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Review Article

Radiation Use Efficiency: Unrevealing its Potential for Crop Yield Optimization

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Abstract

Radiation Use Efficiency (RUE) refers to how efficiently plants capture solar energy through their canopy and convert it into biomass or grain. Crop yield is determined by three factors: the amount of intercepted radiation (IR), radiation use efficiency, and the harvest index (HI). Significant efforts have been made to enhance IR and HI in crop breeding, but these have nearly reached their limits. Therefore, improving RUE presents another promising avenue for increasing yield. Currently, RUE in crops ranges from 2-3%, leaving considerable room for improvement in crop breeding. RUE varies across different species and crops, with C3 crops generally having lower RUE compared to C4 crops. RUE is influenced by radiation interception, which is in turn, affected by incoming radiation and the traits that contribute to photosynthesis. However, the availability of these comprehensive information on RUE is still scanty. Hence, the present review compiles various physiological, molecular, anatomical, biochemical and agronomical approaches which can be used for improving RUE. This compiled information will be useful for researchers and breeders for improving RUE in various crops for increasing yield to meet the future food demand.

Abbreviations

IPAR: Intercepted Photosynthetically Active Radiation

fAPAR: Fraction of Absorbed Photosynthetically Active Radiation

APAR: Absorbed Photosynthetically Active Radiation

HI: Harvest Index

Key words: Radiation use efficiency, Crop improvement, Photosynthetically active radiation , C3 crops, C4 crops, Canopy orientation

1. Introduction

The current rates of increasing crop yield are insufficient to meet the global food demands anticipated by 2050 (Grafton *et al.,* 2015; Roy *et al.,* 2024). In 2023, approximately 733 million people experienced hunger, representing about one in every eleven individuals worldwide, according to the most recent State of Food Security and Nutrition in the World (SOFI) report (FAO, 2024). To feed the growing population, we must either expand agricultural land for crop cultivation or enhance crop yields on existing farmland. Extreme weather events driven by climate change have reduced arable land through soil degradation, and additional shifts in dietary choices have a detrimental

effect on agricultural output (Dawson *et al.,* 2016; Yuan *et al.,* 2024). Agronomic techniques and advancements in the harvest index (HI) have been largely responsible for the growth in agricultural productivity since the Green Revolution (Fischer *et al.* 1998). Conversely, source-related characteristics like as increased stomatal conductance and photosynthetic rate have been linked to improvements in crop output (Fischer *et al.,* 1998; Fischer, 2007; Yu Wang, 2024). Other photosynthesis-related parameters, including biomass (above ground), radiation use efficiency (RUE), stem water-soluble carbohydrate content (WSC), and crop growth rate (CGR), have been linked to increased yield in various crops (Shearman *et al.* 2005; Aisawi 2011).

RUE (g MJ^{-1}) is widely used to estimate the efficiency of photosynthesis, biomass accumulation and yield of crops. RUE is calculated as the amount of dry matter produced over a specific time period per unit of intercepted radiation, and it is frequently divided in important developmental stages of the crop's life cycle. The slope of the relationship between the amount of crop biomass accumulated and the amount of radiation collected represents the RUE. It changes more between years than within a growing season across a variety of management variations, as observed in corn and soybean (Hatfield, 2014). Plant productivity in terms of primary production of biomass is simply a measure of the total photosynthesis of the plants subtracting respiration, which occurred during its growth (Mukherjee *et al.,* 2014). The accessibility of these radiation dynamics is associated with the leaf area index (LAI) and crop canopy characteristics in order to maximise the crop yield. Thus, both photosynthetically active radiation (PAR) and RUE are the key players in crop growth, development and in improving overall crop productivity. Furthermore, increasing photosynthesis at the single-leaf level would be a beneficial goal for raising agricultural productivity and output, as seen by the high positive association found between photosynthesis at the leaf level, total plant dry mass, and grain production (Yamori *et al.,* 2016). Similarly, improving the vertical distribution of photosynthetic resources and optimising the architecture of the canopy will increase RUE. At crop level RUE will be enhanced by prolonging the canopy cover duration attained by early vigour and stay green types while concurrently reducing crop respiration losses (Yin and Struik, 2015). There are several external and internal factors which affect RUE. External factors include environmental factors such as radiation, temperature, air humidity and fertilisers along with plant's nutritional and water status (Stöckle and Kemanian, 2009), internal factors includes plant morphology, leaf traits and plant processes (Fig. 1).

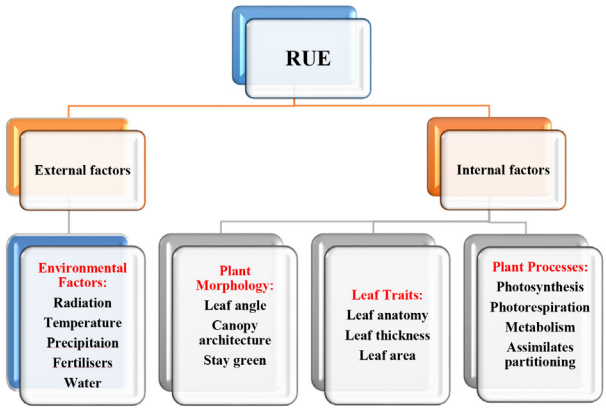

Fig. 1: Different factors affecting radiation use efficiency.

Crop production in every farming system depends largely on the interception of PAR of the crop canopy and the conversion of collected radiation into biomass (Yuan *et al.,* 2020) while the area of arable land has been declining for decades due to damage caused by erosion, pollution, sea level rise, urban development, soil salinization, and water scarcity driven by global climate change. In order to overcome this conflict, there is an urgent need to adapt conventional agriculture to water-limited and hotter conditions with plant crop systems that display higher water-use efficiency (WUE). It has been revealed that the amount of dry matter produced is linearly related to the amount of PAR that crop absorbs (Monteith, 1972). The intercepted PAR is the most important factor in crop growth and 39% of extra terrestrial solar energy is in 400700 nm wavelength range (Gueymard, 2004). RUE, is a fundamental measure based on resource use efficiency which has been employed in crop growth studies (Stöckle and Kemanian, 2009). According to Sadras *et al.,* (2016), photosynthesis accounts for the majority (85–90%) of the dry matter accumulated in a crop. The energy efficiency of photosynthesis, i.e. the ratio of energy stored in chemical form and incoming solar radiation, which has a maximum value of around 6 %, but actual efficiency in agricultural crops usually, does not exceed 2–3% (Geeta *et al.,* 2022). The leaf absorbs 85–90% of the PAR, with the remaining 15 % is reflected or transmitted. RUE is important in plant physiology because of its strong connection with

yield, which explains around 40% of its variability and highlights the roles of light capture and key plant processes connected to leaf biochemistry that drive biomass and yield (Hubbart *et al.* 2018; Molero *et al.* 2019). Enhancing RUE, which is less than half of its theoretical maximum, remains a major challenge in increasing yields for many key food crops (Slattery and Ort, 2015). However, the comprehensive information on different approaches to improve RUE are still scanty. Hence, this review aims to compile physiological, molecular, anatomical, biochemical, agronomical, and plant breeding approaches to improve RUE. This knowledge can assist researchers in various crop improvement programs to enhance yield.

2. Approaches to improve RUE

2.1. Physiological approaches

Increasing RUE is more easily attained through increased photosynthetic capacity and efficiency (Furbank *et al.,* 2020). The radiation intercepted by a plant is affected by leaf angle, leaf surface properties, leaf thickness, chlorophyll concentration, leaf phyllotaxy, vertical stratification of crop, and radiation distribution. Targets for traits engineering includes Rubisco improvement, increased Rubisco expression (Salesse-Smith *et al.,* 2018), reduction of photorespiration, CO_2 concentrating mechanisms (Long *et al.,* 2015; Von Caemmerer *et al.,* 2012), photorespiratory bypasses (Shen *et al.,* 2019; South *et al.,* 2019) etc. Increased expression of the thylakoid cytochrome b6f complex for ATP production (Ermakova *et al.,* 2019; Simkin *et al.,* 2017), enzymes crucial for ribulose-1,5-bisphosphate (RuBP) and sedoheptulose bisphosphatase regeneration (Driever *et al.,* 2017; Lefebvre *et al.,* 2005), and adjustments to photoprotection mechanisms may also enhance the RUE (Kromdijk and *et al.,* 2016). Recently attempts have been made for improving the functionality and effectiveness of light harvesting by increasing the absorption spectrum (by around 25 nm) in the near infra-red range that improved the RUE (Elias *et al.,* 2021; Giraldo *et al.,* 2014). The use of alternative pigments can be used to enhance the wavelength of light absorbed by plants, and additionally to optimise light interception and use (Slattery and Ort, 2021). Modification of mesophyll conductance and stomatal conductance provide better access of CO_2 to Rubisco has also been explored as an engineering target using proposed CO_2 porins to improve RUE (Condon, 2020; Groszmann *et al.,* 2017).

The fractions of incident radiation at various depths in the canopy profile have also increased with year of cultivar release in the case of wheat varieties representing five decades of breeding in Australia, which have favoured the RUE of individual leaves (Sadras *et al.,* 2016). The most crucial stage for determining RUE is between stem elongation and anthesis stage. In this instance, lightsaturated photosynthesis and respiration measured in the flag leaf at anthesis were unrelated to year of cultivar release (Sadras *et al.,* 2012). Giunta *et al.,* (2009) observed that triticale has higher RUE than durum wheat, which could be due to the higher stomatal conductance of triticale. Major plant functions like transpiration and photosynthesis are influenced by the quantity and quality of light. Triticale produced more biomass than durum wheat with comparable amounts of radiation intercepted and water used due to its higher RUE and higher stomatal conductance in pre-anthesis (Motzo *et al.,* 2013). Despite having a similar transpiration efficiency at the leaf level, triticale had higher transpiration efficiency at the crop level. Zhang *et al.* (2020) proposed that, ear photosynthesis, along with proper spike light interception and RUE needs to be incorporated into crop models.

2.2. Anatomical approaches to improve RUE

Kranz structure and vein thickness are expected to improve the working of C4 chemistry into the C3 framework (Feldman *et al.,* 2014; Mckown and Dengler, 2007; Smillie *et al.,* 2012). All C4 crop plants show decreased mesophyll:bundle sheath cells proportion which shortens the way length of photosynthesis and speeds up quick dispersion of metabolites (Mckown and Dengler, 2007). According to these studies, high vein thickness is regarded as an essential component of the photoassimilate movement. To foster C4 rice, Worldwide C4 Rice Consortium was laid out in 2006 and extended that 15 years of trials will be expected to present C4 pathway which is not considered to accomplish by customary rearing methodologies (Mitchell and Sheehy, 2008). Venation patterns might affect how C4 metabolism is incorporated into C3 plants. In order to engineer venation patterns in C3 crops, potential regulators of C4 vein density operating early in vascular development can be explored (Kumar and Kellogg, 2019; Rizal *et al.,*

2015). According to Lundgren *et al.,* (2019), developmental proliferation of veins can be sufficient with the required morphological preconditions to establish a viable C4 leaf morphology, providing an evolutionary entry point into sophisticated C4 metabolism which intern can be used to improve RUE in crops.

2.3. Molecular approaches to improve RUE

Molecular approaches include the identification of genes and QTLs associated with the different processes which contributes to RUE. In wheat Molero *et al.* (2018) has identified 94 single nucleotide polymorphisms (SNPs) through marker-trait-association, which are significantly associated with yield, agronomic and phenology related traits along with RUE and biomass at various growth stages that showed 7–17% of phenotypic variation. Common SNP markers were identified for grain yield, final biomass and RUE on chromosomes 5A and 7A. Marker-Trait Associations (MTAs) related to source traits were discovered at various stages of development, including biomass accumulation, RUE and light interception (Molero *et al.* 2019). MTAs for biomass and physiological maturity (BM & PM) were discovered on chromosomes 6A, 7B, and 7D, as well as multi-trait markers on 5A and 5B and 7A is also linked to RUE at various stages and yields. The identification of MTAs associated with biomass and RUE at different growth stages is key to optimize the photosynthetic potential of the plant along the whole crop cycle if all the genomic regions of interest are presented together in a single genotype. MTAs for RUE were discovered at different developmental stages on chromosomes 1A, 1D, 2A, 2D, 3B, 5A, 6A, and 7A (Table 1). The marker for grain filling is located on 5A which likely plays a significant role in biomass accumulation in the later stages of plant development. During candidate gene search, discovered the coleoptile phototrophism 1 (CPT1) gene, which has been shown to affect phototropism in rice and may have an effect on RUE (Haga *et al.,* 2005). The genetic control of leaf angle is found to be complex, with only a few genes controlling it. In rice, wheat, and other crops, genomic regions (QTL) and genes (e.g., D61/OsBRI1, ILI1, LC2, ILA1, RAV6, OsARF19, OsBCL2 and SLG) governing leaf angle or erectness have been outlined which in-turn affects RUE (Hirano *et al.,* 2017; Jang *et al.,* 2021; Liu *et al.,* 2019; Marone *et al.,* 2020; Zhi *et al.,* 2022).

Table 1: Marker-Trait Associations (MTAs) with RUE in wheat

Trait	Number of MTAs	Chromosomes
RUE_E40InB (g/MJ)	4	2A, 2D, 3B. 6A
RUE_GF (g/MJ)	5	1A, 1D, 2A, 5A, 6A
RUET (g/MJ)	5	3D, 5A(2), 6A, 7A

RUE_E40InB: Radiation use efficiency from canopy closure to initiation of booting

RUE_GF: RUE from 7 days after anthesis until physiological maturity

RUET: Radiation use efficiency from canopy closure to physiological maturity

2.4. Biochemical approaches to improve RUE

RUE can also be increased by Non photochemical quenching (NPQ), which is regulated by the xanthophyll cycle and involves the pigment violaxanthin being reversibly deep oxidized to zeaxanthin via antheraxanthin (Demmig-Adams *et al.,* 1989; Jahns *et al.,* 2009). The enzyme violaxanthin deepoxidase (npq1) influences the amount of zeaxanthin, which converts violaxanthin (inactive in quenching) to zeaxanthin (active in quenching) and vice versa (npq2). Mutants lacking npq1, lack the ability to protect themselves from light in Arabidopsis. Mutants of npq2 (allelic to aba1) overproduce zeaxanthin but are deficient in ABA (Niyogi *et al.,* 1998). The precise manipulation of these genes in both upper and lower leaves to boost RUE can contribute to better performance. Photochemical Reflectance Index (PRI) can be used to monitor the xanthophyll cycle, and PRI expresses the relative down regulation of RUE, caused primarily by high light intensities. PRI is a an optical index used to measure photosynthetic light use efficiency, particularly by monitoring changes in carotenoid pigments, including xanthophylls, which are indicative of photosynthetic activity. It is a potential measure to detect conversion of the xanthophyll cycle in photosystem II (Mohamed *et al.,* 2025). Solar-induced fluorescence (SIF) primarily involves the release of photons from photosynthetic membranes, it is closely related to the flux of photons absorbed by chlorophyll and the biochemical processes that regulate how these photons are processed by PSII. Overexpression of PsbS protein which is a light-stress sensor essential for plant photo protection and a crucial non-photochemical quenching (NPQ) regulator, is found to boost thylakoid photoprotection and enhances RUE and grain yield (Hubbart *et al.,* 2018).

2.5. Agronomical approaches

2.5.1. Intercropping systems: The simultaneous cultivation of two or more crops in the same area, in intercropping system, can increase the utilisation of solar radiation due to canopy characteristics (Awal *et al.,* 2006; Lithourgidis *et al.,* 2011). Intercropping can boost solar interception, radiation usage efficiency, and production per unit incident radiation (Wang *et al.,* 2015). The greater the light intake into the canopy and light harvesting area, the greater the photosynthetic activity. In intercropping systems, the combined plant canopies can quickly cover the planting area which resulted in maximal light interception into the plant canopies and minimum light escape. Tsubo *et al.* (2001) discovered that, PAR was greater in intercropping maize and legumes than in maize monoculture. Intercropping increases the RUE and biological yield of an intercropping system (Nassiri *et al.,* 2015). Selecting the ideal crop mix to increase production is crucial (Yadav *et al.,* 2017), select the crops that have the least amount of plant competition possible by using effective soil nutrient extraction techniques, as well as thoughtful planting density and spatial layout (Seran *et al.,* 2010).

2.5.2. Canopy structure and leaf orientation: Canopy structure and its distribution influences the amount of light intercepted on plant leaves as well as its ability to absorb light (Zhu *et al.,* 2008). The vertical leaf canopy has a better photosynthetic efficiency (up to 40%) than the horizontal leaf canopy (Long *et al.,* 2006). Vertical orientation of maize leaves at the canopy's top, boost the light penetration to the canopy's bottom and photosynthetic rate is more uniform throughout the canopy(Hammer *et al.,* 2009). Photosynthetic rate is also affected by leaf position and its arrangement (Hatfield and Dold, 2019). Canopies with upright leaf angles permit the penetration of radiation to the lower canopy layers, ensuring a more homogenous light distribution over different canopy layers and consequently higher canopy photosynthesis (Marchiori *et al.,* 2010). This improved light distribution is typically associated with low light extinction coefficient and high biomass (Zhu *et al.,* 2020).

The relationships between WUE and RUE were linear across the leaf and canopy scales under different soil drying patterns in maize. Water stress and nutrition reduce leaf area index to a smaller size and greater leaf senescence. The smaller size of LAI agrees with light capture and thus crop growth, decreasing the efficiency of radiation (Bhattacharya Amitav, 2019; Zhou *et al.,* 2021). Wajid *et al.* (2007) reported that when drought stress was imposed before or after anthesis, the primary cause of reduced radiation-use efficiency was a decrease in intercepted light, which ultimately reduced the photosynthetic products being sent to the economical organ of the plant. Under limited nitrogen application radiation-use efficiency in wheat has been reported to be reduced (Muurinen and Peltonen-Sainio, 2006). The efficiency of utilizing the absorbed photosynthetically active radiation for biomass production, can change with variations in leaf chlorophyll content, plant growth stage, and field management practices and environmental stress levels. Depending on the timing of stress, drought reduced either the amount of absorbed radiation or radiation-use efficiency in barley (Jamieson *et al.,* 1995).

2.5.3. Improving light distribution: RUE is a suitable indicator for assessing radiation usage by plants (Shibles and Weber, 1966; Williams *et al.,* 1965; Deng *et al.,* 2024; MoroyoquiParra *et al.,* 2024) and an essential quantifier of crop output in connection to photosynthesis, as it integrates both the quantity of radiation captured by the crop and dry matter production. According to Quiroz *et al.* (2017) diffuse light reduces variations in light intensity, thereby minimizing restrictions on leaf photosynthesis. The plant canopy has an impact on photosynthetically active radiation incident that crops are able to absorb (Driever *et al.,* 2017). Photosynthetic photon flux density (PPFD ie. the amount of light that actually reaches to the plants within the PAR region) can alter plant RUE by influencing photosynthetic rate (Jayalath and van Iersel, 2021), stomatal behaviour (Knapp and Smith, 1990; O'Carrigan *et al.,* 2014), photosynthate distribution (He *et al.,* 2019; Onoda *et al.,* 2014), and chlorophyll concentration (Liu *et al.,* 2019). Incident solar radiation (SR) and intercepted photosynthetically active radiation (IPAR) absorption are directly related to leaf surface, with higher radiation during the maximum leaf area expension phase resulting in higher dry matter production and yield (Tohidi *et al.,* 2012). Among crops, the ideal PPFD for high RUE varies. RUE is maximum in lettuce with a PPFD of 200 mol $m^{-2}s^{-1}$ and basil with a PPFD of 250 mol $m^{-2}s^{-1}$ (Pennisi *et al.,* 2020). RUE is also affected by light quality. Furthermore, light intensity and quality can influence

tomato blooming, which is the primary predictor of yield (Dieleman and Heuvelink, 1992; Nanya *et al.,* 2012). These findings clearly show that increased PPFD causes higher dry mass and lower specific leaf area and increasing PPFD has enhanced the individual leaf photosynthetic rates (Pn) and also RUE (Ke *et al.,* 2022).

2.5.4. Increasing planting density combined with reduced nitrogen rate: Previous research has demonstrated that plant density and N rates have a major impact on canopy structure, resulting in changes in IPAR and RUE, which ultimately influence yield (Dai *et al.,* 2015; Shah *et al.,* 2004). High maize yields under varied N rates and planting density can be attributed to higher IPAR, RUE, or a combination of the two (Zahedi *et al.,* 2015). Radiation interception and LAI are linked to higher crop growth driven by nitrogen fertilisation (Caviglia and Sadras, 2001). Previous research has revealed that high grain yield and NUE may be obtained by combining planting density and N application rate (Ciampitti and Vyn, 2011; He *et al.,* 2019; SHI *et al.,* 2016; Zhang *et al.,* 2020). A two-year field experiment was performed to assess the cumulative impact of planting density and N rate (240 and 204 kg N ha^{-1}) on maize yield, NUE, canopy radiation capture and radiation use efficiency. The study's findings revealed that increasing plant density by 30% while reducing basal nitrogen (N) by 15% led to a 24.7% rise in N partial factor productivity (NPFP) and a 6.6% increase in maize grain yield compared to the conventional high-N, low-density planting approach. Improved IPAR and RUE played a crucial role in enhancing productivity under higher planting density with reduced nitrogen input in maize. (Du *et al.,* 2021). Plant density of 44.4 hills m^{-2} and its application of 180 kg N ha^{-1} was optimal for better growth and RUE of transplanted rice (Swarna *et al.,* 2017).

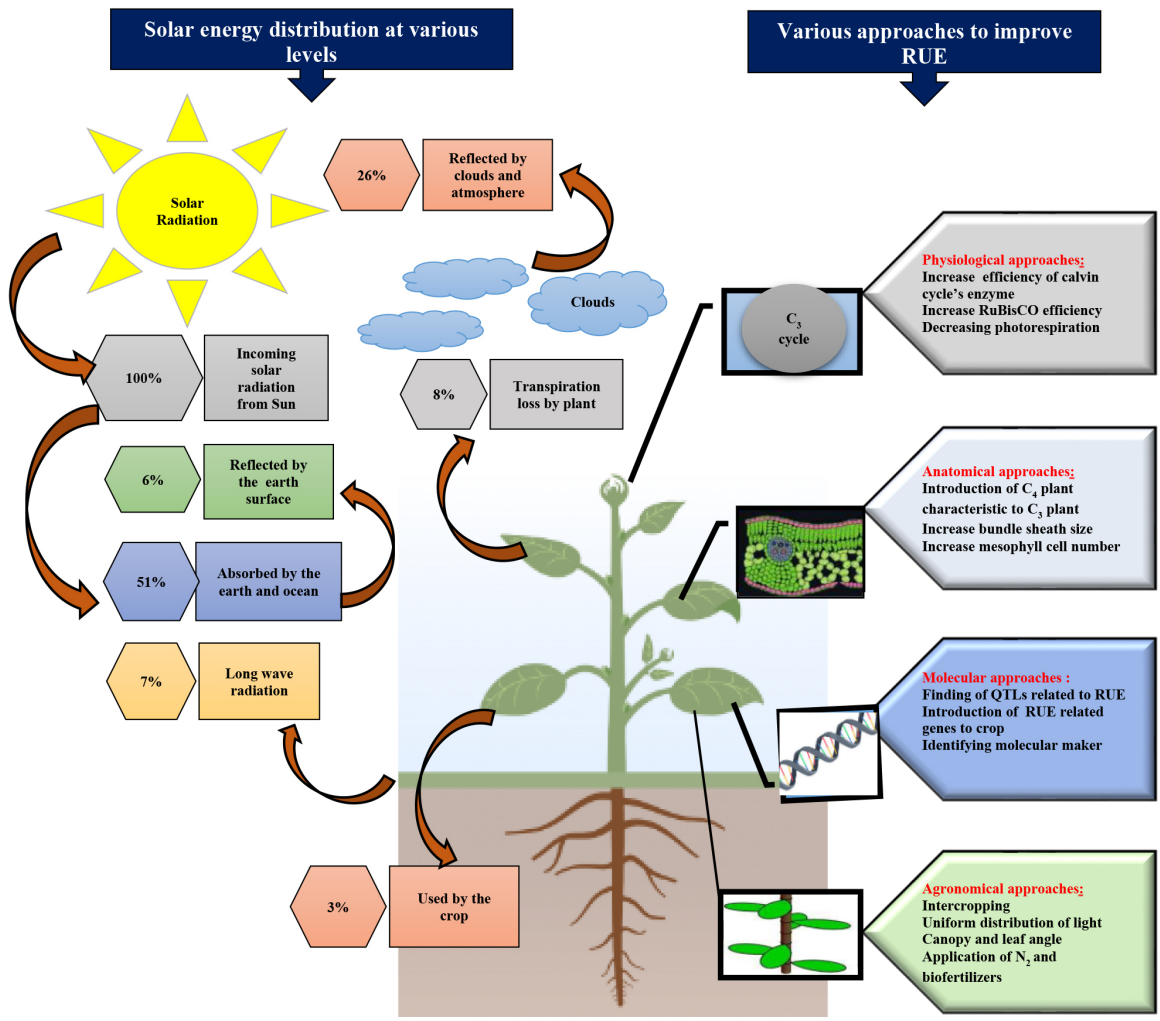

Fig. 2: Schematic representation of the solar energy distribution and various approaches to improve RUE

2.5.5. Application of biofertilizers: Applying the appropriate amount of fertiliser to the plants can also result in increased RUE. Biofertilizer inoculation reduced the time required by 15 days to achieve the maximum leaf area index, resulting in the highest fraction of absorbed radiation and, consequently, the highest sesame dry matter production at 60 days post-emergence. (Jahan *et al.,* 2013). In a field study conducted in sesame crop, RUE was higher in Biosulfur® (SSB), containing sulfur-solubilizing bacteria (Thiobacillus ssp.) and Nitroxin containing Azotobacter sp. and Azospirillum sp. in comparison to control. In numerous crop species, RUE response to nitrogen have been thoroughly studied, Yin and Struik (2015) showed that the application of biochar (20 tha^{-1}) has significantly increased the post-heading RUE, the ratios of NUpost/SLW and NUpost/LAI, and post-heading nitrogen uptake (NUpost). These findings supports the hypothesis by showing that the post-heading nitrogen uptake and RUE of field-grown rice can be improved by the application of biochar. The overall solar energy distribution at different levels, the amount of solar energy used by crops and the various approaches used for improving RUE are presented in consolidated way in Fig. 2.

For improving radiation use efficiency (RUE), understanding the underneath attributes is very much necessary. Implications of RUE can be improved by better understanding of the trait and its methods for quantification of trait to explore the genetic variability. Understanding RUE can be utilized for crop yield optimization which can be done by selection of parents with higher RUE to develop high yielding varieties. Different crop specific studies have been explained for improving RUE. Further, site specific application of N fertilizers can further improve crop health and RUE. Tailoring agronomic practices to specific crop requirement and environmental conditions can significantly enhance light interception and biomass production, ultimately improving RUE and crop yield.

Conclusion and Future prospective

RUE is a complex trait influenced by both environmental and internal factors. RUE is a key area for future research as light interception is so inextricably linked to biomass and productivity. A multidisciplinary approach integrating physiological, anatomical, biochemical, molecular and agronomical tools is essential to maximize RUE and improve future productivity. In the majority of breeding programmes, fixed traits are controlled by additive effects, the efficiency at which sunlight is converted into biomass through photosynthesis is also an additive effect. Incorporating synthetics, wild species and landraces into breeding programmes can be a promising approach to improve RUE significantly in cultivated crops for sustained yield production. The future of RUE improvement lies in leveraging advanced genetic tools, enhancing photosynthesis efficiency, AI- driven precision farming and exploring climate-adaptive breeding techniques. Utilizing the big data analysis to model light use patterns will help to optimize RUE for improved production. These efforts could significantly boost crop yield, helping to meet the growing global food demand.

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Author contributions

PR wrote the main manuscript text, MHM, RK and GR edited and Reviewed the manuscript, ZW, YK and OP contributed in literature survey, figure and table, RT overall guidance and support. All authors read and approved the manuscript.

Declaration of Competing Interest

The authors declare that there is no competing interest.

Ethical Approval

The article doesn't contain any study involving ethical approval.

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No

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