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# Water Use Efficiency in Crop Plants: Advances, Challenges and Breeding Opportunities

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Water scarcity is a major constraint to global crop productivity, necessitating innovative breeding strategies to enhance water use efficiency (WUE) in crop plants. Traditionally expressed as biomass or yield per unit of water consumed, WUE is a complex trait influenced by physiological, morphological and genetic factors and their interaction with the environment. Key components influencing crop yield under water-limited conditions, including transpiration efficiency, root architecture, canopy development, harvest index and carbon isotope discrimination ($\Delta^{13}C$), are discussed. Advances in conventional and molecular breeding, high-throughput phenotyping and genomic tools have enabled more precise selection for WUE-related traits. The review underscores that improving effective water use, rather than maximising WUE alone, is central to achieving stable yields. Future breeding efforts must integrate physiological insight with modern genomics to develop climate-resilient, water-efficient crop cultivars.

**Keywords:** Water Use Efficiency, Plant breeding, Carbon isotope discrimination ($\Delta^{13}C$), Assimilation-to-transpiration ratio (A/T).

## Introduction

The slogan "More crop per drop" (Kijne *et al.*, 2003) gained prominence as a guiding concept for crop improvement under water-limited environments, particularly in scientific discourse. Although appealing and easy to communicate, the phrase can be misleading when applied to plant breeding, especially in rainfed agriculture. It has fostered the assumption that genetic gains in yield under water scarcity can be achieved simply by increasing production per unit of water consumed. This interpretation has also contributed to the mistaken belief that higher water-use efficiency (WUE) inherently reflects drought tolerance or superior yield performance under stress. While management interventions such as improved soil fertility and agronomic practices can indeed enhance productivity per unit water, genetic improvement follows a far more complex pathway. Therefore, this review focuses specifically on the genetic and physiological aspects of improving crop performance in water-limited environments, rather than providing a comprehensive treatment of WUE as a whole (Condon *et al.*, 2004).

Extensive use of carbon isotope discrimination (Δ) has improved understanding of the relationships among transpiration efficiency (TE), water-use efficiency (WUE) and yield under different water regimes. However, Δ reflects leaf-level TE rather than whole-crop WUE and its interpretation has often been misleading. Across crops and environments, relationships between Δ and yield are highly inconsistent, ranging from positive to negative or no association at all, and are frequently influenced by traits such as phenology, plant height or harvest index. This variability shows that WUE is not a reliable or universal indicator of productivity or drought resistance in rainfed systems, although it remains useful for saving irrigation water. Evidence from several crops demonstrates that drought-resistant genotypes often have deep and dense root systems that maintain transpiration and water uptake, resulting in high biomass but low WUE.

Consequently, favourable plant water status under drought is usually associated with low WUE. Genetic variation in WUE under limited water is driven more by differences in water use than biomass production, meaning that selection for high WUE often favours traits that restrict water use, such as early flowering or small leaf area. Such strategies improve yield only in environments with stored soil moisture. Overall, drought resistance is frequently linked with low WUE and selecting solely for high WUE may inadvertently favour drought-susceptible genotypes under water-limited conditions.

## Water Use Efficiency as a breeding target

Breeding for water-related traits requires a clearly defined goal and the identification of heritable traits that contribute to that goal. Water-use efficiency (WUE) can be defined differently depending on the level of measurement. At the physiological level, WUE refers to the amount of carbon fixed in photosynthesis per unit of water lost through transpiration (A/T). In contrast, farmers and agronomists are concerned with agronomic WUE, which is the harvested yield produced from the total water available to the crop through rainfall or irrigation. Although agronomic WUE is the ultimate breeding objective, it can be better understood by breaking yield into key components: total water used by the crop (ET), the fraction of that water used in transpiration (T/ET), the efficiency with which transpired water produces biomass (W), and the proportion of biomass converted into grain, known as harvest index (HI). These components are interrelated, but each offers potential for genetic improvement. Leaf-level WUE (A/T) is most directly related to transpiration efficiency (W), yet it can also influence ET, T/ET and HI indirectly (Sheshshayee *et al.*, 2003). A physiological perspective, A/T depends on the balance between $CO_2$ uptake and water loss through stomata. It can be improved either by reducing internal $CO_2$ concentration relative to the atmosphere (Ci/Ca) or by lowering the vapour pressure gradient driving transpiration. Thus, leaf-level traits can contribute to yield, but only when aligned with whole-crop water use and partitioning processes.

## Role of $\Delta^{13}C$ on WUE

Recent research shows that improving agronomic water-use efficiency through breeding is possible by targeting specific plant traits. However, the success of any trait depends strongly on the environment in which the crop is grown. For example, a high assimilation-to-transpiration ratio (A/T) may increase yield in certain environments but may have little benefit or even reduce yield in others. In wheat, selection for high A/T using low carbon isotope discrimination ($\Delta^{13}C$) in well-watered plants has led to the development of high-yielding varieties in eastern Australia. These varieties were bred for regions where crops rely on stored soil moisture, and careful use of water early in the season is essential for good seed formation and grain filling. In contrast, in Mediterranean-type and irrigated environments, higher yields are often linked with high $\Delta^{13}C$ values, which are associated with rapid early crop growth and quick leaf area development that shades the soil and reduces evaporation losses (Sheshshayee *et al.*, 2003). Selection strategies promoting fast leaf area expansion have proven effective in Mediterranean environments. Combining rapid early growth with high A/T could further improve yields in rainfed systems, although genetic links between high vigour and high $\Delta^{13}C$ may complicate breeding efforts, particularly in wheat. The usefulness of such trait combinations depends on the timing and severity of water stress and how A/T is influenced by stomatal behaviour or photosynthetic capacity. Simple methods now exist to measure these traits. In groundnut, high A/T improves biomass but may reduce harvest index (HI). Progress has been achieved by selecting simultaneously for high A/T and high HI, though better understanding of this relationship could further accelerate breeding gains (Blum, 2009).

## Why to optimize WUE in crop breeding?

1. **Trait-environment interaction**: The effectiveness of breeding for specific traits, like high A/T (assimilation/transpiration ratio), depends on the crop's environment, as some traits benefit yield in certain conditions but may be detrimental in others.
2. **Successful breeding in wheat**: Low-$\Delta^{13}$C selection has led to high-yielding wheat varieties in eastern Australia, optimising water use by managing stored soil moisture for seed set and growth.
3. **Mediterranean and irrigated systems**: In Mediterranean-type and irrigated environments, high-$\Delta^{13}$C is linked to fast crop growth and better soil shading, enhancing yield potential.
4. **Challenges and future strategies**: Combining high early vigour with high A/T in wheat may be difficult due to genetic correlations, but success in crops like groundnut, where A/T is linked to biomass but negatively to HI, suggests targeted breeding can improve outcomes.

## Role of $CO_2$ in Water-Use Efficiency (WUE)

$CO_2$ plays a critical role in determining Water-Use Efficiency (WUE) in plants, which is the ratio of carbon gained (photosynthesis) to water lost (transpiration). Here's how:

1. **Stomatal regulation & transpiration:** Plants take in $CO_2$ through stomata, which also leads to water loss *via* transpiration. Higher atmospheric $CO_2$ levels cause partial stomatal closure, reducing water loss while maintaining or even increasing carbon assimilation.
2. **Photosynthesis enhancement:** Increased $CO_2$ concentration boosts photosynthetic rates, leading to higher biomass production. C3 plants (*e.g.*, wheat, rice, pearl millet) benefit more from elevated $CO_2$ than C4 plants (*e.g.*, maize, sorghum) because they are more limited by $CO_2$ availability.
3. **Impact on Water-Use Efficiency (WUE)**: Elevated $CO_2$ generally improves WUE by increasing carbon gain per unit of water lost. This effect is more pronounced in water-limited environments, where plants optimize water conservation while maintaining productivity.
4. **Long-term adaptations & breeding considerations:** Future crop breeding programs may leverage $CO_s$-driven WUE improvements. Selecting for traits like high A/T ratios (carbon assimilation to transpiration) and efficient stomatal responses can further optimize WUE under changing climatic conditions.

## Breeding strategies to improve Water-Use Efficiency (WUE) in plants (Blum, 2009)

Improving Water-Use Efficiency (WUE) through breeding involves selecting traits that optimize carbon assimilation (photosynthesis) while minimizing water loss (transpiration). Here are key breeding strategies:

**1. Selection for high A/T ratio (Assimilation/Transpiration):** Targeting low-$\Delta^{13}$C (carbon isotope discrimination) in C3 crops like wheat, which correlates with higher WUE. Used successfully in wheat breeding for drought-prone regions (*e.g.*, Australia).

**2. Optimizing stomatal traits:** Breeding for partial stomatal closure under high $CO_2$ conditions to reduce transpiration without limiting photosynthesis. Selection for stomatal density and size to optimize water loss regulation.

**3. Enhancing root architecture:** Developing deep-rooted genotypes to access deeper soil moisture. Selecting for efficient water extraction and retention in root systems.

**4. Improving canopy & leaf traits:** Breeding for faster leaf area development to shade the soil and reduce evaporation. Selecting for leaf waxiness and reduced cuticular water loss to improve drought tolerance.

**5. Integrating photosynthetic efficiency:** Improving Rubisco efficiency and $CO_2$ assimilation rates in C3 plants. Enhancing C4 photosynthesis traits in C3 crops through genetic engineering.

**6. Harnessing genetic & genomic approaches:** Marker-assisted selection (MAS) for WUE-related genes; Genome editing (CRISPR-Cas9) to fine-tune stomatal function and root traits.
**7. Crop-specific strategies:** In Mediterranean crops, breeding for fast early growth and high transpiration efficiency to maximize soil moisture use. In groundnuts, simultaneous selection for high A/T and high Harvest Index (HI) to balance biomass production and grain yield.

## Importance of improving water-use efficiency (WUE)

Enhancing Water-Use Efficiency (WUE) in plants through breeding is crucial for sustainable agriculture, food security, and climate resilience. Here's why:
**1. Ensuring crop productivity in water-limited areas:** Drought and water scarcity threaten agricultural yields, especially in arid and semi-arid regions. Improved WUE enables crops to produce more biomass and grain per unit of water consumed, ensuring stable yields under water-limited conditions.
**2. Climate change adaptation:** Rising temperatures and erratic rainfall patterns increase the frequency of drought stress in major cropping areas. WUE-focused breeding helps crops cope with changing climatic conditions by optimizing water uptake and conservation.
**3. Sustainable water resource management:** Agriculture accounts for ~70% of global freshwater usage; developing high-WUE crops reduces irrigation demand, preserving groundwater and freshwater sources for future generations.
**4. Enhancing food security & economic stability:** Efficient water use ensures consistent crop production, reducing reliance on unpredictable rainfall. Helps smallholder farmers in drought-prone areas maintain stable incomes and food supply.
**5. Reducing environmental impact:** High-WUE crops lower soil erosion and salinity issues by reducing excessive irrigation. Minimizes the carbon footprint associated with water-intensive irrigation systems.
**6. Increasing agricultural efficiency with limited resources:** Water-efficient crops enable higher productivity on marginal lands where water availability is restricted. Supports sustainable rainfed agriculture, reducing dependency on irrigation infrastructure.

## Challenges in breeding for Water-Use Efficiency (WUE)

Despite its importance, breeding for improved Water-Use Efficiency (WUE) presents several challenges:
**1. Complex genetic control:** WUE is controlled by multiple genes interacting with environmental factors. Identifying and isolating key genes for WUE improvement is difficult.
**2. Trade-offs between WUE & yield:** High WUE often results in slower transpiration, which can limit nutrient uptake and photosynthesis, potentially reducing yield. In some cases, traits that improve WUE may also slow crop growth and biomass accumulation.
**3. Environmental variability & trait expression:** WUE-related traits behave differently under varying soil moisture, temperature and humidity conditions. A trait beneficial in one environment may be ineffective or even detrimental in another.
**4. Difficulty in measuring WUE efficiently:** WUE assessment requires advanced physiological measurements like carbon isotope discrimination ($\Delta^{13}C$) and gas exchange analysis, which are time-consuming and expensive. Large-scale screening of WUE traits in breeding programs is logistically challenging.
**5. Stomatal behaviour & photosynthetic constraints:** Breeding for partial stomatal closure (to conserve water) may reduce $CO_2$ intake, potentially limiting photosynthesis and biomass production. Striking the right balance between stomatal regulation and carbon assimilation is complex.
**6. Long breeding cycles & genetic bottlenecks:** Developing high-WUE varieties through conventional breeding is time-intensive, requiring multiple generations. Limited genetic variation in domesticated crops restricts breeding potential for further WUE improvements.
**7. Adaptation to different cropping systems:** WUE strategies vary across rainfed, irrigated, and arid cropping systems; a single breeding approach may not be universally effective for different environments.

**8. Challenges in transferring WUE traits to major crops:** Some high-WUE traits from wild relatives or minor crops are difficult to transfer into staple crops (wheat, maize, rice) without negatively affecting other agronomic traits. Genetic modification (GM) and CRISPR offer potential solutions but face regulatory and public acceptance challenges.

## Future thrusts to improve WUE through breeding

To enhance Water-Use Efficiency (WUE) in crops, future breeding strategies must integrate advanced genetics, precision agriculture and climate resilience. Key focus areas include:

**1. Advanced genomic approaches:** Genome editing (CRISPR-Cas9) to fine-tune genes controlling stomatal function, root architecture and photosynthesis. Marker-assisted selection (MAS) for rapid identification and breeding of WUE-related traits. Speed breeding to accelerate the development of high-WUE varieties.

**2. Breeding for climate-resilient crops:** Developing crops with high WUE under elevated $CO_2$ and rising temperatures. Enhancing drought-tolerant genes to improve survival under extreme water stress. Selecting flexible transpiration rates to optimize water use in variable environments.

**3. Root system optimization for water absorption:** Breeding deep-rooted crops to access subsoil moisture in dry conditions. Improving root hydraulic conductivity for efficient water uptake. Microbiome-assisted breeding, using beneficial soil microbes to enhance root efficiency.

**4. Photosynthesis enhancement for higher WUE:** Improving Rubisco efficiency to enhance carbon assimilation with less water loss. Introducing C4-like traits into C3 crops to boost water-use efficiency. Genetic engineering for higher mesophyll conductance to increase $CO_2$ uptake.

**5. High-throughput phenotyping & AI integration:** Drones, remote sensing and AI for real-time monitoring of WUE traits in field trials. Using machine learning models to predict high-WUE genotype performance under different conditions. Smart breeding programs integrating phenotypic and environmental data for precision selection.

**6. Multi-trait selection for sustainable yield:** Combining high WUE with high biomass production to maintain yield potential. Selecting for stomatal behaviour, leaf anatomy, and rapid leaf area expansion in dryland crops. Integrating WUE traits with pest and disease resistance to ensure robust crop performance.

**7. Farmer-centric & region-specific breeding:** Developing location-specific varieties tailored to different rainfall patterns and soil types; Participatory breeding involving farmers and local communities for adoption of high-WUE crops; Strengthening seed distribution networks for WUE-improved cultivars.

## Conclusion

Water-use efficiency (WUE) is a valuable but complex concept in crop breeding and it cannot be treated as a simple substitute for drought tolerance or yield stability under water-limited conditions. Evidence clearly shows that high WUE, particularly when assessed through leaf-level traits or $\Delta^{13}C$, does not consistently translate into higher yield across environments. In many rainfed systems, drought-resistant genotypes achieve superior performance through greater water capture and sustained transpiration rather than conservative water use. Therefore, breeding efforts must move beyond the slogan "more crop per drop" and focus on understanding how water use, biomass production, and harvest index interact within specific environments. Optimizing, rather than maximizing, WUE is essential for improving crop productivity under diverse water regimes.

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