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Enhancing Citrus Resilience: Strategies and Advances in Abiotic Stress Management: A Review

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ABSTRACT

Citrus, a major global agricultural crop is highly valued for its nutritional benefits and widespread consumption. However, as a subtropical plant, citrus is particularly sensitive to abiotic stresses such as salinity, drought, waterlogging, nutrient deficiency, high irradiance and cold temperatures. These stresses pose significant challenges to citriculture, reducing yield and fruit quality. Traditional methods like rootstock selection and plant breeding have been used to improve stress tolerance to some extent. Recent advancements in genetic engineering and biotechnology have enhanced our understanding of the molecular mechanisms behind stress tolerance. Identifying and isolating specific genes and transcription factors have led to novel agricultural practices that economically benefit citriculture and mitigate the adverse effects of abiotic stress. This review paper emphasizes and summarises the citrus responses to abiotic stress and strategies developed to enhance stress tolerance in citrus plants.

Key words: Abiotic stress, Citriculture, Citrus, Stress management, Tolerance mechanisms.

Abiotic stresses significantly hinder sustainable agricultural growth, posing challenges to meeting global food demand (Sah *et al*., 2016). These stresses negatively impact plant well-being and necessitate adaptive strategies for survival (Mittler, 2002). Major environmental factors affecting plant growth include light, water, temperature, minerals and nutrients (Zhu, 2016). Fluctuations in these conditions cause biochemical, physiological and morphological changes, affecting plant reproduction and yield leading to economic losses (Osakabe *et al*., 2013; De Storme and Geelen, 2014).

Citrus fruits, which are cultivated worldwide, have been known among the most highly consumed fruits as a natural source of energy, nutrients and health supplements. Various species of citrus are consumed primarily as fresh fruit, raw materials for juices or are available in canned form (Lv *et al*., 2015). Citrus-derived secondary metabolites, including phenolics flavonoids, alkaloids, carotenoids, limonoids, coumarins and essential oils, are highly valued for their bioactive properties, which include antioxidative, anticancer, cardiovascular protective and neuroprotective effects. Moreover, citrus fruits are known to be used as additives, spices, cosmetic ingredients and chemoprophylactic agents in various industrial sectors (He *et al*., 2011; Keleb and Selli, 2011).

Over the past 60 years, global citrus production has surged nearly 5.5 times. The last decade (2011 to 2021) saw the most significant increase, particularly in tangerine production, which rose by over 1.44 million tons annually. During the same period, orange production grew by 312 thousand tons per year, while lemon and lime production increased by 578 thousand tons annually. Among the leading producers, China, Brazil and India stand out. China's high productivity is primarily attributed to its substantial tangerine and other citrus fruit production. Brazil is notable as the largest producer of oranges and the top exporter of orange juice. Meanwhile, India leads the world in lemon and lime production. Other key citrus-producing countries in 2021 included Mexico, Spain, the United States, Turkey, Egypt, Nigeria and Iran, rounding out the top ten producers (Pereira Gonzatto and Scherer Santos, 2023). The citrus production has been significantly affected by both biotic and abiotic stresses (Ali and Moktan, 2014; Patra *et al*., 2017).

Citrus, typically a warm-climate fruit tree belonging to the rutaceae family thrives best in subtropical regions where seasonal changes are minimal and freezing temperatures are rare. While citrus can adapt to a variety of soil types and is tolerant of both high and low pH levels, temperature and soil moisture are the primary environmental factors influencing the health and quality of

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citrus trees (Syvertsen and Hanlin, 2008). They generally do not tolerate soil flooding, drought, chilling temperature further saline or alkaline soils should always be avoided for citrus. It is evident from numerous studies that citriculture is severely obstructed by abiotic stresses, such as temperature stress (Zhu *et al*., 2011), water stress (Zou *et al*., 2017), salt stress (Zhang *et al*., 2016), mineral nutrient stress (Liu *et al*., 2018) and waterlogging stress (Wu *et al*., 2013). This review focuses on the impacts of abiotic stresses on citrus plants and their cultivation, highlighting the roles of various biochemical factors, enzymes and genes in stress response and mitigation. It also discusses strategies adopted in citriculture to overcome the effects of these stresses on citrus production.

Impact of abiotic stresses on citrus

Salinity stress

Salinity is considered as one of the major factor affecting the crop production throughout the world (Sinky *et al*., 2024). Salinity either in water or soil represents one of the major abiotic stresses specifically in arid and semi-arid regions, which can severely limit the production of agricultural crops (Nayem *et al*., 2020; Sharma and Sachan, 2024). High concentration of salt leads to hyper osmotic stress and ionic imbalance in cellular system which consequently leads to oxidative damages. Such damages in plants are responsible for growth retardation, membrane disruption, molecular alterations and even death. For the plant to be saline tolerant, their homeostatic mechanism along with detoxification machinery must be boosted (Zhu, 2016; Alam *et al*., 2020). Citrus are typically categorised as "salt-intolerant" because irrigation with saline water results in drastic decline in their growth compared to many other crops (Prior *et al*., 2007). In citriculture, electrical conductivity (EC) values exceeding 3 dS m^{-1} and sodium adsorption ratios over 9 in saturated soil extracts are considered critical thresholds for cultivation survival (Santana-Vieira *et al*., 2016).

Salinity-induced osmotic stress occurs when the dissolved salt concentration in water is high enough to inhibit crop growth. In citrus, the indirect movement of water within leaf tissues can lead to the accumulation of Cl^- ions, which negatively impacts the transpiration rate and photosynthesis (Moya *et al*., 2003). Citrus species vary in their tolerance to salinity; their tolerance level depends on their capacity to exclude toxic Na^+ and Cl^- ions from the cellular system (Khoshbakht *et al*., 2015; Moya *et al*., 2003). A research conducted by (Hepaksoy, 2000), revealed that that fruit yield of citrus crop was reduced by approximately 13% when subjected to soil with higher electrical conductivity of the saturated soil extract. The other reported effects of salinity in citrus are decline in stomatal conductance leading to reduced CO_2 diffusion eventually, affecting the photosynthetic efficiency (García-Sánchez and Syvertsen, 2006) and elevated ion accumulation (Brumos *et al*., 2010). Though some of the citrus species are found to be salt tolerant like, Sunki mandarin (*Citrus sunki* Hort. ex Tan.), Rangpur lime (*Citrus limonia* Osbeck) and Cleopatra mandarin (*Citrus reshni* Hort. ex Tan.) while trifoliate orange (*Poncirus trifoliata* (L.) Raf.) and its hybrids such as Carrizo citrange [*Citrus sinensis* (L.) Osbeck × *P. trifoliata* (L.) Raf.] are characterized as salt sensitive as reviewed by (Hussain *et al*., 2012).

Drought stress

Given the global impact of abiotic stresses on tree physiology and productivity, drought stress is recognized as one of the most harmful factors. Drought stress induced crop yield loss is generally more significant then losses from other biotic and abiotic stresses, primarily because severity and duration of drought stress are critical (Eesha *et al*., 2024). The excessive formation of reactive oxygen species during drought stress results in oxidative damage and cell death (Kumar *et al*., 2024). During drought stress, disruptions in plant water relations lead to decreased water use efficiency. Citrus plants under drought conditions suffer significant losses in growth and cellular metabolic functions, resulting in reduced yield and fruit quality (Pérez-Pérez *et al*., 2008). Drought stress also causes declines in physiological parameters such as stomatal conductance, net CO_2 assimilation and leaf transpiration in citrus plants (Syvertsen and Garcia-Sanchez, 2014). As demonstrated by (García-Tejero *et al*., 2012) the fruit growth and flowering stages were the most sensitive periods in relation to irrigation water deficit and yield loss. Drought stress imposed a yield loss of up to 20% during the flowering stage whereas yield losses of nearly 10% and 6% were observed during the fruit growth or ripening stages respectively. Moreover under stress condition, significant loss in length, dry weight and fresh weight of both root and shoot accompanied with low germination percentage was recorded in Cleopatra sprouts (Zaher-Ara *et al*., 2016). The ability of citrus to withstand water deprivation varies by genotype, with the following order of drought resistance: *Citrus reticulata* > *Citrus* × *limonia* > *Citrus* × *limon* > *Poncirus trifoliate* > *Citrus chuana* > *Citrus* × *sinensis* > *Citrus verrucose* > *Citrus* × *paradisi.* (Rodríguez-Gamir *et al*., 2011; Zaher-Ara *et al*., 2016).

Water logging

The recent trends in climate change is responsible for increase in temperatures and altered water cycles, as evident by the increasing severity of droughts and aberrant precipitations consequently leading to waterlogging and flooding (Pérez-Jiménez and Pérez-Tornero, 2021). Flooding or waterlogging creates hypoxia, which triggers a wide spectrum of metabolic, biochemical, developmental and physiological changes in fruit trees (Habibi *et al*., 2023). This leads to the occurrence of desiccation symptoms; delayed root growth and transporter-driven ion uptake are also inhibited due to defective root respiration. Hypoxia is of special relevance to citrus plants due to lack of a specific adaptation *i.e.* aerenchyma formation or lenticel hypertrophy (Arbona and Gomez-Cadenas, 2008).

The major cause of waterlogging is the poor soil drainage system, excessive rainfall or irrigation and destruction of soil structure. The effects of flooding on plants mainly relate to the decline of energy shortage, therefore a reduced ion uptake and less energy for root growth (Rodríguez-Gamir *et al*., 2011). When plants are waterlogged, they cannot uptake water, leading to wilting of the foliage and shoots, a symptom that becomes more pronounced in warm weather. If root damage is extensive or soils remain waterlogged for prolonged periods, more severe symptoms can occur, including reduced chlorophyll levels, stunted growth and leaf senescence (Ashraf, 2012). However, the ability to endure waterlogging stress varies by genotype, with different citrus genotypes exhibiting a wide range of responses to waterlogging (Garcia-Sanchez *et al*., 2007). For instance, 'Cleopatra' is known to be very sensitive to flooding (Arbona and Gomez-Cadenas, 2008), whereas 'Forner Alcaide no. 5' has shown excellent tolerance to flooding conditions (Forner *et al*., 2003).

Cold stress

Exposure to low and very low temperatures is one of the most common environmental stresses affecting plants. In citrus, low temperatures can cause chilling and freezing injuries, thereby limiting crop production and yield (Zhang *et al*., 2011). Citrus fruits, especially at the ripening stage, can tolerate only 2-3 hours of temperatures dropping to -2 to -3°C; otherwise, the fruits decay. The ripening stage during January and February is the most vulnerable period for citrus crop yield (Zabihi *et al*., 2016). Citrus crops, which are among tropical and subtropical fruits, are generally classified as cold-tender plants, making them vulnerable to freezing stress (Fotouhi *et al*., 2008). Chilling results in the loss of membrane integrity and an increase in active oxygen radical production, leading to leaf damage and electrolyte leakage. The integrity of intracellular organelles is also disrupted, causing a loss of compartmentalization, impaired photosynthesis, reduced chlorophyll pigments, disrupted protein assembly and overall metabolic dysfunction (Mahajan and Tuteja, 2005). Young citrus shoots die at threshold temperature around -12°C, although some citrus fruits can tolerate temperatures as low as -10°C (Vu and Yelenosky, 1991). *Poncirus trifoliata* (L.) Raf. is noted as the most cold-tolerant citrus rootstock (Wang *et al*., 2015).

Above mentioned all the abiotic stresses lead to the production of reactive oxygen species (ROS) such as superoxide radicals, hydroxyl, hydrogen peroxide and singlet oxygen. ROS produced in chloroplasts and mitochondria during metabolic processes, can damage essential cellular components including proteins, membranes, pigments and nucleic acids (Rad *et al*., 2017). Moreover, significant increase in ROS accumulation and antioxidant enzyme activity has been reported in citrus plants under various abiotic stresses (Ziogas *et al*., 2021).

Tolerance mechanism towards abiotic stresses

Abiotic stresses, such as salinity, drought and temperature extremes, pose significant challenges to sustainable agricultural growth by impairing plant metabolic pathways. Salinity reduces photosynthetic efficiency and increases reactive oxygen and nitrogen species, prompting citrus plants to enhance antioxidant defenses (Hasanuzzaman *et al*., 2020; Ziogas *et al*., 2021). Na^+ transporters HKT1 and SOS1 help maintain ion balance under salt stress, with HKT1 preventing Na^+ overaccumulation in photosynthetic organs and SOS1 extruding Na^+ from root cells (Wang *et al*., 2014). In woody perennials like citrus,

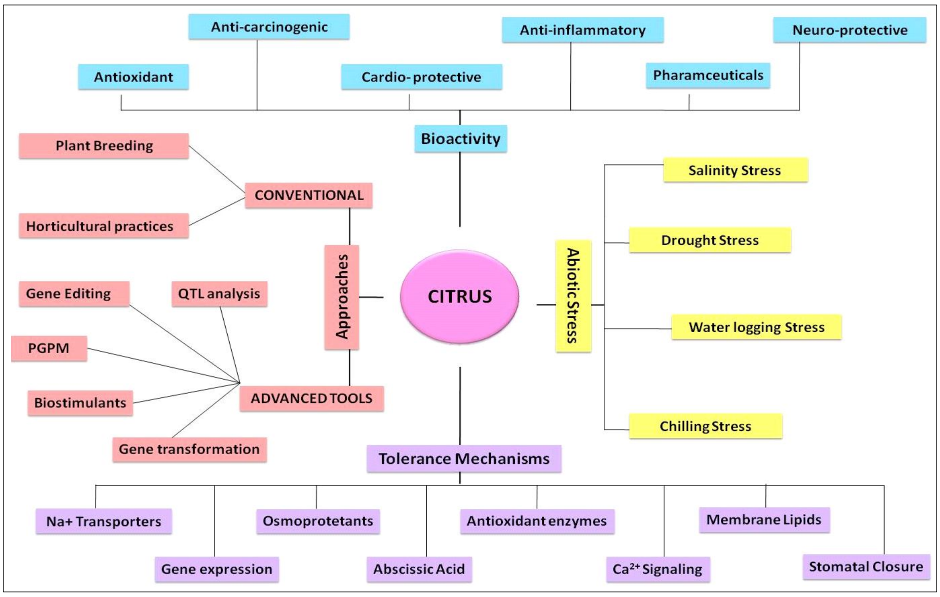

Fig 1: Aspects of abiotic stress management in citriculture.

excess Na^+ recovered by HKT1 may accumulate in woody tissues. The expression of SOS1 and HKT1 genes is linked to the ability of Cleopatra mandarin and trifoliate orange to exclude Na^+ (Martínez-Alcántara *et al*., 2015).

Under drought or high saline conditions, abscisic acid (ABA) acts as a crucial stress-signaling hormone (Bartels and Sunkar, 2005). It regulates stomatal closure, synthesis of compatible osmolytes and the upregulation of genes for adaptive responses. Increased ABA levels are linked to the upregulation of 9-cis-epoxycarotenoid dioxygenase (NCED), which converts 9-neoxanthin to xanthoxin, a key step in ABA biosynthesis. Moreover, active ABA can be removed by conjugation with hexoses via ABA O-glycosyl transferase (AOG), forming ABA-glycosyl ester (ABAGE) (Priest *et al*., 2006). Active ABA can be released from ABAGE degradation through the action of ABAGE β-glycosidase (BG18) (Schroeder and Nambara, 2006). Proline is synthesized from glutamate *via* glutamate semialdehyde and D1-pyrroline-5-carboxylate (P5C) through the actions of P5C synthetase (P5CS) and P5C reductase (P5CR). The genes encoding these enzymes are strongly upregulated under drought stress (Hare *et al*., 1999). Proline accumulation, triggered by free radicals from oxidative stress, protects plants during various environmental stresses. Proline levels are tightly regulated and only increase when synthesis outpaces degradation, as excessive proline is toxic to cells (Deuschle *et al*., 2001). Carbohydrates are also crucial for plant biomass, osmotic regulation and drought response. Progressive drought leads to a significant increase in soluble sugar content in some citrus crops, likely due to increased starch conversion into soluble sugars or decreased sugar utilization (Zaher-Ara *et al*., 2016). Drought stress typically enhances starch hydrolysis and reduces sucrose translocation, resulting in the accumulation of reducing sugars in leaf tissue, which provides osmotic protection (Campos *et al*., 1999; Zaher-Ara *et al*., 2016).

Waterlogging triggers hypoxia, leading to various physiological and molecular changes, including reduced photosynthetic activity and stomatal closure to increase water use efficiency (Martinez-Alcantara *et al*., 2012). A primary response to flooding is stomatal closure (Perez-Jimenez *et al*., 2017), which reduces gas exchange, lowers transpiration and increases water use efficiency to avoid dehydration. This response has been observed in previous citrus waterlogging studies (Li *et al*., 2006; Rodriguez-Gamir *et al*., 2011). Moreover, *Citrus* rootstocks' ability to regenerate roots has been found to influence their waterlogging tolerance (Pérez-Jiménez and Pérez-Tornero, 2021).

When plants detect stress, membrane destabilization occurs, which is the primary cause of plant damage from freezing (Steponkus and Webb, 1992). During acclimatization, the cryostability of the plasma membrane increases due to changes in lipid composition, enhancing resistance to dehydration. This involves an increased proportion of phospholipids, particularly di-unsaturated species of phosphatidylcholine and phosphatidylethanolamine and a reduced proportion of cerebroside lipids (Uemura *et al*., 1995). Calcium signaling involving specific kinases and transcription factors like HY5, plays a crucial role in cold response (Primo-Capella *et al*., 2021). The rise in calcium levels is transient, showing a characteristic peak facilitated by a specific vacuolar calcium antiporter, the calcium exchanger (CAX1 Ca^{2+}/H^+), which helps plants repeatedly respond to low-temperature signals. This calcium influx reaches receptor kinases regulated by calmodulin 1 and 2 (CRLK1 and CRLK2), initiating a signaling cascade specific to the cold response pathway (Yang *et al*., 2010). Plants process and integrate signals related to seasonal changes and light, which is crucial for acclimatization and cold tolerance. Hypocotyl 5 (HY5) transcription factor, a key modulator of light signaling and plant development, regulating other genes through various sub-networks (Catala *et al*., 2011). HY5 is overexpressed at low temperatures and induces genes responsive to cold stress by binding to the Z-box of promoters, part of the LTRE (low-temperature response element) domain. This light-mediated cold stress response is also present in citrus (Huang *et al*., 2019). In cold stress-tolerant plants, many genes involved in synthesizing osmoprotectants like proline, quaternary amines, sugars and sugar alcohols are highly expressed to combat stress adversities (Livingston and Henson, 1998). Proteins likely involved in stress tolerance include chaperones, late embryogenesis abundant (LEA) proteins, osmotin, antifreeze proteins, mRNA-binding proteins, key enzymes for osmolyte biosynthesis, fatty acid metabolism enzymes and lipid-transfer proteins (Holmberg and Bulow, 1998). Genes responsive to dehydration and cold stress encode various protective proteins, highlighting the need for multifaceted genetic approaches to enhance stress tolerance.

Strategies to combat abiotic stresses in citrus plants

Researchers have employed various strategies to enhance abiotic stress tolerance in crop plants ranging from traditional breeding methods to modern CRISPR/Cas9 technique (Ahmar *et al*., 2020; Zafar *et al*., 2020). Citriculture, in particular, faces significant challenges from drought and salinity, reducing citrus yield and fruit quality. Developing and disseminating strategies to help farmers adopt economically beneficial agricultural practices that minimize abiotic stress is crucial. Traditional breeding programs have produced improved citrus varieties, highlighting plant breeding as a key method for achieving stress adaptation (Govindaraj *et al*., 2015; Hasan *et al*., 2019). Research has shown that rootstocks are essential for a plant's ability to withstand water scarcity by influencing physiological performance through variations in leaf water potential, hydraulic conductance and stomatal conductivity (Rodriguez-Gamir *et al*., 2011). The genetic traits of the rootstock determine the scion's robustness and survival under water stress (Miles and Wayne, 2008). For instance, orange trees (cv. Lane Late) grafted onto Cleopatra mandarin rootstock show higher water use efficiency and osmotic adjustment under drought conditions compared to those grafted onto Carrizo citrange hybrid rootstock (Garcia-Sanchez *et al*., 2007; Zaher-Ara *et al*., 2016). Additionally, horticultural practices such as using hydrogels, shading and treatments with persistent analogs of abscisic acid and polyamines have been successfully implemented to improve citrus performance under abiotic stress (Gimeno *et al*., 2014).

Genetic improvement for salinity tolerance in citrus species can be achieved through identifying natural variations via direct selection or quantitative trait loci (QTL) mapping. Due to limited success in direct selection under field conditions, breeders have focused on identifying transferable genes and gene products. Techniques like marker-assisted breeding and genetic transformation have gained prominence. QTL analysis involves crossing two parents with different quantitative traits to identify specific genes responsible for desired traits (Singh and Sharma, 2018). Notably, QTL mapping identified 70 potent QTLs in a BC1 population (*Citrus grandis* × (*Citrus grandis* × *Poncirus trifoliata*), with 69% related to salinity (Tozlu *et al*., 1999).

Salinity is more problematic on poorly drained clay or silt soils than on permeable sandy or gravelly soils. Citrus crops are commonly irrigated using drip or micro-sprinkler methods, ensuring water does not contact leaves to prevent salt burn. Salts can be leached from the root zone by applying large amounts of water to the soil once or twice a year (Simpson *et al*., 2014). Chemical priming is a promising method in plant stress physiology and crop management. Plants can develop “stress memory” after initial stress exposure, leading to better adaptation to subsequent stresses. Priming triggers responses to various stresses, offering low-cost protection under high-stress conditions (Colmenero-Flores *et al*., 2020). Exogenous application of nutrients and plant hormones has proven effective in making plants tolerant to flood stress. Scientists worldwide are researching this approach. For example, Ashraf *et al*. (2011) showed that exogenous potassium application, both in soil and as a foliar spray, alleviated waterlogging stress in cotton plants. Similarly, Yiu *et al*. (2009) found that exogenous application of spermidine and spermine led to biochemical and physiological adaptations in onions under flooding stress.

The use of biostimulants has become common among farmers for their protective effects against abiotic stress and positive contributions to overall plant growth (Van Oosten *et al*., 2017). Recent data show that bio stimulants aid in citrus root development and regulate osmoregulatory mechanisms in plant cells (Conesa *et al*., 2020). For example, orange trees (*Citrus sinensis* L.) sprayed with a commercial extract of *Ascophyllum nodosum* showed improved water relations and water use efficiency when irrigated with 50% of evapotranspired water (Spann and Little, 2011). The overuse of chemical fertilizers and pesticides has degraded soil quality, highlighting the need for sustainable agricultural techniques. Plant-growth-promoting microbes have emerged as a crucial strategy for enhancing plant growth and protection against abiotic stresses (Kumar *et al*., 2017). Arbuscular Mycorrhizal fungi, for instance, improve water deficit tolerance in the roots of Trifoliate orange by regulating polyamine homeostasis (Zou *et al*., 2021).

Traditional breeding methods for improving stress tolerance in crops have had limited success due to the complexity of these traits and low genetic variance under stress conditions. Advances in plant biotechnology over the past two decades have led to the identification and isolation of transcription factors related to cold stress tolerance. These include genes involved in the biosynthesis of Osmo protectants, membrane lipid modification, LEA proteins and detoxifying enzymes (Primo-Capella *et al*., 2021). The discovery of C-repeat binding factor (CBF) genes has been significant for low temperature adaptation and signal transduction (Forner-Giner *et al*., 2009). Overexpression of CBF4 in *Arabidopsis*, for instance, has enhanced tolerance to freezing and drought (Huang *et al*., 2015).

Minimizing the adverse effects of abiotic stresses requires precise and sophisticated agricultural practices that consider crop needs and resource availability. Manipulating specific plant genes to enhance production capacity and stress tolerance is becoming increasingly important. With climate threats affecting citrus crop production, advanced genomic and biotechnological techniques are essential for mitigating environmental impacts on citriculture.

CONCLUSION

Effective management of abiotic stress is crucial for achieving better yield and quality in agricultural crops. Although some citrus species have developed defense mechanisms against various stresses, most remain susceptible. Extensive research in genomics, proteomics and metabolomics, along with additional physiological approaches, is essential to understand the mechanistic roles of various factors in signal transduction pathways, their interactions and how they perceive and transmit signals to specific downstream responses under stress. Noteworthy stress management strategies proposed by researchers, combined with recent advancements in genetic engineering and biotechnological tools, offer new hope. Recent significant progress in understanding the complex mechanisms governing stress tolerance in citrus plants holds great potential for improving abiotic stress management in citriculture.

Conflict of interest

Authors declare no conflict of interest.

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