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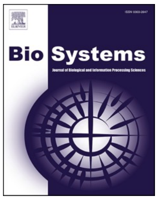

Maize root behavior as three-inputs-three-outputs logical gates due to positive gravitropism and nutritropism

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ABSTRACT

Root growth and their interactions can provide valuable information for the development of asynchronous logic systems. Here, maize root behavior due to positive gravitropism and nutritropism is evaluated as three-inputs-three-outputs logical gates. Using plant roots as the element for unconventional computing, the Boolean functions of each root tropism were constructed through arithmetic-logical operations. One gravity gate (rGG) and two nutrient gates (rNG1 and rNG2) were fabricated using additive manufacturing. The rGG platform was oriented with roots directly pulled down by gravity which computes $(x, y, z) = (xz + yz, x + \bar{y}z + y\bar{z}, xy + yz)$, whereas specific output channels in rNG1 and rNG2 were fertigated with high phosphorus concentration resulting in $(x, y, z) = (x + y + z, xy + xz, xyz)$ for rNG1 and $(x, y, z) = (xyz, x\bar{y}z + xy\bar{z}, x + y + z)$ for rNG2. For rGG, rNG1, and rNG2, the symbols x, y, and z pertain to “root presence” in the related channel, whereas top bar on the symbols indicates “root absence”. Anatomical traits of roots were evaluated to assess possible differences in vascular tissues due to gravitropic and nutritropic responses. Overall, maize primary roots showed prominent positive gravitropism and nutritropism, and the roots that were most attracted by gravitational or nutritional stimuli showed an increase in the diameter of phloem and xylem. The logic exhibited by roots was dependent on the gravitropic and nutritropic stimuli to which they were exposed in the different logic gates. The responsiveness of maize roots to environmental stimuli such as gravity and nutrients provided valuable information to be used in computational bioelectronics.

1. Introduction

Plant roots can respond to external stimulation through directional movements termed tropisms. Root tropisms are characterized by movements of root apexes and morpho-anatomical alterations of root tissues (Izzo and Aronne, 2021; Hetherington, 2019). Tropistic responses of roots include chemotropism (Izzo et al., 2019), electrotropism (Wolverton et al., 2000), halotropism (van den Berg et al., 2016), hydrotropism (Dietrich, 2018), gravitropism (Geisler et al., 2014), magnetotropism (Bilyavska and Polishchuk, 2014), oxytropism (Eysholdt-Derzsó and Sauter, 2017), phonotropism (Rodrigo-Moreno et al., 2017), phototropism (Izzo et al., 2022), thermotropism (van Zanten et al., 2021), and thigmotropism (Massa and Gilroy, 2003). Directional movements of plant roots are exerted through differential cell development in tissues of the root apex (Gilroy, 2008). If a certain plant organ (e.g. root) moves toward a certain stimulus, then this exhibits positive tropism. Conversely, tropistic movements away from a stimulus are defined as negative tropism (Gilroy, 2008). Plant gravitropism has been largely explored since Darwin and, currently, there is a large body of information regarding root gravitropism, especially for model species such as *Arabidopsis thaliana* (Muthert et al., 2020). Plant roots can also exhibit positive tropism toward nutrients based on the concentrations existing in a particular soil region or growth substrate (Yamazaki et al., 2019). Nutritropism is distinguished from chemotropism and halotropism since the latter two are based on a specific chemical or salinity concentration, respectively. Furthermore, halotropism is generally an escape response of roots to avoid stressful conditions of salinity (Galvan-Ampudia et al., 2013). Overall, deepening the

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mechanisms of these tropistic responses of roots may help improve agricultural practices and enhance plant productivity.

In the perspective of bioelectronics, root growth generates specific patterns and can mimic logic gate operations based on Boolean algebra. The cognition of plants has been proven because of the Information Integration Theory (IIT) which characterizes the tropism of both shoot and root systems (Segundo-Ortin and Calvo, 2021). Unconventional computing involves a non-traditional computational technique in developing technological innovations and concepts which are based on physics, biochemistry, and biology models (Adamatzky, 2019; Beasley et al., 2021). In Fredkin-Toffoli conservative logic, two colliding objects from different angles and velocities may create localization (Ghosh and Sarkar, 2020). This localization changes the velocities of the objects, annihilates the object with weaker velocity, or fuses with the other. Computation is manifested through the response of objects as the localization information values are transformed.

Aside from Margolus and Belousov-Zhabotinsky gates (de Lacy Costello and Adamatzky, 2005), one of the realizations of this collision-based computation is the two-inputs-two-outputs plant root logic gate (Adamatzky et al., 2017). This biological logic gate operates based on how fast the two roots elongate to the junction point between x and y channels and exit via channels p or q (Fig. 1a). The faster the root reaches the junction, the more choices are available as to what direction it can proceed as long as the root apex is attracted by tropistic stimuli (Fig. 1b and c). There could also be a tendency that a root blocks or allow the passage of the others based on root bending which can alter the information values (Fig. 1d and e). The presence and absence of the root in a channel are denoted by 1 and 0, respectively, following the Boolean algebra. Root topology and trajectory contained in a patterned physical location represent the biological computation of roots. In the natural conditions, roots grow underground and can be impacted by soil cues including hardness, moisture content, and the presence of rocks that can obstruct certain regions of interest. Indeed, physical properties of soil can affect the formation of roots and their growth (Forster et al., 2020; Fujiwara et al., 2021). Using a two-inputs-two-outputs logic gate, humidity-dependent root propagation exhibited x and $\bar{x}y$ logic operations (Adamatzky et al., 2017). However, synchronization issues have been reported for this setup by performing a gravity experiment using channels oriented horizontally and filled with Phytagel tissue-culture media (Adamatzky et al., 2017). In this regard, the design of more accurate logic gates is required to advance studies on plant-based bioelectronics.

Plant roots offer a viable and sustainable computing system due to their uneven growth and biochemical rates in interacting with environmental stimuli which produce the disparity in information values. This is analogous to the digital logic principle which requires varying the clock frequency in a square wave oscillator resulting in waveform lapses, making sure there is an uneven combination of the input variables. In plant roots, this is done naturally through tropisms where the interaction of root apexes with environmental stimuli (attractants and repellants) manifests computation, and these changes in information values may be utilized as an avenue in developing phytosensors and plant decision-making processes and responses (Volkov, 2016).

In the present study, maize root behavior due to positive gravitropism and nutritropism was investigated as three-inputs-three-outputs logical gates. Three-inputs-three-outputs logical gates resolved the previous issue of being limited to possible logic complexities in characterizing root tropisms, improving the two-inputs-two-outputs plant root logical gates that can only handle the operations innate to universal electronic logic gates and a 2-bit summing circuit as presented in (Adamatzky et al., 2017). Using plant roots as the element for unconventional computing, the Boolean functions of each root tropism were constructed using arithmetic-logical operations. One gravity gate (rGG) and two nutrient gates (rNG1 and rNG2) were fabricated using additive manufacturing for testing. Logic channels were intendedly desynchronized to compute the complexity of root reactions. Light microscopy was also performed to investigate possible changes in root vascular tissues due to gravitropism and nutritropism. Furthermore, differently from previous studies which dealt with root tropisms in a miniaturized controlled platform, this study employs soil-based interaction with plant roots that mimics more the natural conditions of plants growing in the field.

This study contributes to: (1) the understanding of gravitropism and nutritropism of roots developed in patterned channels for potential application in improving plant cultivation systems; (2) the analysis of gravitropic and nutritropic responses in plant vascular tissues; and (3) the development of advanced real-life technological applications based on root logic.

2. Materials and methods

2.1. Plant material and logic gate channel prototyping

The maize (*Zea mays* L.) genotype used in this study is PSB Cn 97-92 (Bureau of Plant Industry, Manila). It was chosen because of its ability to germinate faster and evenly compared to other commercially available genotypes (Concepcion et al., 2021). Seeds were stored in a controlled chamber at 4 °C until sown. Seeds were placed in a container filled with distilled water for 12 h before sowing. Viable seeds used for the experiments were selected by performing a floatation test. Three patterns of logical gates (rGG, rNG1, and rNG2) were modeled using Google Sketchup 2019 (Trimble Inc.) with a base plate dimension of 10.16 cm × 10.16 cm and a height of 1 cm for the actual embossed channels to hold the soil and function as a conduit for root development (Fig. 2). The rGG refers to the root gravity gate, whereas rNG1 and rNG2 refer to the root nutrient gate designs 1 and 2, respectively. The lengths of the channels from input to joint and joint to output section were intendedly desynchronized to characterize the actual root interactions. Polylactic acid (PLA, $(C_3H_4O_2)_n$) and 3D printer (Ender-3 Pro 3D Printer, Creality, China) are respectively the filament material and the device used to prototype the three logical gate designs.

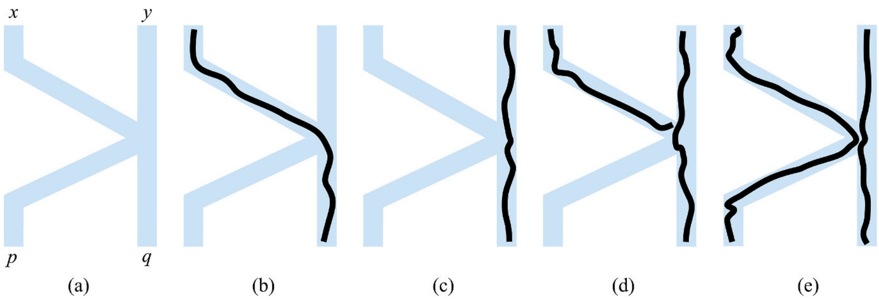

Fig. 1. Two-inputs-two-outputs plant root logical gates in which two roots cannot fit in a single channel. (a) Scheme where x and y are input channels and p and q are output channels. (b) $x = 1, y = 0$. (c) $x = 0, y = 1$. (d) $x = 1, y = 1$, root apex y reaches first the junction. (e) $x = 1, y = 1$, both apexes reach the junction at the same time. Inspired by (Adamatzky et al., 2017).

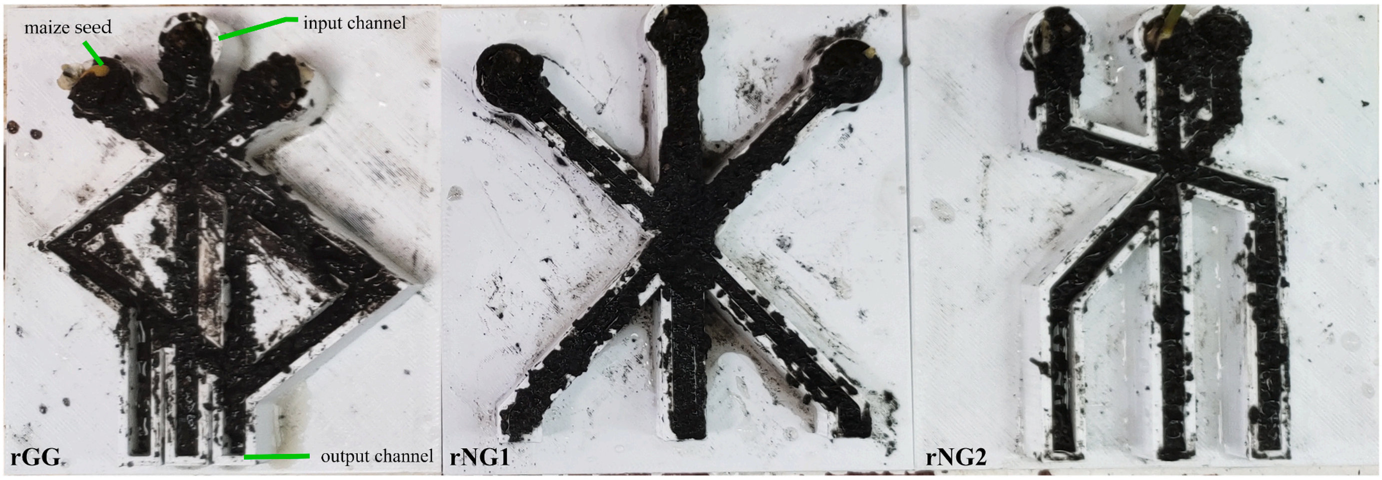

Fig. 2. Actual printed logic gate patterns (white) filled with soil mixture inspired from (Adamatzky et al., 2017). Maize seeds are sown in each rounded input channel on top (rGG = root gravity gate, rNGI and rNG2 = root nutrient gate 1 and 2).

2.2. Gravity gate

The gravity gate experiment utilized the rGG prototype (Fig. 2). This gravity attraction gate was placed in vertical orientation with root apex expected to go straight downward due to positive gravitropism (1*g*). This orientation with channels parallel to the pull of gravity is intended to mimic the soil depth that roots could possibly encounter in the real environment. Experiment duration was 7 days from sowing to root sampling. Soil mixture was composed of 30% sand, 10% perlite, 40% loam, and 20% vermiculite. Soil mixture was watered uniformly to avoid possible hydrotropic responses of roots due to an uneven distribution of water. Controlled environment configuration included a temperature range of 24–27 °C, relative humidity of 55–65%, and 16-h photosynthetic light of 650 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from broadband white LEDs. Fertigation was employed with a nutrient mixture containing 6 mM KNO_3, 4 mM $Ca(NO_3)_2$, 2 mM NH_4H_2PO4, 2 mM $MgSO_4$, 1 mM KCl, 1 mM H_3BO_3, 1 mM $MnSO_4$, 1 mM $ZnSO_4$, 1 mM $CuSO_4$, 1 mM $(NH_4)Mo_7O_{24}$, and 1 mM Fe-EDTA^2. Root growth was inspected after 3, 5, and 7 days from sowing to evaluate root interactions at the junctions of channel patterns and if there were roots already exiting the output channels. The operations were done by carefully removing thin layers of soil above the junctions j_1 to j_5 (Fig. 2). Truth table showing the actual root-exhibited logic operations affected by gravity and the corresponding logic circuit were constructed. Combinations of AND, OR, and NOT gates were used in constructing the circuit. There is a total of 8 input combinations (x, y, and z) with 0 and 1 possible states pertaining to *no root presence* and *root presence*, respectively, based on Boolean algebra's 2^n where n is the number of inputs. Ten replicates of this rGG trial were performed. The output of the gravity gate development are Boolean functions having the following mathematical topology: $\{p, q, r\} = f(x, y, z)$ where p, q, and r represent output channel states.

2.3. Nutrient gates

Nutrient gates are attraction gate based on the different concentration of nutrients in soil regions to act as attractant for the maize primary roots used in this study. The nutrient gate trials were based on the fact that root grows towards the area with higher nutrient concentration due to positive nutritropism (Yamazaki et al., 2019). By using the fabricated logic channels rNG1 and rNG2 (Fig. 2), two nutrient concentrations were employed in the different channels: control (T1) and phosphorus-deficient (T2). It is known that phosphorus is the primary macronutrient used for root development (Strock et al., 2018), hence reducing its concentration may result in reduced growth. T1 mixture was composed of 6 mM KNO_3, 4 mM $Ca(NO_3)_2$, 2 mM NH_4H_2PO4, 2 mM $MgSO_4$, 1 mM KCl, 1 mM H_3BO_3, 1 mM $MnSO_4$, 1 mM $ZnSO_4$, 1 mM $CuSO_4$, 1 mM $(NH_4)Mo_7O_{24}$, and 1 mM Fe-EDTA^2. T2 mixture contained the same set of inorganic fertilizers as T1 with the exception of 0.05 mM $NH_4H_2PO_4$ and 1 mM $(NH_4)_2SO_4$ salt. Both soil mixtures (T1 and T2) were watered uniformly to avoid possible hydrotropic responses of roots due to an uneven distribution of water. For rNGI logic pattern (Fig. 2), T1 was applied to p channel up to j junction only. P-deficient T2 was applied to q and r channels up to j junction. For rNG2 logic pattern (Fig. 2), control T1 was applied to p and q channels up to j junction. P-deficient T2 was applied to r channel up to j junction only. The whole logic channel platform was oriented horizontally during the experiment to avoid interference with gravitropic response of roots. Soil mixture, controlled environment configuration, construction of truth table, and the process of developing the Boolean functions of actual root interaction and propagation were the same of the gravity gate already described. The output of the nutrient gate development are Boolean functions having the following mathematical topology: $\{p, q, r\} = f(x, y, z)$ where x, y, and z are the input channel states and p, q, and r represent the output channel states. The two designs for nutrient gate and the variation of the channel in which control T1 is applied were designed to evaluate root interactions in desynchronized information channels simulating the conditions of an outdoor soil system.

2.4. Analysis of root vascular tissues

Light microscopy of transverse sections of primary roots was performed to evaluate possible differences in root anatomy, particularly vascular tissues, due to gravitropic and nutritropic responses. The roots that reached the output channel parallel to gravity in rGG and the nutrient-rich channel in rNG1 and rNG2 were referred to as fastest roots, differently from the others which were referred to as slowest roots. Root samples were thoroughly uncovered from the soil and washed with distilled water to remove soil residues. Thin sections of roots were cut at 1 cm from the germinated seed using a razor blade and were stained with 1% toluidine blue (TBO, Sigma-Aldrich) for 30 s, cleansed with 25% diluted glacial acetic acid, and washed with distilled water for 30 s for 3 times before mounting in a glass slide with a drop of water. Light microscopy was performed using a trinocular microscope (Howell Medical Supply, Philippines). Imaging of transverse sections of roots was done using ToupView software (ToupTek, China). The mean diameter of xylem, metaxylem, and phloem tissues was measured using ImageJ software in 10 roots per treatment and graphed using Microsoft Excel 2018. One-way analysis of variance ($\alpha = 0.05$) and Tukey pairwise comparison were performed using the Minitab 20.4 (Minitab, LLC) to evaluate significant differences of anatomical traits between roots.

3. Results

3.1. Maize root behavior in gravity gate

The proposed experimental gravity gate prototype (Fig. 3) resolved the previous issue in which there should be a specific root that enters a junction first (Adamatzky et al., 2017). The present gravity gate (rGG) is constructed of multiple channels strengthening the concept of desynchronization to characterize the natural information value that can be obtained from roots. The rGG consists of bent channel segments a and b that converge at junction j_1 (Fig. 3a). On the other hand, there is a straight path from input channel y to output channel q. In our trials, it was observed that the root y, because of the gravity directly pulling down to junction j_1, reaches faster the junction j_1 than the other roots when either or both roots x and z are present (Table 1). There were other cases in which only one seed germinated within the 7-day cultivation. When root z emerged solo ($z = 1$), it passed the junction j_1 and exited via channel q following the direction of gravity (Fig. 3b). When root y emerged solo ($y = 1$), it smoothly passed the junction j_1 and exited via channel q (Fig. 3c). When the root x emerged solo ($x = 1$), it passed the junction j_1 following the pattern of channel x and then curved down towards channel q (Fig. 3e).

A more complex condition happened when two roots grew from different channels and interacted at a certain joint. When both roots y and z emerged ($y = 1$ and $z = 1$), root y reached first the junction j_1 while root z pushed a portion of root y causing it to flex laterally towards segment b down to channel r (Fig. 3d). The growth rate of root z was altered by the inclined channel z even if it has the same length as channel y. There was also a circumstance when both roots x and z reached at almost the same time the junction j_1 ($x = 1$ and $z = 1$), which resulted in root apexes colliding with each other and bending laterally from channel a to p and b to r, respectively (Fig. 3f). When both roots x and y emerged ($x = 1$ and $y = 1$), root y reached first the junction j_1 whereas root x bent laterally towards segment a down to channel p (Fig. 3g). Furthermore, when all input roots emerged ($x = 1$, $y = 1$, and $z = 1$), root y developed faster than root x and z because of the inclined channels x and z (Fig. 3h).

Table 1
Actual logic operations exhibited by three-inputs-three-outputs gravity gate (rGG). Boolean values of 0 and 1 represent no root presence and root presence, respectively, in the corresponding channel.

x	y	z	$(xz + yz)$	$(x + \bar{y}z + y\bar{z})$	$(xy + yz)$	Root Interactions
0	0	0	0	0	0	No root emerges in the input channels
0	0	1	0	1	0	Root in channel z exits via channel q
0	1	0	0	1	0	Root in channel y exits via channel q
1	0	0	0	0	0	Root in channel x exits via channel q
0	1	1	0	1	1	Root in channel y exits via q while root in z bends to r
1	0	1	1	0	1	Roots in x and z meet at junction j_1 and bend to channels p and r
1	1	0	1	1	0	Root in y exits via q while root in x bends towards p
1	1	1	1	1	1	Root in y exits via q while roots in x and z bend to p and r

In the case of all root emergence, the sidewall roots x and z, which arrived at the junction when root y has already grown across it, bended laterally towards channel segments a and b, respectively. The actual logical operations of maize roots using rGG is reported in Table 1 and the

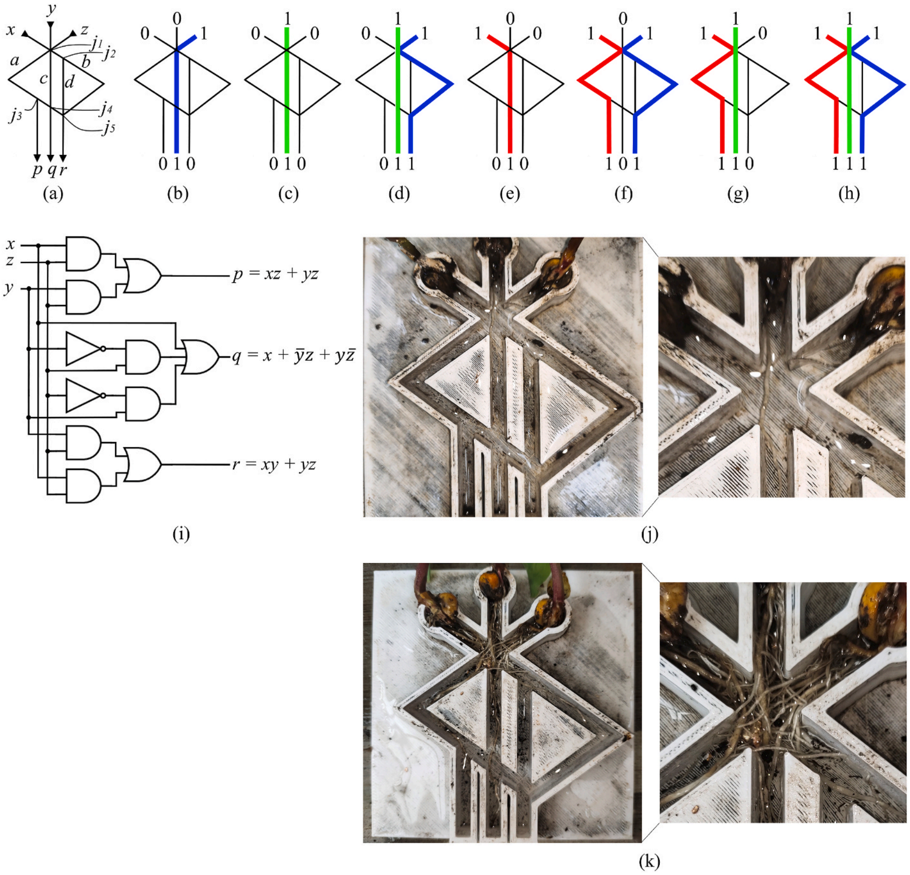

Fig. 3. (a) Scheme of three-inputs-three-outputs plant root gravity gate (rGG) where x, y, and z are input channels and p, q, and r are output channels. (b) $x = 0$, $y = 0$, $z = 1$. (c) $x = 0$, $y = 1$, $z = 0$. (d) $x = 0$, $y = 1$, $z = 1$. (e) $x = 1$, $y = 0$, $z = 0$. (f) $x = 1$, $y = 0$, $z = 1$. (g) $x = 1$, $y = 1$, $z = 0$. (h) $x = 1$, $y = 1$, $z = 1$. (i) Equivalent logic circuit. Possible scenarios of root interactions in 1g with logic gate platform orientated vertically: (j) middle primary root reaches faster the junction and blocks other roots to enter the middle output channel and (k) primary roots in place with seminal roots networking at the top of the channels.

corresponding logic circuit is illustrated in Fig. 3i using the combinations of classical logic gates (AND, OR, and NOT gates). The interactions of maize roots in a three-inputs-three-outputs rGG computes the following sum-of-products (SOP) Boolean functions: $p = xz + yz$, $q = x + \bar{y}z + y\bar{z}$, and $r = xy + yz$, where $\bar{y}$ is the NOT signal of input root y (NOT for inversion like 1 to 0 and 0 to 1) and same with $\bar{z}$ for input root z. The rGG system with only root y germination is presented in Fig. 3j with dismantled soil layers and carefully cleansed channels showing the smooth passage to the vertically aligned output channel q. However, it can also be noticed that there is an entropy in the information value which happens when seminal roots interact with each other across channels (Fig. 3k). Indeed, the numerous seminal roots may hinder the growth of the primary roots or redirect them by obstructing certain channels. Nevertheless, the primary roots x, y, and z had faster emergence and growth rate than the seminal roots to timely get in place into their channels separately.

3.2. *Maize root behavior in nutrient gate*

Nutrient gate is an experimental prototype aimed to investigate the influence of nutrient concentration in guiding root growth underground and its logic. In this study, we prototyped two nutrient gates, rNG1 (Fig. 4a) and rNG2 (Fig. 5a), in which the control attractant (T1) is placed on exit channels p and r, respectively, whereas the remaining channels are supplemented with phosphorus-deficient fertilizer (T2).

As for rGG, rNG allows the interaction of one, two or three primary roots coming from different seeds at the same time (Table 2). In rNG1, when root z emerged solo ($z = 1$), it passed the junction j and exited via channel p attracted by the higher nutrient concentration in channel p (P = 0.2 mM) than channels q and r (P = 0.05 mM) (Fig. 4b). When root y emerged solo ($y = 1$), it passed the junction j and exited via channel p (Fig. 4c). When root x emerged solo ($x = 1$), it passed the junction j and exited via channel p (Fig. 4e). It is clear that when the root is at junction j, whatever is the starting channel, the root is attracted to the channel with a high concentration of nutrients (channel p).

When two roots emerged from different channels in rNG1, only one root was able to enter the channel with a high nutrient concentration, whereas the other root moved towards the adjacent channel with a lower P concentration. When roots y and z reached at the same time the junction j ($y = 1$ and $z = 1$), root y bended towards channel p, whereas root z bended towards channel q (Fig. 4d). This is likely because at junction j, root y is relatively closer than root z to channel p. When both roots x and z reached at the same time the junction j ($x = 1$ and $z = 1$), root z grew directly into channel p obstructing the entry of root x (Fig. 4f). Differently, when roots x and y emerged ($x = 1$ and $y = 1$), because both roots require a curvature to grow into the channel p and root x is relatively closer than root y, root x exited via channel p whereas root y grew towards channel q (Fig. 4g). Similarly, when all three maize seeds germinated ($x = 1$, $y = 1$, and $z = 1$), root x blocked the entry in channel p of both roots y and z at junction j. Indeed, root x reached quickly the junction j in a favorable position for bending towards the channel with the attractor (higher nutrient concentration).

The actual logical operations of maize roots using rNG1 are reported in Table 2 and the corresponding logic circuit is illustrated in Fig. 4i using the combinations of classical logic gates. The interactions of maize roots in a three-inputs-three-outputs rNG1 computes the following SOP Boolean functions: $p = x + y + z$, $q = xy + xz$, and $r = xyz$. In our experiment, there was also a case where rNG1 exhibited the root z exiting via channel p and root x bending towards channel z (Fig. 4j). In this case, interestingly, the seminal roots of x followed the same path (channel p) as the primary root, whereas seminal roots of y were also attracted by the high P concentration resulting in the physical network of roots x and y (Fig. 4k).

Similar to rGG and rNG1, rNG2 is a three-inputs-three-outputs gate that allows the interaction of one, two or three primary roots coming from different maize seeds at the same time (Table 3). Different from

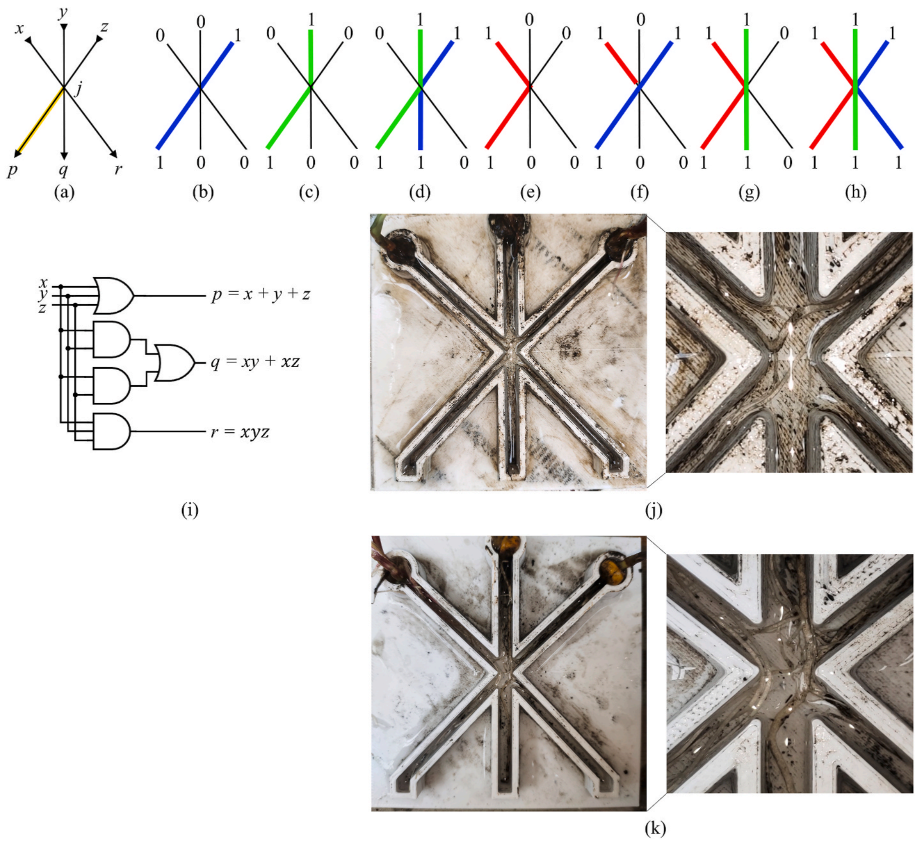

Fig. 4. (a) Scheme of three-inputs-three-outputs plant root nutrient gate (rNG1) where x, y, and z are input channels and p, q, and r are output channels. (b) $x = 0, y = 0, z = 1$. (c) $x = 0, y = 1, z = 0$. (d) $x = 0, y = 1, z = 1$. (e) $x = 1, y = 0, z = 0$. (f) $x = 1, y = 0, z = 1$. (g) $x = 1, y = 1, z = 0$. (h) $x = 1, y = 1, z = 1$. (i) Equivalent logic circuit. Possible scenarios of root interaction in 1g with logic gate platform orientated horizontally and optimal nutrient concentration supplemented in the r output channel: (j) rightmost root grow fastest and blocks the leftmost root to enter the rightmost output channel and (k) primary roots in place with seminal roots networking across all channels.

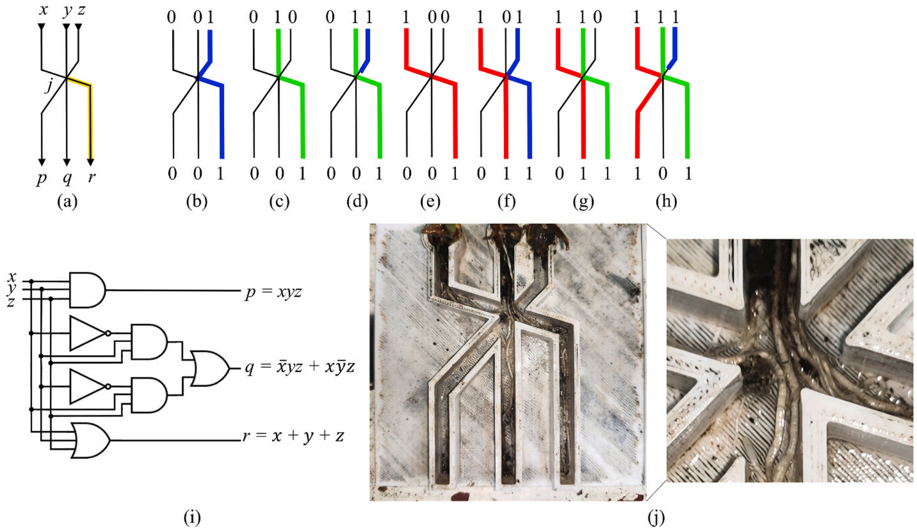

Fig. 5. (a) Scheme of three-inputs-three-outputs plant root nutrient gate (rNG2) where x, y, and z are input channels and p, q, and r are output channels. (b) $x = 0, y = 0, z = 1$. (c) $x = 0, y = 1, z = 0$. (d) $x = 0, y = 1, z = 1$. (e) $x = 1, y = 0, z = 0$. (f) $x = 1, y = 0, z = 1$. (g) $x = 1, y = 1, z = 0$. (h) $x = 1, y = 1, z = 1$. (i) Equivalent logic circuit. Possible scenario of root interactions in 1g with logic gate platform oriented horizontally and optimal nutrient concentration injected in the r output channel: (j) middle root grow faster than other roots towards the nutrient-rich channel r.

Table 2
Actual logic operations exhibited by three-inputs-three-outputs nutrient gate (rNG1). Boolean values of 0 and 1 represent no root presence and root presence, respectively, in the corresponding channel.

x	y	z	$(x + y + z)$	$(xy + xz)$	(xyz)	Root Interactions
0	0	0	0	0	0	No root emerges in the input channels
0	0	1	1	0	0	Root in channel z exits via channel p
0	1	0	1	0	0	Root in channel y exits via channel p
1	0	0	1	0	0	Root in channel x exits via channel p
0	1	1	1	1	0	Root in y exits via p while root in z bends to q
1	0	1	1	0	0	Roots in x and z meet at junction j with x exiting via p
1	1	0	1	1	0	Roots in x and y meet at junction j with x exiting via p and y via q
1	1	1	1	1	1	Root in y exits via q, while roots in x and z bend to p and r

Table 3
Actual logic operations exhibited by three-inputs-three-outputs nutrient gate (rNG2). Boolean values of 0 and 1 represent no root presence and root presence, respectively, in the corresponding channel.

x	y	z	(xyz)	$(x\bar{y}z + xy\bar{z})$	$(x + y + z)$	Root Interactions
0	0	0	0	0	0	No root emerges in the input channels
0	0	1	0	0	1	Root in channel z exits via channel r
0	1	0	0	0	1	Root in channel y exits via channel r
1	0	0	0	0	1	Root in channel x exits via channel r
0	1	1	0	0	1	Root in y exits via r, blocking root z
1	0	1	0	1	1	Roots in x and z meet at junction j with z exiting via r and x via q
1	1	0	0	1	1	Roots in x and y meet at junction j with y exiting via r and x via q
1	1	1	1	0	1	Root in y exits via r, deviating x to p and blocking z

rNG1, rNG2 has desynchronized channel segments x, y, and z. In addition, rNG2 has the high P concentration located in the output channel r.

In rNG2 trials, when root z emerged solo ($z = 1$), it passed the junction j and exited via channel r attracted by the higher concentration of nutrients in this channel (P = 0.2 mM) than channels p and q (P = 0.05 mM) (Fig. 5b). In this circumstance, the root apex redirected its growth towards the nutrient-enriched area. When root y emerged solo ($y = 1$), it passed the junction j and exited via channel r (Fig. 5c). When root x emerged solo ($x = 1$), it passed the junction j and exited via channel r (Fig. 5e). In the case when two roots emerged from different channels, still, only one root entered the channel with high concentration of nutrients, whereas the other curved towards the adjacent channel with lower P concentration. When roots y and z reached at the same time the junction j ($y = 1$ and $z = 1$), root y curved towards channel r obstructing the entry of root z (Fig. 5d). When both roots x and z reached at the same time the junction j ($x = 1$ and $z = 1$), root z grew directly into channel r impeding root x to enter the channel q (Fig. 5f). Similarly, when roots x and y emerged ($x = 1$ and $y = 1$), since both roots require a curvature to grow into the channel r and root y is relatively closer than root x, the latter curved towards channel q whereas root y followed the higher nutrient concentration (Fig. 5g). Significantly, when all three maize seeds germinated ($x = 1$, $y = 1$, and $z = 1$) and their roots grew towards junction j, root y blocked the passage of root z and deflected root x towards channel p (Fig. 5h). Despite the emergence of all roots, root y having the shortest distance to junction j ensured to enter first the channel with higher P concentration. The actual logical operations of maize roots using rNG2 is reported in Table 3 and the corresponding logic circuit is illustrated in Fig. 5i. The interactions of maize roots in a three-inputs-three-outputs rNG2 computes the following SOP Boolean functions: $p = xyz$, $q = x\bar{y}z + xy\bar{z}$, and $r = x + y + z$.

3.3. Dependency of vascular tissues on gravity and nutrient concentration

Anatomical traits of vascular tissues of roots sampled from rGG, rNG1, and rNG2 trials showed significant differences according to gravity and nutrient availability in the soil (Fig. 6). For the analysis, the roots that reached the output channel q in rGG, the nutrient-rich channel p in rNG1 and channel r in rNG2, were referred to as fastest roots, differently from the other roots referred to as slowest. The slowest roots generally exhibited more pronounced root trichomes, especially in rGG and rNG1 (Fig. 6a). On average, the root diameter at 1 cm from the seed showed no differences between logic gates and only the slowest roots in rGN2 resulted thinner compared to fastest roots (Fig. 6a). In addition, there was a general reduction of metaxylem count in slowest roots compared to fastest roots (Fig. 6a). Differenlty, the metaxylem average diameter was similar between rGG, rNG1, and rNG2, fastest and slowest roots (Fig. 6c). Based on the ANOVA test, the average phloem and xylem diameters showed significant differences between fastest and slowest

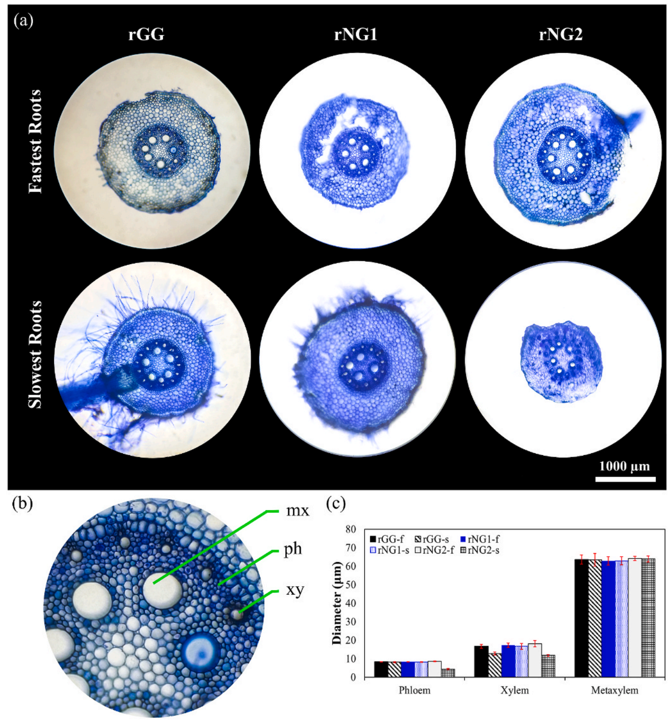

Fig. 6. (a) Transverse sections of maize primary roots grown in gravity (rGG) and nutrient gates (rNG1 and rNG2). (b) Details of root anatomy showing the metaxylem (mx), phloem (ph), and xylem (xy). (c) Comparison plot of phloem, xylem, and metaxylem mean diameters of roots in gravity and nutrient gates (suffixes f and s pertain to the fastest and slowest roots respectively; bars in red are standard errors; different letters indicate statistically significant differences with $P < 0.05$).

roots for rGG, rNG1, and rNG2. Specifically, the slowest roots in rGG and rNG2 treatments developed a phloem with reduced diameter compared to fastest roots (Fig. 6c). Similarly, xylem diameter of the slowest roots in rGG and rNG2 treatments exhibited a reduced size compared to slowest roots (Fig. 6c).

4. Discussion

AND, OR, and NOT logic gates were used in constructing the operations of the experimental logic gates rGG, rNG1, and rNG2, following the theory of Margolus and Belousov-Zhabotinsky gates (de Lacy Costello and Adamatzky, 2005) integrated with Boolean algebra. For all constructed gates, maize seeds were placed in the input channels to implement $x = 1$, $y = 1$, and $x = 1$ (Figs. 3–5). The attractants superimposed in this study were the gravity (i.e. altered orientation of the gates) and the phosphorus-rich soil region in the fabricated channels to study the dynamics of information values that may be derived according to gravitropism and nutritropism of roots.

It is known that phosphorus availability in the soil largely influence root growth and morphology with implications also in gravitropic responses of roots (Malhotra et al., 2018; Ge et al., 2000). Using rNG1 and rNG2 we computed logical operation of root growth in relation to phosphorus availability in soil mimicking natural conditions in which multiple roots compete for nutrient uptake. The bending of slower roots in rGG, rNGI, and rNG2 when two or more roots reach a junction resembled a similar scenario already reported in literature (Volkov, 2016), especially considering the suppression of root x. When a root reached first the nutrient-rich channel, it disabled other roots to enter the same channel (Fig. 5j). Since the volume of each channel can host multiple roots at the same time, the redirection of roots towards channels not enriched with phosphorus could be explained considering that the first root entering the channel already reduced the nutrient availability in the soil. This agrees with previous studies indicating that the absorption of immobile resources such as phosphate largely affect root localization and competition (Ho et al., 2004). Root competition is generally defined as a reduction of resource availability, including nutrients, water, and space, that is caused by other roots either by depletion or by inhibiting access to the resource (Schenk, 2006). In this regard, a growing body of research indicate that plants can engage in many sophisticated behaviors including complex decision-making processes in nutrient foraging and root competition (Segundo-Ortin and Calvo, 2022), and such behaviors are based on phenotypic plasticity and consist of directional growth of plant organs to adapt to the surrounding environment (Karban, 2008). Individual roots can induce a change in the growth direction of neighboring roots, ultimately resulting in a swarm behavior that optimize soil scanning to detect nutrient patches, as shown in maize (Ciszak et al., 2012). Indeed, roots can perceive and react to the presence of other roots or inert objects in the soil even before contact and this ability may benefit resource acquisition by redirecting root growth in heterogeneous soil (Ho et al., 2004). However, the nature of the signals perceived by the roots remains unknown and a possible role of electrical signals or root exudates has been hypothesized (Ho et al., 2004).

One substantial difference with our study is the derivation of a mathematical function based on three-inputs-three-outputs gates which are by definition more complex than the two-inputs-two-outputs gates reported in literature (Adamatzky et al., 2017) as the third root may act as an additional suppressor/deflector for the development of other roots. Regardless of the channel pattern, rNG1 and rNG2 root operations had inverse identical information values due to transferring the nutrient attraction from output channel p to r. Moreover, in rNG1, where the attractant is in channel p, the channel p computes $x + y + z$ and channel r computes xyz. On the other hand, for rNG2 in which the attraction is effective at channel r, r computes the $x + y + z$ information value. For rGG, in the case when the middle root deflected other roots, this produced a deformation of the section of root y at the junction j_1. This is due to the force exerted by the roots coming from channel x and z trying to merge with root y along segment c.

Differently from onion roots growing in the two-inputs-two-outputs logic gates (Adamatzky et al., 2017), maize exhibited many lateral and seminal roots in the current study, which might have influenced the primary root propagation and morphology. In this regard, thigmotropism may act as an additional response in orienting roots as there will be multiple maize roots networking across channels. Moreover, the use of natural soil in a patterned channel was not yet employed in previous studies (Rodrigo-Moreno et al., 2017; Adamatzky et al., 2017; Baluska et al., 2010; Masi et al., 2015), which might result in a different behavior of roots but better mimicking natural conditions of root growth. Root traits and environmental conditions show complex interactions especially regarding soil properties such as texture, structure, porosity or the presence of objects, barriers, and nutrients (Dunbabin et al., 2013). Indeed, root growth and development are influenced by the interaction with soil that also involve thigmotropic responses of roots, and this must be taken into account to better predict root growth in natural environment. Indeed, the use of soil in our experimental setup aids in the scale up of our laboratory study providing more accurate information for the design principle of plant root-based robots as proposed in Fig. 7. Provided that the intention is to have a root robot that penetrates the soil underground in exploring freshwater source, the developed three-input-three-output gates are recommended as the developed Boolean functions characterized soil texture with the impact of moisture gradient, whereas the soilless platform in (Adamatzky et al., 2017) may result in a sporadic root growth direction as root's environment is purely filled with water and unconstrained. In this very essence, soil-based rGG, rNG1, and rNG2 caused a directional root propagation that makes the root system to unconventionally compute the channel it needs to traverse going to the water source with minimal energy exertion. The

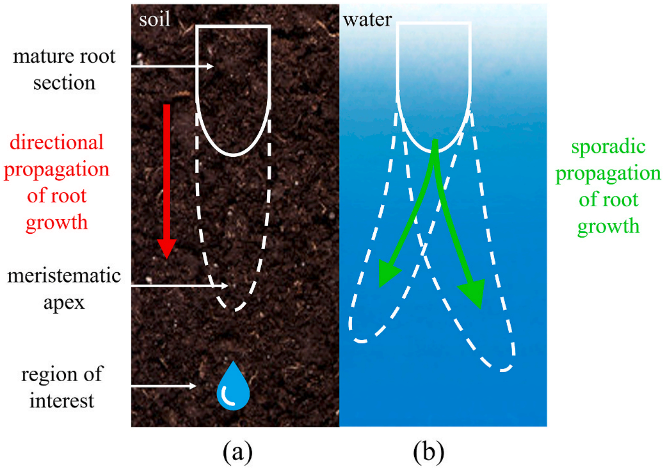

Fig. 7. Comparison of the direction of root propagation in (a) soil-based and (b) soilless environments as the basis of design principle of plant root robot.

Boolean functions formulated in (Adamatzky et al., 2017) are primarily not applicable for actual application in soil exploration as the channel forming the paths are only made using artificial materials while the three-input-three-output gates developed considered the small rocks, rock beds, and different soil materials making the partitions in the developed root logic channel in Fig. 2. Entropies in root information values can be caused by the mechanical interaction of maize seminal roots across channels at the top of the gates. In this case, touch stimuli and collisions may affect root growth direction (Ponce et al., 2017Ponce et al., 2017), especially when many seminal roots are networking. Furthermore, when thigmotropism is activated, both gravitropism and nutritropism may be attenuated according to the interactions between tropisms and their relative strengths (Muthert et al., 2020). Nevertheless, logic gates and Boolean algebra allowed asynchronicity by having NOT operator that makes information value resistive to entropy, as exhibited by rGG (Fig. 3). Interestingly, it can also be noticed that there are multiple onion seeds used per input channel (7 and 4 germinated seeds on the first and second channel respectively) in (Adamatzky et al., 2017) whereas there is only one germinated maize seed per input channel in the current study. Having multiple seeds per input channel may further introduce entropy as there is the presence of multiple sensing root tips. It is also very impractical to have an unbalanced count of germinated seeds in the channel inputs as the target plant root robot requires balance input sensing elements. From the perspective of digital electronics and control systems that are significantly considered as the building principles for plant root-based robot, a three-input-three-output root gate such as rGG, rNG1 and rNG2 have the higher potential to provide more decisions (propagation of root robot end effectors) than a two-input gate. As proposed in the current study, the decision rule is 2^n where n is the number of inputs, resulting in a total of eight defined decisions. On the other hand, the work in (Adamatzky et al., 2017) is characterized only by four decisions that may be too under fitted when exposed to the real soil environment. With an emphasis on the number of outputs of two root logic gates in comparison, the three-output gate of the current study poses a higher potential for more actual root end effectors and in that case, underground exploration will be swifter than what a two-output could provide. It should be taken into consideration that a higher number of gate outputs could induce complexity in the decision, but a higher number of gate inputs could introduce more rules to trigger the movement of a robot.

Overall, the roots most attracted by gravitational and nutritional stimuli in rGG and rNG2 showed an increased phloem and xylem diameter. This suggests that both positive gravitropism and nutritropism may have strengthened vascular tissues for water and nutrient transport. Roots in rGN2 that did not enter the channel containing high nutrient concentration developed thinner roots and narrower vascular tissues which is likely due to the low availability of P, which is known to be a fundamental element for root development (Malhotra et al., 2018). However, the same did not happen for the roots in rNG1 which does not have desynchronized channels like rNG2.

In relation to the information values that can be derived from root interactions in rNG, tropistic response towards nutrients is the main driver for computing logical operations. Overall, rNG1 and rNG2 proved that information values from tropistic responses of primary roots change depending on the nutrient availability in the soil. In the context of logical operations computed by plant roots by growing and shaping their morphology towards attractants, the competition for nutrients has large potential to be exploited in developing technological biosystems. The redirection of a root implies an undesired energy consumption which contrasts with the logic of energy minimization, analogous to inertia, in which roots do not change their growth direction if the environmental parameters remain constant.

Revisiting the case of two-inputs-two-outputs gate (Adamatzky et al., 2017), the construction of three-inputs-three-outputs logical functions is particularly interesting as cascading OR, AND, and XOR root gates based on humidity influence yielded a half-adder (HA) circuit which can add the characteristic (logic state) of 2-bit data (2 inputs). However, this complex HA circuit is still a theory and has not yet experimented. The current study also investigated the combined influence of gravity (z axis $= 1g$) and nutrients, instead of focusing on a single stimulus. To have a more comprehensive understanding on how roots are influenced by multiple stimuli like certain toxic elements, sounds, light, water, and temperature, there is a need of developing much more complex gates in terms of design and costs. The construction of three-inputs-three-outputs logical functions based on maize root behavior encompasses unconventional computing and plant biology to robotics and bioelectronics (Parker et al., 2021). One significant extension of the rGG and rNG logical gates developed in this study may be the development of a root-based robot for underground exploration (Sadeghi et al., 2017). This robot may extend its body through pneumatic means by following the set of root responses to environmental stimuli. This robot may be instrumentalized in tandem with capacitive resistive underground imaging in finding freshwater resource or other soil-based exploration. Hence, this root-based robot will decide on its own according to the logical operations embedded in it. Arithmetic logic units (ALU) based on plant root interactions may also be developed in the future. Drought is usually visible through plant leaves. However, belowground, root is the core functional part of the plant that absorbs moisture from the soil also detecting and avoiding water-limited soil areas. This orientation in which the root structure with channels is in parallel to the pull of gravity is intended to mimic the soil depth that roots could possibly encounter in the real environment. The roots are expected to sense the downward path where there is significant moisture. Adaptive fertigation system is also one of the target applications of plant root unconventional computing when there is significant number of roots. This orientation in which the root structure with channels is in parallel with the pull of gravity is intended to mimic the soil depth that roots could possibly encounter in the real environment. The roots are expected to sense the downward path where there is significant moisture by growing through an artificial sink just like the channels of the attraction gates in this study, that means there is gradient of drought or insufficient nutrients nearby causing the roots to deflect towards a specific soil region. The rGG and rNG models developed in the current study can be used as pre-programmed routers in automated manufacturing of other bioelectronic devices.

Consequently, the implementation of plant-based bioelectronics in open field scenario where there are multiple tropistic stimuli simultaneously affecting root propagation is complex and requires some constraints to process the ambiguity in data. This is supported by preliminary studies in plant root and leaf computing that mostly dealt with simulations (Adamatzky, 2019; Adamatzky et al., 2017). In the case of gradient distribution of phosphate nutrient in unconstrained soil system, there are no boundaries to consider which may result to a chaotic digital system. To exploit the potential of plant-based bioelectronics, artificial restrictions should be employed such as the use of gravity and nutrient gates. In more practical perspective, a computing system based on root propagation can be housed in an underground facility and trigger some feedback in agricultural practices like fertigation optimization. Despite the early staging of this unconventional computing study, the aspects of information value processing are an immense field that may also touch plant-based biomedical devices, controlled environment agriculture (CEA) automation triggering (Dadios et al., 2022), neurobiology (Brenner et al., 2006), and bioregenerative life support system operations in altered gravity (De Pascale et al., 2021). This can be done by cascading rGGs and rNGs in creating more practical system applications. Still, substantial effort is required to characterize plant root behavior using different logic channels, other crops and tropistic stimuli to advance plant-based bioelectronics.

5. Conclusion

Positive gravitropism and nutritropism influence root growth and development which provided information values through multiple interaction of roots in three-inputs-three-outputs logic gates. Roots that quickly elongated to output channels enriched with phosphorus caused other roots to redirect to other channels, ensuring a substantial uptake of nutrients from the soil. However, entropy artefacts might be related to other tropistic responses such as thigmotropism that can manifest in certain experimental conditions due to the fabricated channels or the networking of seminal roots. In this regard, further investigation to elucidate root responses in dynamic environmental conditions with multiple stimuli will enhance information quality to be used in developing plant-based bioelectronics. Considering the large body of information that could be gathered from the wide range of tropistic responses identified in plant roots, there is still broad research areas to be explored to deepen how roots grow and interact under multiple stimulations and how the obtained information values can be extended to computational electronics and technological applications.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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