Tease out the future: How tea research might enable crop breeding for acid soil tolerance

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https://doi.org/10.1016/j.xplc.2021.100182

ABSTRACT

Unlike most crops, in which soil acidity severely limits productivity, tea (Camellia sinensis) actually prefers acid soils (pH 4.0–5.5). Specifically, tea is very tolerant of acidity-promoted aluminum (Al) toxicity, a major factor that limits the yield of most other crops, and it even requires Al for optimum growth. Understanding tea Al tolerance and Al-stimulatory mechanisms could therefore be fundamental for the future development of crops adapted to acid soils. Here, we summarize the Al-tolerance mechanisms of tea plants, propose possible mechanistic explanations for the stimulation of tea growth by Al based on recent research, and put forward ideas for future crop breeding for acid soils.

Keywords: aluminum, acid soil, tea, Camellia sinensis, breeding

Ding Z.J., Shi Y.Z., Li G.X., Harberd N.P., and Zheng S.J. (2021). Tease out the future: How tea research might enable crop breeding for acid soil tolerance. Plant Comm. 2, 100182.

INTRODUCTION

Acid soils occupy approximately 30% of the world’s total land area and as much as half of the world’s potentially arable lands (i.e., lands located in tropical and subtropical zones that have sufficient solar energy and rainfall for plant growth) (Kochian, 1995; von Uexküll and Mutert, 1995). In acid soils, aluminum (Al), the most abundant metal in the earth’s crust, is released as soluble phytotoxic ions from insoluble aluminosilicate or oxide forms (Kochian, 1995). Al³⁺ ions inhibit the root growth of most plants at very low micromolar concentrations (Ma et al., 2001), and Al toxicity has thus been considered the major factor that limits crop yield on acid soils (Kochian, 1995, 2015). Development of Al-resistant crops is therefore fundamental if sustainable agricultural production on acid soils is to be achieved. Although significant efforts have been made to translate the understanding of Al-resistance mechanisms from many crops or model plants that are non-acidophiles (Delhaize et al., 2004; Magalhaes et al., 2007; Maron et al., 2013; Kochian et al., 2015), it may be that research on species completely adapted to acid soils will provide additional important information that will enhance the breeding of acid- and Al-tolerant crops. Tea is a good candidate for this approach, as it prefers acid soil conditions, is highly tolerant of Al, and even requires Al for optimum growth (Konishi et al., 1985; Hajiboland et al., 2013b). It would be a major advance if other crops could be enabled to acquire a similar capacity for coping with Al.

Tea (Camellia sinensis) is a warm-weather evergreen in the Theaceae family and was first named by C. von Linné in 1753 (v. Linné, 1753; Yang and Hong, 2013). As is well known, the tea drink is usually made from young tea leaves and is the oldest and most popular caffeine-containing beverage in the world (Xia et al., 2017). The earliest credible records indicate that tea was used as a medicinal drink in China during the Shang dynasty, as early as 3000 BC (Xia et al., 2017). However, tea was not popularized as a beverage until 780 AD when The Classic of Tea (Ch’a Ching) was written by Lu Yu (Harbowy et al., 1997). In modern times, tea is planted in more than 60 countries worldwide, and world production stands at 8.57 million tons with a plantation coverage of 6.3 million hectares (FAO, 2017). Tea is believed to have originated at the intersection of northeast India, northern Burma, and southwest China (Wight, 1959; Mondal et al., 2004). Due to cross-pollination, the genus Camellia had 82 species in 1958 (Sealy, 1958; Mondal et al., 2004) and more than 325 species in 2000 (Mondal and Chand, 2002), and it now has approximately 1500 cultivars worldwide (Drew, 2019), indicating a high genome diversity. Cultivated tea varieties belong mainly to two major groups: C. sinensis var. sinensis (Chinese type), the most widely...
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distributed type in China and the world, and C. sinensis var. assamica (Assam type), which is named after the Assam region in India where it was first grown and which has much larger leaves than the Chinese type (Yang and Hong, 2013; Sanlier et al., 2018). Although considerable efforts have been made to determine the relationships between these tea strains over the past 20 years using various sophisticated genetic tools (Kaundun et al., 2000; Balasaravanam et al., 2003; Yao et al., 2008; Megahakumbura et al., 2018), the identity of the wild tea progenitor remains uncertain (Drew, 2019).

The high worldwide popularity of the tea drink is due not only to its stimulative properties, attractive aroma, and pleasant taste but also to its numerous potential health and medicinal benefits, e.g., the prevention of cancer, protection against neurodegenerative diseases, and alleviation of metabolic syndromes (Cabrera et al., 2006; Yang and Hong, 2013). These effects probably arise from the characteristic secondary metabolites present in tea leaves, which include polyphenols, caffeine, and theanine (Harbowy et al., 1997; Yang and Hong, 2013). Accordingly, the increased production of these specific metabolites has been a major target trait in tea breeding, alongside increased yield. Recently, high-throughput “omics”-based technologies, such as transcriptomics, proteomics, and metabolomics, have been employed in efforts to identify genes potentially involved metabolic pathways and stress responses in tea plants (Li et al., 2015; Ding et al., 2017; Xu et al., 2017a, 2017b; Zhao et al., 2017; Chen et al., 2018), greatly accelerating tea research in the last 4 years. In particular, tea genomes have been sequenced, showing that the Chinese-type cultivar has a 3.1-Gb genome (Harbowy et al., 2008; Meegahakumbura et al., 2018), the identity of the wild tea progenitor remains uncertain (Drew, 2019).

Because understanding of the tea response to Al is still very limited, this perspective aims to prompt further dissection of the mechanisms whereby tea plants tolerate and utilize Al, thereby paving the way for future breeding of crops that are tolerant of acidic soils. We first briefly introduce the various features of tea growth and its environmental requirements, then focus on the mechanisms underlying the responses of tea plants to Al. Furthermore, we outline proposals for the use of tea and Al research results to inform the future development of crops tolerant of acid soils.

GENERAL ENVIRONMENTAL CUES FOR TEA GROWTH

Tea is a perennial plant with a productive lifespan of over 100 years and a typical economically viable production period of between 30 and 60 years (Mondal et al., 2004; Hajiboland, 2017). The tea tree grows naturally to a height of roughly 15 m, but a bush height of 0.6–1 m is maintained in cultivation for ease of harvesting the tender young leaves (de Costa et al., 2007). The flowers of tea are white in color and borne singly or in pairs at the axils. Fruits are green, with two or three seeds, and plants become fruit bearing within 5–6 years (Mondal et al., 2004). Tea bushes can be raised from seeds, cuttings, or tissue culture. Vegetative propagation is a common practice because it is high yielding, inexpensive, and fast and can save elite varieties from loss (Hajiboland, 2017). The general growth and development of tea plants are affected by a variety of environmental cues, including temperature, sunlight, water, and soil nutrients. The optimum temperature for tea growth is between 18°C and 30°C (Harbowy et al., 1997; Hajiboland, 2017). Higher or lower temperatures reduce tea leaf photosynthesis and affect productivity and quality (Carr, 1972). Unlike many crops, the tea plant originated as an understory species in tropical rainforests, and its photosynthesis is therefore adapted to shade (Mohotti and Lawlor, 2002). Thus, the optimum light intensity for tea growth varies from 500 up to 1500 μmol m⁻² s⁻¹ in different cultivars (Carr, 1972; Hajiboland et al., 2011), and the optimum shading level is 30%–40% (Hajiboland, 2017). Water availability is another factor that strongly influences tea productivity. Water stress, such as drought, is responsible for a 14%–20% reduction in tea yield and 6%–19% mortality (Cheruiyot et al., 2008). The optimum soil moisture content is considered to be 70%–80%, whereas soil moisture less than 60% inhibits tea growth. Annual rainfall of 1000–2000 mm and humidity of 80%–90% are particularly suitable for tea growth, but humidity less than 50% leads to growth inhibition.

The plucked parts of the tea plant have a high nutrient content, with nitrogen (N) being the most abundant element, followed by potassium (K), calcium (Ca), phosphorus (P), sulfur (S), magnesium (Mg), and zinc (Zn) (Sultana et al., 2014; Hajiboland, 2017). High tea yields of 5800–6400 kg ha⁻¹ year⁻¹ require heavy supplies of N fertilizer (up to 600 kg ha⁻¹ year⁻¹), a requirement probably associated with the stimulation of increased N uptake and assimilation by the frequent harvesting of the shoots (Ruan and Wu, 2004; Cheruiyot et al., 2009). Similar to rice and potato, tea prefers NH₄⁺ to NO₃⁻ as its N source and is well adapted to NH₄⁺-rich environments, having a high capacity for root NH₄⁺ assimilation (Ruan et al., 2007). In contrast to its N requirement, tea has a much lower P requirement than many other crop species and is highly tolerant of P deficiency (Salehi and Hajiboland, 2008). On the other hand, K is considered the most important nutrient for tea after N because large amounts of K are removed from the soil through continued harvesting (Sultana et al., 2014). With respect to micronutrients, boron (B) and Zn deficiencies are common syndromes in tea culture (Hajiboland, 2017). Whereas foliar application of Zn can readily rescue Zn-deficiency symptoms, it is technically difficult to improve tea yield under B deficiency through the application of B-containing fertilizers because the range of soil B concentrations between deficiency and toxicity is very narrow (Bradley et al., 2012; Kumar et al., 2014). Finally, Al accumulates to high concentrations in tea plants and actually promotes tea growth (Matsumoto et al., 1976; Hajiboland et al., 2013b; Sun et al., 2020), making tea Al responses very different from those of most other crops.

AL IS A SPECIAL ELEMENT FOR TEA GROWTH

Tea grows preferentially in acid soil (pH 4.0–5.5), in which Al is partially released from its inactive insoluble form to its active...
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Table 1. Responses of various crops and tree species to aluminum.

| Common name | Species            | [Al] for a significant inhibition of root growth (μM)<sup>a</sup> | References                                                   |
|-------------|--------------------|---------------------------------------------------------------|---------------------------------------------------------------|
| Rice        | Oryza sativa       | <30 (15.48)                                                   | Yamaji et al. (2009); Xia et al. (2010)                       |
| Barley      | Hordeum vulgare    | <5 (1.27)                                                     | Delhaize et al. (2004)                                        |
| Rye         | Secale cereale     | <50 (24.32)                                                   | Gallego and Benito (1997)                                     |
| Wheat       | Triticum aestivum  | <20 (9.66)                                                    | Kinraide and Parker (1987); Sasaki et al. (2004)             |
| Sorghum     | Sorghum vulgare    | <27<sup>b</sup>                                               | Caniato et al. (2007)                                        |
| Maize       | Zea mays           | <6<sup>b</sup>                                                | Pellet et al. (1995)                                         |
| Buckwheat   | Fagopyrum esculentum | <25 (12.93)                                        | Zheng et al. (2005)                                          |
| Tomato      | Solanum lycopersicum | <25 (6.72)                                            | Simon et al. (1994)                                          |
| Rice bean   | Vigna umbellata    | <25 (3.62)                                                    | Fan et al. (2014)                                            |
| Soybean     | Glycine max        | <25 (6.3)                                                    | Noble et al. (1988)                                          |
| Rapeseed    | Brassica napus     | <25 (12.93)                                                   | Wang et al. (2013)                                           |
| Tea         | Camellia sinensis  | >1000 (195.7)                                                | Morita et al. (2008); Chen et al. (2011); Xu et al. (2016); Sun et al. (2020) |
| Aspen       | Populus tremula    | <250 (59.5)                                                   | Grisel et al. (2010)                                         |
| Honey locust| Gleditsia triacanthos | <50 (12)                                        | Sucoff et al. (1990)                                         |
| Red oak     | Quercus rubra      | <120 (75.97)                                                  | Kelly et al. (1990)                                          |
| Sugar maple | Acer saccharum     | <250 (64.6)                                                   | Kelly et al. (1990)                                          |
| Beech       | Fagus sylvatica    | <500 (143.5)                                                  | Kelly et al. (1990)                                          |
| Red spruce  | Picea rubens       | <250 (55.32)                                                  | Raynal et al. (1990)                                         |

<sup>a</sup>The rough threshold concentration above which Al causes obvious root growth inhibition in most ecotypes of a species is shown (inhibition rate 30%–60%). The concentration of bioactive Al<sup>3+</sup> given in parentheses was calculated using Visual MINTEQ software (https://vminteq.kwr.kth.se/). Bioactive Al concentrations for sorghum, maize, and honey locust are provided in the references.

<sup>b</sup>These references only provided the concentrations of bioactive Al<sup>3+</sup>.

In most plants, soluble Al<sup>3+</sup> ions usually confer a characteristic spectrum of cellular damage symptoms, such as plasma membrane disintegration, cytoskeletal disruption, and DNA damage (Kochian, 1995). These effects inhibit root growth and function and consequently reduce crop yield, especially under conditions of additional environmental stress, such as water stress and nutrient deficiency (Kochian et al., 2015). The root growth of most plants is usually quickly inhibited to varying degrees by exposure to Al<sup>3+</sup> ions at low micromolar concentrations (e.g., less than 50 μM), and Al tolerance also varies among plant species (Table 1). For example, rye is one of the most Al tolerant of grain cereal crops and displays approximately 2–3 times greater Al tolerance than barley, wheat, and triticale (Li et al., 2000; Yang et al., 2005). In marked contrast, the tea plant is considerably more Al tolerant than almost all other known crops and many tree species (including aspen and red oak) (Table 1). In general, tea can withstand a concentration of at least 1000 μM Al without negative effect on normal growth (Konishi et al., 1985; Fung et al., 2008; Hajiboland et al., 2013b). For example, it is well known that Al<sup>3+</sup>, but not low pH, directly stimulates the growth of tea plants and other acidophiles, including Melastoma malabathricum, Hydrangea macrophylla, and Melaleuca cajuputi (Osaki et al., 1997). An experimental range of external Al concentrations (0.3–2.5 mM) that is lethal to most plants increases the biomass of tea seedlings of various cultivars by 30%–200% (Konishi et al., 1985; Fung et al., 2008; Morita et al., 2008; Chen et al., 2011; Hajiboland et al., 2013b; Xu et al., 2016). During the initial period of Al exposure, tea root growth, including that of the primary root, lateral roots, and root hairs, is dramatically promoted, whereas shoot growth remains largely unchanged, implying that Al more effectively promotes tea root growth than shoot growth. In addition to its effects on intact tea plants, Al also stimulates the growth of excised tea roots in liquid culture and of suspension-cultured tea cells in a simple salt solution (Tsuij et al., 1994; Ghanati et al., 2005), suggesting that the response of tea to Al occurs not only at the level of the intact plant but also at the tissue and cellular levels. In fact, tea grows poorly in the absence of Al, and this is especially true of root growth in hydroponic cultivation (Fung et al., 2008). By contrast, the shoots accumulate up to 30 000 mg/kg of Al in old leaves on a dry weight basis, and less Al (<800 mg/kg) is present in young leaves (Matsumoto et al., 1976).
et al., 2008) (Figure 1). Roots grown in the absence of Al become brown and grow relatively slowly with limited lateral root outgrowth compared with control roots grown in the presence of Al. Under Al supply, tea roots grow more vigorously and are mostly white in color. Because the white:brown root ratio is positively correlated with healthy growth (Chamuah, 1988), Al appears to be an indispensable element for tea growth and development. In addition, when tea is grown in alkaline soils, the shoots display obvious chlorosis, an effect that can be rescued by foliar Al application (Chenery, 1955).

MECHANISMS OF TEA PLANT AL TOLERANCE

In general, there are two distinct higher plant mechanistic strategies that enable Al resistance. The first strategy is Al exclusion, in which Al ions are prevented from entering the root apex by secretion of Al chelators, such as organic acid anions, into the rhizosphere (Ma et al., 2001). The second mechanism is Al tolerance, which involves sequestration or compartmentalization of Al ions once they enter the root cytosol (symplastic detoxification) and modification of the root cell wall to change its Al-binding capacity (apoplastic detoxification) (Kochian et al., 2015). Because tea is an Al hyperaccumulator, Al tolerance is likely to be the major mechanism by which it copes with Al. Research based on 27Al nuclear magnetic resonance spectroscopy indicates that various chemicals, including phenolics, oxalate, fluoride, and citrate, are involved in chelating Al ions for detoxification in tea roots and shoots (Bojórquez-Quintal et al., 2017). Phenolics, particularly the catechins, have been shown to be the primary Al chelators in tea leaves (Nagata et al., 1992), with catechins and their derivatives making up as much as 30% of leaf dry weight (Wörth et al., 2000). Al application significantly increases the soluble phenolic fraction in both leaves and roots. In addition, high phenolic content is found in the cell wall, where cell-wall-bound phenolics are potential targets for Al (Hajiboland and Poschenrieder, 2015). It is therefore likely that phenolics function in Al tolerance both inside and outside the cell. By contrast, in tea roots, oxalate has been proposed to be mainly responsible for Al detoxification (Morita et al., 2008), and increased levels of Al–oxalate complexes within tea roots are correlated with increased exposure to Al. Furthermore, Al stimulates oxalate secretion from tea roots (Morita et al., 2011), which to some extent prevents Al from entering root cells. In addition, during root-to-shoot Al translocation, an Al-citrate (1:1) complex was found to be the major form of Al in the xylem sap (Morita et al., 2004), and other chemicals, such as fluoride, may also play a role in Al detoxification in tea (Gao et al., 2014). Al chelation may therefore be a primary strategy for efficiently maintaining Al at non-toxic levels following uptake by tea plants.

Next, the mechanisms whereby Al is distributed organically and subcellularly also make tea plants highly tolerant of Al. Following attempts to determine the location of Al in tea roots and shoots, Al was observed predominantly in root hairs, root tips, and the leaf epidermis (Hajiboland and Poschenrieder, 2015; Bojórquez-Quintal et al., 2017), suggesting a tissue preference for Al storage. With respect to subcellular distribution, higher levels of Al were detected in the cell wall and apoplastic soluble fractions than in the symplastic fraction (Fung et al., 2008; Gao et al., 2014). Roughly 25%–30% of total Al was present in the symplast of tea (Fung et al., 2008; Gao et al., 2014), whereas less than 15% of total Al was found in the symplast of non-Al accumulators such as barley and tobacco (Clarkson, 1967; Chang et al., 1999). Because of its relatively high Al content, tea has symplastic Al levels much higher than those of non-Al-accumulating plants, indicating an extremely strong capacity for cellular Al detoxification in tea. Consistent with this assertion, a high Al tolerance was found in tea suspension
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Figure 2. Mechanisms of Al tolerance in tea plants.
A model illustrating the currently understood mechanisms of Al tolerance in tea plants, mostly involving cell-wall fixation and vacuolar sequestration based on the chelation of Al^{3+}. The majority of Al^{3+} ions are fixed into the cell walls by binding to specific cell-wall components, e.g., wall-bound phenolics, HC1 (hemicellulose I), pectin, and others. The remaining smaller Al^{3+} fraction is taken up into cells via unknown transporters. Once present in the cytosol, Al^{3+} is further complexed by phenolic compounds, oxalate, and fluoride. It is subsequently sequestered into the vacuoles via specific transporters whose identity is also unknown. In root cells, Al^{3+} is present mostly in the form of Al-oxalate complexes and, to a lesser extent, in Al-phenolic and Al-fluoride complex forms (lower right), whereas in leaf cells, Al^{3+} is predominantly in the Al-phenolic complex form (upper right). The roots can also secrete oxalate, thus promoting Al exclusion. In the xylem, Al^{3+} is translocated mostly in Al-citrate complex form (middle right). The bold arrows and letters indicate greater contributions to Al tolerance.

In addition to symplastic Al detoxification, apoplastic detoxification may also be involved in the Al tolerance of tea plants (Figure 2). It is commonly agreed that the binding of Al to the cell wall limits cell-wall expansion, thus inhibiting root elongation (Kochian, 1995). Al^{3+} ions are able to interact with wall components both electrostatically with the negatively charged carboxyl groups in wall pectins and by adsorption to uncharged hemicellulose polymers (Yang et al., 2011). Furthermore, modification of pectin or hemicellulose by specific enzymes (e.g., cell-wall pectin methyltransferases, xyloglucan endotransglucosylase/hydrolases, O-acetyltransferases) can affect cell-wall Al-binding capacity and hence Al tolerance (Schmohl et al., 2000; Zhu et al., 2012, 2014; Li et al., 2020). Therefore, a reduced cell-wall Al adsorption capacity generally leads to increased Al tolerance. In keeping with this, the ratio of Al content in the cell wall to that in the symplast is reduced in tea plants compared with other crops (Clarkson, 1967; Fung et al., 2008; Gao et al., 2014). Understanding the underlying mechanism that controls subcellular Al distribution in tea plants is therefore an important question. Nonetheless, because tea is an Al hyperaccumulator, its cell walls still harbor a much higher Al content than those of many other plants. The key question is why such a high abundance of Al in the cell wall does not inhibit tea root cell elongation, and hence root growth, and how this can happen. Future work in this area may be focused on the specifics of cell-wall components in tea plants, although the high content of cell-wall-bound polyphenols may already provide a clue (Hajiboland and Poschenrieder, 2015).

Mechanisms of Tea Plant Growth Stimulation by Al

Although tea displays relatively high Al tolerance, more research attention has been given to the paradoxical stimulatory effect of Al on tea growth, a phenomenon first discovered by Chenery in 1955 (Chenery, 1955). Several different mechanisms have been proposed as possible explanations for the Al stimulation of tea growth, including that Al (1) activates a proton ATPase in the plasma membrane, and thus alleviates proton toxicity at low pH (Osaki et al., 1997); (2) stimulates P absorption in tea roots (Konishi et al., 1985); (3) promotes the growth of beneficial microorganisms on the root surface (Konishi, 1990); (4) replaces some function of B (Yokota et al., 1997); (5) stimulates the uptake of N, Ca, Mg, K, and Mn (Fung et al., 2008; Bojórquez-Quintal et al., 2017); (6) reduces Fe uptake and transport, thus alleviating Fe toxicity (Hajiboland et al., 2013a); (7) elevates the activities of antioxidant enzymes, leading to increased membrane integrity and delayed lignification and aging (Li et al., 2011); and (8) enhances photosynthesis, resulting in higher carbohydrate supply and better protection against reactive oxygen species (Hajiboland et al., 2013b). Although these various hypotheses may in some ways explain the beneficial effects of Al on tea growth, several of them were called into question following the demonstration that Al stimulates the growth of suspension-cultured tea cells.
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in a simple salt solution containing proper concentrations of CaCl₂ and sucrose with no additional nutrients (Ghanati et al., 2005).

Based on the evidence presented here, we propose two further scenarios (A and B) that may explain how Al promotes tea growth:

(A) Perhaps Al is an essential nutrient for tea and for other plants that are well adapted to acid soils. Al meets the requirements for being a nutrient for tea in that (1) Al has a direct beneficial effect on tea growth, (2) tea plants grow poorly and cannot even complete their life cycle in the absence of Al, and (3) the physiological role of Al in tea growth is irreplaceable (i.e., Al cannot be replaced by alternative elements). In line with this proposal, several elements not previously considered to be nutrients, including silicon (Si) and nickel (Ni), are now known to be essential nutrients that promote the growth of certain plants. In accordance with scenario A, Al promotes the division of suspension-cultured tea cells (Ghanati et al., 2005) and facilitates nutrient uptake and photosynthesis of roots and shoots, respectively (Konishi et al., 1985; Fung et al., 2008; Hajiboland et al., 2013b). Furthermore, very recent research reveals that Al is required for the maintenance of tea root meristematic activity, probably because nuclear-localized Al³⁺ ions function in the protection of DNA integrity (Sun et al., 2020). In addition, spraying Al solutions onto the leaves of tea plants grown in alkaline soil can promote recovery from chlorosis (Chenery, 1955). In fact, Al can to varying degrees stimulate the growth of a broad range of non-acidophobe plant species (Bojórquez-Quintal et al., 2017), such as rice (Osaki et al., 1997), and the Al concentration that provides beneficial effects may vary among species. Although Al was previously thought not to be preferred by metabolic systems (because the Al ion is very small and consequently has a very slow exchange rate; Williams, 1999), the potential beneficial physiological role of Al should be given more serious consideration in the future.

(B) In the context of long-term adaptation, perhaps tea and other plants have evolved to respond to Al as a stress signal. According to this scenario, Al induces both stress responses and additional specific developmental responses. For example, Al at non-toxic levels might directly affect cellular hormonal signaling, thus stimulating cell division and elongation. In this case, the rapid root morphological response to Al (Barceló et and Poschenrieder, 2002) could be an initial step, with the increased nutrient uptake and improved shoot growth attributed to Al being more indirect effects. The resultant expanded root surface would thus promote the uptake of various nutrients, including nitrogen. The elevated nitrogen content would in turn stimulate photosynthesis in tea leaves, promoting greater carbon assimilation (Stitt and Krapp, 1999) and thereby improving the growth of tea plants in the presence of Al. In addition to hormonal signaling, the promotion of root growth by Al could occur via various alternative mechanisms. For instance, Al stimulates the excretion of caffeine from tea roots to inhibit callose deposition in root tips, and it is possible that this callose deposition may prevent cell-wall extension and subsequent root elongation (Morita et al., 2002). Alternatively, Al may trigger a unique response in tea plants, resulting in biochemical modification of the cell wall, regulation of the activity of cell-wall loosening agents, and resultant root elongation (Safari et al., 2018).

Nevertheless, in addition to the above scenarios, there remains the possibility that, for tea and other Al-accumulator species that are completely adapted to acid soils, the internal mechanisms that evolved to detoxify Al may negatively affect growth in the absence of Al. For example, an excess of polyphenols or organic acids, while effectively detoxifying Al, may, in the absence of Al, inactivate other essential mineral elements (Watanabe and Osaki, 2002). This possibility should also be given further attention in the future.

DESIGNING FUTURE CROPS FOR ACID SOILS

Because acid soils account for a substantial portion of the world’s cultivable land area, a large number of crop species, including many tree crops (e.g., 90% of coffee species, 60% of cocoa, 100% of oil palm), legumes (e.g., 35% of soybean), root and tuber crops (e.g., 60% of white potatoes, 80% of sweet potatoes, 100% of cassava), and cereals (20% of barley, 20% of maize, 13% of rice), are susceptible to Al stress (von Uexküll and Mutert, 1995). With increasing nitrogenous fertilizer inputs and increasing rain acidification, soil acidification is becoming much more of a problem than it was in the past. For example, soil pH in the major Chinese crop-production areas has decreased by 0.13–0.8 in the past decades (Guo et al., 2010). As a result, many more crops now face Al stress. In addition, Al toxicity has been identified as an important contributor to forest decline (Ulrich et al., 1980). Therefore, the development of Al-tolerant species is not only fundamental for sustaining agricultural production and global food security but also essential for forest restoration and thus, in some ways, for improvement of the global ecological environment.

Current objectives for the breeding of crops with increased Al tolerance are focused mainly on Al tolerance itself. However, because tea plants are not only extremely tolerant to Al but also actually require Al for optimal growth, they perhaps provide a better model for future Al-tolerant crops: more than simple Al tolerance, such crops could exhibit Al stimulation of growth and productivity, making them completely adapted to acid soils. Following this view, the future breeding of Al-tolerant crops could involve three distinct steps (Figure 3). First, a high capacity for Al resistance must be acquired, perhaps through a combination of efficient Al-exclusion and compartmentalization mechanisms (e.g., highly inducible expression of Al transporter genes responsible for the sequestration of Al into vacuoles or translocation of Al to insensitive tissues; increases in the Al-binding capacity of the cell wall without changes in its extension or expansion properties achieved through the manipulation of specific genes that contribute to cell-wall properties; highly inducible accumulation of Al chelators through the modification of specific secondary metabolic pathways; enhanced Al-induced/activated organic acid secretion from the root apex). Because tea plants possess highly efficient versions of many of
these Al-resistance mechanisms, molecular identification of the key responsible genes is an important topic for future tea research. Second, crops must acquire the capacity for growth stimulation by Al. Achieving this important second step is highly dependent on advances in tea research and specifically on an enhanced understanding of how tea plants utilize Al and how Al stimulates tea growth at both the molecular and genetic levels. In particular, the future discovery of the key genes and pathways that mediate the Al-dependent growth promotion of tea plants will enable molecular breeding of these mechanisms into other crops. Third, an acquired ability to restrict the translocation of Al into edible crop tissues is essential. Because Al is a potential neurotoxicant that causes cell injury (Yokel, 2000) and has also been linked to Alzheimer’s disease (Exley, 2007), the Al content of edible crop parts must be strictly controlled so as to prevent its accumulation to dangerous levels. Such control could be achieved by the high-level expression of tonoplast-localized Al transporters, thus enabling efficient sequestration in the specific tissues or cells that lead to the edible parts. In the case of tea itself, the younger leaves used for making tea contain much lower levels of Al than the older leaves, and the Al in those younger leaves is further fixed in the cell wall or chelated by phenolics. For these reasons, the Al concentration, and in particular the Al bioavailability in tea infusions, is extremely low (Flaten, 2002), making tea drinking safe and healthy.

FUTURE PERSPECTIVES

Given its excellent performance on acid soils and the recent release of its whole genome sequence, tea could become an important novel model for the study of both Al tolerance and Al growth-stimulatory mechanisms. Precise understanding of these mechanisms may be pivotal for the future development of crops that are completely adapted to acid soils. However, one remaining obstacle to tea’s use as a powerful model is the lack of efficient transformation systems. Traditional Agrobacterium-mediated gene transformation has only a very low efficiency in tea, perhaps because the high levels of polyphenols in tea plants have germicidal properties (Mondal et al., 2004). Very recently, various labs have established novel high-efficiency, species-independent plant transformation systems, including nanomaterial-based gene delivery (Demirer et al., 2019; Kwak et al., 2019) and zygote-based transformation and regeneration (Toda et al., 2019). These novel methods may be applicable for enhancing the transformation efficiency of tea.

Despite these remaining problems, “omics”-based approaches nevertheless provide valuable opportunities for the identification of key genes involved in Al tolerance or Al growth stimulation, and such attempts have recently been made through transcriptomic, proteomic, and ionomic studies of whole tea root or leaf samples (Li et al., 2017; Xu et al., 2017a; Yamashita et al., 2020). Root tips are the primary source of the cells that drive root growth, and in most plants, they are also the primary vulnerable targets of plant Al toxicity. Despite this, Al accumulates without negative effect predominantly in the tea root tips, where it actually promotes root development and function. These considerations indicate that cross talk between the specific signaling pathways responsible for Al tolerance and Al growth-stimulation mechanisms occurs in the tea root apex. Accordingly, “omics”-based approaches should be more focused on understanding how tea root tips respond over time to Al exposure. Moreover, several woody plants and some herbaceous species show exudation of oxalate. However, to date, the transporter responsible for oxalate efflux from the root apex is unknown. Future studies with tea plants may identify the oxalate transporter, providing new ways to improve Al resistance in several plant species. In addition, atmospheric CO₂ concentration has been predicted to increase in future decades, and elevated CO₂ appears to affect root exudation and plant tolerance to abiotic stresses (Dong et al., 2021).
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Future research needs to address the impact of climate changes (e.g., elevated CO₂) on the Al tolerance of tea plants. In addition, genome-wide association studies aimed at the discovery of key genes in metabolic pathways will also enable the identification of genetic loci that regulate both Al tolerance and Al growth stimulation in tea plants.

ACKNOWLEDGMENTS
The authors have no conflicts to declare.

Received: December 3, 2020
Revised: February 28, 2021
Accepted: March 23, 2021
Published: March 24, 2021

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