like *Magnaporthe oryzae*, a concern for various grains, offers a window into potential cereal defense mechanisms (Peraldi et al., 2011). With the advent of advanced genetic tools, from CRISPR-Cas systems to vast mutant libraries, *Brachypodium* stands at the nexus of functional genomics breakthroughs. Tapping into these resources, cutting-edge research has spotlighted genes pivotal for adapting to environmental vicissitudes, nudging the door ajar for reinforcing resilience in crops ranging from rice to millets (Borrill, 2020). In summation, the arc of *Brachypodium's* role in translational genomics, spanning a decade or more, underscores its invaluable contribution. As we navigate a world grappling with climatic unpredictability, such research provides an anchor for sustainable cereal cultivation strategies.

7. ECOLOGICAL FOOTPRINTS: *BRACHYPODIUM'S* NICHE IN CHANGING CLIMATES

Brachypodium's ecological role extends beyond its genetic blueprint. Distributed primarily across the Mediterranean and parts of Western Asia, its interactions with the environment have rendered invaluable insights, particularly in the context of a rapidly changing climate.

The genus *Brachypodium*, notably species like *B. distachyon*, *B. stacei*, and *B. hybridum*, has occupied a myriad of niches, ranging from woodland clearings to open grasslands, and disturbed zones along roadsides (Catalan et al., 2015). *B. stacei's* predilection for the warmer and drier niches of the Iberian Peninsula and *B. distachyon's* adaptation to cooler climates offer contrasting ecological tales, each elucidating distinct environmental interactions (López-Alvarez et al., 2015).

With the onset of climate change, *Brachypodium's* ecological dynamics are evolving. Historically confined to native regions, anecdotal evidence has pointed towards the potential invasive tendencies of species like *B. distachyon*. Some reports even suggest its establishment in newer ecosystems, such as North America (Scholthof et al., 2018).

However, the shifting environmental patterns, characterized by fluctuating temperatures and erratic precipitation, have also influenced *Brachypodium's* distribution. As per predictions, *B. distachyon* might capitalize on the new habitats formed due to climatic disturbances, possibly expanding its geographical expanse (López-Alvarez et al., 2015). Similarly, *B. stacei* and *B. hybridum*, with their inherent genetic resilience, could witness shifts in their ecological niches. Future climatic projections indicate a more dynamic ecological landscape for *Brachypodium*. As these species respond, adapt, and possibly migrate, understanding their ecological trajectories becomes paramount. Such knowledge not only unravels *Brachypodium's* ecological narrative but also offers insights into potential responses of other similar grasses and cereals in a changing global environment.

8. *BRACHYPODIUM*: A SENTINEL FOR CEREAL HEALTH UNDER STRESS

In the realm of plant science, sentinel species provide an early warning of potential challenges, and *Brachypodium* stands out prominently in this role for cereals. While its genomics and environmental adaptability have been explored, its position as a vanguard, flagging potential threats and opportunities for major crops, is pivotal. *Brachypodium's* nuanced interactions with diverse pathogens set the stage for

anticipating disease outbreaks in cereals. For instance, its encounters with novel strains of *Magnaporthe*, which can affect rice and wheat, highlight emergent threats even before they strike primary crops, aiding in proactive management strategies (Inoue et al., 2021). As global agriculture confronts soil health challenges, particularly nutrient imbalances and deficiencies exacerbated by climate change, *Brachypodium's* behavior under nutrient stress provides foresight. Its ability to thrive in soils with varied phosphorus or nitrogen levels could be used as a benchmark for anticipating cereal responses and developing adaptive fertilization strategies (Zhao et al., 2018). Moreover, its rapid phenological shifts in response to environmental cues offer predictive data. By monitoring *Brachypodium's* flowering times, germination rates, or growth patterns under different scenarios, we can infer potential adjustments major cereals might need in terms of sowing periods or harvest schedules (Ream et al., 2014). Additionally, the intricate interplay of *Brachypodium's* microbiome in mediating stress responses can guide us in optimizing root microbiomes of cereals to enhance nutrient uptake, stress resilience, and overall health (Romero-Gamboa, 2019).

9. FUTURE AGRONOMY: HARNESSING *BRACHYPODIUM* TRAITS FOR SUSTAINABLE AGRICULTURE

As the global agricultural paradigm shifts toward sustainable practices, the spotlight on model grasses like *Brachypodium* intensifies. Its myriad traits, honed over millennia of evolution, are a treasure trove for crop improvement, providing a roadmap for the next phase of sustainable cereal agriculture.

9.1. Resource Efficiency and Sustainability

Traditional agricultural practices often rely heavily on inputs, be they water, fertilizers, or pesticides. *Brachypodium*, particularly species like *B. distachyon*, has highlighted remarkable resilience with minimal resources (Brkljacic et al., 2011). Its efficient water-use strategies, adaptive nutrient uptake systems, and natural resistance to certain pests present a blueprint for low-input, high-output agriculture, aligning with modern sustainable farming (Catalan et al., 2015).

9.2. Deep-Diving into Genetics for Agronomic Traits

Modern genomics, combined with advanced bioinformatics, has unlocked vast data from the *Brachypodium* genome. Recent discoveries have spotlighted genes governing traits like drought resistance, nutrient absorption, and disease resistance, opening doors for potential transfers to staple cereals (Hasterok et al., 2022).

9.3. Eco-friendly Pest Management

Beyond its genetic attributes, *Brachypodium's* interactions with pests and its associated microbiome offer pathways for environmentally friendly pest control. Its symbiotic relationships with specific bacterial strains have been shown to deter harmful pests, presenting potential biocontrol avenues (Romero-Gamboa, 2019).

9.4. Climate-Ready Crops

With the impending challenges of climate change, *Brachypodium's* adaptability becomes a central focus. For instance, studies on *B. stacei's* tolerance to increasing salinity or *B. hybridum's* resilience against sporadic rainfall provide insights for breeding cereals ready for tomorrow's climates (López-Alvarez et al., 2015; Neji et al., 2022).

9.5. Conservation Tillage and Ecosystem Health

Brachypodium's natural propensity to thrive in varied terrains, including those disturbed or degraded, hints at its potential role in conservation agriculture. Its integration could support conservation tillage practices, promoting soil health, moisture retention, and biodiversity (Dasgupta et al., 2020).

9.6. Towards Precision Agriculture

The rapid life cycle and amenability to genetic modifications make *Brachypodium* a linchpin in high-throughput phenotyping and genotyping studies. Insights from these could drive precision agriculture, optimizing inputs and enhancing yields (Hsia et al., 2017). Conclusively, *Brachypodium* stands at the crossroads of tradition and innovation. Its ancient wisdom, combined with modern scientific explorations, holds the promise of ushering in an era of agriculture that is not just productive but harmonizes with the planet's ecological rhythms.

10. BEYOND ABIOTIC STRESSES: BRACHYPODIUM IN BIOTIC INTERACTIONS AND CLIMATE DYNAMICS

Brachypodium, while being a linchpin for studying abiotic stress responses, also holds crucial information on plant-biotic interactions in the context of changing climates. Its interactions with a myriad of organisms, ranging from beneficial symbionts to pests and pathogens, provide a window into the intricate dynamics of plant ecosystems and their evolution in a changing world. In the symbiotic realm, *Brachypodium* has established relationships with various mycorrhizal fungi and nitrogen-fixing bacteria, which aid in nutrient acquisition and stress mitigation. These interactions are not just beneficial for the plant but are vital for soil health and fertility (Hacquard et al., 2013). However, climate change threatens to disrupt these symbioses. Elevated temperatures and altered precipitation patterns might influence the microbial community structure in soils, potentially affecting the quality and efficiency of these partnerships (Compant et al., 2021). Conversely, *Brachypodium's* interactions with pests and pathogens offer insights into the challenges crops may face in warmer and more erratic climates. For instance, warmer winters can lead to increased survival and proliferation of certain pests, necessitating preemptive control strategies. Studies on *Brachypodium*-pathogen dynamics, such as its interaction with *Magnaporthe oryzae*, are enlightening, revealing potential vulnerabilities and resistance pathways that could be crucial for safeguarding future cereal crops (K. Inoue et al., 2020).

The changing climate also influences plant-insect dynamics. For example, *Brachypodium's* role as a host to certain herbivores and the resultant effects on plant health and productivity can be seen as a model to predict challenges for larger cereal crops. The dynamics of herbivore attack, plant defense, and the potential shifts in these interactions due to changing weather patterns are of paramount importance (Des Marais et al., 2017). Lastly, *Brachypodium's* interactions are not just at the microbial or insect level. Its position in ecosystems, how it competes or collaborates with neighboring plants, and its role in larger trophic cascades (like being fodder for certain herbivores, which in turn influence predator populations) showcase its integrated role in climate and biotic dynamics (Schwartz et al., 2010). Drawing it all together, *Brachypodium* stands as a sentinel, signaling the complex interplay of biotic interactions in the face of global climate change. Its experiences, challenges, and successes can help guide

sustainable and resilient agricultural practices for the staple cereals that feed the world.

11. CONSERVATION IMPLICATIONS: PRESERVING *BRACHYPODIUM* DIVERSITY FOR FUTURE GENERATIONS

The profound value of *Brachypodium* in scientific research and its potential as a blueprint for future sustainable agriculture underscores the importance of conserving its diversity. As we navigate the challenges of the Anthropocene, where human influence shapes global ecosystems, ensuring the conservation of *Brachypodium* becomes a task of paramount significance.

11.1. Genetic Reservoir

The genetic diversity within *Brachypodium* species serves as a reservoir of traits that can be pivotal for food security and ecological sustainability. This diversity is a result of millennia of evolution, adapting to varied climatic conditions, terrains, and biotic interactions. It offers a plethora of genes that could hold the answers to drought tolerance, pest resistance, and efficient nutrient utilization (Vogel & Hill, 2008).

11.2. Biodiversity Hotspots and Threats

Several *Brachypodium* species, especially *B. stacei*, are endemic to specific biodiversity hotspots, often areas with unique flora and fauna but increasingly under threat from urbanization, agricultural expansion, or climate change-induced habitat shifts (López-Alvarez et al., 2015). Protecting these habitats ensures the conservation of genetic resources that might be crucial for future agricultural innovations.

11.3. Seed Banks and In Situ Conservation

While ex situ conservation strategies, like seed banks, have been employed to store *Brachypodium* seeds for future use, in situ conservation, which involves protecting the natural habitats of these species, is equally important. Natural habitats offer an evolutionary theater, allowing species to adapt and evolve in response to environmental changes (Hasterok et al., 2022).

11.4. Ecosystem Services

Beyond its direct agricultural implications, *Brachypodium* plays roles in its native ecosystems that should not be overlooked. Its interactions with pollinators, soil microorganisms, and even its role in soil

conservation highlight its ecological significance (Scholthof et al., 2018).

11.5. A Model for Conservation

Brachypodium, with its rapidly increasing research prominence, can also serve as a flagship species, drawing attention to broader conservation issues. Its story can be a vehicle to raise awareness about habitat preservation, sustainable agriculture, and the importance of conserving genetic diversity (Bettgenhaeuser et al., 2017). In sum, as we increasingly look to *Brachypodium* for answers to some of the pressing agricultural challenges of our times, it is imperative to also champion its conservation. Preserving its diversity is not just about safeguarding a research model; it is about holding onto a legacy of evolutionary resilience, adaptability, and potential that future generations might lean on.

12. ECONOMIC IMPLICATIONS: *BRACHYPODIUM*'S ROLE IN FUTURE FOOD SECURITY AND CROP SUSTAINABILITY

In the evolving landscape of global agriculture, where food security concerns intersect with sustainability imperatives, *Brachypodium* has emerged as a beacon of both hope and innovation. While at first glance, this small grass may not seem directly relevant to global economic structures, its potential impact on the world's agricultural markets and, by extension, economies, is profound.

12.1. Food Security and the Cereal Connection

Major cereals like wheat, rice, and barley are the cornerstone of global food supplies. Given the shared evolutionary history and genomic similarities between *Brachypodium* and these cereals, research on this model plant holds promise for enhancing yields, improving resistance against pests and diseases, and ensuring consistent food supplies. Ensuring stable cereal yields has direct economic benefits, stabilizing prices and preventing potential market volatilities (Opanowicz et al., 2008).

12.2. Climate Change and Agricultural Resilience

With the advancing threats of climate change, unpredictable weather patterns and increasing incidences of extreme events pose serious risks to global crop yields. The economic consequences of crop failures are devastating, often leading to spikes in food prices and socio-

economic unrest. *Brachypodium*, with its rich genetic resource for abiotic stress tolerance, can serve as a template to engineer more resilient crops, potentially safeguarding billions in annual agricultural revenue (Brkljacic et al., 2011).

12.3. Innovations in Bioenergy

Beyond food, *Brachypodium*'s potential role in bioenergy is of considerable economic interest. As nations grapple with depleting fossil fuel reserves and the environmental fallout of their usage, there is a pressing need to pivot to sustainable energy sources. *Brachypodium*'s rapid growth, adaptability to marginal lands, and potential as a biofuel source can make it a frontrunner in the emerging bioenergy economy (Coomey et al., 2020).

12.4. Reducing Dependency on Agrochemicals

Pesticides, fungicides, and synthetic fertilizers, while essential in modern agriculture, are not just environmentally contentious but also represent a significant economic burden for farmers. By leveraging *Brachypodium*'s insights on natural resistance mechanisms and symbiotic relationships, it might be possible to reduce this dependency, leading to more sustainable and cost-effective farming (Priest et al., 2014).

12.5. Socio-economic Ripple Effect

At the grassroots level, enhanced crop yields, reduced input costs, and new avenues for farming (like bioenergy crops) can uplift farmer incomes, improve community livelihoods, and foster rural development. This not only bolsters national economies but also plays a role in poverty alleviation and improved socio-economic metrics. In the grand tapestry of global economies, *Brachypodium* might appear as a minuscule thread. Yet, the potential economic ramifications of its research could reverberate across continents, shaping food markets, energy sectors, and socio-economic landscapes for generations to come.

12.6. Ecological dynamics and effects of global climate change in *B. distachyon* complex

The intricate ecological dynamics observed in *B. distachyon* and its relatives have far-reaching implications for plant ecosystems and global climate change. These species, characterized by diverse ecological adaptations, are embedded in different habitats, with their distribution and abundance closely linked to factors such as soil

composition, moisture content, and temperature ranges. Within their respective ecosystems, interactions encompass a whole spectrum of dynamics, including competition and coexistence with other plant species, shaping community structure, and influencing biodiversity. Beyond these direct ecological relationships, *Brachypodium* species become sentinels of climate variability. Their specific responses to fluctuations in climatic conditions affect growth, reproduction, and general fitness and provide valuable insights into their adaptability to climate change. In the overall structure of plant ecosystems, these species contribute significantly to biodiversity and ecosystem stability (Priest et al., 2014). However, their potential invasive tendencies pose a challenge to the functioning of ecosystems and influence their dynamics. A closer look at their functional role shows that *Brachypodium* grasses play a key role in nutrient cycling, soil stabilization, and habitat provision. This nuanced understanding helps to appreciate the ecosystem services they provide and underlines their importance in maintaining ecological balance. In the context of global climate change, *Brachypodium* grasses have a significant impact. Their role in carbon storage contributes to efforts to mitigate climate change. Furthermore, the potential of grasses to shift their range and change their distribution patterns in response to climate variability adds complexity to the assessment of climate change impacts (Hasterok et al., 2022). The intricate interplay of *Brachypodium* species in ecosystems contributes to feedback loops, which in turn can influence the wider climate. Therefore, a comprehensive understanding of the ecological dynamics of *Brachypodium* and its relatives is of utmost importance. This knowledge serves as a basis for predicting, managing, and mitigating the ecological consequences of environmental change. In the face of global climatic challenges, the importance of these species goes beyond their immediate habitats and emphasizes the need for a holistic approach to environmental conservation.

13. CONCLUSION

While the story of *Brachypodium* is rooted in the annals of botanical research, its influence extends far beyond the confines of academic laboratories and into the broader issues of global food security, sustainability, and ecological balance. As we journeyed through the various facets of *Brachypodium*'s importance, from its genetic intricacies and mechanisms of stress

resistance to its conservation and economic impact, it became clear that this tiny grass has outsized potential. In an era characterized by rapid environmental change and unprecedented challenges to global agriculture, *Brachypodium* is both a sentinel and a savior. Its genetic richness, a product of millennia of evolution, provides a roadmap for improving the resilience of staple crops that form the basis of life for billions of people. Its interactions with the biological world offer insights into sustainable agriculture that could potentially revolutionize farming practices and reduce our dependence on polluting inputs. Furthermore, its potential role in the bioenergy sector represents a promising path to a greener, more sustainable future. Although *Brachypodium* holds great promise, one must proceed with a mixture of optimism and caution. Preserving the rich biodiversity, understanding the nuanced interactions with the environment, and the ethical considerations of utilizing genetic resources are challenges that lie ahead. These hurdles are not only scientific in nature but also intertwined with socio-economic, political, and ethical dimensions. In the face of the climate crisis and the growing world population, the story of *Brachypodium* is more than just a botanical curiosity; it is a clear call for collaboration. Building bridges between geneticists, ecologists, farmers, policy makers and consumers will be crucial. In *Brachypodium*, we see the embodiment of hope, but it is a hope that can only be realized through collaborative efforts, foresight, and a shared vision for a sustainable future. *Brachypodium* may have started its journey as an "underdog" in the world of plants, but as this report shows, it is poised to become a cornerstone in our collective quest for a resilient, sustainable, and secure future.

REFERENCES

- Abdul Aziz, M., Sabeem, M., Mullath, S. K., Brini, F., & Masmoudi, K. (2021). Plant group II LEA proteins: Intrinsically disordered structure for multiple functions in response to environmental stresses. *Biomolecules*, 11(11), 1662.
- Álvarez, S., Acosta-Motos, J. R., & Sánchez-Blanco, M. J. (2023). Morphological performance and seasonal pattern of water relations and gas exchange in *Pistacia lentiscus* plants subjected to salinity and water deficit. *Frontiers in Plant Science*, 14, 1237332. <https://doi.org/10.3389/fpls.2023.1237332>
- Arif, Y., Singh, P., Siddiqui, H., Bajguz, A., & Hayat, S. (2020). Salinity induced physiological and biochemical changes in plants: An omic approach towards salt stress tolerance. *Plant Physiology and Biochemistry*, 156, 64–77. <https://doi.org/10.1016/j.plaphy.2020.08.042>
- Barrera-Figueroa, B. E., Gao, L., Wu, Z., Zhou, X., Zhu, J., Jin, H., Liu, R., & Zhu, J.-K. (2012). High throughput sequencing reveals novel and abiotic stress-regulated microRNAs in the inflorescences of rice. *BMC Plant Biology*, 12(1), 132. <https://doi.org/10.1186/1471-2229-12-132>
- Bettgenhaeuser, J., Corke, F. M., Opanowicz, M., Green, P., Hernández-Pinzón, I., Doonan, J. H., & Moscou, M. J. (2017). Natural variation in *Brachypodium* links vernalization and flowering time loci as major flowering determinants. *Plant Physiology*, 173(1), 256–268.
- Bevan, M. W., Garvin, D. F., & Vogel, J. P. (2010). *Brachypodium distachyon* genomics for sustainable food and fuel production. *Current Opinion in Biotechnology*, 21(2), 211–217.
- Borrill, P. (2020). Blurring the boundaries between cereal crops and model plants. *New Phytologist*, 228(6), 1721–1727. <https://doi.org/10.1111/nph.16229>
- Brkljacic, J., Grotewold, E., Scholl, R., Mockler, T., Garvin, D. F., Vain, P., Brutnell, T., Sibout, R., Bevan, M., & Budak, H. (2011). *Brachypodium* as a model for the grasses: Today and the future. *Plant Physiology*, 157(1), 3–13.
- Budescu, D. V., Por, H.-H., Broomell, S. B., & Smithson, M. (2014). The interpretation of IPCC probabilistic statements around the world. *Nature Climate Change*, 4(6), 508–512.
- Catalan, P., Chalhoub, B., Chochois, V., Garvin, D. F., Hasterok, R., Manzaneda, A. J., Mur, L. A., Pecchioni, N., Rasmussen, S. K., & Vogel, J. P. (2014). Update on the genomics and basic biology of *Brachypodium*: International *Brachypodium* Initiative (IBI). *Trends in Plant Science*, 19(7), 414–418.
- Catalan, P., López-Álvarez, D., Díaz-Pérez, A., Sancho, R., & López-Herránz, M. L. (2015). Phylogeny and Evolution of the Genus *Brachypodium*. In J. P. Vogel (Ed.), *Genetics and Genomics of Brachypodium* (Vol. 18, pp. 9–38). Springer International Publishing. https://doi.org/10.1007/7397_2015_17
- Catalán, P., Müller, J., Hasterok, R., Jenkins, G., Mur, L. A., Langdon, T., Betekhtin, A., Siwinska, D., Pimentel, M., & López-Álvarez, D. (2012). Evolution and taxonomic split of the model grass *Brachypodium distachyon*. *Annals of Botany*, 109(2), 385–405.

- Chen, S., Luo, Y., Wang, G., Feng, C., & Li, H. (2020). Genome-wide identification of expansin genes in *Brachypodium distachyon* and functional characterization of BdEXPA27. *Plant Science*, 296, 110490.
- Compant, S., Cambon, M. C., Vacher, C., Mitter, B., Samad, A., & Sessitsch, A. (2021). The plant endosphere world – bacterial life within plants. *Environmental Microbiology*, 23(4), 1812–1829. <https://doi.org/10.1111/1462-2920.15240>
- Coomey, J. H., Sibout, R., & Hazen, S. P. (2020). Grass secondary cell walls, *Brachypodium distachyon* as a model for discovery. *New Phytologist*, 227(6), 1649–1667. <https://doi.org/10.1111/nph.16603>
- Dasgupta, P., Das, A., Datta, S., Banerjee, I., Tripathy, S., & Chaudhuri, S. (2020). Understanding the early cold response mechanism in IR64 indica rice variety through comparative transcriptome analysis. *BMC Genomics*, 21(1), 425. <https://doi.org/10.1186/s12864-020-06841-2>
- Des Marais, D. L., Lasky, J. R., Verslues, P. E., Chang, T. Z., & Juenger, T. E. (2017). Interactive effects of water limitation and elevated temperature on the physiology, development and fitness of diverse accessions of *Brachypodium distachyon*. *New Phytologist*, 214(1), 132–144.
- Dinakar, C., Vishwakarma, A., Raghavendra, A. S., & Padmasree, K. (2016). Alternative Oxidase Pathway Optimizes Photosynthesis During Osmotic and Temperature Stress by Regulating Cellular ROS, Malate Valve and Antioxidative Systems. *Frontiers in Plant Science*, 7. <https://www.frontiersin.org/articles/10.3389/fpls.2016.00068>
- Duan, H., Lu, X., Lian, C., An, Y., Xia, X., & Yin, W. (2016). Genome-wide analysis of microRNA responses to the phytohormone abscisic acid in *Populus euphratica*. *Frontiers in Plant Science*, 7, 1184.
- Garcia Molina, M. D., Botticella, E., Beleggia, R., Palombieri, S., De Vita, P., Masci, S., Lafiandra, D., & Sestili, F. (2021). Enrichment of provitamin A content in durum wheat grain by suppressing β -carotene hydroxylase 1 genes with a TILLING approach. *Theoretical and Applied Genetics*, 134(12), 4013–4024. <https://doi.org/10.1007/s00122-021-03944-6>
- Garcia deblás, B., Senn, M. E., Bañuelos, M. A., & Rodríguez - Navarro, A. (2003). Sodium transport and HKT transporters: The rice model. *The Plant Journal*, 34(6), 788 – 801. <https://doi.org/10.1046/j.1365-313X.2003.01764.x>
- Gordon, S. P., Contreras-Moreira, B., Levy, J. J., Djamei, A., Czedik-Eysenberg, A., Tartaglio, V. S., Session, A., Martin, J., Cartwright, A., & Katz, A. (2020). Gradual polyploid genome evolution revealed by pan-genomic analysis of *Brachypodium hybridum* and its diploid progenitors. *Nature Communications*, 11(1), 3670.
- Hacquard, S., Kracher, B., Maekawa, T., Vernaldi, S., Schulze-Lefert, P., & Ver Loren Van Themaat, E. (2013). Mosaic genome structure of the barley powdery mildew pathogen and conservation of transcriptional programs in divergent hosts. *Proceedings of the National Academy of Sciences*, 110(24). <https://doi.org/10.1073/pnas.1306807110>
- Hasterok, R., Catalan, P., Hazen, S. P., Roulin, A. C., Vogel, J. P., Wang, K., & Mur, L. A. (2022a). *Brachypodium*: 20 years as a grass biology model system; the way forward? *Trends in Plant Science*, 27(10), 1002–1016.
- Hasterok, R., Catalan, P., Hazen, S. P., Roulin, A. C., Vogel, J. P., Wang, K., & Mur, L. A. (2022b). *Brachypodium*: 20 years as a grass biology model system; the way forward? *Trends in Plant Science*, 27(10), 1002–1016.
- Hirayama, T., & Shinozaki, K. (2010). Research on plant abiotic stress responses in the post - genome era: Past, present and future. *The Plant Journal*, 61(6), 1041 – 1052. <https://doi.org/10.1111/j.1365-313X.2010.04124.x>
- Hsia, D. S., Grove, O., & Cefalu, W. T. (2017). An update on SGLT2 inhibitors for the treatment of diabetes mellitus. *Current Opinion in Endocrinology, Diabetes, and Obesity*, 24(1), 73.
- Hsu, P., Dubeaux, G., Takahashi, Y., & Schroeder, J. I. (2021). Signaling mechanisms in abscisic acid - mediated stomatal closure. *The Plant Journal*, 105(2), 307 – 321. <https://doi.org/10.1111/tpj.15067>
- Inoue, K., Takahagi, K., Kouzai, Y., Koda, S., Shimizu, M., Uehara-Yamaguchi, Y., Nakayama, R., Kita, T., Onda, Y., & Nomura, T. (2020). Parental legacy and regulatory novelty in *Brachypodium* diurnal transcriptomes accompanying their polyploidy. *NAR Genomics and Bioinformatics*, 2(3), lqaa067.
- Inoue, Y., Vy, T. T. P., Tani, D., & Tosa, Y. (2021). Suppression of wheat blast resistance by an effector of *Pyricularia oryzae* is counteracted by a host specificity resistance gene in wheat.

- New Phytologist, 229(1), 488–500.
<https://doi.org/10.1111/nph.16894>
- Julkowska, M. M. (2020). Tuning to the Signal of Stress: Subcellular Regulation of Abscisic Acid Receptor Abundance by E3 Ubiquitin Ligases. *American Society of Plant Biologists*.
<https://academic.oup.com/plphys/article-abstract/182/4/1531/6116256>
- Kandhol, N., Jain, M., & Tripathi, D. K. (2022). Nanoparticles as potential hallmarks of drought stress tolerance in plants. *Physiologia Plantarum*, 174(2), e13665.
<https://doi.org/10.1111/ppl.13665>
- Lehman, T. A., Rosas, M. A., Brew - Appiah, R. A. T., Solanki, S., York, Z. B., Dannay, R., Wu, Y., Roalson, E. H., Zheng, P., Main, D., Baskin, T. I., & Sanguinet, K. A. (2023). BUZZ : An essential gene for postinitiation root hair growth and a mediator of root architecture in *Brachypodium distachyon*. *New Phytologist*, 239(5), 1723–1739. <https://doi.org/10.1111/nph.19079>
- Lei, L., Gordon, S. P., Liu, L., Sade, N., Lovell, J. T., Rubio Wilhelmi, M. D. M., Singan, V., Sreedasyam, A., Hestrin, R., & Phillips, J. (2023). The reference genome and abiotic stress responses of the model perennial grass *Brachypodium sylvaticum*. *G3: Genes, Genomes, Genetics*, jkad245.
- López - Alvarez, D., Manzaneda, A. J., Rey, P. J., Giraldo, P., Benavente, E., Allainguillaume, J., Mur, L., Caicedo, A. L., Hazen, S. P., Breiman, A., Ezrati, S., & Catalán, P. (2015). Environmental niche variation and evolutionary diversification of the *Brachypodium distachyon* grass complex species in their native circum - Mediterranean range. *American Journal of Botany*, 102(7), 1073 – 1088.
<https://doi.org/10.3732/ajb.1500128>
- Mahood, E. H., Bennett, A. A., Komatsu, K., Kruse, L. H., Lau, V., Rahmati Ishka, M., Jiang, Y., Bravo, A., Louie, K., Bowen, B. P., Harrison, M. J., Provart, N. J., Vatamaniuk, O. K., & Moghe, G. D. (2023). Information theory and machine learning illuminate large-scale metabolomic responses of *Brachypodium distachyon* to environmental change. *The Plant Journal*, 114(3), 463–481.
<https://doi.org/10.1111/tpj.16160>
- Marro, N., Lidoy, J., Chico, M. Á., Rial, C., García, J., Varela, R. M., Macías, F. A., Pozo, M. J., Janoušková, M., & López - Ráez, J. A. (2022). Strigolactones: New players in the nitrogen - phosphorus signalling interplay. *Plant, Cell & Environment*, 45(2), 512–527.
<https://doi.org/10.1111/pce.14212>
- Martínez, L. M., Fernández-Ocaña, A., Rey, P. J., Salido, T., Amil-Ruiz, F., & Manzaneda, A. J. (2018). Variation in functional responses to water stress and differentiation between natural allopolyploid populations in the *Brachypodium distachyon* species complex. *Annals of Botany*, 121(7), 1369–1382.
<https://doi.org/10.1093/aob/mcy037>
- Martínez-Peña, R., Rezzouk, F. Z., del Carmen Díez-Fraile, M., Nieto-Taladriz, M. T., Araus, J. L., Aparicio, N., & Vicente, R. (2023). Genotype-by-environment interaction for grain yield and quality traits in durum wheat: Identification of ideotypes adapted to the Spanish region of Castile and León. *European Journal of Agronomy*, 151, 126951.
- Mayer, B. F., & Charron, J. (2021). Transcriptional memories mediate the plasticity of cold stress responses to enable morphological acclimation in *Brachypodium distachyon*. *New Phytologist*, 229(3), 1615–1634. <https://doi.org/10.1111/nph.16945>
- Meng, Y., Varshney, K., Incze, N., Badics, E., Kamran, M., Davies, S. F., Oppermann, L. M. F., Magne, K., Dalmais, M., Bendahmane, A., Sibout, R., Vogel, J., Laudencia - Chingcuanco, D., Bond, C. S., Soós, V., Gutjahr, C., & Waters, M. T. (2022). KARRIKIN INSENSITIVE2 regulates leaf development, root system architecture and arbuscular - mycorrhizal symbiosis in *Brachypodium distachyon*. *The Plant Journal*, 109(6), 1559 – 1574.
<https://doi.org/10.1111/tpj.15651>
- Minadakis, N., Williams, H., Horvath, R., Caković, D., Stritt, C., Thieme, M., Bourgeois, Y., & Roulin, A. C. (2023). The demographic history of the wild crop relative *Brachypodium distachyon* is shaped by distinct past and present ecological niches. *Peer Community Journal*, 3. <https://doi.org/10.24072/pcjournal.319>
- More, S. J., Bardhan, K., Ravi, V., Pasala, R., Chaturvedi, A. K., Lal, M. K., & Siddique, K. H. M. (2023). Morphophysiological Responses and Tolerance Mechanisms in Cassava (*Manihot esculenta* Crantz) Under Drought Stress. *Journal of Soil Science and Plant Nutrition*, 23(1), 71–91.
<https://doi.org/10.1007/s42729-023-01127-4>
- Muluneh, M. G. (2021). Impact of climate change on biodiversity and food security: A global perspective—a review article. *Agriculture & Food Security*, 10(1), 36.
<https://doi.org/10.1186/s40066-021-00318-5>
- Neji, M., Geuna, F., Gandour, M., Hessini, K., Taamalli, W., & Abdelly, C. (2022). Patterns of morpho-phenological and genetic variation of

- Brachypodium distachyon (L.) P.Beauv. Complex in Tunisia. *Genetic Resources and Crop Evolution*, 69(2), 577–586. <https://doi.org/10.1007/s10722-021-01242-0>
- Neji, M., Geuna, F., Taamalli, W., Ibrahim, Y., Smida, M., Badri, M., Abdelly, C., & Gandour, M. (2015). Morpho-phenological diversity among Tunisian natural populations of *Brachypodium hybridum*. *The Journal of Agricultural Science*, 153(6), 1006–1016.
- Neji, M., Tlahig, S., Hessini, K., Taamalli, W., Abdelly, C., & Kouas, S. (2021a). Variation of forage quality traits in Tunisian populations of *Brachypodium hybridum* in response to phosphorus deficiency. *Crop Science*, 61(6), 4038–4054. <https://doi.org/10.1002/csc2.20613>
- Neji, M., Tlahig, S., Hessini, K., Taamalli, W., Abdelly, C., & Kouas, S. (2021b). Variation of forage quality traits in Tunisian populations of *Brachypodium hybridum* in response to phosphorus deficiency. *Crop Science*, 61(6), 4038–4054. <https://doi.org/10.1002/csc2.20613>
- Opanowicz, M., Vain, P., Draper, J., Parker, D., & Doonan, J. H. (2008). *Brachypodium distachyon*: Making hay with a wild grass. *Trends in Plant Science*, 13(4), 172–177.
- Pachauri, R. K., Allen, M. R., Barros, V. R., Broome, J., Cramer, W., Christ, R., Church, J. A., Clarke, L., Dahe, Q., Dasgupta, P., Dubash, N. K., Edenhofer, O., Elgizouli, I., Field, C. B., Forster, P., Friedlingstein, P., Fuglestvedt, J., Gomez-Echeverri, L., Hallegatte, S., ... van Ypserle, J.-P. (2014). *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. In R. K. Pachauri & L. Meyer (Eds.), EPIC3Geneva, Switzerland, IPCC, 151 p., pp. 151, ISBN: 978-92-9169-143-2 (p. 151). IPCC. <https://epic.awi.de/id/eprint/37530/>
- Peng, Y.-L., Wang, Y.-S., Fei, J., & Sun, C.-C. (2020). Isolation and expression analysis of two novel C-repeat binding factor (CBF) genes involved in plant growth and abiotic stress response in mangrove *Kandelia obovata*. *Ecotoxicology*, 29(6), 718–725. <https://doi.org/10.1007/s10646-020-02219-y>
- Peraldi, A., Beccari, G., Steed, A., & Nicholson, P. (2011). *Brachypodium distachyon*: A new pathosystem to study *Fusarium* head blight and other *Fusarium* diseases of wheat. *BMC Plant Biology*, 11(1), 100. <https://doi.org/10.1186/1471-2229-11-100>
- Priest, H. D., Fox, S. E., Rowley, E. R., Murray, J. R., Michael, T. P., & Mockler, T. C. (2014). Analysis of global gene expression in *Brachypodium distachyon* reveals extensive network plasticity in response to abiotic stress. *PLoS One*, 9(1), e87499.
- Ream, T. S., Woods, D. P., Schwartz, C. J., Sanabria, C. P., Mahoy, J. A., Walters, E. M., Kaeppler, H. F., & Amasino, R. M. (2014). Interaction of Photoperiod and Vernalization Determines Flowering Time of *Brachypodium distachyon*. *Plant Physiology*, 164(2), 694–709. <https://doi.org/10.1104/pp.113.232678>
- Romero-Gamboa, S. (2019). *Brachypodium distachyon* GNRF, SWAM1 and SWAM4 are transcriptional regulators of secondary cell wall biosynthesis. Doctoral Dissertations. <https://doi.org/10.7275/14117186>
- Scarlett, V. T., Lovell, J. T., Shao, M., Phillips, J., Shu, S., Lusinska, J., Goodstein, D. M., Jenkins, J., Grimwood, J., & Barry, K. (2023). Multiple origins, one evolutionary trajectory: Gradual evolution characterizes distinct lineages of allotetraploid *Brachypodium*. *Genetics*, 223(2), iyac146.
- Scholthof, K.-B. G., Irigoyen, S., Catalan, P., & Mandadi, K. K. (2018). *Brachypodium*: A monocot grass model genus for plant biology. *The Plant Cell*, 30(8), 1673–1694.
- Schwartz, C. J., Doyle, M. R., Manzaneda, A. J., Rey, P. J., Mitchell-Olds, T., & Amasino, R. M. (2010). Natural Variation of Flowering Time and Vernalization Responsiveness in *Brachypodium distachyon*. *BioEnergy Research*, 3(1), 38–46. <https://doi.org/10.1007/s12155-009-9069-3>
- Shahzad, A., Ullah, S., Dar, A. A., Sardar, M. F., Mehmood, T., Tufail, M. A., Shakoor, A., & Haris, M. (2021). Nexus on climate change: Agriculture and possible solution to cope future climate change stresses. *Environmental Science and Pollution Research*, 28(12), 14211–14232. <https://doi.org/10.1007/s11356-021-12649-8>
- Shikha, D., Jakhar, P., & Satbhai, S. B. (2023). Role of jasmonate signaling in the regulation of plant responses to nutrient deficiency. *Journal of Experimental Botany*, 74(4), 1221–1243. <https://doi.org/10.1093/jxb/erac387>
- Shiposha, V., Marques, I., López-Alvarez, D., Manzaneda, A. J., Hernandez, P., Olonova, M., & Catalán, P. (2020). Multiple founder events explain the genetic diversity and structure of the model allopolyploid grass *Brachypodium hybridum* in the Iberian Peninsula hotspot.

- Annals of Botany, 125(4), 625–638.
<https://doi.org/10.1093/aob/mcz169>
- Tyler, L., Fangel, J. U., Fagerström, A. D., Steinwand, M. A., Raab, T. K., Willats, W. G., & Vogel, J. P. (2014). Selection and phenotypic characterization of a core collection of *Brachypodium distachyon* inbred lines. *BMC Plant Biology*, 14(1), 25.
<https://doi.org/10.1186/1471-2229-14-25>
- Vogel, J., & Hill, T. (2008). High-efficiency *Agrobacterium*-mediated transformation of *Brachypodium distachyon* inbred line Bd21-3. *Plant Cell Reports*, 27(3), 471–478.
<https://doi.org/10.1007/s00299-007-0472-y>
- Vogel, J. P. (2015). The Rise of *Brachypodium* as a Model System. In J. P. Vogel (Ed.), *Genetics and Genomics of Brachypodium* (Vol. 18, pp. 1–7). Springer International Publishing.
https://doi.org/10.1007/7397_2015_14
- Waditee-Sirisattha, R., Singh, M., Kageyama, H., Sittipol, D., Rai, A. K., & Takabe, T. (2012). *Anabaena* sp. PCC7120 transformed with glycine methylation genes from *Aphanothece halophytica* synthesized glycine betaine showing increased tolerance to salt. *Archives of Microbiology*, 194(11), 909–914.
<https://doi.org/10.1007/s00203-012-0824-z>
- Waters, E. R., & Vierling, E. (2020). Plant small heat shock proteins – evolutionary and functional diversity. *New Phytologist*, 227(1), 24–37.
<https://doi.org/10.1111/nph.16536>
- Woods, D. P., Dong, Y., Bouché, F., Mayer, K., Varner, L., Ream, T. S., Thrower, N., Wilkerson, C., Cartwright, A., Sibout, R., Laudencia-Chinguanco, D., Vogel, J., & Amasino, R. M. (2020). Mutations in the predicted DNA polymerase subunit POLD3 result in more rapid flowering of *Brachypodium distachyon*. *New Phytologist*, 227(6).
<https://doi.org/10.1111/nph.16546>
- Wu, H. (2018). Plant salt tolerance and Na⁺ sensing and transport. *The Crop Journal*, 6(3), 215–225.
<https://doi.org/10.1016/j.cj.2018.01.003>
- Yoshida, K., Kondoh, Y., Nakano, T., Bolortuya, B., Kawabata, S., Iwahashi, F., Nagano, E., & Osada, H. (2021). New Abscisic Acid Derivatives Revealed Adequate Regulation of Stomatal, Transcriptional, and Developmental Responses to Conquer Drought. *ACS Chemical Biology*, 16(8), 1566–1575.
<https://doi.org/10.1021/acscchembio.1c00451>
- Zhang, C., Simpson, R. J., Kim, C. M., Warthmann, N., Delhaize, E., Dolan, L., Byrne, M. E., Wu, Y., & Ryan, P. R. (2018). Do longer root hairs improve phosphorus uptake? Testing the hypothesis with transgenic *Brachypodium distachyon* lines overexpressing endogenous RSL genes. *New Phytologist*, 217(4), 1654–1666.
<https://doi.org/10.1111/nph.14980>
- Zhao, P., Wang, L., & Yin, H. (2018). Transcriptional responses to phosphate starvation in *Brachypodium distachyon* roots. *Plant Physiology and Biochemistry*, 122, 113–120.
<https://doi.org/10.1016/j.plaphy.2017.11.010>