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Research Article

Adaptive Potential, Stress Tolerance, and Fruit Quality in Pomegranate (*Punica granatum* L.): A Review

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Abstract *Punica granatum* L. has gained global importance as a high-value fruit crop because of its nutritional, nutraceutical, and commercial significance, particularly in arid and semi-arid regions. Sustainable pomegranate production depends on the interaction of several biological factors, including phenological adaptation, fruit quality, abiotic stress tolerance, disease resistance, and genetic diversity. This review summarizes current knowledge regarding the adaptive potential, stress tolerance, and quality-related traits of pomegranate, with emphasis on the physiological, biochemical, and molecular mechanisms underlying cultivar performance. Phenological characteristics such as bud differentiation, flowering behavior, and reproductive development are closely associated with environmental adaptation and orchard productivity. Fruit quality is strongly genotype dependent and influenced by morpho-pomological traits, juice composition, antioxidant capacity, anthocyanin accumulation, vitamin C content, and seed biochemical properties. Drought and cold tolerance involve complex physiological processes, including osmotic adjustment, maintenance of membrane stability, antioxidant defense, regulation of plant water status, and preservation of photosynthetic activity. In addition, fungal and bacterial pathogens substantially reduce both preharvest and postharvest performance, highlighting the importance of integrated disease management and resistance breeding. Recent advances in RAPD, SSR, SNP, transcriptomic, and genome-based approaches have improved germplasm characterization and facilitated the identification of valuable genetic resources for breeding programs. However, significant gaps remain in marker validation, multi-environment evaluation, and integration of omics technologies with field phenotyping. Overall, current evidence supports integrated breeding strategies aimed at developing climate-resilient pomegranate cultivars with superior fruit quality and stable productivity.

Key words Pomegranate, *Punica granatum* L., adaptive potential, fruit quality, abiotic stress tolerance, biotic stress resistance, molecular characterization, breeding strategies

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Introduction

Punica granatum L. is one of the oldest cultivated fruit crops and has gained increasing global and regional importance because of its nutritional, medicinal, and economic value. The species is widely cultivated in arid and semi-arid regions of Asia, the Middle East, the Mediterranean basin, and other subtropical areas, where it is valued for both its adaptability to marginal environments and its commercial potential. In recent years, pomegranate cultivation has expanded considerably as a result of rising consumer demand, diversification of production systems, and growing recognition of the fruit as a high-value horticultural commodity (da Silva et al. 2013; Holland et al. 2014). In many producing countries, pomegranate has become increasingly important

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for both local consumption and export-oriented markets, particularly under conditions where water scarcity and climatic instability limit the cultivation of less resilient fruit crops.

The economic importance of pomegranate is closely associated with its fruit quality and nutraceutical value. Pomegranate fruit is rich in sugars, organic acids, vitamins, anthocyanins, phenolic compounds, and other bioactive metabolites that contribute to its antioxidant capacity and functional-food value (Viuda-Martos et al. 2010). Its juice, arils, peel, and seeds have all attracted scientific and industrial interest because of their potential health-promoting properties, including antioxidant, anti-inflammatory, antimicrobial, and cardioprotective properties (Viuda-Martos et al. 2010). Fruit quality in pomegranate is a multidimensional, genotype-dependent characteristic determined by morpho-pomological traits, edible fraction, juice yield, sugar-acid balance, color, antioxidant composition, and seed biochemical attributes (Tehranifar et al. 2010). This complexity means that quality must be interpreted in relation to the intended end use, since fresh-market preference, processing suitability, and nutraceutical value do not always coincide in the same genotype.

Despite its relative ecological adaptability, pomegranate production is increasingly challenged by abiotic and biotic stresses. Among abiotic factors, drought remains one of the most critical constraints because it affects plant water relations, stomatal regulation, membrane stability, gas exchange, osmotic adjustment, and ultimately fruit yield and quality. Low-temperature stress also represents a major limitation in many production areas, particularly where seasonal cold events damage tissues, impair growth, and reduce orchard productivity. In addition, fungal and bacterial pathogens can significantly reduce plant performance, fruit marketability, and postharvest quality through blight, wilt, fruit rot, and latent infections (Munhuweyi et al. 2016). These combined pressures have become more important under ongoing climate change, which is intensifying environmental fluctuations and increasing the need for cultivars with improved resilience. Therefore, stress tolerance in pomegranate should be understood as a complex and integrated phenotype involving coordinated physiological, biochemical, and molecular responses rather than as a single adaptive trait.

A major strength of pomegranate as a crop lies in its substantial genotype variability. Considerable diversity has been reported among accessions for fruit morphology, biochemical composition, drought response, cold hardiness, and disease susceptibility, indicating that the available germplasm constitutes a valuable resource for cultivar improvement (Patil et al. 2020b; Sarkhosh et al. 2009). However, much of the available literature remains fragmented, with studies often focusing separately on fruit quality, stress physiology, disease incidence, or molecular characterization. Such separation limits a comprehensive understanding of how adaptive potential, fruit quality, and stress tolerance interact in breeding-oriented contexts. For this reason, breeding programs increasingly require integrative approaches that combine morpho-pomological evaluation, physiological screening, biochemical profiling, and molecular tools, including DNA markers, genome resources, and marker-assisted selection, to identify superior genotypes with both high fruit quality and stress resilience (Harel-Beja et al. 2015; Patil et al. 2020a; Yuan et al. 2018).

In this context, the present review aims to synthesize current knowledge on the adaptive potential, fruit quality, abiotic and biotic stress tolerance, and breeding perspectives of Punica granatum L. Particular emphasis is placed on the global and regional importance of pomegranate, the biochemical and nutraceutical basis of fruit quality, the major physiological and molecular responses to drought, low temperature, and pathogen pressure, and the role of genotype variability in modern improvement strategies. By integrating these dimensions, this review seeks

to provide a coherent framework for future research and breeding efforts aimed at developing high-quality, stress-resilient pomegranate cultivars suitable for arid and semi-arid production systems.

Phenology and Growth Traits Relevant to Adaptation

Phenological development in Punica granatum L. is closely linked to environmental adaptation and directly influences reproductive performance, yield formation, and orchard management. Available evidence indicates that pomegranate is better suited to warm, subtropical, and semi-arid environments than to strictly temperate conditions, as vegetative growth, bud break, flowering, and fruiting are strongly regulated by temperature and seasonal climatic cues (Ferrara et al. 2023; Rajaei et al. 2015). Bud burst timing may shift according to year-to-year climatic variation, particularly under changes in temperature and precipitation, suggesting that phenology in pomegranate is highly responsive to environmental conditions rather than being fixed across seasons (Rajaei et al. 2015). This plasticity is agriculturally important because the synchronization of bud break and flowering with favorable environmental windows contributes directly to reproductive success and cultivar adaptation.

Bud differentiation is a key component of growth behavior in pomegranate because it determines whether shoots remain vegetative or enter reproductive development. It has been reported that pomegranate produces structurally and functionally distinct buds, including smaller buds on twigs and larger buds on spurs, with variation among cultivars in number, position, and developmental fate (Ferrara et al. 2023; Rajaei et al. 2015). Large buds are more frequently associated with reproductive potential, whereas narrower buds often give rise only to vegetative shoots (Rajaei et al. 2015). This differentiation is important for adaptation because the balance between vegetative and reproductive growth affects canopy renewal, flowering intensity, and the ability of the tree to maintain productivity under different environmental conditions. In practical terms, knowledge of bud fate can improve pruning strategies and support cultivar-specific orchard management.

Flowering traits further determine reproductive efficiency and adaptation. Pomegranate flowers may be hermaphrodite or staminate, and their proportion varies among cultivars and across seasons, thereby influencing fruit set and final productivity (Ferrara et al. 2023; Wetzstein et al. 2011). Hermaphrodite flowers are generally larger and more abundant than staminate flowers and play the principal role in successful fruit development, whereas male flowers frequently abscise and contribute little to yield (Ferrara et al. 2023; Wetzstein et al. 2013a; Wetzstein et al. 2013b). Environmental conditions affecting floral differentiation, timing of flowering, and branch growth therefore have direct consequences for reproductive success. Overall, phenology and growth traits in pomegranate should be viewed as adaptive traits of high agronomic relevance, since they mediate the interaction between genotype, seasonal climate, and reproductive performance.

Fruit Quality and Biochemical Characteristics

Fruit quality in *Punica granatum* L. is a multidimensional and strongly genotype-dependent trait shaped by morpho-pomological characteristics, juice chemistry, antioxidant composition, and seed biochemical properties. Structurally, pomegranate fruit consists of peel, septa, locules, arils, seeds, juice, and seed oil fractions, all of which contribute differently to its nutritional and commercial value (Fig. 1). The edible arils generally account for about 45-52% of whole fruit weight, whereas the peel may represent approximately 49-55%, depending on the cultivar. Seeds usually account for about 18-20% of fruit weight and contain oil-rich tissues with recognized nutraceutical importance (Holland et al. 2009; Viuda-Martos et al. 2010). In addition, Mediterranean germplasm shows substantial variability in fruit size, aril yield, soluble solids, titratable acidity, phenolic content, anthocyanin accumulation, vitamin C concentration, and seed oil composition, indicating that pomegranate quality cannot be defined by a single universal standard (Ferrara et al. 2011; Radunić et al. 2015). Instead, fruit quality should be interpreted according to intended end use, since fresh-market, processing, and nutraceutical value do not necessarily coincide in the same genotype.

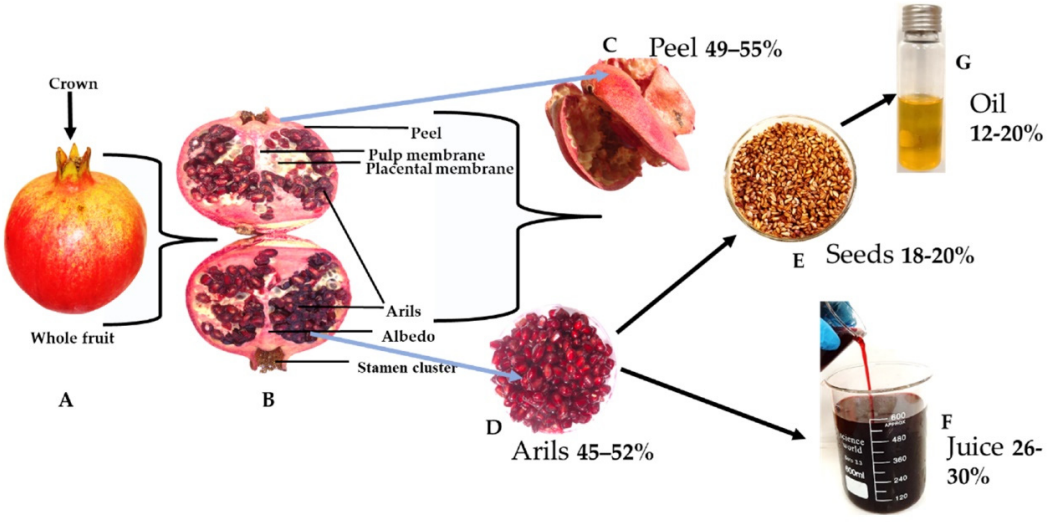

Fig. 1. Botanical structure and principal fractions of *Punica granatum* L. fruit: (A) whole fruit; (B) anatomical structure; (C) peel; (D) arils; (E) seeds; (F) juice; and (G) seed oil. (Magangana et al. 2020).

Morpho-pomological traits

Morpho-pomological traits constitute the first level of fruit quality because they directly determine fresh-market acceptability and processing efficiency. Studies on Italian and Croatian accessions have shown wide variation in fruit weight, fruit size, aril size, aril mass, and edible fraction, confirming that physical fruit quality is highly genotype-dependent (Ferrara et al. 2011; Radunić et al. 2015). Large-fruited genotypes are generally preferred for fresh consumption and industrial processing, while smaller fruits may still be valuable when associated with superior biochemical profiles. Likewise, traits such as seed/aril ratio and total aril yield are especially relevant

for consumer preference, since a lower proportion of woody tissue improves palatability and eating quality (Barone et al. 2001; Martinez et al. 2006). These observations indicate that morpho-pomological performance reflects not only genotype but also adaptation to local production environments.

Juice chemistry and antioxidant profile

Juice quality is primarily governed by the balance between soluble solids and organic acids, together with phenolic composition, antioxidant activity, pigment profile, and vitamin C concentration. Across regional germplasm, soluble solids and titratable acidity vary widely, resulting in clear differentiation among sweet, sour-sweet, and sour types (Ferrara et al. 2011; Radunić et al. 2015). Sensory quality therefore depends more strongly on sugar-acid balance than on sugar concentration alone, making the maturity index and related ratios highly informative descriptors of organoleptic performance (Martinez et al. 2006; Melgarejo et al. 2000). In parallel, biochemical quality is closely associated with antioxidant composition. Pomegranate juices are rich in phenolic compounds and exhibit strong antioxidant activity, although substantial genotype-dependent variation has been reported in total phenolics, anthocyanins, and vitamin C (Gil et al. 2000; Seeram et al. 2008; Tehranifar et al. 2010). Importantly, analytical comparisons indicate that phenolic estimates may differ depending on method, particularly between chromatographic and spectrophotometric assays, which complicates direct comparison across studies (Escarpa et al. 2001). Overall, antioxidant quality in pomegranate appears to result from the combined contribution of phenolic compounds, anthocyanins, and ascorbic acid rather than from a single dominant metabolite class.

Seed biochemical composition

Seed biochemical composition extends the concept of fruit quality beyond the edible arils and juice fraction. Although seeds are often considered a by-product of processing, they represent a valuable source of oil rich in unsaturated fatty acids and conjugated linolenic acid isomers, particularly punicic acid (Ferrara et al. 2011). Available studies indicate that seed oil content varies markedly among genotypes, whereas the qualitative fatty acid profile is comparatively more stable (Fadavi et al. 2006). This suggests that seed traits have important nutraceutical and industrial relevance, especially for by-product valorization and functional food development. Therefore, pomegranate fruit quality should be regarded as a use-specific, multi-trait system in which commercial value depends on the integrated contribution of fruit morphology, sensory balance, antioxidant chemistry, and seed lipid composition.

Abiotic Stress Tolerance

Pomegranate (*Punica granatum* L.) is widely recognized as a relatively resilient fruit crop adapted to arid and semi-arid environments, yet its growth, productivity, and fruit quality are still substantially constrained by drought and low temperature. In this species, abiotic stress tolerance is best interpreted as an integrated

adaptive phenotype involving maintenance of plant water status, stabilization of photosynthetic activity, osmotic adjustment, membrane protection, antioxidant defense, and recovery capacity after stress release. Available evidence further indicates that these responses are strongly genotype dependent, which makes cultivar-level screening essential for breeding and orchard management under increasingly unstable climatic conditions (da Silva et al. 2013; Pourghayoumi et al. 2017; Sirooeinejad et al. 2020).

Drought tolerance

Drought tolerance in pomegranate is closely associated with the ability to maintain hydration, preserve gas exchange, and reduce cellular injury under water deficit. Greenhouse and field studies on Iranian cultivars have shown that drought progressively decreases relative water content, stem water potential, photosynthetic rate, transpiration, and stomatal conductance, while increasing membrane damage and stress-related metabolite accumulation. However, the magnitude of these changes varies markedly among cultivars, confirming that drought adaptation is not uniform within the species (Faraji et al. 2020; Pourghayoumi et al. 2017). Tolerant genotypes generally maintain higher relative water content, smaller reductions in photosynthesis, and lower membrane injury than susceptible ones, indicating a more effective balance between water conservation and metabolic continuity.

Additional physiological screening of commercial Iranian cultivars further supports this interpretation. Under progressive drought, photosynthetic rate, transpiration, stomatal conductance, intercellular CO_2 concentration, and leaf relative water content all declined, while leaf temperature and electrolyte leakage increased. Yet cultivars such as ‘Rabab Neyriz’ and ‘Malas Yazd’ retained greater photosynthetic stability, higher leaf hydration, and lower electrolyte leakage than more sensitive genotypes such as ‘Nadery Badroud’, indicating stronger physiological resilience under dehydration. These findings show that drought tolerance in pomegranate can be efficiently differentiated through integrated physiological markers related to gas exchange, water relations, and membrane stability, rather than through any single variable alone (Gholami et al. 2012; Hassani et al. 2015; Medrano et al. 2002). The practical implication is that drought-tolerant pomegranate ideotypes should be selected not only for survival under stress, but also for their ability to sustain functional carbon assimilation and recover after rewatering.

Cold tolerance

Cold tolerance in pomegranate is a dynamic seasonal process regulated by acclimation, maximum mid-winter hardiness, and subsequent deacclimation. Although the crop is cultivated mainly in subtropical and warm temperate environments, low and subfreezing temperatures can cause severe injury to shoots, buds, and productive tissues, especially in regions with unstable winter conditions (da Silva et al. 2013; Soloklui et al. 2012). Seasonal evaluation of freezing tolerance has shown that cold hardiness differs substantially among cultivars and is strongly associated with acclimation behavior rather than with a fixed varietal threshold (Sirooeinejad et al. 2020).

The most cold-tolerant cultivars generally accumulate higher levels of soluble carbohydrates, proline, and phenolic compounds during acclimation, while also maintaining lower lipid peroxidation and stronger antioxidant protection.

For example, 'Poostsyah Shirin' was shown to attain greater freezing tolerance and stronger resistance to deacclimation than more sensitive cultivars, indicating that both maximum hardiness and delayed loss of hardiness are important components of cold adaptation (Sirooeinejad et al. 2020). Recent transcriptomic evidence further supports these physiological observations by showing that low-temperature stress in pomegranate affects hormone signaling, photosynthetic pathways, carbon fixation, and carbohydrate metabolism, confirming that cold adaptation involves coordinated molecular and physiological reprogramming rather than a purely passive seasonal response (Guan et al. 2023).

Physiological and biochemical stress markers

Across both drought and cold stress, several physiological and biochemical traits emerge consistently as useful markers of abiotic stress tolerance in pomegranate. Relative water content, stem water potential, chlorophyll stability, electrolyte leakage, gas-exchange traits, and leaf temperature are among the most informative physiological indicators because they directly reflect plant hydration status, membrane integrity, and photosynthetic performance under stress (Pourghayoumi et al. 2017; Sirooeinejad et al. 2020). At the biochemical level, soluble carbohydrates, proline, antioxidant enzymes such as superoxide dismutase, catalase, and peroxidase, and oxidative damage markers such as malondialdehyde are frequently associated with cultivar differences in tolerance.

Importantly, not all stress-responsive traits should be interpreted as tolerance markers in the same way. In some cases, high proline or anthocyanin accumulation may reflect stress severity rather than adaptive superiority, whereas lower electrolyte leakage, reduced malondialdehyde accumulation, and greater chlorophyll stability more consistently indicate effective protection of cellular function (Guan et al. 2023; Pourghayoumi et al. 2017). Therefore, the available evidence supports the use of integrated physiological and biochemical profiling rather than single-trait screening for identifying drought- and cold-tolerant pomegranate germplasm. Such an approach is especially valuable for breeding programs, where combining stress resilience with stable productivity and fruit quality is the primary objective.

Biotic Stress Resistance

Biotic stress is a major factor limiting the sustainable production, storage performance, and marketability of pomegranate (*Punica granatum* L.). In this crop, disease losses arise not only from visible field symptoms but also from latent infections established during flowering or early fruit development and expressed later during ripening, storage, or transport. This latent nature of infection is particularly important in pomegranate because fruit may appear externally healthy while internal tissues are already colonized, leading to serious hidden losses in commercial chains (Michailides et al. 2010; Munhuweyi et al. 2016; Thomidis 2014; Tziros et al. 2008). Accordingly, biotic stress resistance in pomegranate should not be viewed simply as the absence of visible symptoms, but rather as the ability to restrict early infection, suppress quiescent pathogen development, and preserve fruit and tree integrity throughout preharvest and postharvest stages.

Major fungal and bacterial diseases

The disease spectrum of pomegranate includes both fruit-decay pathogens and systemic vascular or foliar pathogens, indicating that host defense must operate across multiple tissues and developmental stages. Among fungal diseases, heart rot and black spot associated mainly with *Alternaria alternata* are especially important because they illustrate two distinct epidemiological syndromes: one characterized by hidden internal decay and another by visible rind lesions (Ezra et al. 2010; Munhuweyi et al. 2016; Tziros et al. 2008). Heart rot is particularly destructive because infection often begins during flowering and remains asymptomatic until fruit maturation, allowing infected fruit to enter storage and marketing systems unnoticed (Michailides et al. 2008; Michailides et al. 2010). This makes floral susceptibility, latent colonization, and internal tissue protection as important as rind resistance in evaluating cultivar performance.



Fig. 2. Representative images from a pomegranate fruit-disease dataset used for deep-learning applications: (A) healthy fruit; (B) bacterial blight; (C) anthracnose; (D) Cercospora disease; and (E) Alternaria disease. (Revathi et al. 2025). Dataset available at https://data.mendeley.com/datasets/b6s2rkpmvh/1.

Other major fungal pathogens further demonstrate the diversity of infection routes in pomegranate. *Botrytis cinerea* is a key storage pathogen capable of colonizing calyx and crown tissues and spreading under humid cold-storage conditions, while *Penicillium* spp. behave more typically as wound pathogens whose success depends

strongly on rind injury and postharvest handling quality (Munhuweyi et al. 2016; Palou et al. 2006; Thomidis 2014). *Coniella granati* and *Colletotrichum gloeosporioides* add further complexity because they affect fruit, shoots, and leaves and may also exhibit latent behavior before visible symptom expression (Munhuweyi et al. 2016; Sataraddi et al. 2011). At the orchard level, wilt caused mainly by *Ceratocystis fimbriata* and bacterial blight caused by *Xanthomonas axonopodis* pv. *punicae* are among the most destructive diseases because they compromise not only fruit quality but also branch viability, canopy structure, and long-term orchard productivity (Jadhav et al. 2009; Munhuweyi et al. 2016). Taken together, these pathosystems show that biotic stress resistance in pomegranate is multidimensional, involving floral, fruit, foliar, vascular, and storage-related defense capacity rather than a single disease-resistance trait (Fig. 2).

Defense mechanisms and management implications

Current evidence suggests that effective resistance in pomegranate depends on both host-associated and management-mediated mechanisms. At the host level, resistance likely includes the capacity to limit pathogen ingress through floral tissues, maintain rind and calyx integrity, reduce lesion expansion, tolerate or suppress latent colonization, and restrict oxidative and structural deterioration of infected tissues. However, compared with the substantial literature on disease description, epidemiology, and control, direct knowledge of the genetic and physiological basis of host resistance remains relatively underdeveloped in pomegranate (Munhuweyi et al. 2016). Existing reports of cultivar- or germplasm-level resistance, including screening against *Coniella granati* and other pathogens, indicate that useful variation exists, but it remains fragmentary and insufficiently integrated into breeding pipelines (Kumari et al. 2015). Thus, the crop still relies more heavily on disease management than on well-defined resistant ideotypes.

From a management perspective, the biology of major pomegranate pathogens makes integrated disease control indispensable. Since inoculum may arise from mummified fruit, infected debris, diseased wood, soil, contaminated tools, irrigation water, and propagation material, orchard sanitation and clean planting stock are fundamental preventive measures (Jadhav et al. 2009; Jamadar et al. 2011). Because several important pathogens infect during flowering or remain quiescent until after harvest, disease control must begin in the orchard rather than being postponed to postharvest stages. At the same time, postharvest protection remains crucial, particularly for pathogens such as *Botrytis* and *Penicillium*, whose development is strongly influenced by wounding, condensation, and storage humidity (Munhuweyi et al. 2016; Palou et al. 2006; Thomidis 2014). This dual preharvest-postharvest character of pomegranate disease epidemiology means that resistance is partly biological and partly managerial.

An important contemporary trend is the move away from exclusive dependence on synthetic fungicides toward more integrated and ecologically safer systems. Concerns over fungicide residues, pathogen resistance, and environmental impact have stimulated interest in biological control and biopesticide approaches, including *Trichoderma*-based treatments and antagonistic microbial strains against bacterial blight and fungal fruit rots (Chavan et al. 2016; Munhuweyi et al. 2016; Sataraddi et al. 2011). Although these alternatives are promising, the long-term improvement of biotic stress resistance in pomegranate will require a stronger breeding-oriented framework. Future research should therefore focus on systematic multi-pathogen screening of diverse germplasm, clarification of latent-infection

resistance at floral and fruit stages, development of rapid molecular diagnostics for pathogen detection, and integration of host resistance with orchard sanitation, biocontrol, and postharvest management. Overall, the most realistic strategy for improving biotic stress resistance in pomegranate is not reliance on a single control method, but the convergence of host resistance, epidemiological understanding, and integrated disease management.

Molecular Characterization and Advanced Breeding Strategies

Molecular characterization has become increasingly important in pomegranate because morpho-pomological traits alone are often insufficient for accurate discrimination of cultivars, germplasm management, and breeding-oriented selection. In *Punica granatum* L., many economically important traits, including fruit quality, seed hardness, stress adaptation, and disease response, are influenced by genotype × environment interactions, which can obscure classification based only on phenotype. For this reason, molecular markers and genomic tools have become essential for clarifying genetic relationships, identifying elite accessions, avoiding duplication in germplasm collections, and supporting parent selection for breeding programs (Ophir et al. 2014; Patil et al. 2020a; Sarkhosh et al. 2009). Overall, the available literature shows a clear transition in pomegranate research from conventional marker systems toward genome-assisted and transcriptome-informed breeding strategies.

Molecular markers for germplasm characterization

Early molecular studies in pomegranate relied mainly on RAPD, AFLP, and related marker systems to estimate genetic diversity and classify regional germplasm. RAPD-based studies were particularly useful in showing that phenotypically similar accessions may differ genetically, and that morphological and molecular clustering do not always coincide, especially in soft-seeded or locally named materials (Sarkhosh et al. 2009; Zamani et al. 2007). This was an important step because it demonstrated that molecular data are necessary for reliable genotype discrimination, even when fruit traits appear highly informative. However, RAPD markers also have well-known limitations in reproducibility, locus specificity, and transferability, which restrict their usefulness for advanced breeding applications.

SSR markers represented a major improvement because of their codominant inheritance, higher reproducibility, and stronger discriminatory power. Studies using genomic SSRs, EST-SSRs, and later hypervariable SSR markers confirmed moderate to high polymorphism among cultivated, exotic, and wild pomegranate accessions, and consistently showed that wild and landrace materials often retain broader allelic diversity than commercial cultivars (Jian et al. 2012; Patil et al. 2020a; Soriano et al. 2011). Importantly, SSR-based analyses revealed population structure patterns broadly associated with geographical origin and germplasm history, demonstrating their value for core collection development, parent selection, and germplasm conservation. Thus, SSRs remain one of the most practical marker systems for pomegranate diversity analysis and pre-breeding, particularly where cost-effective and medium-throughput genotyping is needed.

SNPs, transcriptomics, and genome-enabled resources

A major conceptual advance in pomegranate genetics came with the development of transcriptomic and genome-enabled marker resources. Transcriptome sequencing made it possible to move beyond anonymous polymorphism toward gene-associated variation, thereby linking diversity analysis more directly with functional biology. The study of Ophir et al. (2014) was especially important in this regard because it used de novo transcriptome assembly to discover SNP markers and demonstrated that transcriptome-derived polymorphisms could successfully resolve broad germplasm structure in pomegranate (Ophir et al. 2014). This work showed that pomegranate diversity could be analyzed on a broader genomic basis than previously possible with local marker sets alone, and it established SNP discovery as a realistic foundation for future genomics-assisted breeding.

Subsequent progress in whole-genome sequencing further strengthened this transition. Draft and reference genome assemblies, including those of cv. Tunisia and Dabenzi-related resources, enabled genome-wide marker mining, improved SSR development, and facilitated the identification of loci associated with fruit quality and developmental traits (Patil et al. 2020; Qin et al. 2017; Yuan et al. 2018). These resources are especially valuable because they provide the structural framework required for high-density marker development, comparative genomics, and candidate-gene analysis. In practical breeding terms, this means that pomegranate is no longer limited to low-resolution marker surveys; it is increasingly moving toward genome-informed trait dissection.

Transcriptomic analyses also have broader significance beyond marker discovery. They provide access to stress-responsive genes, metabolic pathways, and transcriptional networks involved in fruit quality, seed traits, and abiotic stress adaptation. In this sense, transcriptomics acts as a bridge between diversity analysis and functional breeding. While classical germplasm studies answer the question “how diverse?” transcriptome-based approaches begin to answer “which genes and pathways are diverse?” which is far more relevant for precision breeding.

Marker-assisted and integrated breeding perspectives

Despite significant progress in molecular characterization, pomegranate breeding remains less advanced than in many major fruit crops, largely because trait inheritance, marker validation, and breeding pipelines are not yet fully integrated. The current literature suggests that marker-assisted selection (MAS) in pomegranate is promising, but still at an emerging stage. The development of genetic maps enriched with transcript-linked markers and QTLs for fruit quality traits indicates that the species is becoming increasingly suitable for marker-trait association studies and more informed hybridization strategies (Harel-Beja et al. 2015). However, most breeding efforts still rely heavily on phenotypic evaluation, and validated markers for routine selection of major commercial traits remain limited.

Integrated breeding is therefore particularly important. In pomegranate, no single data layer is sufficient for effective selection. RAPD and SSR studies provide broad diversity patterns; SNPs and transcriptomics offer functional resolution; genome resources enable dense marker development; and phenotypic evaluation remains indispensable for traits such as fruit quality, seed hardness, yield stability, and stress resilience. Therefore, the most effective future strategy is not the replacement of conventional breeding by molecular tools, but their integration. A

robust pomegranate breeding framework should combine germplasm characterization, phenotypic screening, genome-wide marker resources, and candidate-gene information to identify parents, define heterotic or divergent pools, and accelerate the selection of elite ideotypes.

From this perspective, wild accessions, landraces, and exotic germplasm deserve particular attention because several studies indicate that they harbor broader genetic variation than established cultivars and may serve as sources of useful alleles for fruit quality improvement, stress adaptation, and resilience breeding (Ophir et al. 2014; Patil et al. 2020a). Thus, molecular characterization in pomegranate should be viewed not merely as a classification exercise, but as the foundation of a modern integrated breeding system.

Knowledge Gaps and Future Perspectives

Despite the growing body of research on *Punica granatum* L., important knowledge gaps still limit the development of a fully integrated improvement strategy. Current studies have generated substantial information on fruit quality, abiotic stress tolerance, biotic stress resistance, and molecular diversity, yet these components are often examined separately rather than within a unified breeding framework. As a result, pomegranate improvement remains stronger at the descriptive level than at the predictive and application-oriented level.

A major limitation is the incomplete translation of molecular resources into practical breeding. Although RAPD, SSR, SNP, transcriptomic, and genome-based studies have significantly improved germplasm characterization, only a limited number of markers have been validated for routine selection of key traits such as fruit quality, seed softness, drought tolerance, cold hardiness, and disease resistance. Similarly, many physiological and biochemical studies have been conducted under greenhouse or single-location conditions, which may not fully represent the long-term behavior of mature orchard trees under field environments. Greater emphasis is therefore needed on multi-environment validation, long-term phenotyping, and stronger genotype × environment analysis.

Future research should prioritize the integration of phenotypic, physiological, biochemical, and molecular datasets into breeding-oriented platforms. Wild accessions, landraces, and exotic germplasm should receive particular attention as potential sources of useful alleles for fruit quality and stress resilience. At the same time, omics-based approaches, including transcriptomics, metabolomics, and candidate-gene validation, should be more closely linked with field performance and horticultural value. Such integration will be essential for developing pomegranate cultivars that combine superior fruit quality with stable adaptation to climatic and pathological constraints.

Conclusions

Pomegranate (*Punica granatum* L.) is a high-value fruit crop whose agronomic and commercial importance continues to increase under arid and semi-arid conditions. The evidence reviewed here shows that its improvement

depends on the interaction of multiple biological dimensions, including phenological adaptation, fruit quality, abiotic stress tolerance, biotic stress resistance, and molecular diversity. Fruit quality is strongly genotype dependent and should be regarded as a use-specific, multi-trait phenotype involving morpho-pomological, biochemical, and nutraceutical characteristics.

At the same time, both drought and cold tolerance are complex adaptive traits associated with water-status maintenance, membrane protection, antioxidant defense, and preservation of physiological activity, whereas biotic stress resistance depends on the combined effects of host defense, pathogen biology, and integrated disease management. Molecular tools such as RAPD, SSR, SNP, transcriptomics, and genome resources have substantially strengthened germplasm characterization and created new opportunities for advanced breeding, although their practical deployment remains incomplete.

Overall, future progress in pomegranate will depend on integrated breeding strategies that combine precise phenotyping, molecular characterization, and multi-environment validation. Such an approach is essential for developing cultivars that unite high fruit quality with resilience to environmental and pathological stresses.

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Author Contributions

IAA: Conceptualization, Supervision, Writing - review & editing, UXY: Conceptualization, Formal analysis, Methodology, Investigation, Writing - original draft, Writing - review & editing, BAS: Investigation, Data curation, Writing - review & editing, ANX: Investigation, Validation, UXT: Investigation, Resources, USB: Investigation, Formal analysis, Writing - review & editing, KGM: Resources, Validation, AAD: Supervision, Methodology, Writing - review & editing.

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