

Review

# Breeding Maize for Tolerance to Acidic Soils: A Review

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**Abstract:** Acidic soils hamper maize (*Zea mays* L.) production, causing yield losses of up to 69%. Low pH acidic soils can lead to aluminum (Al), manganese (Mn), or iron (Fe) toxicities. Genetic variability for tolerance to low soil pH exists among maize genotypes, which can be exploited in developing high-yielding acid-tolerant maize genotypes. In this paper, we review some of the most recent applications of conventional and molecular breeding approaches for improving maize yield under acidic soils. The gaps in breeding maize for tolerance to low soil pH are highlighted and an emphasis is placed on promoting the adoption of the numerous existing acid soil-tolerant genotypes. While progress has been made in breeding for tolerance to Al toxicity, little has been done on Mn and Fe toxicities. More research inputs are therefore required in: (1) developing screening methods for tolerance to manganese and iron toxicities; (2) elucidating the mechanisms of maize tolerance to Mn and Fe toxicities; and, (3) identifying the quantitative trait loci (QTL) responsible for Mn and Fe tolerance in maize cultivars. There is also a need to raise farmers' and other stakeholders' awareness of the problem of Al, Mn, and Fe soil toxicities to improve the adoption rate of the available acid-tolerant maize genotypes. Maize breeders should work more closely with farmers at the early stages of the release process of a new variety to facilitate its adoption level. Researchers are encouraged to strengthen their collaboration and exchange low soil pH-tolerant maize germplasm.

**Keywords:** maize; low soil pH; toxicity; breeding; tolerance

## 1. Introduction

Maize (*Zea mays* L.) is among the most widely grown crops in the world after rice (*Oriza sativa* L.) and wheat (*Triticum aestivum* L.). It forms the basis for food security in some of the world's poorest regions in Africa, Asia, and Latin America and is produced on nearly 100 million hectares in 125 developing countries [1]. One of the major abiotic constraints of maize production is the occurrence of acidic soils, caused by a low potential of hydrogen (pH). Considerable grain yield reductions of maize under low soil pH have been reported in numerous studies. Dewi-Hayati et al. [2] reported that grain yield reduction in acid soils varied from 2.8 to 71%, whereas Tandzi et al. [3] found maize yield reduction under acid soils to be up to 69%. The variation in yield reduction under low soil pH is based on the level of acidity in the soil, the agro-climatic conditions of the environment, and the genetic potential of maize genotypes. Improving grain yield under acidic soil conditions is a major objective of maize breeding programs in many regions of the world. An estimated 3950 million ha, or 30% of global

arable land, is covered by acidic soils [4–6]. The largest amount of potentially arable acid soils exists in the humid tropical zones, and comprises about 60% of the acid soils of the world [5]. The poor fertility of acidic soils is due to a combination of mineral toxicities (Al, Mn, and Fe) and nutrient deficits caused by the leaching or decreased availability of phosphorus (P), calcium (Ca), magnesium (Mg), sodium (Na), and micronutrients such as molybdenum (Mo), zinc (Zn), and boron (B) [7].

The development of high-yielding maize cultivars has been the target of selection and breeding procedures in tropical and subtropical regions with acid soils. Grain yield is often the product of interactions between plant genotypes and the environment during the cropping cycle [8]. A high level of heterosis and good combining ability are prerequisites for developing good, economically viable maize hybrids [9]. Conventional breeding, based on testcross data, has been widely used to estimate heterosis between populations or inbred lines, and used to assign inbreds to heterotic groups [10–15]. Combining ability analyses assess the potential value of inbred lines and identify the nature of gene action controlling various quantitative characters. This information is essential for maize breeding focusing on developing hybrids, synthetics, and improved open pollinated cultivars [16] under low soil pH. The advent of molecular genetics has enabled the use of DNA markers to tag genomic regions associated with tolerance to low soil pH, and the subsequent utilization of marker-assisted selection (MAS) to enhance the efficiency of maize breeding programs [17]. Additionally, the identification of key physiological processes associated with yield improvement and the determination of gene-to-phenotype associations can potentially increase the efficiency of breeding for acid tolerance, either through traditional or molecular methods [18].

This paper reviews maize improvement for tolerance to acidic soils using conventional and molecular technologies, with a special focus on the experimentations that have improved the acid tolerance of some maize genotypes. It also reviews the genetic, physiological, and biochemical mechanisms by which plants tolerate low soil pH stress. The adoption of existing and improved acid-tolerant maize genotypes is also taken into account. Challenges faced in breeding for acid tolerance are identified and suggestions for overcoming them are provided. Areas with limited information and research attention are also identified. The intensification of research efforts to fill the identified gaps in information could improve on the efforts already made in the development of high-yielding and high-quality acid-tolerant maize cultivars.

## 2. Acid Soils

### 2.1. Distribution of Acidic Soils

Acidic soils occur mainly in two global belts: the northern belt, with a cold, humid temperate climate, and the southern tropical belt, with warm and humid conditions [5,6,19]. The global distribution of acid soils is as follows: 40.9% in the Americas, 26.4% in Asia, 16.7% in Africa, 9.9% in Europe, and 6.1% in Australia and New Zealand. About 67% of the acid-soil area is under forests, 18% under savannas and prairie vegetation, 4.5% under arable lands, and less than 1% under perennial tropical lands [5]. In Cameroon, acid soils cover 75% of arable land [20,21], whereas in Kenya they cover only 13% of the total land area [22]. In South Africa, 5 million ha of soils are severely acidified with an estimated 11 million ha being moderately acidic [23]. In KwaZulu Natal, 85% of soils have pH < 5 and about half of these have an acid saturation of >10% [24]. The distribution of low soil pH (pH < 5) in the world is presented in Figure 1.

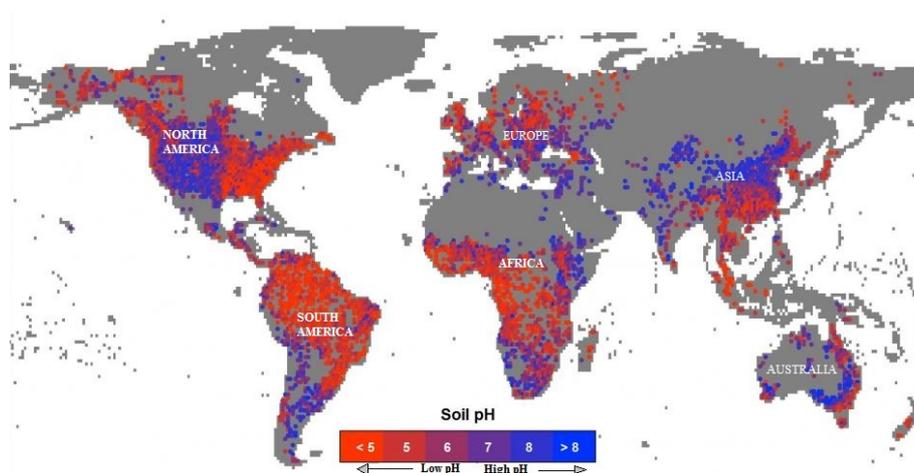


Figure 1. World distribution of soil pH (modified from [25]).

## 2.2. Acidification of Soils

Acidic soils are defined as soils with pH < 5.5 in the top layer [4–6]. The amount of hydrogen cation ( $H^+$ ) activity in the soil solution determines the soil pH and is influenced by edaphic, climatic, and biological factors. High rainfall affects the rate of soil acidification when rainfall washes away bases ( $Ca^{2+}$ ,  $Mg^{2+}$ ,  $K^+$ ,  $Na^+$ , and carbonate ion ( $CO_3^{-2}$ )) from the soil. Hydrolysis results in a reduction in soil pH when a metal is dissolved in water, releasing protons. The hydrolytic displacement of base cations and the provision of additional acids from oxidation reactions are the main natural causes of soil acidification, which lead to base-deficient, aerated sands under strong leaching conditions such as high rainfall and drainage [26]. Poor agricultural practices (use of ammonium fertilizers and crop removal) also contribute to the acidification of the soil [27]. Soil acidification is intensified by the removal of cations through the harvesting of crops and by acid precipitation from polluted air [28,29].

## 2.3. Toxication of Acid Soils

Acid soil toxicity is caused by a combination of high solubility of toxic heavy metal elements (iron, copper, manganese, zinc, and aluminum), a lack of essential nutrients (phosphorus, magnesium, calcium, potassium, sodium), and low soil pH [30,31]. Low soil pH can therefore generate excesses of aluminum, iron, and manganese, which hamper crop production [32]. High Al and Fe oxides and hydroxide in low soil pH are responsible for P fixation, making it unavailable to plants [33–35]. All of these toxicities (Al, Mn, and Fe) should be considered when breeding for maize tolerance to low soil pH around the world.

### 2.3.1. Aluminum Toxicity

Al toxicity limits agricultural productivity by preventing crops to reach their yield potential [36–39]. Al toxicity (60 to 300  $\mu g$  per liter of water in soil) can cause 25–80% yield losses in various crop plants [40]. Under Al toxicity, nitrogen (N), P, and potassium (K) uptake, which are essential nutrients responsible for the stimulation of root growth [41], become unavailable. Strong subsoil Al toxicity reduces plant rooting depth, increases susceptibility to drought, and decreases the use of subsoil nutrients [28]. Al toxicity effects result in root damage, which hamper nutrient uptake ability, resulting in nutrient deficiency in the plant [42,43]. Under Al toxicity, P deficiency leads to stunted plant growth, and thin and spindly stems with purpling leaves, which results in the reduction of grain yield [44,45]. The determination of the content of available Al (exchangeable and in the soil solution) is essential for an evaluation of the risk for plant production in acid soils. While most of the attention on acidic soils has been focused on Al toxicity, limited attention has been placed on Fe and Mn toxicities.

### 2.3.2. Iron Toxicity

Iron is the fourth most abundant mineral in the earth's crust after oxygen (O<sub>2</sub>), silicon (Si), and Al. Fe toxicity is a disorder associated with large concentrations of reduced iron (Fe<sup>2+</sup>) in the soil solution, which occurs in flooded soils [46]. The hydrolysis of Fe is more acidic than Al hydrolysis. Acidity resulting from Fe toxicity is normally buffered by Al hydrolysis reactions. However, once most of the soil Al ions have reacted, Fe hydrolysis takes over, leading to a profound decrease in soil pH [47].

In low soil pH, the anaerobic bacteria provide very high amounts of ferrous ion, which become toxic to plants. Acid soils that are poorly aerated or compacted can increase iron content to the point of toxicity. A high concentration of Fe<sup>2+</sup> in the rhizosphere has antagonistic effects on the uptake of essential nutrients (P, K, and Zn) by the plants, causing the accumulation of harmful organic acids or hydrogen sulphides, and consequently leading to plant yield reduction [48]. Yield reductions of 12 to 100% have been previously observed in rice growing in iron toxic soils [49–51], depending on the level of iron toxicity, genetic background of genotypes, and soil fertility status. High iron availability in the soils can also lead to direct or indirect toxicity in the plants [52]. High toxic levels of accumulated Fe in plants can damage lipids, proteins, and deoxyribonucleic acid (DNA). Direct effects of iron toxicity also include damage to cell structures leading to reduced plant growth and injury to foliage [53–56]. In tolerant genotypes, excess iron is known to precipitate on roots, forming an iron plaque that acts as a barrier against iron while ensuring the utilization of essential nutrients by those plants (a process known as indirect iron toxicity). In contrast, an imbalance of nutrients has been observed in susceptible plants growing in soils with toxic levels of iron [48,57,58]. The critical concentration of iron toxicity symptoms varies from 10 to 500 mg/L depending on the nutrient status in the plants and the presence of the reduction products in the environment [51].

### 2.3.3. Manganese Toxicity

Manganese (Mn) is an essential trace element throughout all stages of plant development, which becomes toxic when taken up in excessive quantities. Mn is deficient in maize plants when its level is less than 15 ppm; it is low when it is between 15 and 25 ppm; sufficient between 26 and 150 ppm; high between 151 and 200 ppm; and excessive or toxic when its concentration is higher than 200 ppm [59].

Mn toxicity is associated with Al and Fe hydrolysis, the primary reactions causing soil acidity. Soil acidification further enhances the solubility of Mn, and thus increases its bioavailability to toxic levels in natural and agricultural systems [60,61]. The effects of Mn toxicity are more pronounced in sensitive plants with a decrease in soil pH, which further increases the solubility of Mn [47,61]. The first symptoms of Mn toxicity appear on the oldest leaves of plants as chlorosis, which later progresses to necrosis [62]. In addition, plants exposed to excess Mn exhibit a very strong inhibition of chloroplast structure and functions, reduced photosynthetic and transpiration rates, and inhibition of carbon dioxide (CO<sub>2</sub>) fixation as a result of stomatal closure [63,64]. To date, there is a very limited number of published reports on manganese toxicity in plants. Therefore, this area of study requires more investigations.

## 2.4. Management of Acidic Soils

A number of management practices are used to correct low soil pH. Liming is the most commonly recommended management practice [65–67]. Kisinyo [68] found that the application of both lime and P fertilizer are important for P and N fertilizer recovery efficiencies necessary for healthy maize growth under acid soils. However, the application of lime and/or fertilizer is not always affordable for small-scale farmers and is not environmentally friendly [12,69]. Additionally, liming affects the topsoil and does not remove acidity in the subsoil, where it poses a severe problem to developing roots [70,71]. Mwangi et al. [72] reported that farm yard manure is a better amendment for correcting soil pH because it has a strong buffering capacity that contains both soil acidity and alkalinity. However, the general recommendations are very high (10 tons per hectare) and the manure is not always available [73].

The addition of crop residues to soils can result in an increase in soil pH [74–76]. Hoyt and Turner [74] found an increase in soil pH of about 0.5 of a pH unit when lucerne meal was added to acid soil, but observed a decline of pH 20 days after incubation. It has been generally observed that the addition of residues causes an initial rise in soil pH, which is then followed by a decline in pH [75,77]. The use of acid-tolerant maize cultivars constitutes an efficient and permanent alternative to increase yields in acidic soils [78].

### 3. Mechanisms of Tolerance to Low Soil pH

The mechanisms of tolerance to low soil pH occur at physiological, biochemical, and molecular levels. However, some of the mechanisms are still poorly understood, and thus require more research. Knowledge of the mechanisms of tolerance of maize genotypes to Al, Fe, and Mn toxicities could facilitate the development of acid soil-tolerant genotypes.

The exclusion of Al in the root apoplast as well as intracellular tolerance to Al toxicity [79,80] have been suggested as important mechanisms for Al tolerance in maize [36–38]. Aluminum exclusion is related to the ability of Al-tolerant plants to excrete organic acids (predominantly citric acid and oxalate in maize) and phenolics from the root apex [37,81,82]. The secreted organic anions (OA) bind with Al to form a complex (Al–OA) which protects the root apex, thus allowing it to continue growing [38,80,81]. The exudation of other organic compounds may be important for the chelation of Al in the root apex [38], even though little is known about their mechanisms of action [79]. Other ligands released in the root apex include phenolic compounds, flavonoids, succinates, phosphates, uridine diphosphate-glucose, and polysaccharides in the form of mucilages [38,79–81,83,84]. Mucilage is a gelatinous material made of high molecular weight polysaccharides exuded from the most external layers of the root apex and is an important mechanism of resistance to metals [79,85].

Physiological, molecular, and biochemical studies have shown that the modification of the cell wall composition imparts resistance to Al toxicity to some genotypes [79,84–86]. The most important internal tolerance mechanisms are Al-binding proteins, the chelation of Al using organic acids (such as citric acid) and other organic ligands in the cytosol, the compartmentalization or sequestration of Al in the vacuoles, the evolution of Al-tolerant enzymes (such as Nicotinamide adenine dinucleotide phosphate—specific isocitrate dehydrogenase), elevated enzyme activity [37,86,87], and the Al-induced synthesis of callose (such as 1, 3-glucan) [78,88]. The phospholipid composition of the plasma membrane plays an important role in Al toxicity since it creates a negative charge on the surface of the membrane and increases the sensitivity to Al [79,89].

The mechanisms of tolerance to Mn toxicity are not clearly established [64]. Different plant species and genotypes respond differently for tolerance to Mn toxicity [64,90]. The tolerance of maize plants to Mn toxicity has been attributed to tolerance to high tissue concentrations of Mn [63]. Stoyanova et al. [64] evaluated four cultivars of maize under high and toxic concentrations and found that the most tolerant genotype, Kneja 434, expressed a stronger internal capacity of protection against the phytotoxicity of Mn and a higher potential of Mn detoxification. More research is needed to better understand the mechanisms of plant tolerance to Mn and Fe toxicities. Connolly and Guerinot [53] stated that cells store iron with specialized iron-storage proteins called ferritins, which play an important role in iron homeostasis, but the significance of this finding remains unclear.

### 4. Breeding Maize for Tolerance to Low Soil pH

Tolerance to mineral elements can be defined as the ability of a plant to grow better, produce dry matter, develop fewer deficiency symptoms when grown at low or toxic levels of the mineral element, and give better yield [91,92]. The breeding of maize for tolerance to low soil pH has largely used conventional and molecular approaches, as elucidated in the following sections.

#### 4.1. Conventional Breeding Methods

Breeding programs place emphasis on the grain and forage production of maize plants for human consumption and animal feed. Selection is therefore directed toward the improvement of plant growth characteristics under stress conditions. Conventional breeding makes use of heterosis, heterotic patterns, and heterotic groups, and combinability to develop improved maize hybrids with tolerance to low soil pH. Screening for tolerance to low pH can be performed in the laboratory using hematoxylin and nutrient culture assays [93–96], in the greenhouse or glasshouse [97,98], and under field conditions in sites that are characterized as ‘hot spots’ for soil acidity [3,12,99–101]. However, the use of nutrient growth solution is a poor predictor for genetic selection under Al toxic soils in the field. Ouma et al. [94] found that the nutrient culture screening for Al toxicity can predict field selection under Al toxic soils with an accuracy of 24 to 35%, depending on the saturation level of Al in a particular soil and the level of available phosphorus. Under low soil pH, Al ions tend to form highly stable complexes with phosphorus [102]. Under these conditions, maize cultivars with high P use efficiency have a good acid soil tolerance capacity.

##### 4.1.1. Heterosis, Heterotic Patterns, and Heterotic Groups for Maize Tolerance to Low Soil pH

Heterosis (hybrid vigor) is the phenomenon in which the progeny of crosses between inbred lines or pure-bred populations perform better than the expected average of the two parents (mid parent heterosis) for particular traits [103] or better than the best parent (high parent heterosis). There are three probable causes of heterosis and none involves additive variance. The dominance hypothesis involves the action and interaction of favorable dominant alleles. The over dominance hypothesis proposes that heterozygous loci are superior to homozygous loci. The epistasis hypothesis involves the interaction of alleles from different loci, which is what occurs with regulatory loci that can turn other genes on or off. Ceballos et al. [104] found in their study in Mexico that in acidic soils, dominance was the most important source of variation, accounting for about 55% of the total variation. Additive and epistatic variance components each accounted for 22.5% of the total genotypic variation in the same study. Heterosis has been efficiently used in the development of high-yielding maize hybrids tolerant to low soil pH.

Inbreds can be classified into specific heterotic groups or patterns depending on their similarity in combining ability and heterotic response when crossed with genotypes from other genetically distinct groups [103]. Twenty-eight maize open pollinated cultivars (OPVs) were crossed in all possible combinations and the 378 varietal hybrids derived from the crosses were evaluated in 10 environments with acid soils in Brazil. From that study, the cultivars were classified into four heterotic groups based on combining ability data. The consistency of the proposed heterotic groups was confirmed by comparing intra- and inter-group first generation progeny ( $F_1$ ) values and mid parent heterosis [105]. More often, significant differences have been recorded among environments and line  $\times$  tester interaction across environments, which have highlighted the different responses of genotypes in various environments [12,13,15,106]. Four distinct heterotic groups were identified under acid soil and across environments in Cameroon based on the specific combining ability and yield superiority of  $F_1$  hybrids over the best hybrid check from inbred line  $\times$  tester crosses conducted in 2012–2014 [15]. In India, six parental inbreds were classified into three heterotic groups based on their specific combining ability for yield under low soil pH. In this case, the superior heterotic pattern was flint  $\times$  dent [107].

The standard public sector view of heterosis is based on statistical estimates and often presents a complex view of heterosis and heterotic groups that is different from most private sector programs. In most private sector programs, breeders develop heterotic groups by using elite inbred lines as testers. The general process is to cross two inbreds with different desirable traits but which both combine well with an elite tester. The  $F_1$  of this cross is selfed to produce a source population from which new inbreds are developed. The new inbreds are selected by the evaluation of hybrids between them and the tester. Any tester hybrids that outperform the best check hybrid by 10% or more are advanced and the new inbred is classed into an anti-tester heterotic group [15]. In practice, commercial maize hybrids

consist of crosses of two unrelated inbreds, each derived from different families or heterotic groups. The diversity increases on pooling germplasm from different heterotic groups. The application of these methods could be useful in developing high-yielding maize genotypes with tolerance to low soil pH. Several research studies [12,13,15,103–107] have been conducted during the past few years under low soil pH conditions using conventional methods (including combinability and heterotic grouping) with the goal of developing high-yielding and tolerant maize genotypes. Despite the efforts and progress made by researchers, the grain yield loss of maize due to low soil pH is still very high. This might be because low soil pH is associated with others stresses such as water stress and poor soil fertility, thus making the selection process more complex.

#### 4.1.2. Combining Abilities and Heritability of Maize Genotypes for Tolerance to Low Soil pH

The concept of combining ability is important in hybrid development, where you compare the performance of lines in hybrid combinations. Combining ability or productivity in crosses is defined as the ability of a parent or an inbred line to transmit desirable traits to a hybrid. There are two types of combining ability: general (GCA) and specific (SCA). SCA is the interaction of genes of two parents involved in a cross with a specific inbred in relation to its contributions in crosses with an array of other inbreds. It relates to non-additive gene effects and depends on how genes from each inbred complement the other [108]. Meanwhile, GCA refers to the average performance of a given genotype or parent in a series of hybrid combinations.

The nature and magnitude of gene action is an important factor in developing an effective breeding program [16]. In Cameroon, the evaluation of 121 testcross hybrids under acid soil environments showed that three parental inbred lines (Cam Inb gp1 17, 4001, and 9450) produced hybrids with the best specific combining ability [15]. Pandey et al. [99] found that parents versus crosses mean squares of grain yield were highly significant, indicating the importance of heterosis and non-additive gene effects for grain yield under acidic soil environments. Under low soil pH, Parentoni et al. [109] and Chen et al. [110] also found the non-additive gene effects to be more important than the additive effects for tolerance to low P. Moreover, Ouma [96] detected both additive and non-additive gene effects under high and low P in Kenyan acid soils. Under low soil pH, the yield-related traits are generally controlled by additive and non-additive gene effects with the predominance of non-additive gene effects. The breeding value and gene effects of maize genotypes for tolerance to low soil pH are presented in Table 1.

**Table 1.** Gene effects for maize tolerance to low soil pH.

| Type of Maize Genotype               | Combining Abilities in Low Soil pH   | References        |
|--------------------------------------|--|-------------------|
| Hybrids                              | Importance of both additive and non-additive gene effects for yield and yield components in acid soil environments.                                    | [100,101,103,111] |
| F <sub>1</sub> progenies             | Both additive and non-additive gene actions with the predominance of non-additive effects were observed under acid soils.                              | [11,12,15,99]     |
| Maize populations                    | Epistasis accounts for the higher proportion of the total variability of the total sum of squares in acid soil locations.                              | [104]             |
| Maize hybrids (single and top cross) | Tolerance to Al toxicity in soil acidity was controlled by additive as well as non-additive gene effects, with the preponderance of additive effects.  | [111–117]         |
| Single cross hybrids                 | In acid soil with manganese toxicity, the contribution of non-additive gene effects was greater than the additive effects of genes.                    | [116,117]         |
| Testcross hybrids                    | At Nkolbisson in Cameroon, where the soil acidity contains Mn toxicity, the effect of additive genes was higher than the effect of non-additive genes. | [14]              |

Grain yield is the most important quantitative trait and it involves multiple genetic effects. In the development of high-yielding maize hybrids, it is important to know the gene actions and their relative contribution in the expression of yield-related traits. Under low soil pH, yield is controlled by additive and non-additive gene actions [100,101,114] with the predominance of non-additive gene effects [11,12,15,99,103]. It is difficult to select for yield directly so the yield components that are

usually controlled by additive gene effects are evaluated. Several researchers have reported high heritability and high genetic variance for different yield components in maize [118,119]. Rafique et al. [118] reported high heritability (>80%) for all of the traits collected (plant height, ear height, ear length, ear diameter, grain yield, kernel per row) showing heritable variation among genotypes. Rafiq et al. [119] found high heritability estimates (>80%) for all of the traits indicating the preponderance of additive gene action. Bello et al. [120] reported high phenotypic and genotypic coefficient of variations as well as high heritability for the number of grains per ear, ear weight, and plant and ear heights, and found that these traits were under the control of additive gene effects. Therefore, effective selection could be possible for the improvement of these yield components under normal conditions. Khan et al. [121] reported moderate heritability estimates under normal conditions for plant height (38.5%), ear height (32.6%), days to 50% tasseling (48.4%), 100-kernels weight (42.3%), ear length (49.5%), ear diameter (40.0%), and cob diameter (28.5%). Opposingly, Tandzi et al. [3] observed low heritability for all of the agronomic traits (anthesis-silking interval (9%), plant height (27%), ear height (40%), ear per plant (14%), ear aspect (28%), plant aspect (17%), and yield (8%)) recorded under low soil pH.

#### 4.1.3. Secondary Traits Associated with Tolerance to Acidic Soils

The identification of secondary traits is very useful in breeding maize for tolerance to low soil pH due to their correlations with yield. Since yield is mostly controlled by non-additive gene action, secondary traits could be used as indirect predictors of yield in acid soil environments. In addition, secondary traits can also be useful for the genotypic characterization of plants in response to low soil pH stress. Baligar et al. [122] reported that at 41% Al saturation, tolerant maize genotypes produced high shoot and root weight as well as high nutrient efficiency ratio (NER) for P, Ca Mg, and Fe. The greater grain yield of newer acid-tolerant Argentinean maize hybrids was mainly related to an increase in harvest index [123]. Increased harvest index was more associated with a greater increase in grain yield components including kernel number and/or kernel weight than with an increase in shoot biomass. The characteristic most frequently associated with genetic yield improvement in maize under stress conditions is delayed leaf senescence or “stay green” [124,125]. Different secondary traits associated with tolerance to low soil pH at different stages of maize development have been identified over the years (Table 2). Welcker [101] observed moderately strong to strong correlations of anthesis-silking interval, plant height, and ears per plant with yield under low soil pH conditions. However, Tandzi et al. [3] observed weak to moderately weak correlations of anthesis-silking interval and plant height with yield, suggesting the unreliability of these traits as predictors of performance under low soil pH conditions. Leaf area, photosynthetic rate, stress tolerance index, and stress susceptibility index showed strong correlations with yield (Table 2); these traits could be reliable predictors of yield due to their probable stability across environments. Some secondary traits are specific to certain mineral toxicities in the soil. For instance, chlorophyll content could be a useful secondary trait under Mn toxicity [64].

**Table 2.** Secondary traits associated with tolerance to low soil pH.

| Secondary Traits *  | References |
|---|------------|
| Anthesis silking interval (−0.65 in 1999 and −0.66 in 2000), plant height (+0.65 in 1999, +0.71 in 2000), and ears per plant (+0.50 in 1998, +0.74 in 1999 and +0.74 in 2000) were strongly related to yield.   | [101]      |
| Leaf area (+0.75) and photosynthetic rate (+0.78) were highly and positively correlated with grain yield.   | [101]      |
| Seminal root length measured at leaf stage 4 appeared to be the most sensitive trait for tolerance to low pH under laboratory conditions.   | [12,101]   |
| Relative Net Root Growth (RNRG) was found to predict field performance under Al toxic soils by between 24% and 35%.   | [96]       |
| Plant height (0.36), ear height (0.28), and stress tolerance index (0.94) were highly and positively correlated with yield.<br>Anthesis-silking interval (−0.13), plant aspect (−0.4), ear aspect (−0.47), and stress susceptibility index (−0.90) were negatively correlated with yield. | [3]        |

\* Values in brackets refer to correlation coefficients between yield and secondary trait.

#### 4.2. Application of Molecular Tools in Breeding for Maize Tolerance to Acidic Soils

Molecular approaches have led to significant achievements of higher tolerance and the identification of genes responsible for acidic soil tolerance, specifically Al tolerance [29]. Molecular markers have been used in maize breeding to map blocks of genes associated with economically important traits, often termed as quantitative trait loci (QTL) [126]. Molecular markers are modern diagnostic tools, which may therefore help breeders to develop cultivars with tolerance to Al, Fe, and Mn toxicities. Molecular markers could be used in marker-assisted selection (MAS) [127], once genes linked to each of these toxicities have been identified.

Members of two different families of transporters, *ALMT* (Al-activated malate transporter) and *MATE* (multidrug and toxic compound extrusion), have been identified to facilitate organic acid anion efflux in Al-tolerant plants [128–131]. Using maize association mapping population and three independent F<sub>2</sub> populations derived from the crosses B73 × CML247, B73 × CML333, and B73 × NC350, Krill et al. [131] identified six candidate genes, including *ALMT2*, in response to Al toxicity. However, only four of the candidate genes, *Zea mays AltSB like* (*ZmASL*), *Zea mays aluminum-activated malate transporter2* (*ALMT2*), *S-adenosyl-L-homocysteinase* (*SAHH*), and *Malic enzyme* (*ME*), were identified by both the association and linkage mapping studies. Froese and Carter [132] found that the positive allele of marker wmc331 linked to *ALMT1* was not widely present in the winter wheat germplasm used in their study but was present only in the most tolerant cultivar. In addition to Al tolerance, genes in the *ALMT* family are also known to influence other physiological processes such as guard cell regulation, fruit quality, and seed development [102].

The *MATE* gene has been cloned and identified in several crops such as *Arabidopsis* [55], barley [133], wheat [134], sorghum [129], rice [135], bean [136], poplar [137], soybean [138], and maize [130,131] (Table 3). The Al-tolerant allele for the *MATE1* locus was found to contain a tandem gene triplication and to have higher levels of gene expression compared to the sensitive allele with a single gene copy [131]. A gene-specific marker, Cit7, was developed based on sequence of the barley *HvMATE* gene to improve the marker-assisted selection of barley genotypes under Al toxicity [139]. The presence of three copies of *MATE1* in Al-tolerant maize lines, Al237, C1006, and IL677a, originating from regions of highly acidic soils in South America and Africa underscores the role of gene copy number variation in the adaptation of plants to acidic soils, and further suggests that genome structural changes may be a rapid evolutionary response to new environments [131].

Mattiello et al. [140] identified 44 candidate genes located within or near intervals of QTL for Al tolerance, with several functions such as cyclins (RNA binding protein, a protease inhibitor) and xyloglucan endo transglycosylase protein 8 precursor that may work together and contribute to maintaining root growth in acid soil with toxic levels of Al. The use of more powerful genomic technics such as the Hi-C sequencing method could provide new evidence for the existence of spatial Al-tolerant gene clusters [141].

To date, there are no reports on genes or QTL associated with tolerance to Fe and Mn toxicities. The identification of QTL linked to secondary traits correlated with yield performance under conditions of either Fe or Mn toxicity could further enhance the efficiency of maize breeding for tolerance to low soil pH. QTL associated with secondary traits such as days to silking, anthesis-silking interval, and stay green characteristic under stressed environments [142,143] could have the potential to be utilized as indirect molecular predictors of performance of plants exposed to Fe and Mn toxicities. Moreover, it is relevant to check whether any of the previously identified genes or QTL for Al tolerance have pleiotropic effects for tolerance to Fe and Mn toxicities. Also, there is need for the application of the recent advances in proteomic and metabolomics to provide a greater understanding of the mechanisms involved in the tolerance of plants to low soil pH.

**Table 3.** Genes associated with Al tolerance in different crops.

| Gene   | Crop  | Reference             |
|--|---|-----------------------|
| <i>MATE</i> (multidrug and toxic compound extrusion)   | Maize   | [129–131]             |
|  | <i>Arabidopsis</i>                              | [55]                  |
|  | Sorghum   | [129]                 |
|  | Rice  | [135]                 |
|  | Bean  | [136]                 |
|  | Poplar  | [137]                 |
|  | Soybean   | [138]                 |
| <i>Zea mays</i> AltSB like ( <i>ZmASL</i> ),<br><i>Zea mays</i> aluminum-activated malate transporter2 ( <i>ALMT2</i> ),<br><i>S</i> -adenosyl-L-homocysteinase ( <i>SAHH</i> ),<br>Malic enzyme ( <i>ME</i> ) | Maize   | [139]                 |
| <i>HvMATE</i>  | Barley  | [135,139]             |
| <i>ALMT</i> ( <i>Al</i> -activated Malate Transporter)   | Wheat, rice, tobacco, barley                    | [128,132,134,144,145] |
| <i>BnALMT1</i> and <i>BnALMT2</i><br><i>GmALMT1</i><br><i>ScALMT1</i>  | Rape<br>Soybean<br>Rye                          | [146–148]             |
| <i>MsALMT1</i><br><i>HlALMT1</i>   | <i>Medicago sativa</i><br><i>Holcus lanatus</i> | [149,150]             |

### 5. Successes in Breeding for Low Soil pH-Tolerant Maize Genotypes

The International Maize and Wheat Improvement Center (CIMMYT), in collaboration with several National Agricultural Research Systems (NARS) all over the world, have developed soil acidity-tolerant maize cultivars to increase maize productivity per unit area. Acid soil-tolerant maize populations have undergone recurrent selections to improve these populations for grain yield under both acid and normal soils [151].

Significant progress has been made in the development of tolerant maize genotypes to low soil pH since 1997. Case studies showing grain yield improvements of some maize genotypes under acidic soil conditions are summarized in Table 4. Means of yield, percentage yield reduction, and percentage yield increase of the genotypes (general, hybrids, single cross, best single cross, three-way cross, best three-way cross, OPV, and the best commercial check) are summarized in Table 4. The mean yield reduction percentage of genotypes varied from 36 to 51% in Latin America and Asia, and from 37 to 40% in Cameroon. These variations were influenced by several factors such as the level of acidity, the agro-climatic conditions, and the tolerance status of the genotypes to low soil pH. The average grain yield of acid soil-tolerant OPVs such as Sikuni was 3.2 t/ha when evaluated across 13 acid soil environments. On the other hand, top cross hybrids developed in 1995 from crosses of OPVs and inbred lines had an average grain yield of 3.84 t/ha when evaluated across six acid soil environments [151]. Reference [103] reported that an addition of 60 kg ha<sup>-1</sup> of phosphorus did not produce a significant grain yield difference for the acid soil-tolerant cultivar ATP-SR-Y but significantly increased the grain yield of the susceptible cultivar, Tuxpeno Sequia, indicating that ATP-SR-Y is a P-efficient cultivar. In Cameroon, a maize yield increase of 51% was obtained with some varieties under low soil pH, while a general yield reduction of 37% was observed in other varieties [3,12]. In Kenya, some single cross hybrids (KML 036 × MUL 863, KML 036 × S39615-1, MUL 863 × MUL 1007, MUL 125 × POOLB 26-1, MUL 817 × MUL 125) expressing superior tolerance to Al toxicity were identified [98]. The most common standard acid-tolerant maize cultivar developed in CIMMYT is CIMCALI 97 Balopia SA<sub>4</sub>, referred to as 97BASA<sub>4</sub> [95].

**Table 4.** Case studies showing grain yield improvements of some maize genotypes evaluated under selected acidic soil environments from 1998 to 2015.

| Genotype              | Latin America and Asia (1997–2000) |                   |                  | Cameroon (1996–2014) |                      |                  |
|-----------------------|------------------------------------|-------------------|------------------|----------------------|----------------------|------------------|
|                       | Mean                               |                   |                  |                      |                      |                  |
|                       | Yield (t/ha)                       | % Yield Reduction | % Yield Increase | Yield (t/ha)         | % of Yield Reduction | % Yield Increase |
| General               | 2.62                               | 44.6              | 19.5             | 3.15                 | 37.3                 | 5.7              |
| Hybrids               | 2.64                               | 44.9              | 20.1             | 3.0                  | 39.5                 | 1                |
| Single cross          | 2.56                               | 46.7              | 17.6             | 3.38                 | 39.5                 | 12.1             |
| Best single cross     | 2.86                               | 50.8              | 26.2             | 6.5                  | 39                   | 51.2             |
| Three-way cross       | 2.70                               | 41.6              | 21.8             | -                    | -                    | -                |
| Best three-way cross  | 3.10                               | 41.3              | 31.9             | -                    | -                    | -                |
| OPV                   | 2.11                               | 35.9              | -                | 2.97                 | 36.9                 | -                |
| Best commercial check | -                                  | -                 | -                | 3.17                 | 40                   | 6.3              |

General = overall mean of genotypes, % yield reduction = the proportion of the yield that is lost under low soil pH compared to the control environment, % yield increase = proportion of yield gain under low soil pH compared to the check. Sources: [3,12,99].

Even though the expected yield of maize genotypes that are tolerant to low soil pH is still low compared to normal conditions, several OPVs and hybrids tolerant to this stress have already been developed and made available to producers. In addition to a high level of expression of the Al tolerance gene *MATE1*, some Maize cultivars such as Cateto also contain high copy numbers of the gene [129]. Several inbred lines and hybrids have been developed from crosses involving the cultivar Cateto. Perentoni et al. [45] classified two maize hybrids (L3 × Cateto and 228-3 × L22) as being P-use efficient based on their mean yield under low and high P environments. These single cross hybrids could be highly tolerant to low soil pH since they are capable of efficiently using phosphorus in a stress environment. Collaborative research should be encouraged in the regions where low soil pH is a major problem to maize production, as this may lead to improvements in the commercialization of low soil pH-tolerant cultivars.

## 6. Adoption of Acid Soil-Tolerant Maize

The adoption of improved maize cultivars remains an important issue in developing countries. Some acid soil-tolerant maize cultivars have not been adopted by farmers even when available, because farmers' selection criteria are generally not considered in the breeding process [51]. About 80% of farmers recycle improved cultivars, including hybrids, contrary to the recommendations [152] in most African countries. Although the superiority of hybrids compared to OPVs has been reported, OPVs will continue to be more important than hybrids under acid soils over the coming years due to the limited resource-base of smallholder farmers [151]. For instance, several high-yielding, low soil pH-tolerant top crosses and hybrid maize genotypes have been identified in Cameroon but have not yet been released [3,12].

Numerous studies have provided insight into the selection criteria of farmers in different parts of Africa. Tolerance to acidic soils was never mentioned in these studies, despite the prevalence of the problem. In the bimodal humid forest area of Cameroon, smallholder farmers are willing to adopt high-yielding maize cultivars tolerant to poor soil fertility if they produce good quality grain and are soft and sweet tasting [68]. Regression analysis showed that household size, level of education, contact with extension agents, access to credit, and yield of improved maize cultivars were the factors that influence the adoption of improved maize cultivars in Nigeria [153]. Gender, age, farm size, income, and lack of access to extension influenced the low adoption rate of maize technologies in Western Kenya. Therefore, it has been recommended that policies should consider household structure, empower smallholder farmers economically, and improve access to extension services to enhance the adoption of improved maize in the country [154]. The provision of social infrastructure, especially access roads to market centers, and the extension of agricultural education to farmers would increase

the spread of improved maize cultivars in Kenya [155]. The use of these approaches might also facilitate the adoption of acid-tolerant cultivars.

Farmers, in most cases, are not aware when breeders release new high-yielding cultivars with tolerance to low soil pH. More demonstration plots combined with farmer training and farmer field days could enhance the adoption rate of improved cultivars. Researchers should apply participatory selection approaches in maize breeding to share knowledge with farmers and other stakeholders who regularly interact with farmers. It is not clear whether the majority of researchers actually believe in involving farmers when evaluating new cultivars. Without farmer involvement, practitioners end up issuing blanket recommendations that are not context-specific. Researchers should organize some workshops explaining practical aspects to be taken into account to deal with the problem of soil acidity. This could involve designing simpler ways in which farmers could measure soil pH, as well as the identification of indicator plants that grow in acidic soils. The adoption of acid-tolerant cultivars can be expected to improve once farmers have a good appreciation of the problem, as well as simple ways of detecting soil acidity in their fields. Farmers could also be encouraged to share seeds of some Al-tolerant cultivars to facilitate their widespread use.

## 7. Conclusions

Low soil pH is often combined with other stresses such as drought, low N, low P in the soil, and poor soil fertility. Several maize genotypes with different levels of tolerance to acidic soils have been developed and commercialized throughout the world, but the yield losses to soil acidity still remain high. Tailoring the crop to fit acidic or less fertile soils is more effective and more economically and environmentally friendly than changing the soil to fit the crops. There is a need to use combining ability and heterosis to efficiently develop high-yielding and more adapted acid-tolerant maize genotypes. The integrated use of molecular tools such as marker-assisted selection already applied in some areas is highly encouraged. In countries, mostly in Africa, where the application of molecular markers is non-existent or very limited due to lack of facilities, financial resources, and skilled personnel, the establishment of modern state-of-the-art laboratories and the training of human resources are critical. Researchers are encouraged to strengthen their collaboration through the sharing of data, findings, and germplasm exchange. The availability of maize germplasm with a broad genetic base for tolerance to low soil pH would increase the potential for the development of high-yielding cultivars with high levels of tolerance to low soil pH as well as toxicities of Al, Fe, and Mn. The mechanisms of Mn and Fe tolerance in maize are still not clearly established. More research should be devoted to maize tolerance to Mn and Fe toxicities. To raise the level of adoption of improved maize cultivars under acidic soils, farmers should be involved in the selection process through participatory breeding and selection approaches.

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## Abbreviations

|     |                          |
|-----|--------------------------|
| Al  | aluminum                 |
| Mn  | manganese                |
| Fe  | iron                     |
| pH  | potential of hydrogen    |
| QTL | quantitative trait locus |
| P   | phosphorus               |

|                                  |  |
|----------------------------------|--|
| Ca                               | calcium  |
| Mg                               | magnesium  |
| Na                               | sodium   |
| Mo                               | molybdenum   |
| Zn                               | zinc   |
| B                                | boron  |
| DNA                              | deoxyribonucleic acid                                  |
| ha                               | hectare  |
| H <sup>+</sup>                   | hydrogen cation  |
| Ca <sup>2+</sup>                 | calcium cation   |
| Mg <sup>2+</sup>                 | magnesium cation                                       |
| K <sup>+</sup>                   | potassium cation                                       |
| Na <sup>+</sup>                  | sodium cation  |
| (CO <sub>3</sub> ) <sup>-2</sup> | carbonate ion  |
| O <sub>2</sub>                   | oxygen   |
| Si                               | silicon  |
| ppm                              | parts per million                                      |
| CO <sub>2</sub>                  | carbon dioxide   |
| OA                               | organic anion  |
| OPVs                             | open pollinated cultivars                              |
| SCA                              | specific combining ability                             |
| GCA                              | general combining ability                              |
| F <sub>1</sub>                   | first generation progeny                               |
| ALMT                             | aluminum-activated malate transporter                  |
| MATE                             | multidrug and toxic compound extrusion                 |
| F <sub>2</sub>                   | second generation progeny                              |
| CML                              | CIMMYT maize line                                      |
| CIMMYT                           | International Maize and Wheat Improvement Center       |
| NARS                             | National Agricultural Research Systems                 |
| t/ha                             | tons per hectare                                       |
| ATP-SR-Y                         | acid tolerant population streak resistant yellow       |
| ZmMATE                           | zea multidrug and toxic compound extrusion             |
| HvMATE                           | Hordeum vulgare multidrug and toxic compound extrusion |
| AltSB                            | aluminum tolerant in sorghum                           |
| ALMT2                            | aluminum-activated malate transporter 2                |
| SAHH                             | S-adenosyl-L-homocysteinase                            |
| ME                               | malic enzyme   |
| RNA                              | ribonucleic acid                                       |
| ALMT1                            | aluminum-activated malate transporter 1.               |

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