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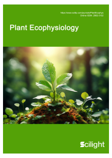

Review

Does Leaf Rolling Serve as a Phenotype Index for Drought Tolerance in Grasses? A Review

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Abstract: Leaf rolling is a distinct morphological response to drought stress observed in grasses, including major cereal crops such as rice, wheat, and maize. While parameters associated with leaf rolling are often proposed as potential criteria for screening and selecting drought-tolerant genotypes, their efficacy and reliability as definitive indicators of drought tolerance remain subjects of ongoing debate. In this review, we first summarize common patterns of leaf rolling and provide a critical overview of quantification methods, ranging from subjective visual scoring and simple indices like the leaf rolling index to objective morpho-geometric measurements, advanced image analysis techniques, and integrated or remote sensing approaches. We also summarize the significant inter- and intraspecific variations observed. Subsequently, we delve into the physiological mechanisms linking leaf rolling to both avoidance and tolerance. Recent evidence suggests a tight temporal correlation between the initiation of visible rolling and critical physiological thresholds, such as the bulk leaf turgor loss point and substantial stomatal closure. This supports the hypothesis that bulliform cells might act not only as the effectors executing the rolling movement but also as highly sensitive physiological sensors monitoring internal water status. Furthermore, the initiation phase of rolling—potentially governed by the sensory function of bulliform cells—may provide novel insights into physiological tolerance, even if the extent of rolling remains an equivocal trait for breeding selection. Finally, potential future research directions stemming from this analysis are also discussed.

Keywords: leaf turgor loss point; bulliform cells; quantifying leaf rolling; drought resistance

1. Introduction

Leaf rolling is a distinct morphological response observed in grasses, including major cereal crops such as rice, wheat, and maize, particularly under drought conditions (Fernandez & Castrillo, 1999; O'Toole & Cruz, 1980; Sirault, 2007). This adaptive mechanism involves the inward curling of the leaf blade along its central axis, effectively reducing the surface area exposed to the atmosphere and thereby mitigating water loss through transpiration (O'Toole, Cruz, & T. Singh, 1979). As such, leaf rolling in grasses is considered to serve as a drought avoidance strategy by conserving water through reduced transpiration and light interception (Kadioglu & Terzi, 2007).

Recently, several studies have suggested that leaf rolling may also function as a drought tolerance trait (Wang et al., 2023). The phenomenon, often assessed by measuring its degree, physiological impacts, or temporal dynamics (Baret et al., 2018), is considered to help plants conserve water. When leaves roll, they reduce the surface area exposed to the sun and wind, thereby decreasing water loss through transpiration. The timing and degree of leaf rolling can have various physiological implications for drought response, fundamentally impacting the water balance and metabolic processes of plants. For instance, delayed and light rolling is suggested as an indicator of higher drought tolerance (Jiang et al., 2021; Saglam et al., 2014), as a tolerant plant is expected to maintain cellular turgor and sustain photosynthetic activity under drought conditions. In contrast, a rapid and extensive rolling indicates that the plant is quickly succumbing to water stress, experiencing a significant loss of turgor pressure and a sharp decline in internal water status. However, its functional significance as a reliable index of drought tolerance remains a subject of debate, fueled by conflicting empirical findings (Cal et al., 2019; Li et al., 2022; Zhang et al., 2021). For instance, while some advocate for its use in screening drought-tolerant genotypes (Desta et al., 2025; Lafitte, Blum, & Atlin, 2003; Verulkar & Verma, 2014), other studies report inconsistent correlations between the extent of rolling and critical outcomes such as leaf water status (Cal et al., 2019). A major contributing factor to these discrepancies is the complex interplay of physiological mechanisms underlying leaf rolling in response to drought (Kadioglu et al., 2012).

This review aims to synthesize the current understanding of drought-induced leaf rolling in grasses, mainly in cereals. We explicitly exclude instances where leaf rolling is driven by structural traits under non-stress conditions, which are believed to play a significant role in enhancing light-use efficiency (Ali et al., 2022). The primary goal is to clarify the functional significance of drought-induced leaf rolling. To achieve this aim, we first examine common patterns, interspecific and intraspecific variations, and methodologies for quantifying leaf rolling status in response to drought. Furthermore, we analyze the physiological mechanisms underpinning leaf rolling and its relationships with both drought avoidance and tolerance traits, exploring how these interactions contribute to overall plant resilience under water-limited conditions. By emphasizing the ecophysiological implications, we seek to clarify the role of drought-induced leaf rolling as an index of drought avoidance and drought tolerance.

2. Characteristics and Dynamics of Drought-Triggered Leaf Rolling in Grasses

2.1. Common patterns of leaf rolling in response to drought

Grasses generally exhibit two distinct patterns of leaf rolling under drought conditions: adaxial rolling (inward toward the upper surface) and abaxial rolling (outward toward the lower surface; Figure 1C). The specific direction of rolling often depends on the relative abundance of the primary water-losing structures (stomata) and the position and function of specialized cells known as bulliform cells, which drive the rolling movement (Zou et al., 2014; Figure 1).

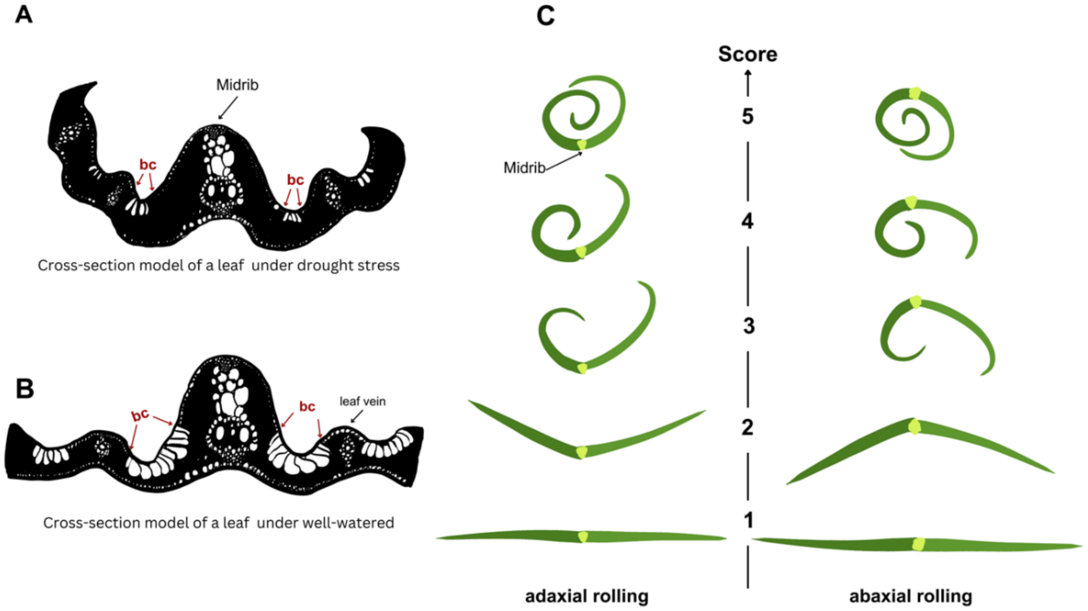

Figure 1. Leaf responses to water availability and a corresponding visual scale for quantifying leaf rolling. (**A**) Transverse anatomical view of a leaf under drought stress, characterized by pronounced adaxial rolling potentially driven by changes in bulliform cells (bc). (**B**) Comparative transverse section of a leaf under well-watered conditions, exhibiting a less curved profile. (**C**) A standardized 1-to-5 scoring system used to visually assess the severity of leaf rolling, illustrating different degrees of adaxial (inward) and abaxial (outward) curling. Key structures including the midrib, bc, and leaf vein are labeled in panels A and B.

Adaxial (inward) rolling is more common among grass species and is characterized by the leaf margins rolling or folding inward toward the adaxial surface of the leaf blade (Figure 1). This movement is typically orchestrated by rows of large, thin-walled epidermal cells—the bulliform cells—located predominantly on the adaxial surface (Mader et al., 2020; Xu et al., 2021). Under well-hydrated conditions, bulliform cells remain turgid, maintaining the leaf in a flattened, open state optimal for light interception and photosynthesis. However, as water deficit develops, these cells lose turgor pressure more rapidly than surrounding epidermal or mesophyll cells (Mader et al., 2020; Matschi et al., 2020). This loss of turgor causes the bulliform cells to shrink and inflate in bionic research, generating tension that pulls the leaf blade inward (Mader et al., 2020). In rice cultivar BY240 which exhibits reversible leaf rolling under water deficit, bulliform cells take part in the process of leaf curling, their function is bi-directional through turgor pressure regulation (Li et al., 2010). Inward rolling reduces the total leaf surface area exposed to environmental stresses such as intense solar radiation and desiccating winds. Moreover, it creates a pocket of relatively still, more humid air within the rolled leaf, thereby increasing the boundary layer resistance and significantly reducing water loss via transpiration through the enclosed adaxial stomata (Kadioglu & Terzi, 2007; O'Toole, Cruz, & T. Singh, 1979).

In contrast, abaxial rolling involves the leaf margins curling outward and downward, away from the adaxial surface and toward the abaxial (lower) surface. This pattern is generally less common across grass species. The mechanisms underlying abaxial rolling are more variable and less comprehensively understood than those of adaxial rolling (Li et al., 2010). Abaxial rolling may involve bulliform cells located on the abaxial surface or differential changes in cell turgor or cell wall properties between the upper and lower surfaces, resulting in outward curling (Zou et al., 2014). This pattern is often observed in grass species where stomata are predominantly located on the abaxial surface (Redmann, 1985). In such cases, outward rolling serves a similar protective function by shielding the primary sites of transpiration, thereby mitigating excessive water loss (Ali et al., 2022). Additionally, abaxial rolling may confer specific adaptive advantages under arid or high-radiation environments, where protection of the stomata-rich abaxial surface contributes to reduced water loss and improved drought tolerance (Latif et al., 2023; Toon et al., 2015).

2.2. Methods and indices in quantifying leaf rolling

Over the years, various methods have been developed to quantify leaf rolling, capturing different facets of this complex trait. These approaches range from simple visual assessments to sophisticated image analyses. Broadly, they can be categorized into subjective and objective methods (Table 1), each offering distinct advantages depending on the specific research context. The following sections detail these approaches, beginning with subjective techniques before exploring various objective methodologies based on geometric principles, image analysis, and integrated or remote sensing approaches.

Table 1. Summary of Common Methods and Indices for Quantifying Leaf Rolling Status. **(**LRI, Leaf Rolling Index; RA, Rolling Angle; CI, Curvature Index (often related to Curvature Radius); LAR, Leaf Area Reduction; CHP, Convex Hull Perimeter; WLR, Width-to-Length Ratio; RLV, Rolled Leaf Volume; PID, Pixel Intensity Distribution; FD, Fractal Dimension; STI, Stress Tolerance Index; CLIR, Canopy-Level Index of Rolling; NDVI, Normalized Difference Vegetation Index; CT, Canopy Temperature; LAI, Leaf Area Index).

Category	Index	Description	Advantages	Drawbacks	References
Visual Scoring	Leaf Rolling Score, LRI	Ordinal scale or percentage based on visual assessment	Simple, rapid, low-cost, field-scalable, high-throughput	Subjective, observer bias, low precision/sensitivity, potential inconsistency	O'Toole & Cruz 1979; Baret et al., 2018
Morpho-Geometric Methods	RA	Angle formed by the margins of the rolled leaf	Objective, quantitative shape data	Manual measures slow, precision may need imaging/cross-sectioning	King, Vincent, & Harris, 1996
	CI	Mathematical description/measure of leaf surface curvature (e.g., radius)	Objective, quantitative shape data, sensitive measure	Requires imaging or cross-sectioning for accuracy	Sirault et al., 2015; Hay et al., 2020; Liu et al., 2010
	LAR	Proportional decrease in projected leaf area due to rolling	Objective, quantitative area change, relatively intuitive	Can be confounded by non-rolling turgor changes, needs baseline	Kang & Huang, 2023
	CHP	Perimeter of the convex hull encompassing the leaf cross-section	Objective, integrates overall cross-section shape	Requires imaging/cross-sectioning, sensitive to image quality	Sirault et al., 2015
	WLR	Change in the ratio of leaf width to length upon rolling	Objective structure data, WLR relatively simple	Less descriptive than area/curvature metrics	Saruhan, Saglam, & Kadioglu, 2012; Puglielli, Gratani, & Varone, 2017
	RLV	Estimated volume occupied by the conformally changed leaf	Objective, captures 3D structural change	Difficult/destructive to measure accurately	Huang et al., 2024
Image Analysis Methods	PID, Edge Detection, FD	Metrics derived from digital image processing & computer vision	Precise, objective, non-invasive, automatable, high-throughput potential	Requires equipment, complex analysis/calibration, expertise needed, setup sensitive	Wang et al., 2024; Du, Zhai, & Wang, 2013; Gwo, Wei, & Li, 2013
Integrated Indices	STI, CLIR	Combined scores reflecting overall stress tolerance/response	Holistic tolerance view, combines multiple factors	Complex validation needed, weighting can be subjective, interpretation indirect	Fernandez, 1992; Baret et al., 2018
Remote Sensing Methods	NDVI, CT, LAI	Canopy-level indices reflecting vegetation status	Large-scale monitoring (field/region), non-invasive (area)	Indirect measure, confounded by canopy factors, specialized equip./expertise needed	Jiang et al., 2021; Cal et al., 2019; Lu et al., 2011; Berni et al., 2009; Garrigues et al., 2008; Asner, Scurlock, & Hicke, 2003

2.2.1. Subjective methods

Visual scoring systems remain among the most widely employed methods due to their simplicity, low cost, and suitability for rapid assessment of large populations, particularly under field conditions (O'Toole & Cruz, 1980). These systems typically employ a numerical scale (e.g., 0–5 or 0–9) that corresponds to predefined levels of rolling severity, enabling observers to assign scores based on visual inspection (Baret et al., 2018; O'Toole & Cruz, 1980). In addition to visual scores, the Leaf Rolling Index (LRI) offers a quantitative approach by calculating the proportion of leaves exhibiting rolling symptoms within a given sample (Gao et al., 2019). At the individual leaf scale, the one-dimensional (1D) method is commonly used to compute the LRI, which is defined as $LRI = [(Lw - Ln)/Lw] \times 100\%$, where Lw is the maximum width of the leaf when fully expanded, and Ln is the maximum width when the leaf is rolled (Shao, 2005). While practical for high-throughput screening, these methods are inherently subjective, leading to potential variability between observers and across time points, and they often exhibit reduced sensitivity to subtle differences in rolling degree (Hu et al., 2009). Efforts to standardize visual assessments commonly involve the use of diagrammatic guides to enhance scoring consistency.

2.2.2. Morpho-geometric methods

Objective quantification methods overcome subjectivity by using morpho-geometric indices derived from direct measurements or imaging techniques, quantifying physical changes in leaf shape and dimensions. Examples include the Rolling Angle (RA), which measures the angle formed by rolled leaf margins (King, Vincent, & Harris, 1996), and the Curvature Index (CI), describing the degree of leaf surface curvature (often based on calculating the radius of curvature from cross-sections or surface scans) (Hay et al., 2000; Liu et al., 2010; Sirault et al., 2015). Other metrics focus on the overall cross-sectional shape derived from imaging, such as the Convex Hull Perimeter (CHP), which represents the perimeter of the smallest convex shape enclosing the leaf's cross-section (Sirault et al., 2015). Leaf Area Reduction (LAR) quantifies the proportional decrease in visible or projected leaf area onto its maximum fitting plane upon rolling (Kang & Huang, 2023) while morphological indices like the Width-to-Length Ratio (WLR) and estimates of Rolled Leaf Volume (RLV) capture alterations in overall dimensions and structure (Huang et al., 2024; Puglielli, Gratani, & Varone, 2017; Saruhan, Saglam, & Kadioglu, 2012). Although these methods offer reproducible, quantitative data, obtaining high precision, particularly for CI, CHP, or RLV, often requires specialized imaging or careful cross-sectioning techniques. Furthermore, simpler metrics like width reduction used for LAR estimations may sometimes be confounded by environmental fluctuations influencing leaf turgor independently of the specific rolling response.

2.2.3. Image analysis-based methods

Recent advances in digital imaging and computational analysis have opened new avenues for precise and high-throughput quantification of leaf rolling. Image analysis-based indices leverage computer vision techniques to extract objective metrics from digital images. Methods such as Pixel analysis and Edge Detection Algorithms quantify rolling based on changes in leaf appearance, texture, or contour complexity (Gwo, Wei, & Li, 2013). Recent research has used deep learning algorithms, such YOLOv8, which directly analyze pixel data in leaf images to identify and classify leaf rolling. Wang et al. (2024) proposed LRD-YOLO, an improved object detection algorithm that examines pixel data to identify leaves and classify them as 'leaf' (unrolled) or 'rolled' according to established criteria such as the CIMMYT leaf rolling stages.

The Fractal Dimension (FD) of the leaf outline, which typically decreases as the projected shape simplifies with rolling, offers another quantitative metric (Du, Zhai, & Wang, 2013). These approaches provide high precision and non-invasiveness, with significant potential for automation in both laboratory and field settings using various imaging platforms (e.g., RGB, multispectral, 3D imaging). Easlon & Bloom. (2014) developed a method that utilizes a red calibration region of known dimensions within each image to accurately scale leaf area measurements, independent of camera distance or focal length, effectively serving as an internal scale. It calculates leaf area by comparing the number of green pixels corresponding to leaf tissue with the number of red pixels in the calibration zone, employing the formula: leaf area = (green pixel count) × (calibration area/red pixel count). However, they demand considerable investment in hardware, sophisticated image processing algorithms, careful calibration, and expertise in data analysis, and they can be sensitive to variations in lighting and perspective (Perez-Sanz, Navarro, & Egea-Cortines, 2017).

2.2.4. Integrated indices and remote sensing approaches

As remote sensing technologies are widely used in plant science, integrated stress indices and remote sensing techniques are increasingly adopted (Berger et al., 2022; Jiang et al., 2021). Integrated indices, such as the Stress Tolerance Index (STI) and Canopy-Level Index of Rolling (CLIR), synthesize leaf rolling data with physiological, morphological, or agronomic parameters—such as biomass and yield—to provide a holistic evaluation of drought tolerance (Baret et al., 2018; Fernandez, 1992). For instance, in rice, the cultivar IR64 exhibited the lowest STI value (0.22) and the highest leaf rolling score (6.3) during the reproductive stage, indicating its pronounced susceptibility to drought stress (Kumar et al., 2014). Furthermore, Baret et al. (2018) investigated the relationship between visual leaf-rolling scores in maize and alterations in canopy structure using digital hemispherical photographs to estimate the fraction of intercepted diffuse photosynthetically active radiation ($FIPAR_{dif}$). They proposed a CLIR that is normalized for differences in $FIPAR_{dif}$ observed when leaves are unrolled. The significant correlation between leaf-level rolling score and CLIR suggests that remote sensing methods could quantify changes in canopy architecture due to leaf rolling.

At larger spatial scales, remote sensing approaches, including drones and satellites, utilize indices such as the Normalized Difference Vegetation Index (NDVI), Canopy Temperature (CT), and Leaf Area Index (LAI) to infer changes related to leaf rolling at the canopy or field level (Asner, Scurlock, & Hicke, 2003; Berni et al., 2009; Cal et al., 2019; Garrigues et al., 2008; Jiang et al., 2021). In rice, the change in NDVI over measurement times (ΔNDVI) has been used to represent the degree of leaf rolling due to drought stress, which is based on the idea that as leaves roll, the canopy cover decreases, and NDVI values are also reduced. ΔNDVI was calculated as the difference between NDVI measurements on earlier and latter dates during drought stress, representing the reduction in NDVI due to stress-induced leaf rolling (Cal et al., 2019). Similarly, in maize, Lu et al. (2011) assessed ΔNDVI by comparing NDVI measurements taken in the morning and afternoon of the same day. They observed that NDVI values were significantly higher in the morning than in the afternoon under water stress, particularly in genotypes with severe leaf rolling. In contrast, genotypes without visual signs of leaf rolling exhibited minimal diurnal variation in NDVI. These findings underscore the utility of NDVI—particularly ΔNDVI—as a proxy for assessing leaf rolling in maize and rice under drought stress. However, it is crucial to acknowledge a limitation with ΔNDVI; namely, that changes in leaf angle or leaf shedding can produce effects on NDVI that are indistinguishable from those caused by leaf rolling, even in the absence of actual rolling. Therefore, while powerful for large-area monitoring, these remote sensing indices provide indirect estimates influenced by overall canopy structure and health, thus requiring careful interpretation and validation through ground-based observations (Berni et al., 2009). It is important to note that remote sensing techniques are indirect measurements and hence only allow for semiquantitative estimation of the actual leaf rolling state.

2.2.5. Considerations for method selection

The selection of an appropriate method for quantifying leaf rolling is largely contingent upon the specific research objectives, the spatial and temporal scale of the study, resource availability, and the desired balance between precision, throughput, and cost. Visual scoring remains advantageous for large-scale screening due to its simplicity and low cost, whereas geometric, morphological, and image-based analyses offer more detailed and objective insights into the physical characteristics of leaf rolling (Baret et al., 2018; Sirault et al., 2015). Integrated and remote sensing approaches allow for broader assessments of tolerance and large-scale monitoring. While these methods do not directly quantify leaf rolling, they can support the evaluation of associated canopy-level changes. In addition, a comprehensive understanding of the physiological implications of leaf rolling—such as its effects on photosynthesis and plant water relations—as well as its temporal dynamics, including the onset and recovery rates, can yield deeper insights into plant responses to abiotic stress (Wang et al., 2024). However, such assessments typically require specialized instrumentation and real-time monitoring protocols.

3. Intra- and Interspecific Variations of Leaf Rolling in Response to Drought

Leaf rolling in response to drought stress exhibits significant variability within species (intraspecific) and among species (interspecific). Intraspecific variation in leaf rolling as a response to drought is generally significant, reflecting both underlying genetic variation and phenotypic plasticity within a species. For instance, substantial intraspecific variation of *Oryza sativa* in leaf rolling has been investigated by several research groups, with studies showing differences based on plant type, such as tall varieties being more responsive than modern semi-dwarf ones, and dryland cultivars rolling at higher (less negative) leaf water potentials than wetland types (Jiang et al., 2021; Turner et al., 1986; Wang et al., 2023). Specific rice genotypes also exhibit considerable diversity in the leaf water potential thresholds that trigger rolling; for example, initial rolling thresholds varied from −1.04 MPa to −1.95 MPa among four genotypes studied by Wang et al. (2023), and genetic differences in leaf rolling under drought were suggested to be linked to morphological traits (e.g., leaf area, blade width, length, and dimensional ratios) (Cal et al., 2019). Furthermore, changes in physiology attributes characterize phenotypic plasticity. For example, osmotic adjustment to alter these leaf water potential thresholds, as demonstrated in the IR36 rice variety, is a physiological expression of phenotypic plasticity (Hsiao et al., 1984). Comparable intraspecific variation is evident in wheat, where the cultivar H45 exhibits a greater propensity to roll than Silverstar, a disparity attributed to differences in leaf morphology, particularly in transverse mean curvature (Sirault, 2007). Similarly, durum wheat cultivars show wide variability in leaf rolling scores under water-limited conditions, highlighting substantial genetic diversity for this trait (Amal et al., 2020). In maize, genetic variability is also apparent in differential rolling responses among cultivars. A drought-tolerant variety was observed to roll later and maintain higher leaf water potential compared to a drought-sensitive counterpart (Saglam et al., 2014). Additionally, maize exhibits phenotypic plasticity in its diurnal rolling patterns, which vary in response to climatic conditions and water availability. These responses are suggested to be linked to differential elastic stretching across the leaf blade, a process ultimately governed by leaf water potential (Baret et al., 2018).

Interspecific variation in leaf rolling has also been observed across different species and genera. However, a deeper understanding of the underlying physiological mechanisms and the precise linkage with leaf water status in an interspecific and evolutionary context is often lacking. For instance, distinct rolling patterns are observed between grass species like *Napier grass* (*Pennisetum purpureum*) and the *Brachiaria* hybrid cv. Mulato II, which shows more pronounced rolling even under milder drought conditions (Cardoso et al., 2015). Significant variation also exists between closely related species, such as within the *Oryza* genus, where *O. glaberrima* genotypes showed greater leaf rolling compared to *O. sativa* and interspecific hybrids (*O. sativa* x *O. glaberrima*) under the same drought stress condition (Efisue, 2006). Furthermore, broader surveys highlight differential use of this trait; among 18 C4 grass species studied by Jardine, Thomas, & Osborne (2021), leaf rolling was observed in some, like *Aeluropus lagopoides* and *Sporobolus indicus*, but was absent in others subjected to similar drought stress. While these studies clearly demonstrate intraspecific and interspecific differences in leaf rolling as a drought response, the absence of detailed physiological characterization, particularly regarding leaf water potential dynamics, limits the insights into the adaptive significance and evolutionary drivers of these diverse responses. This deficiency often restricts the conclusions to descriptive observations, hindering a comprehensive understanding of how varying degrees of drought impact the physiological state of different species and trigger their leaf rolling responses.

4. Linking Leaf Rolling to Drought Resistance

Drought resistance is a complex phenomenon that encompasses various plant strategies to cope with water deficit, which can be broadly categorized into drought escape, drought avoidance, and drought tolerance ("Down-to-Earth Drought Resistance," 2024). Drought escape refers to the capacity of a plant to complete its life cycle rapidly, thereby circumventing exposure to severe drought conditions. Drought avoidance involves minimizing water loss or enhancing water uptake during periods of drought. In contrast, drought tolerance reflects the physiological and biochemical adjustments that enable plants to maintain function and survive under drought (Fang & Xiong, 2015; Kooyers, 2015). As drought escape is apparently less directly linked to instantaneous morphological responses like leaf rolling, in the following sections, we summarize our current understanding of the links between leaf rolling and drought avoidance and tolerance strategies.

4.1. Leaf rolling as a drought avoidance mechanism

Leaf rolling is a widely studied response of many plants, especially grasses such as rice, maize, wheat, and sorghum, to water deficit and other environmental stresses (Sirault, 2007). The rolling response is commonly regarded as a drought avoidance mechanism because it aids in water conservation. By rolling inward, leaves reduce their exposed surface area to solar radiation, creating a microenvironment with increased humidity and great boundary layer resistance. This, in turn, lowers leaf temperature and by reducing VPD, it decreases transpiration rates, effectively minimizing water loss (Dingkuhn et al., 1989). Some studies on rice have demonstrated that leaf rolling occurs before stomata completely close, indicating that rolling plays a role in water conservation even before transpiration is fully halted (Wang et al., 2023). Artificially flattening the highly rolled leaves has been shown to increase the water loss rate by 14% to 68% (S. Singh, T. Singh, & Chauhan, 2011; Wang et al., 2023), whereas manually rolling flat leaves to their maximal rolling state can reduce water loss by 43% to 52% (O'Toole & Cruz, 1980; S. Singh, T. Singh, & Chauhan, 2011). In rice mutants with enhanced rolling phenotype under normal conditions, the leaf water loss rate decreased by 22% to 59% compared to wild-types (Wu et al., 2025; Zhang et al., 2021; Zhang et al., 2015). These findings underscore the effectiveness of leaf rolling in maintaining internal water status and mitigating dehydration damage during drought episodes. Notably, the response is reversible—leaves re-expand under favorable water conditions—allowing plants to dynamically regulate intercepted radiation based on environmental demands.

Beyond water conservation, leaf rolling also plays a role in photoprotection. Under water stressed conditions, when stomatal closure reduces CO_2 uptake, plants are at greater risk of photodamage due to excess absorbed light energy. Leaf rolling can mitigate this risk by reducing both irradiance and leaf temperature. For instance, Saglam et al. (2014). showed that rolled maize leaves were approximately 0.3~0.5 °C cooler than leaves physically constrained from rolling and experienced significantly lower photosynthetically active radiation (PAR) on the leaf surface. Importantly, their results suggested that by reducing light exposure, rolling may help prevent photodamage to the photosystem II (PSII) apparatus, thus preserving photosynthetic function even under stress. In *Ctenanthe setosa*, non-rolling (clamped) leaves exhibited reduced efficiency of PSII (ψ_{PSII}) and photochemical quenching (q_P), along with enhanced non-photochemical quenching (NPQ), in comparison to rolled leaves (Nar et al., 2009). Similarly, in sorghum, leaf rolling effectively prevented the midday decline in PSII efficiency observed in fully exposed leaves, indicating that leaf rolling serves as a photoprotective mechanism by limiting excessive light exposure and mitigating photoinhibition (Corlett et al., 1994).

4.2. Linking leaf rolling to drought tolerance

While traditionally regarded as a drought avoidance mechanism, leaf rolling is increasingly recognized for its close correlation with key physiological and biochemical traits underlying drought tolerance (Li et al., 2017; Zhang et al., 2021; Zhang et al., 2009). Recent studies, particularly in rice, reveal that leaf rolling is not an isolated morphological response but rather an integrated component of a coordinated suite of responses that govern plant water status and survival under drought conditions (Jiang et al., 2021; Wang et al., 2023; Zhang et al., 2021). A recent study demonstrates that a decline in leaf hydraulic conductance precedes major stomatal closure and the onset of leaf rolling in rice (Wang et al., 2023). In their study, the visible initiation of leaf rolling coincides temporally with significant stomatal closure (50–80%) (Wang et al., 2023). This alignment suggests that leaf rolling constitutes part of an integrated drought response system, operating synergistically with stomatal regulation, and might benefit preserving leaf water potential and reducing the risk of hydraulic failure and cellular viability damage, which benefits survival in severe drought and indirectly meaningfully contributes to drought tolerance. This mechanism may align with drought strategies across the isohydric–anisohydric continuum, where the more isohydric plant tends to preserve self-water status before deadly damage (Jardine, Thomas, & Osborne, 2021).

An important insight from the same study pertains to the timing of leaf rolling initiation. Specifically, visible rolling was observed to occur at a leaf water potential very close to the leaf turgor loss point (π_{tlp})—the threshold at which mesophyll cells lose turgor—suggesting that reductions in turgor pressure may occur simultaneously in bulliform and mesophyll cells. The mechanistic basis for this strong association might lie in the specialized function of bulliform cells, which regulate leaf rolling by inducing curvature through turgor-driven changes in their shape and volume. A key insight from recent research is the remarkable consistency observed across different rice genotypes between the leaf water potential triggering initial rolling and the potential at π_{tlp}, a widely accepted physiological index of drought tolerance (Wang et al., 2023). Based on the striking congruence between the water potential thresholds for these two distinct phenomena—the visible morphological change of rolling initiation and the underlying cellular dehydration point. Wang et al. (2023) proposed a compelling hypothesis regarding the function of bulliform cells. They suggest that these cells may serve a dual role, acting not only as mechanical effectors that generate curvature but also as highly sensitive detectors of tissue-water status (Figure 2). In this proposed model, progressive loss of turgor in bulliform cells would signal the approach of the π_{tlp}, thereby initiating leaf rolling before irreversible dehydration occurs.

Nevertheless, the sensor–effector hypothesis remains to be tested. Three questions are especially critical. (i) Does rolling confer an additional water-saving advantage once stomatal conductance has begun to decline? Experiments that physically prevent rolling while allowing normal stomatal regulation (e.g., gentle splints) are required to separate the contributions of the two processes to whole-leaf water loss. (ii) Is shrinkage of bulliform cells an active regulatory event or merely a passive hydraulic consequence of their exposed position and thin cuticle? Direct measurements of turgor pressure and aquaporin activity in bulliform versus mesophyll cells would clarify this issue. (iii) How large are water-potential gradients across the leaf blade at the onset of rolling? High-resolution psychrometric or Raman imaging approaches could reveal whether the adaxial epidermis, where bulliform cells reside, experiences lower water potential than the mid-rib region commonly sampled. Addressing these questions will determine whether the correlation between the onset of rolling and π_{tlp} reflects causal control or coincident responses to dehydration. Furthermore, the strong correlation identified by Wang et al. (2023) raises the possibility that observing the water potential at the onset of leaf rolling could serve as a valuable, potentially non-destructive proxy for estimating the physiologically critical π_{tlp} across different genetic materials, thereby aiding in the assessment of drought tolerance. However, further investigation across a wider range of species and environmental conditions would be needed to fully validate this proposed dual role and the utility of rolling initiation as a reliable physiological indicator.

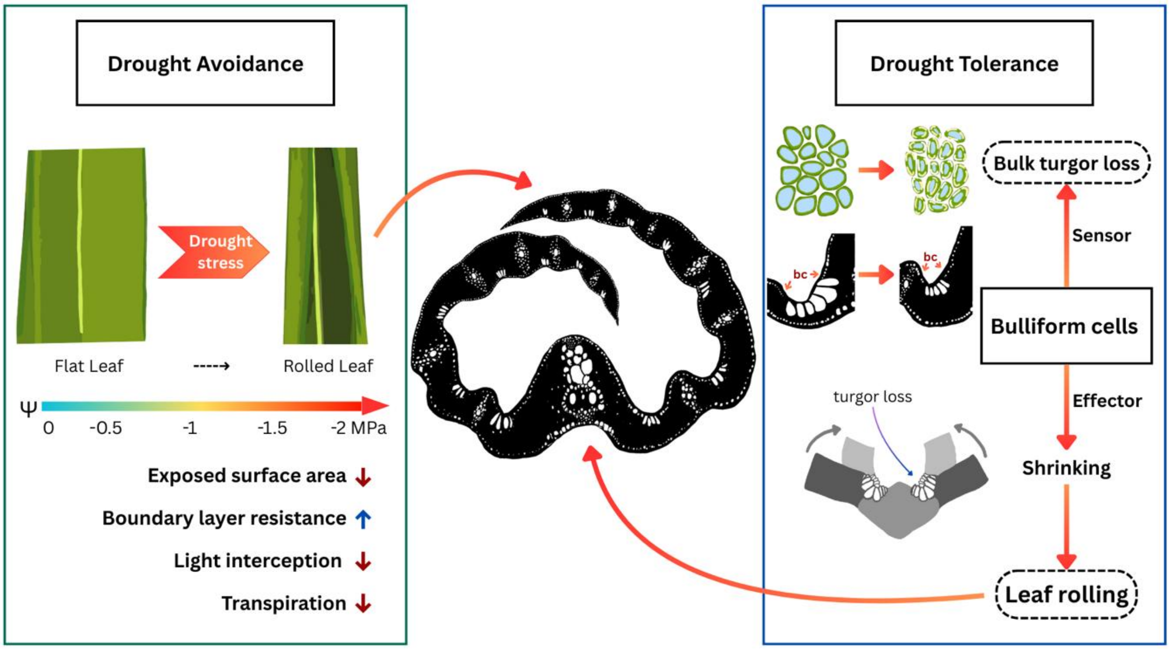

Figure 2. The dual function of bulliform cells (bc) in leaf rolling. Mechanisms of drought avoidance through leaf curvature and their role as sensors and effectors in enhancing drought tolerance.

The study by Wang et al. (2023) also mentioned that while leaf rolling does precede the π_{tlp}, stomatal conductance at 50% decline (g_{sw50}) also occurs prior to π_{tlp} for three of the four rice genotypes. More likely, the linkage of K_{leaf50} (leaf hydraulic conductance at 50% decline) and the timing of initial rolling can provide insight into thresholds and hydraulic function in the outside-xylem and bulliform regulation of leaf rolling. Further research is needed to clarify whether the regulation or decline of outside-xylem conductance drives greater changes in cell hydration and cell volume in bulliform cells relative to other cells. The study found that the leaf water potential threshold for a given functional trait differed significantly among genotypes, with the exception of leaf hydraulic conductance. It is not necessarily surprising that the genotypes did not vary much in their drought tolerance trait thresholds, as this suggests a coordinated response of these traits.

4.3. Evidence questioning a direct link between leaf rolling and drought resistance

Drought resistance means biomass or yield in grasses during drought, so it is frequently used in drought breeding programs (Vadez et al., 2024). Although leaf rolling is proposed to be a water conservation strategy under drought conditions, its correlations with drought resistance, especially concerning yield maintenance remains complex and often tenuous. This ambiguity has historically posed challenges for its use as a reliable selection criterion in crop improvement programs. One potential explanation, as argued by Blum. (2009), is that effective use of water (EUW), rather than mere water-use efficiency (WUE), constitutes the critical determinant of yield enhancement under drought stress. While leaf rolling enhances WUE by minimizing total water use, it may suppress biomass accumulation and, therefore, yield. In contrast, strategies aimed at maximizing soil moisture capture for transpiration and sustaining stomatal conductance are essential for optimal carbon assimilation and biomass production under limited water availability.

Several studies, including analyses of genetically diverse rice populations, have highlighted a weak or inconsistent correlation between leaf rolling and drought resistance (Cal et al., 2019; Lu et al., 2011). The work by Cal et al. (2019) on Aus and tropical japonica rice panels is a prominent example. Their findings across multiple field and greenhouse experiments indicated that leaf rolling scores (as well as the remote sensing related index, NDVI) were generally not correlated with drought resistance indicators such as the maintenance of shoot biomass or grain yield under water stress conditions. Instead, the study found that genetic variation in the propensity for leaf rolling under drought was more strongly linked to constitutive leaf morphological traits, especially in grasses (Baird et al., 2021). Particularly leaf width and length, rather than dynamic physiological parameters like leaf water potential, stomatal conductance, or canopy temperature in these populations. Supporting this, Al-Salman et al. (2023) found that wider sorghum leaves tend to have larger bulliform cells, which may enhance their capacity to regulate leaf rolling and limit desiccation under high transpiration demand. Similar associations between leaf width, bulliform cell development, and leaf rolling have also been observed in rice (Zou et al., 2011), suggesting a broader pattern across graminoid grasses. This suggests that in diverse germplasm, the observable degree of rolling that may reflect the leaf physical capacity to roll (influenced by its structure) is as much as, or more than, the plant's internal water status or its overall ability to sustain productivity under drought. Future studies that investigate if π_{tlp} is associated with the maintenance of shoot biomass or grain yield under water stress conditions are required to validate the π_{tlp}-centered mechanism.

This review proposes that leaf rolling in grasses may serve as a reliable indicator of drought tolerance, as it closely reflects the leaf turgor loss point. To further substantiate this hypothesis, future research should systematically examine the onset and intensity of leaf rolling in conjunction with other critical drought-related hydraulic traits, including leaf capacitance and bulk elastic modulus. In addition, comparative analyses with leaf-shedding responses will be essential to quantify the physiological trade-offs and yield implications of each strategy. These integrative insights will not only furnish plant breeders with more precise physiological targets and empirically grounded selection criteria for breeding drought-resilient ideotypes, but also help explain why leaf rolling has been largely excluded from contemporary breeding programs—primarily due to its weak correlation with yield under drought stress (Cal et al., 2019; Lu et al., 2011; Peleg et al., 2009). Moreover, some studies suggest that leaf rolling may not represent an adaptive mechanism, but rather a passive consequence of turgor decline (Matthews, Azam-Ali, & Peacock, 1990). Furthermore, rolling is associated with the decline in light interception, and stomatal conductance can severely constrain photosynthesis, ultimately compromising growth and yield under prolonged stress conditions.

5. Future Directions

As discussed herein, drought-induced leaf rolling in grasses has been extensively described; however, several key knowledge gaps continue to impede its effective integration into crop improvement strategies. Drought resistance mechanisms involve both avoidance and tolerance strategies. Dehydration avoidance is typically the primary target for improving productivity under drought conditions in most agricultural crops, though specific physiological processes such as grain filling phase may depend more on dehydration resistance. Future research has to elucidate the biophysical processes within bulliform cells that drive leaf rolling, develop robust high-throughput phenotyping techniques, and—most critically—dissecting the hydraulic and anatomical bases of leaf rolling to determine if it is mechanistically linked to drought tolerance. If such a link is established, it will be essential to assess how this trait can be utilized as a reliable screening index and whether it contributes to grain yield stability under the multifaceted drought condition encountered in agricultural systems.

To elucidate the driving forces behind rolling, research must delve into the biophysics of bulliform cells. This requires moving beyond correlations and employing cell-specific techniques, such as pressure probes (Zimmermann et al., 2008), continuous leaf psychrometers (Savage et al., 1983), and advanced microscopy (e.g., cryo-SEM), to directly measure turgor dynamics and stomatal closure relative to surrounding cells during dehydration and rehydration. Understanding the pathways of water loss and the molecular mechanisms governing turgor (e.g., aquaporins, ion channels) is essential for confirming their hypothesized role as sensors linked to the π_{tlp}. Moreover, upcoming research needs to examine the relationship of leaf rolling with key biophysical traits of leaf capacitance and bulk elastic modulus, which determine tissue water storage and ability to change shape upon drought stress. Such parameters may account for the diversity in rolling sensitivity and recovery trajectories among species or genotypes. Comparisons with other drought avoidance mechanisms, i.e., leaf shedding, are also necessary. While rolling reduces water loss by reducing surface area and transpiration, it may impair carbon assimilation. Shedding, which eliminates transpiring surfaces altogether, can protect plant water status at the cost of photosynthetic potential. An understanding of the physiological compromises and environmental conditions under which one strategy is preferable to the other is necessary to evaluate their relative effectiveness in sustaining yield during water shortage.

Concurrent development of robust, high-throughput phenotyping techniques is crucial for large-scale studies and breeding applications. Current methods, especially subjective visual scoring, lack consistency. Future efforts should focus on automated systems using advanced imaging (including 3D) and artificial intelligence to quantify not just the maximum degree but also the dynamics of rolling (onset rate, recovery rate) accurately and efficiently across large populations. Standardizing protocols and validating these high-throughput methods against key physiological parameters are necessary prerequisites. Refining remote sensing approaches also requires careful ground-truthing to ensure they reliably capture rolling status and its physiological implications at the canopy or field scale, isolating the rolling signal from other stress responses.

Most critically, research must rigorously determine if leaf rolling provides a mechanistic contribution to drought tolerance beyond basic water avoidance. This requires experiments, potentially using near-isogenic lines, genotypes where rolling can be manipulated, diverse species within genera, and across species from distinct genera and grass subfamilies to isolate its specific impact on plant survival, physiological function, and growth under drought stress. Understanding the metabolic costs and trade-offs associated with rolling is also vital. Evaluating rolling responses across diverse genotypes under various drought scenarios and interacting other environmental factors within relevant ecological and site-specific contexts will help clarify when and how rolling contributes adaptively (Tardieu, Simonneau, & Muller, 2018). Additionally, establishing whether the timing of rolling initiation serves as a more reliable indicator than the degree of rolling is a key part of this assessment.

Finally, if a clear mechanistic link between leaf rolling and enhanced drought tolerance is firmly established, subsequent research must focus on its practical application. This involves developing reliable, efficient screening protocols based on the most informative aspect of the rolling trait (e.g., initiation threshold or dynamics). Crucially, validation studies will be needed to confirm whether selection for this optimized rolling trait translates into improved and stable grain yield under the complex, variable drought conditions typically experienced in farmers' fields across different genetic backgrounds and target environments.

Author Contributions

NC wrote the first draft along with inputs from XW, SL and DX, DX developed the initial concept of the manuscript. All authors contributed to writing, editing, and figure preparation and agreed to the final version of manuscript. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement

Not applicable.

Conflicts of Interest

Authors declare that they have no competing interests.

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