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Root Architecture Modifications for Enhanced Nutrient Uptake in Maize

Wei Wang ✉, Jinhua Cheng
Institute of Life Science, Jiyang College of Zhejiang A&F University, Zhuji, 311800, China
✉ Corresponding email: tina.wei.wang@jicat.org

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Abstract Maize (*Zea mays*) has a strong dependence on nitrogen fertilizer, but the utilization efficiency of nitrogen is generally low. Root structure (RSA) plays a significant role in the nutrient absorption of maize. Deep roots and steep root angles help to obtain deep water and nitrate nitrogen, while abundant lateral roots and root hairs enhance the absorption capacity of surface phosphorus, potassium and other nutrients. This study summarizes the relationship between the root structure of maize and nutrient absorption, explores the influence of root anatomical characteristics on the absorption efficiency of nitrogen and phosphorus, and summarizes the management measures and rhizosphere microbial interactions that affect the root structure of maize. It also discusses the research progress of the ideal root type of maize and proposes future research directions for improving the root structure, providing theoretical references for maize breeding and field management.

Keywords Maize (*Zea mays*); Root structure; Nitrogen absorption; Phosphorus absorption; Breeding

1 Introduction

Maize (*Zea mays*) is the third most important food crop in the world and has a high demand for nitrogen fertilizer during its production process. However, in actual planting, the utilization rate of nitrogen fertilizer is not ideal. A lot of nitrogen that was put into the fields was not absorbed by the maize but was lost into the environment. Insufficient supply of nitrogen and phosphorus or uneven distribution in the soil affects the growth and yield of maize. If the amount of fertilizer is too large, it is easy to cause a decline in soil quality and increase the risk of environmental pollution (Chen et al., 2022). Maize hybrids with higher nitrogen efficiency usually have more active root systems during the seedling stage and vegetative growth stage (Jan et al., 2025; Kishore et al., 2025).

Root system architecture (RSA) mainly refers to the spatial distribution of roots in the soil, that is, how roots grow in the soil. It includes many aspects, such as how long the roots are, how large the surface area is, what the volume is, how thick the roots are, how many there are, what the Angle is, and in which soil layers different types of roots are distributed, etc. (Guo et al., 2022). Under low-nitrogen conditions, maize genotypes with larger total root length, higher root surface area, and greater root dry weight tend to absorb more nitrogen and have better utilization effects on nitrogen fertilizers (Jan et al., 2025). When the roots grow deeper and the root Angle is steeper, it is more conducive to absorbing water and nitrate nitrogen from the deep soil. A large number of lateral roots and well-developed root hairs can enhance the absorption capacity of the root system for non-mobile nutrients such as phosphorus and potassium in the surface soil (Van Der Bom et al., 2025).

This study sorts out and integrates the latest progress on the relationship between the root structure of maize and nutrient absorption, summarizes the main root structure and anatomical traits that affect the absorption of key nutrients in maize, summarizes different management measures and rhizosphere microbial interactions, discusses the research progress on the ideal type of maize root and related genetic basis, and proposes future research priorities and application prospects. It provides a theoretical framework and practical reference for root-oriented maize breeding and field management.

2 Root Architecture and Its Role in Nutrient Acquisition

2.1 Basic principles of root architecture

Maize has a fibrous root system with many types of roots. It is usually called a “multi-root type” system. It includes primary roots (also called seminal roots), adventitious roots such as crown roots and brace roots, and many lateral roots. This root structure is different from that of typical taproot crops. Even so, maize still depends on both axial roots and a large number of lateral roots to take up water and nutrients from both deep and shallow soil layers (Hochholdinger et al., 2018; Jiang and Whalen, 2025). The root system architecture (RSA) of maize is affected by time and planting density. When maize is planted at high density in the field, the total root biomass usually becomes smaller as density increases. However, the length of axial roots does not change much. Maize adapts to this situation by reducing the number of root nodes and limiting the length and density of lateral roots. In this way, roots grow less within the row but spread more between rows (Shao et al., 2018). In most cases, the highest root length density is found in the topsoil layer, mainly within 0~36 cm. When soil nutrients or water are limited, or when fertilizers are placed deeper in the soil, maize roots can grow further downward. Under these conditions, roots may extend into soil layers deeper than 36 cm (Chen et al., 2022; Zhang et al., 2023).

2.2 Key root traits influencing nutrient uptake

Under low nitrogen and salt stress, root traits change in obvious ways. When roots become longer and the total root surface area increases, shoots usually grow better. Aboveground biomass often goes up, and root and stem mass increase at the same time. These changes are closely linked to each other. However, thicker roots do not always mean better performance. When the average root diameter increases, specific root length often drops. This suggests that plants may be changing how they get nutrients, rather than simply trying to absorb more (Guo et al., 2025; Jiang and Whalen, 2025; Keerthi et al., 2025). Root hairs are especially important for phosphorus uptake, because phosphorus moves very slowly in soil. In field experiments, plants without root hairs absorbed much less P and K than normal plants. Their aboveground growth was also clearly weaker, especially in soils with high adsorption. Simply increasing root length could not fully solve this problem (Lippold et al., 2022; Vetterlein et al., 2022). Lateral roots also matter for nutrient use. When plants have more lateral roots or longer lateral roots, they can better explore small nutrient-rich areas in the soil. This includes local high-P zones or areas around soil aggregates, which helps improve nutrient use efficiency (Zhang et al., 2023).

2.3 Interactions between root architecture and soil nutrient availability

Root morphology is influenced by various environmental conditions, such as gravity, soil compaction, water content, soil texture, aeration, and nutrient supply levels. When the supply of nitrogen and phosphorus is insufficient, crops usually adjust their root system structure. A common change is an increase in the "ratio of root length to aboveground biomass" (Lopez et al., 2023). In the comparative experiments of sandy soil and loam soil, the influence of soil texture on root traits was significant, especially in terms of root hair quantity and root diameter (Vetterlein et al., 2022). When large aggregates of loam are distributed in sandy soil, local areas often have both high nutrient content and greater soil resistance simultaneously. The root system of corn does not enter the interior of the aggregates in large quantities, but rather grows more along the surface of the aggregates. The root system significantly increased root length density and the number of branches at these positions. The application of nitrogen and phosphorus fertilizers at different depths will form band-shaped regions with high contents of NO_3^- and available phosphorus within the soil layer of 16~32 cm, which will stimulate root growth and increase the expression levels of genes related to nitrogen and phosphorus absorption and transport (Chen et al., 2022; Zhang et al., 2023).

3. Mechanisms of Root Architecture Modifications for Enhanced Nutrient Uptake

3.1 Genetic approaches to modifying root architecture

After conducting an integrated analysis of 917 QTLS, 68 root meta-Qtls were identified. Thirty-six results are consistent with the markers reported in previous GWAS studies. Traits such as root length, root Angle, root volume and root enzyme activity are not controlled by a single gene (Karnatam et al., 2023). Wang et al. (2021) conducted a GWAS analysis on the Angle, diameter and quantity of coronal roots, identified 38 QTLS and predicted 113 candidate genes. The AUX/IAA gene, heat shock protein and genes related to cytokinin are all involved in the development process of the coronal root. Li et al. (2024a) conducted GWAS and linkage analyses on 14 traits and identified hundreds of QTLS. Genes related to hormone signaling pathways such as IAA26, ARF2, LBD37 and CKX3 are often located in the same genetic region as root traits. Under drought stress conditions, Li et al. (2023) combined GWAS analysis with differential expression analysis to screen out multiple genetic loci related to 13 root traits and identified candidate genes such as ZmCIPK3.

3.2 Agronomic approaches to enhancing root traits

Applying nitrogen fertilizer to the middle layer of soil at a depth of 16 to 24 cm is very beneficial to the root system, significantly increasing the nitrate nitrogen and available phosphorus in this layer of soil. The number of lateral roots in the 16~32 cm soil layer increases, and the root surface area also expands. Root hairs will elongate and the activity of phosphatase in the root system will increase (Liu et al., 2025). If compound fertilizer is applied to a deeper position, approximately 0.25 meters, the root system will grow downward and outwards. Within the depth range of 0-1.0 m, both the root length density and the root surface area increase. Deep root systems absorb more water, mainly concentrated in the 0.4~1.4 m soil layer, and the inorganic nitrogen content in the root SAP also increases. The water use efficiency and nitrogen absorption efficiency increased by 10%~39%, and the crop yield increased by approximately 14% (Wu et al., 2022). In cold arid and semi-arid regions, the dosage of nitrogen fertilizer and soil moisture content should be considered together. When the soil moisture was maintained at 80% of the field capacity and 200 kg N ha^{-1} nitrogen fertilizer was applied simultaneously, the activity of antioxidant enzymes in the root system was significantly enhanced and the accumulation of reactive oxygen species decreased. The increase in hormone contents such as IAA, GA and zeaxanthin makes the root system state more stable and is also conducive to the absorption of nutrients such as potassium, calcium and magnesium (Chi et al., 2025).

3.3 Environmental influence on root growth and nutrient acquisition

Under drought, low nitrogen, and salt stress, maize roots often change in clear ways (Li et al., 2023; Yu et al., 2024). When there is not enough water in the soil or when nitrogen levels are low, different maize types do not respond in the same way. In some plants, roots grow longer. In others, changes in root surface area or root volume are more obvious (Jiang and Whalen, 2025). Salt stress also affects maize roots. In salty soil, roots usually become thicker, and the total root volume often increases. This helps the plant grow better in hard soil or soil with high salt content. When nitrogen is limited, maize often adapts by extending its roots further into the soil. At the same time, root surface area and specific root length increase. This allows the root system to spread over a larger soil area and take up more nutrients (Keerthi et al., 2025). Soil conditions also play a role in root development. Soil pH and organic matter levels can influence root growth. During drought, the substances released by roots and by microbes around the roots may change. These changes can further affect how fast roots grow and how well they absorb nutrients (Hao et al., 2025).

4 Advances in Root Architecture Modification for Maize

4.1 Breeding programs focused on root architecture

The field soil-digging root phenotypes of six main cultivated maize varieties in the southwest region under the gradient of 0-300 kg N ha^{-1} showed that with the increase of nitrogen application, the total root length, root surface area, root opening Angle and maximum root width all increased significantly, and these four RSA indicators were significantly positively correlated with the yield. The root opening Angle and the maximum root width were significantly positively correlated with nitrogen accumulation in plants. The linear-plateau model fitting showed that when the root opening Angle reached approximately 99.5° and the root width reached 15.2 cm, nitrogen accumulation reached the plateau value within 0~300 kg N ha^{-1} (Guo et al., 2022). In terms of nitrogen-efficient breeding, the phylogenetic root phenotypes and anatomical analyses of 6 hybrids and 9 parents under full nitrogen (180 kg/ha) and low nitrogen (30 kg/ha) conditions revealed that the n-efficient hybrid (EE type) For example, WK702 shows a 6.0%~15.7% narrower root opening Angle, a 11.9%~12.4% larger root projection area, a 16.3%~22.6% deeper maximum root depth, and a 22.6%~37.1% larger cortical ventilation tissue area under low nitrogen conditions (Chen et al., 2025). GWAS analysis of 14,301 field plants identified 81 highly reliable RSA candidate genes, and it was found that 28 known root-related genes were selected during domestication and improvement. Favorable alleles related to "steep root angles" in modern materials continued to accumulate in different breeding eras. Two auxin genes, ZmRSA3.1 and ZmRSA3.2, were functionally verified to regulate root Angle and root depth (Ren et al., 2022).

4.2 Integration of root architecture into maize improvement programs

In the root anatomy-GWAS study conducted on 316 materials, 16 macroscopic root morphological traits, 7 weight traits and 108 microphenotypes of sections were regulated by more than 3 000 genes. Among them, the haplotype frequencies of genes related to root diameter, root length and root area showed significant differences between tropical/subtropical and temperate materials (Guo et al., 2025). Ee-type hybrids are superior to SNE and NN types in terms of root opening Angle, root depth and ventilation tissue, and this dominant root phenotype can be traced back to specific n-efficient parents in the parents. Under low nitrogen conditions, the ventilation tissue area of the EE-type parents can reach 0.92 mm², while that of the low-efficiency parents is only 0.23 mm². Root maximum depth, aerated tissue area and xylem duct area affect yield through different path coefficients (0.19~0.27) (Chen et al., 2025) (Figure 1). The root systems of single-cross hybrids are generally smaller than those of double-cross hybrids. The root length is significantly reduced within the root diameter range of 2465-181 μm. However, there is no significant difference in the field soil water consumption rate (2.6-2.9 mm/d) between the two types of materials. The yield and constituent traits of the single crossbred under various densities and water treatments were significantly higher (P<0.001) (Messina et al., 2021).

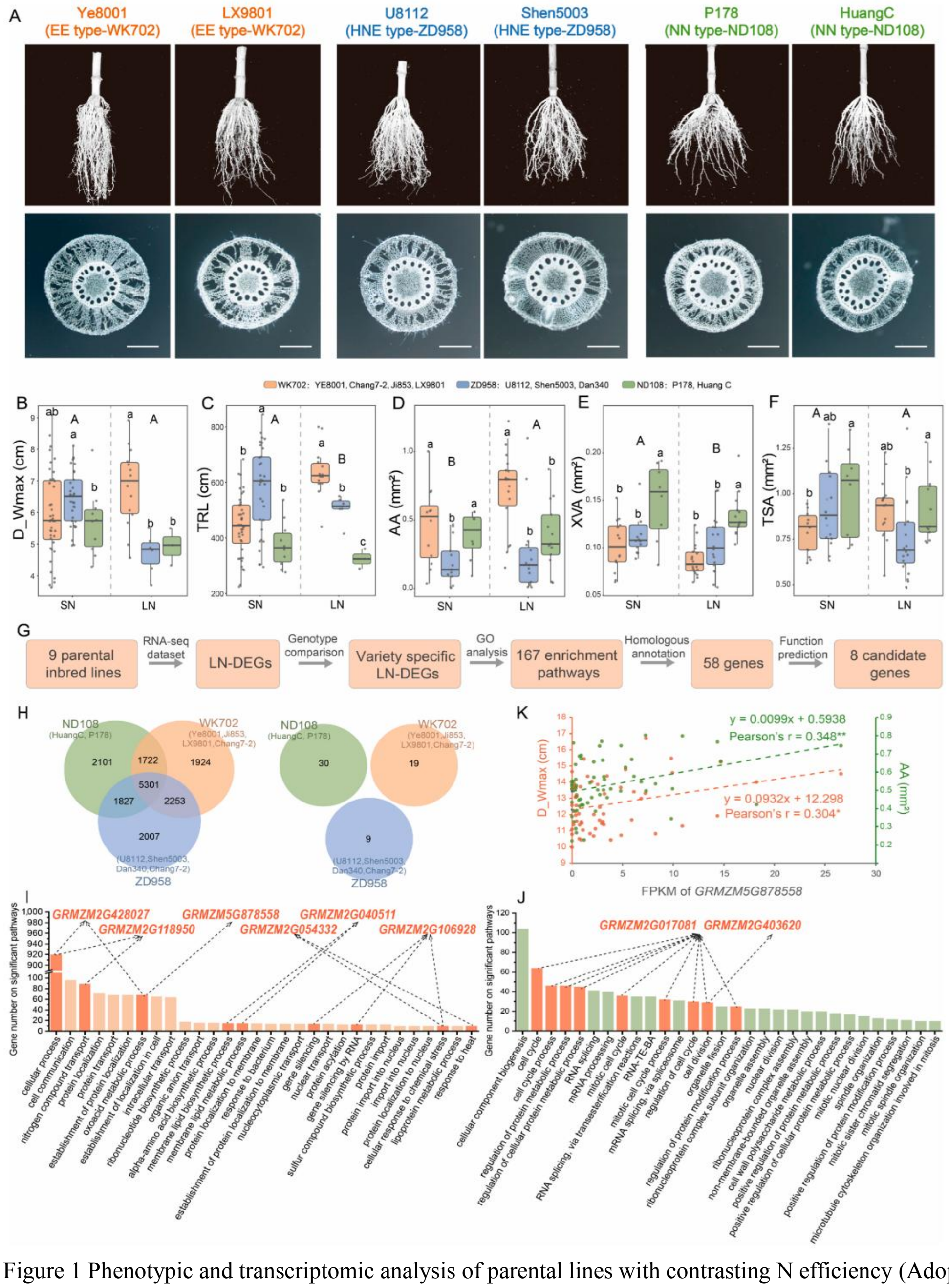

Figure 1 Phenotypic and transcriptomic analysis of parental lines with contrasting N efficiency (Adopted from Chen et al., 2025)

5 Case Studies on Root Architecture Modifications in Maize

5.1 Research study: impact of root architecture on nitrogen uptake

After three consecutive years of field trials, the root growth condition of the large root system test cross combination T-213 was significantly better. During the tasseling stage, the root length density, root surface area and root dry weight of T-213 were all higher than those of the small root system control T-Wu312, with an increase of approximately 9.6%~19.5%. Although the distribution position of the root system in the soil did not change significantly, after silk production, the plant's absorption of nitrogen increased significantly, and the grain yield also rose by 17.3%. The content of nitrate nitrogen in the soil layer below 30 cm decreased significantly (Mu et al., 2015). Under high-nitrogen and low-nitrogen conditions, a comparison was made between 7 inbred lines and 12 hybrids, and it was found that the overall root system performance of the hybrids was stronger. Nitrogen absorption efficiency (NUpE) is significantly positively correlated with multiple root system indicators, including root length (RL, r = 0.73***), root surface area (RSA, r = 0.67***), root volume (RV, r = 0.66***), root density (RD, r = 0.52***), and root dry weight (RDW). r = 0.92***, and the correlation coefficients were all relatively high (r = 0.80***). Nitrogen use efficiency (NutE) is mainly affected by aboveground traits, such as the activities of nitrate reductase and glutamine synthase, as well as photosynthetic indicators such as leaf area index (LAI) (Jan et al., 2025).

Combinations such as Zheng58×PH4CV, 444×PH4CV, 444×MO17 and B73×MO17 exhibit larger root systems and higher NUpE in the early nutritional stage. Under the conditions of 0 N and 150 kg N ha^{-1}, the pillar root Angle and crown root Angle of the newly bred hybrid increased by 7.9%~19.3% respectively compared with the old variety, the number of crown roots increased by 21.4%~30.5%, and the 95% root weight depth D95 increased by 8.5%~10.5%. This type of RSA hybrid vigor enhances N absorption before silk casting and N internal efficiency (NIE) during grain filling (Li et al., 2024b). At 40 μmol/L NO_3^-, the abovground and underground biomass of the N - high-efficiency genotype was almost unaffected, while the abovground and underground dry matter of the N - low-efficiency genotype decreased by approximately 58% and 64% respectively. The former is manifested as the lateral root strategy of "few branches + long elongation". The total lateral root length contributes the most to improving NUE, followed by the axial root length. The N efficiency is significantly positively correlated with the lateral root and axial root elongations at different depths (Wang et al., 2022). F44 has longer crown roots, larger root surface area and volume, as well as higher number and density of lateral roots. It has a strong ability to transport and assimilate nitrate nitrogen, and the activities of NR and asparagine synthase in its roots are significantly higher than those in B73. B73 prefers ammonium N, and in the B73×F44 hybrid, the preference for root form and N form of B73 is completely dominant (Dechorgnat et al., 2018). 478 has a greater total root length, higher root dry weight and higher root-crown ratio both at high and low N in the field. Especially at low N, more and longer axial roots make its N accumulation and yield higher than those of W312. However, the $^{13}NO_3^-$ flux per unit root length and the N absorption rate were actually lower than those of W312 (Liu et al., 2009).

5.2 Case study: root traits and phosphorus efficiency in maize

Under low P conditions in the field, the correlation coefficient between PupE and PUE was 0.48~0.54, while under hydroponic conditions, the correlation coefficient between root morphology indicators and PupE was 0.25~0.30, but had no relation to PutE. Two QTL clusters (Cl-BIN3.04 a/b) were located in the bin3.04 segment of chromosome 3, carrying both PUE, PupE and root trait QTLS. The favorable alleles all originated from the "large root + high PupE" parent. Using these two clusters for label-assisted backcrossing selection and breeding, advanced backcrossing lines with a single cluster were obtained, and their PUE in low-P fields was on average 22%~26% higher than that of the receptor parents. The L224 series that simultaneously integrated Cl - bin 3.04A and Cl - bin 3.04B exhibited higher PupE both in hydroponics and in the field. High and low P treatment experiments were carried out in large columnar POTS in greenhouses and fields using RIL carrying "many short (MS)" or "few long (FL)" lateral root types. Under low P conditions, the P absorption of the MS type system in the greenhouse is 89% higher than that of the FL type system, and the aboveground biomass is 48% higher. Under low P in the field, the 95% root weight depth (D95) of the MS system is 16% shallower than that of FL, the root length density in the 0-20 cm soil layer is 81% higher, the P content and photosynthetic rate of leaves are 49% and 12% higher respectively, and the aboveground biomass is 19% higher. The grain yield was 14% higher (Jia et al., 2018).

Applying different P fertilizers such as single super phosphorus, MAP, UP and APP in 10-20 cm local strips can increase the density and length of first-order lateral roots in the enrichment area by up to 74% compared with uniform fertilization (Wang et al., 2024); In the field experiment of black soil, the yield per plant treated with APP reached 171.8 g, which was significantly higher than that of DAP, FCMP and their combined application. APP significantly increased the proportion of soil TP and inorganic P (REp, FPp, AEp, PHI, PAC) (Dong et al., 2024).

6 Future Prospects and Challenges

6.1 Future of root architecture research in maize

Imaging techniques such as X-ray CT, MRI, and mini root canal are increasingly used in root system research, and they do not damage the plants themselves during the observation process. Medium and high-throughput field phenotypic research platforms such as "Shoveling Field Studies" are also good. Researchers can observe the morphological changes of the root system without having to dig out the plants. The problem that the root system was buried in the soil in the past and was difficult to observe directly is being gradually solved (Keerthi et al., 2025). In terms of genetic improvement, the application of gene editing and transgenic technologies has made the operation more direct, allowing for direct adjustment of target genes, such as those that affect root length, root growth Angle, root hair formation, and nutrient transport capacity (Mmbando and Ngongolo, 2024). The concepts of ideal root systems such as "steep, low, deep" and "topsoil feeding" have also been continuously refined. They are no longer limited to the external morphology of the root system and have begun to pay attention simultaneously to the internal structural changes of the roots, as well as the composition and function of the rhizosphere microbial community (Galindo-Castaneda et al., 2022).

6.2 Challenges in root architecture modifications

There is an inherent contradiction between the root system and the aboveground part in terms of carbon distribution. The carbon obtained by plants is limited. If too much is invested in the root system, the carbon that the aboveground part can receive will decrease, the aboveground biomass may decline, and the grain yield is also likely to be affected (Van Der Bom et al., 2020; Lynch, 2021; Holz et al., 2024). Many studies on root system improvement have been conducted under hydroponic conditions or in small pot experiments. In the field, the root system has to confront soil resistance, and the distribution of nutrients is also uneven. There is also a complex microbial community in the rhizosphere. These factors are often difficult to be truly reflected under artificial conditions (Galindo-Castaneda et al., 2022; Keerthi et al., 2025).

6.3 Practical implications for sustainable agriculture

If the root system develops better, such as longer total root length, larger surface area, and stronger root vitality, it will be easier to absorb nitrogen and also improve the utilization efficiency of nitrogen fertilizer (Jing et al., 2022; Jan et al., 2025). In the case of uneven distribution of soil nutrients, the ability of the root system to utilize nutrient "patches" is also crucial. By increasing the number of lateral roots, enhancing the secretion level of phosphatase, and strengthening the expression of genes related to ammonium transport, it is possible to ensure that crops obtain sufficient nutrients while reducing the amount of fertilizer application (Holz et al., 2024). Types with less deep roots or larger root angles are more conducive to absorbing water and nitrogen from deep soil, and at the same time can promote the accumulation of soil carbon. The root system with more shallow roots and lateral root branches is more suitable for absorbing phosphorus and potassium in the surface soil (Kishore et al., 2025). The mutual cooperation among root hairs, the mucus secreted by the root system, the rhizosphere biofilm and beneficial microorganisms can improve the utilization efficiency of water and nutrients, and also enhance the adaptability of crops to adverse environments.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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