Trends in Plant Science

Feature Review

Lateral Roots: Random Diversity in Adversity

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Lateral roots are essential for soil foraging and uptake of minerals and water. They feature a large morphological diversity that results from divergent primordia or root growth and development patterns. Besides a structured diversity, resulting from the hierarchical and developmental organization of root systems, there exists a random diversity, occurring between roots of similar age, of the same hierarchical order, and exposed to uniform conditions. The physiological bases and functional consequences of this random diversity are largely ignored. Here we review the evidence for such random diversity throughout the plant kingdom, present innovative approaches based on statistical modeling to account for such diversity, and set the list of its potential benefits in front of a variable and unpredictable soil environment.

Structured and Random Diversity of Lateral Roots

Lateral roots are essential for the uptake of minerals and water, as well as for the many interactions with the surrounding soil. They are the first place where architectural responses of root systems to external abiotic and biotic stimuli take place [1,2] suggesting that these responses contribute to the plant acclimation to the various soil conditions encountered. Within a plant, all lateral roots are not equal but rather display contrasting morphological (length, orientation) and anatomical (size of vessels, proportion of stele, etc.) features with consequences on their function [3]. Such diversity is visible in the absence of soil heterogeneity and can thus be considered as an intrinsic property of the plant (Figure 1), in contrast with an environment-induced plasticity component. Intrinsic diversity can be partly accounted for by structural and developmental patterns within the root system. For instance, lateral roots branched on primary roots are often thicker, longer, and display different anatomy than those branched on secondary roots and the same holds for tertiary as compared with secondary roots (e.g., in trees [4] and in grasses [5]; Figure 1A). Similarly, lateral roots close to the parent root apex are shorter because they are younger compared with more distal ones, due to the acropetal sequence of lateral root formation [6]. These sources (and others) lead to what we suggest to be called 'structured diversity' of lateral roots, arising from known sources of variation. Aside from this structured diversity, however, a random diversity term (Figure 1A) can be detected between lateral roots branched into the same region of a parent root (i.e., that are of the same order and of presumably the same age). The random nature of this diversity was recently tested with appropriate statistical tools [7]. Figure 1 conceptualizes the distinction between intrinsic structured and random diversity of lateral roots and illustrates (Figure 1B–E) random diversity in various annual monocots and dicots, as well as in trees. Additional illustrations can be found for sunflower (*Helianthus annuus*) [8], rubber tree (*Hevea brasiliensis*) [9], but also for the model plant *Arabidopsis thaliana* [10,11] suggesting random diversity is a common feature within the plant kingdom. It has been proposed that it is prompted by **developmental instability** (see Glossary), a concept often used to account for variation between individuals of the same genotype within the same (but unpredictable) environment [12] and that was applied to the case of diversity of lateral roots within a single individual plant [13]. Random diversity is visible through differences in length, diameter, and anatomy of neighboring lateral roots [14,15] (Figure 1F) but also of neighbor primordia [16,17]. Within

Highlights

The random diversity of lateral roots has been overlooked and fragmented results suggest the existence of genetic variability for this diversity.

Potential functional benefits of the random diversity of lateral roots are a better efficiency and plasticity in the context of temporally and spatially variable and unpredictable soil environments.

Recent modeling solutions have been proposed to account for the random diversity of lateral roots.

Many signals, such as auxin, cytokinins, sugars, etc., decrease or increase diversity and could be involved in the mediation of diversity responses to environmental variations.

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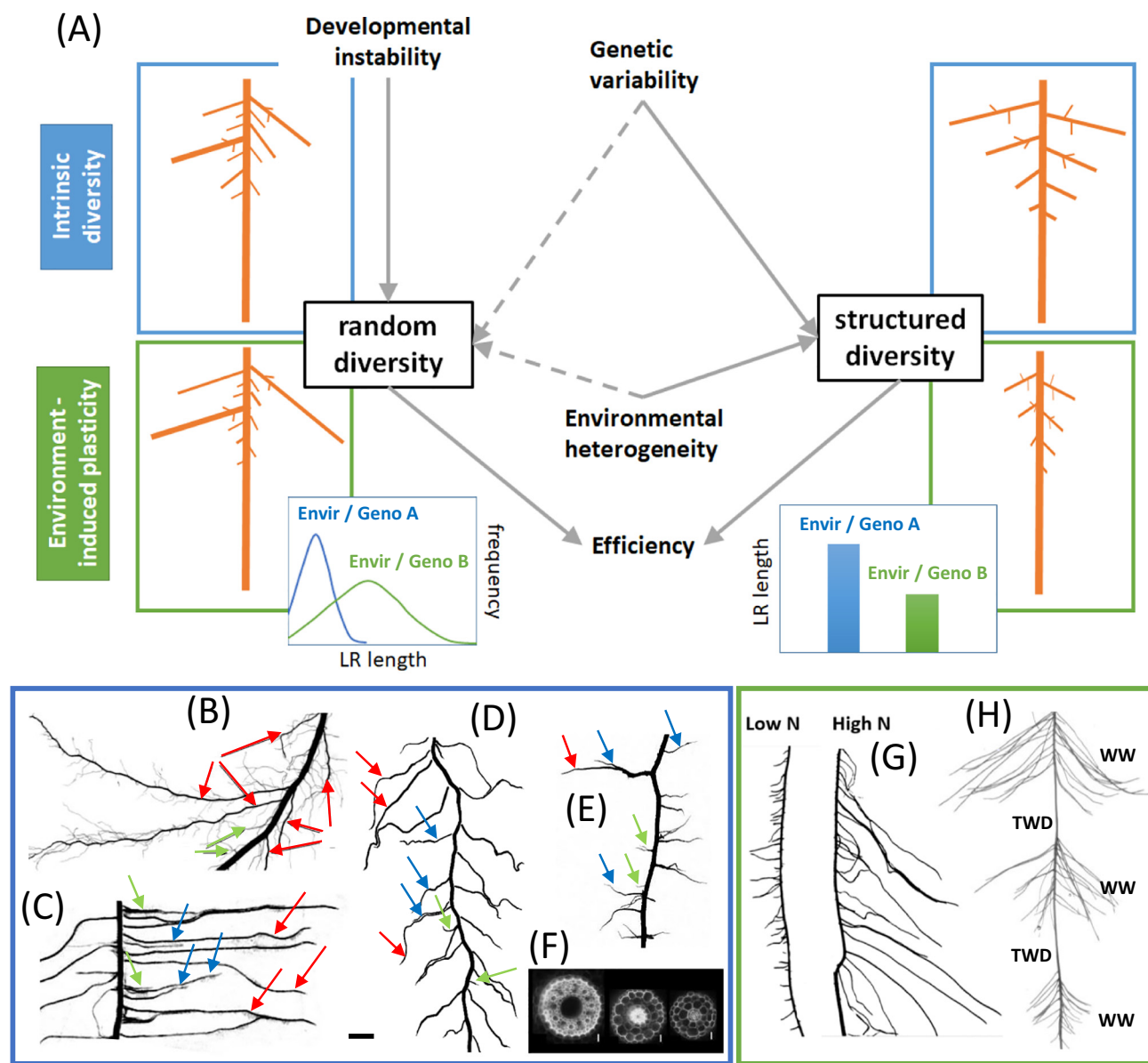
Trends in Plant Science

Figure 1. Structured and Random Diversity of Lateral Roots in Plants. (A) Structured (right) and random (left) morphological and anatomical diversity of lateral roots as intrinsic features of root system architecture in plants. In the structured diversity component, first order laterals are longer and thicker than second order, etc. Within a root order, root lengths and growth patterns are essentially determined by the age of the lateral root and thus the distance from the apex of the parent root, causing a highly regular pattern. In the random diversity component, presumably caused by developmental instability, length and anatomy differ among roots of the same order, branched on the same parent root and of the same age. Both structured and random diversity take place in the absence of environmental heterogeneity and are referred to as intrinsic diversity. Random diversity is detectable in most if not all plant species. Illustrations are given for monocots [(B) rice and (C) maize], annual dicot [(D) pea and tree (oak) dicot (E)], with arrows pointing towards long (red), short (green) or intermediate (blue) lateral roots (scale bar = 5 mm). Diversity in length can be associated with diversity in anatomy, as illustrated with transverse sections in three types of lateral roots in pearl millet [(F) scale bar = 20 μm, note that for the large root on the left, only the stele is shown]. Within species, some genetic variability (upper panel, plain grey arrows) for structured diversity is reported (e.g., genotypes with, on average, longer, or shorter laterals, longer or shorter apical unbranched zone). By contrast, little is known (dotted grey arrow) about the genetic variability of random diversity (i.e., within a species, are there genotypes with more or less diverse laterals). In response to environmental heterogeneity, structured and random diversity respond in a different way. On the structured component of diversity, all roots of the same order and of the same age essentially respond in the same way. An example of this is the 'xerobranching' pattern

(Figure legend continued at the bottom of the next page.)

species, there exists genetic variability for structured diversity of lateral roots (e.g., *Zea mays* L. genotypes with, on average, longer, or shorter laterals [18]). In contrast, very little information (but see [19]) is available on the occurrence of genetic variability of random diversity (i.e., within a species, are there genotypes with more or less diverse lateral roots).

There is evidence that both structured and random diversity contribute to the responses of the root system to spatial and temporal soil heterogeneities [20,21] (Figure 1G), although in a different way. Within the structured component of diversity, similar roots (same order, same age) tend to respond similarly. A clear illustration is the 'xerobranching' pattern induced by transient lack of water [22] (Figure 1H), where all primordia passing by a given developmental window during the stress are permanently arrested, while emerged roots continue to grow or recover. Another example is the development of cluster roots under low phosphorus conditions in some species, such as white lupin (*Lupinus albus*) [23]. By contrast, in the random component, different roots may respond differently. An example is the response to nitrogen spatial heterogeneity with longer roots responding more steeply to high nitrogen (illustrated in Figure 1G).

Paradoxically, while the development of lateral roots and of their primordia has been the matter of intense research during the last two decades, in particular in *Arabidopsis* (Banda *et al.* in this issue of TIPS gives a timely update on the molecular networks operating on these processes), the random diversity of lateral roots has been largely overlooked. While root system architecture is increasingly targeted as a lever to improve plant resource capture efficiency under poor and/or fluctuating (minerals, water) soil [24,25] and more broadly low-input agriculture [18,26], it becomes essential to better figure out: (i) when, where, and how lateral root random diversity takes place; (ii) how it can be accounted for by models; and (iii) what can be the benefits of this diversity in front of an adverse, spatially and temporally variable, and unpredictable soil environment. These points are the matter of the present review.

Lateral Root Random Diversity: When? Where?

In order to understand the outset of lateral root random diversity, we must recall the various stages of lateral root development and localize where random diversity is taking place. The different stages and the **stochastic** representation of the different trajectories of primordia and roots is shown in Figure 2. The current paradigm emanating from the model plant *Arabidopsis* [27] states that regular oscillations of molecular responsiveness to auxin at the basal meristem/elongation zone region of the primary root prime those pericycle cells which flow through this zone during peaks of responsiveness. These early oscillations can be affected by environmental clues, such as an abscisic acid (ABA)-mediated repression by a lack of water [22]. These primed regions, named prebranch sites, become competent for later asymmetrical division and primordia initiation [28]. The activation of cell division of primed cells is, however, not systematic and depends on local and global clues [29]. For example, primordia initiation is promoted under conditions of high auxin [30]. Priming and initiation can thus be formalized by an endogenous, process-dependent probability (occurrence or not of the auxin oscillation, activation or not of prebranch sites; Figure 2). These probabilities are under the control of local environment, such as patches with high nitrate [31], high water availability [32], or low phosphorus in the case of cluster roots [23], and auxin is again a good candidate to integrate these local environmental fluctuations.

Glossary

Developmental instability: the ability of an individual to develop nonidentical phenotype under given environmental and genetic conditions.
Entropy: *sensu* Shanon, entropy is a measure of unpredictability of the state, or equivalently, of its average information content.
**Hydropatterning:** plant roots can sense microscale heterogeneity in water availability across their circumference, which causes dramatic differences in the patterning of tissues along this axis, in particular branching. Auxin biosynthesis and transport is essential for regulating this process.
Markov chain: a stochastic model describing a sequence of possible events in which each event depends only on the previous event.
Stochastic: the randomness of a process.
Xerobranching: an ABA-dependent adaptive mechanism allowing roots to rapidly respond to changes in water availability in their local microenvironment

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leading to a complete absence of primordia due to transient lack of water [20] [(H) shows an image of a barley root]. Another example is the response of cluster roots to low phosphorus in white lupin [23]. In contrast, in the random component, different roots respond differently. This is illustrated by the branching patterns (G) along primary roots of maize exposed to high or low nitrogen in split-roots system, where longer lateral roots respond much more steeply to high nitrogen. Whereas structured diversity is quantified by averages, random diversity must be evaluated by distributions (of lengths, growth rates, etc.), as illustrated by the small inset showing bars for average or distributions. Both structured and random diversity may contribute to efficiency in response to environmental heterogeneity and unpredictability. All pictures from the authors, except (B) from [111], (D) courtesy C. Salon, and (F) from [55]. In (G), half of the laterals are omitted for clarity. Abbreviations: LR, Lateral root; TWD, transient water deficit; WW, well watered.
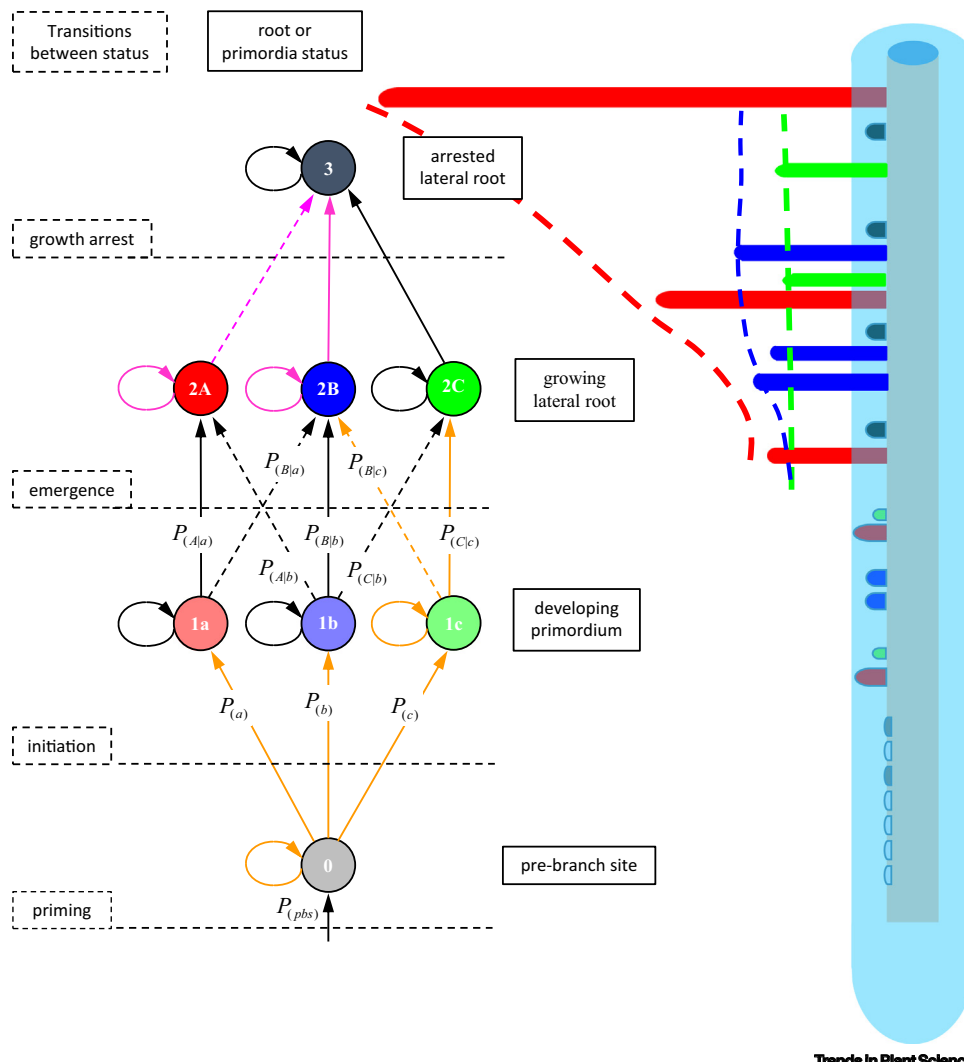
Figure 2. Longitudinal Sequence of Stochastic Events Contributing to the Diversity of Lateral Roots Branched along a Primary Root and Formalized Using a **Markov Chain**. (0) Establishment of prebranch sites following oscillations of the response to auxin in a zone located between the basal meristem and the elongation zone, with a probability $P_{(pbs)}$. (1) Once initiated, primordia develop with a diversity of rates, here arbitrarily discretized into fast (1a), intermediate (1b), or slow (1c), associated with corresponding probabilities ($P_{(a)}$, $P_{(b)}$, $P_{(c)}$). (2) Primordia may or may not emerge. If emerged, lateral roots grow with a diversity of rates for more or less long durations. According to [7], this diversity is not homogenous but can be discretized into types [here three, set as fast and accelerating (2A), slow and rapidly stopping (2C), and slowly decelerating (2B)]. Again, each state is reached with a probability that also depends on the previous status (for instance, $P_{(A|b)}$ is the probability to enter the stage 2A after being a primordia under the 1b status). An ultimate stage (3) represents arrested roots. Diversity of growth patterns translate into a divergence of lateral root length after a few days (red, blue, and green dotted lines showing the shape of the envelope of root tips of the three types). Possible transitions between Markov chain states are represented by straight arrows when an object (primordium, root) moves to a new status and by a loop (called self-transitions) when the object remain in the same status until the next time step. Dashed arrows correspond to the less probable transitions. The colored loops and arrows correspond to nonhomogeneous transition distributions (i.e., distributions are time-dependent, consistent with the idea of developmental window when 'decisions' are made). The self-transitions, the probabilities of which increase with time and converge to 1, are in orange. This is the case of the prebranch sites, which have a delineated window to initiate primordia. Similarly, slowly developing primordia have a probability to arrest, which increases with time. As a consequence, probabilities to exit these states converge to zero (orange arrows). For states 2A and 2B, the self-transition probability decreases, then stabilizes to a value > 0 (pink loop), while the probability of moving to the growth arrest state (pink arrow) increases, then stabilizes to a value < 1, the asymptotic probability of staying in state A being far higher than that to remain in state B.

Once initiated, the fate of primordia is not unique. This can be seen in (rare) studies where primordia size (length, width, cell numbers) is recorded as a function of distance to the parent root apex [16,17]. If primordia initiation is considered acropetal (although there are debates on this depending on species (see [6,29]), a high variance of primordium size at a given distance from the parent root apex means that primordia develop at various rates, possibly equipped with various anatomical attributes (Figure 2). An extreme example of this diversity is the S and L primordia in rice (*Oryza sativa*) that give rise to S (short, determinate growth) and L (long) lateral roots [33] that differ strongly in their anatomy [34]. Beyond auxin [35,36], the list of hormonal and molecular signals able to influence probabilities associated with primordia development is long, starting with cytokinins [37,38] and regularly updated: sugars [39], brassinosteroids [40], ethylene [41], jasmonic acid [42], but also signaling peptides [43], small RNA [44], or more recently, very long chain fatty acids [45] all play their part in this process, often with some crosstalk [38]. How these signals contribute to maintaining or exacerbating lateral root primordia diversity both under nonstressful conditions or as mediators of environmental clues is essentially not known and should attract the attention of the lateral root community.

Ultimately, primordia may or may not emerge. A lack of emergence of a proportion of primordia has been repeatedly observed in response to high [46], but also very low [35,47], nitrate, high phosphorus [10,48], or water stress [49] but it is less acknowledged that this also occurs in the absence of stresses [6,50]. Lucas *et al.* [51] identified auxin again as a major actor governing the succession of arrested primordia/emerged lateral roots in *Arabidopsis.* According to our framework, this means that auxin likely alters the different probabilities associated with primordia development (Figure 2).

Once emerged, lateral roots display a range of growth patterns, from a rapid deceleration leading to growth arrest shortly after emergence, up to a steep acceleration and sustained growth for several days (Figure 2). This diversity is consistently revealed in studies in which time series of lateral root growth rate were measured, for example, *Arabidopsis* [11], oak tree (*Quercus robur*) [52], peach tree (*Prunus persica*) [53], rubber tree [9], sunflower [8], maize, and pearl millet (*Pennisetum glaucum*) [7]. Diversity can take the form of a continuum [11,52], or of distinct types (classically 2–4), that have been either strictly defined (as in the case of rice [54] or millet [55]) or defined with some overlap (as in the case of maize [7]). Short lateral roots are usually thin, with limited transport capacity [55] and their meristem show signs of exhaustion or at least shrinkage [56,57], as in the case of determinate primary roots found in some species such as in Cactaceae [58]. Lateral root length or growth rate are often correlated, though loosely, to apical or basal diameter, displaying an 'envelope curve', suggesting that root diameter (and thus likely the surface area of xylem or phloem vessels and their conductivity) defines a potential growth rate that cannot be exceeded due to conductivity limits [14,59]. The diversity of lateral root fate within that envelope curve occurs in the absence of environmental heterogeneity and contributes to what was defined as random diversity above. In addition, evidence can be found that random diversity also contributes to environment-induced plasticity of lateral root fate. For example, in *Arabidopsis*, root segments in contact with high nitrate patches show increased proportion of long, likely fast growing roots [60], while phosphorus deficiency leads to a reduced number of fast growing and long roots [10,20]. Similarly, the response to soil moisture in rice involves a change of the proportion of L types (and there exists a large genetic variability for this trait [19]). This proportion also depends on internal clues. Once again, auxin is a well-known modifier of the proportion of lateral roots but only within certain temporal limits, outside of which it has little influence [61]. Sugars also stimulate lateral root elongation rate [62] and change the proportion of fast and slow growing roots [11], suggesting that sugars are also an important component

of the signaling landscape influencing probabilities associated with lateral root development (Figure 2).

Recently, using appropriate statistical tools, we found no evidence of any structuration of the occurrence of long, short, or intermediate laterals along primary roots in maize and pearl millet, suggesting this typology results from a random process [7]. The molecular and genetic bases of this random process, largely overlooked, now need careful attention. While genetic regions controlling lateral root density are being revealed and validated at the molecular level [63], an identification of genetic regions controlling lateral root diversity in crops will become the next challenge.

Lateral Root Random Diversity: A Journey through a Progressive Decrease of Entropy

Root biologists conventionally report lateral root descriptors (e.g., diameter, growth rate, angle) that are averaged (see inset in Figure 1) at the level of the plant or group of plants (e.g., genotypes, conditions). This group-centered approach maintains the vision of differentiation as a stereotyped program that all lateral roots execute identically, starting at the specification of the prebranch site. Contrastingly, in the animal domain, there is growing acknowledgement that stochasticity is an essential aspect of differentiation, as illustrated by the great variability of gene expression at the single cell level in undifferentiated tissues [64]. In line with this, some studies refer to the theoretical framework of non-equilibrium thermodynamics, which offers innovative paths to analyze biological processes related to differentiation [65]. In that context, cell differentiation is viewed as a succession of irreversible transition(s) from one steady state to another, entailing a continuous decrease of **entropy** [66]. Between successive transitions along the differentiation journey, cells remain in a (meta)-stable state with a characteristic gene expression profile that is self-maintained by the cell gene regulatory network. Transitions occur through a transient increase of entropy triggered by some tissue signals and are followed by a decrease of entropy as the cell stabilizes in a new state [67]. This theoretical framework also copes with multistability (i.e., multiple possible fates). Importantly, it provides observables, such as Shannon entropy, that can aid identification of key time-points or actors that break the stability of the system required for differentiation [64].

Consistent with this view, we propose that the succession of events leading to the random diversity of primordia and lateral root fates can be seen as a journey through a progressive decrease of Shannon entropy (i.e., an increase of information and a decrease of the deformability of the system; Figure 3). If we unroll the different phases of primordia and lateral root development, the lack of priming of prebranch sites depicted in the previous section is analogous to a steep decrease of entropy, since nonprimed pericycle cells definitely lose their ability to initiate primordia. Primed sites experience a lower decrease of entropy, as they may or may not lead to primordium initiation (Figure 3). Prebranch sites that do not give rise to primordia remain stuck in a steady state with no further possible initiation (entropy sink). Once initiated, primordia developmental trajectories differ. If these trajectories are mirrored by different anatomies, as suspected [7,55], with more or less, smaller or larger xylem and phloem vessels, changes of trajectories may become less likely. Finally, the emergence of lateral roots leads to a decrease of entropy with different amplitudes. Those lateral roots quickly decelerating also fall into an entropy sink, since they most often lose their meristem [56]. Similarly, the meristem of accelerating roots enlarges with time [56], which suggests they are well equipped to grow for a long time. As in the case of primordia, roots with intermediate behavior could exhibit different fates, awaiting signals depending on intrinsic or environmental conditions [7]. Illustrations of the flexibility of these trajectories come from classical studies showing that modifications of sugar supply or local auxin or tissue ABA induce massive changes in lateral root fate at the different transitions (Figure 3) [11,22,32,61,68–70].
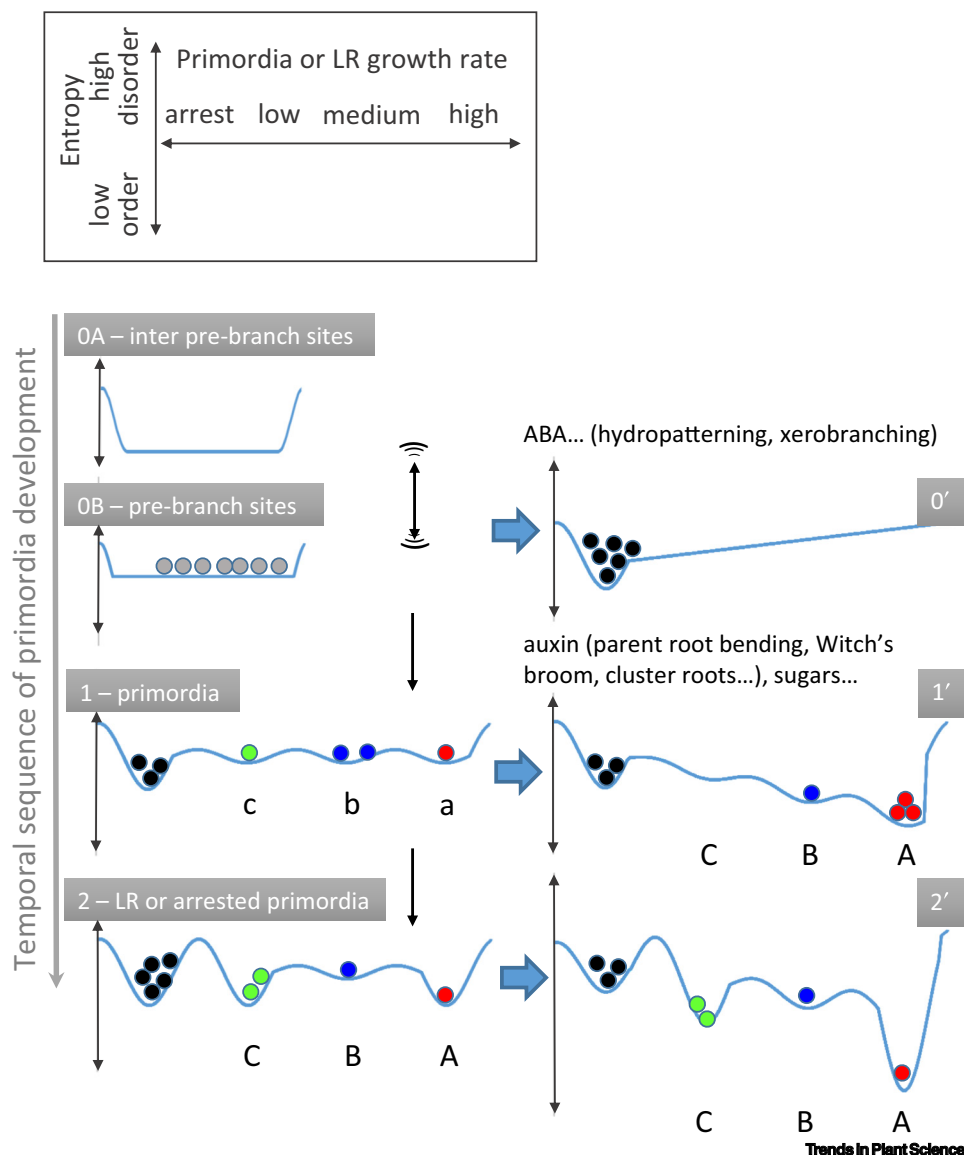
Figure 3. A Journey through a Progressive Decrease of Entropy during Primordia Development. The entropy characterizes the degree of totipotency of a group of cells (prebranch site, primordium, or root tip). The blue line represents the level of entropy in different primordia or lateral roots (LRs) whether they are arrested (black beads) or grow at slow (green beads), intermediate (blue beads), or fast (red beads) rates. The journey starts with the targeting (0A) or not (0B) of prebranch sites (PBS) with a slight (0B) or steep (0A) decrease of entropy. PBS (grey beads) that do not give rise to primordia remain stuck in a stable state in an entropy sink. Initiated primordia develop with different trajectories from large/rapid primordia (a) to small and/or slow growing primordia (c) with possible intermediates (b). Entropy sufficiently decreases so that changes in primordia fate becomes more difficult (symbolized as beads being trapped in an entropy sink). Then, LRs emerge (2) but some primordia do not (additional black beads). At that stage, the fate of LRs from extreme types (A and C) is no longer flexible, while intermediate ones (B) can still behave differently based on external stimuli. The journey can be altered upon environmental and/or hormonal treatments. For instance, the supply of auxin to the root, the excision of the primary root tip, or the local bending of the primary root (the latter two inducing a massive flush of auxin) lead to a drop of entropy (1'). This drives all developing primordia to behaving in the same way (large/fast growing). Sugars also stimulate fast development of primordia. In contrast, auxin has a much lesser impact on emerged laterals, since it occurs at a stage where entropy is too low to allow redirection of fate (2'). Impact of signals is also seen at earlier stages, such as during hydropatterning or xerobranching with abscisic acid (ABA) being an intermediate inhibiting primordia initiation. In that case, all PBS fall in an entropy sink.

Lateral root primordia development therefore sounds like an appropriate material to explore the benefits of using the concept of entropy in plant developmental biology, as recently reviewed [64]. This would require defining a metric for entropy and testing signals (Figure 3), potentially increasing or reducing entropy. It could also stimulate studies on gene expression network at sub-tissue or even single cell levels, as it is currently developing [71], for instance in incipient primordia.

Stochastic Models as a Keystone to Characterize Lateral Root Diversity

In order to consider lateral root diversity as a trait, and characterize genetic and/or environmental impacts, some effort is needed to define variables and ways to measure them. Because diversity in growth patterns has been often related to diversity in diameters [9,55], the coefficient of variation of basal or apical diameter of lateral roots was recently used to characterize the diversity of lateral roots across 140 mono and dicot species [14]. Based on the central role of root apical diameter in determining growth potential, the ArchiSimple model [72] was developed, which satisfactorily reproduces the root architectural features of a large number of species with a low number of parameters (Figure 4A). In this case, the diversity of lateral root growth patterns is modeled by incorporating a stochastic function for the assignment of lateral root diameter at emergence, with lateral root types emerging as a consequence of this stochasticity. Several other root models incorporate stochasticity, which is implemented either directly (each lateral root growth rate is sampled from a normal distribution with mean and standard deviation set by the user) or indirectly through diameters, as in the case of ArchiSimple. A subset of root architectural models accounting for stochasticity and thus lateral root types is listed in Table 1. It notably includes CRootBox [73], DigR [74], OpenSimRoot [75], or RootTyp [76]. These models also have the capacity to define explicitly several lateral root types with additional parameters, including type-specific probabilities of generation by the parent root. In that case, diversity is not an emergent property of the model and requires a more extensive parameterization. As far as we know, neither the effect of environmental clues, nor the effect of genetic variation has been implemented to modulate proportions of lateral root types in these models. This step certainly constitutes a future challenge in order to propose a new generation of root architecture models able to respond to a fluctuating environment through modification of lateral root growth patterns. Another challenge is to couple these root architectural models to soil models in order to evaluate the impact of root architecture, including lateral root random diversity, on resource capture performance [77].

Inasmuch as functional–structural models are perfect tools to closely reproduce real root architectures based on growth and development processes, statistical models are perfect tools to identify patterns of lateral root diversity and thus be used to perform genetic analyses or evaluate the impact of environmental stimuli. In line with this, a new phenotyping pipeline was recently developed and evaluated on two cereals: maize and pearl millet [7]. This pipeline starts with the SmartRoot image-analysis system [78], which is used to reconstruct consistent spatio-temporal data on the basis of successive snapshots of root system architecture, with temporal and spatial statistical models. Daily growth rates of individual lateral roots (Figure 4B) are then analyzed using semi-Markov switching linear models that synthesize the information into a probability to enter a growth stage, a duration before growth cessation, and a linear trend describing the change in growth rate with time. For both maize and pearl millet, three types were identified, with similar characteristics across species [79]. In pearl millet, these types matched anatomical differences in root or stele diameter, as well as in number and size of xylem vessels. Interestingly, introducing genetic (auxin signaling mutant) or environmental (severe shading) perturbations in maize only
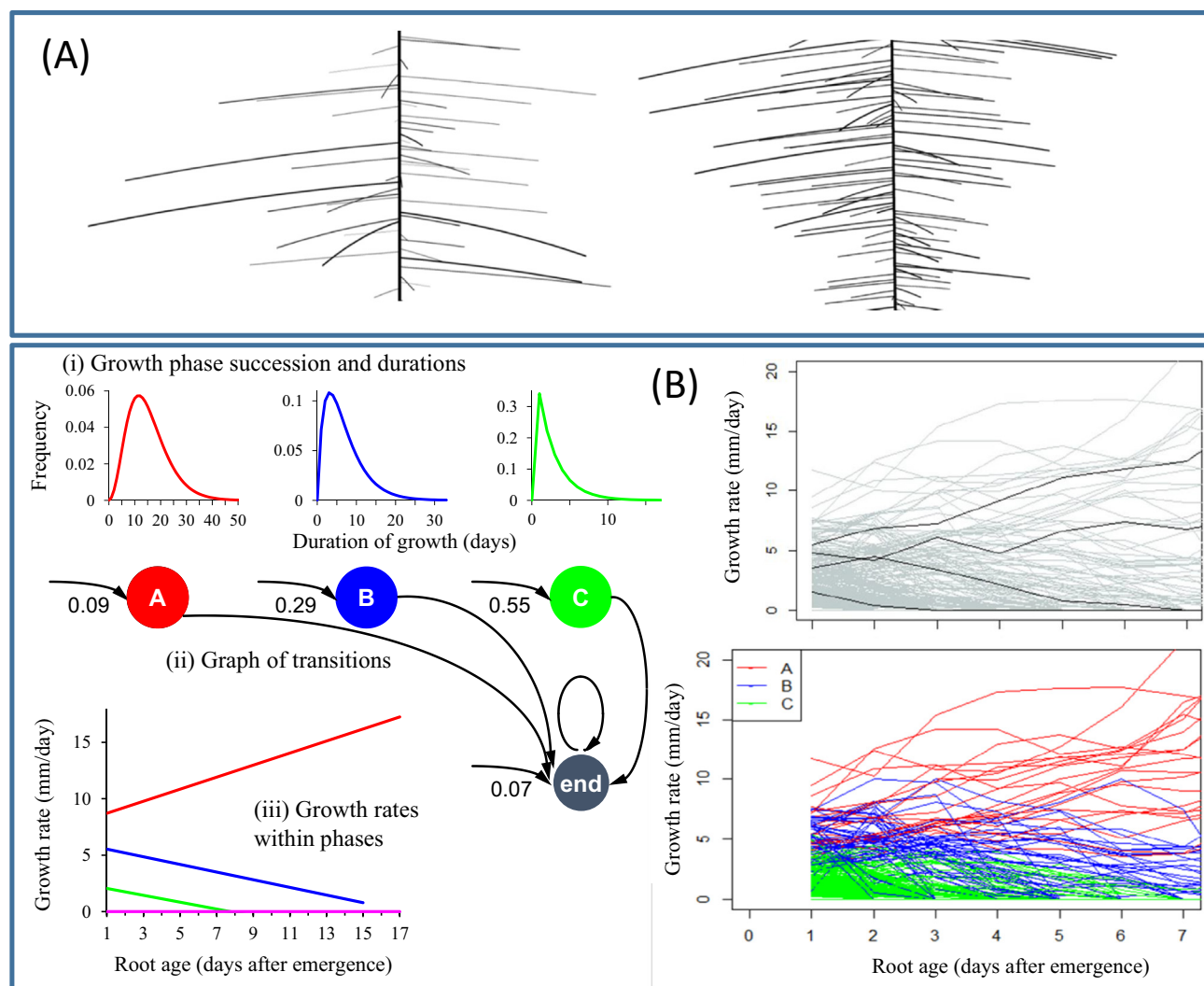
Figure 4. Modeling Approaches to Capture Lateral Root Random Diversity. (A) Representation of two extreme branching patterns along a dicot taproot, either highly diverse (left) or not (right), generated using the ArchiSimple model [70]. The only difference between the two root systems is the variance of lateral root diameter at emergence, which is 2.5 times higher on the left than on the right root system. (B) Model-based characterization of the diversity of lateral root growth patterns. The diversity of growth patterns in pearl millet is represented by the upper right panel, which shows growth trajectories of all laterals from one single maize primary root (grey lines). Four contrasted patterns are shown as black lines. This diversity is analyzed using semi-Markov switching linear model (SMS-LM). In that case, a four-state SMS-LM best accounts for the diversity of patterns [11]. The three growth states correspond to lateral root types called A, (fast and accelerating pattern), B (intermediate, slowly declining), and C (rapidly arrested). All roots may ultimately stop growing (consistent with the formalization shown in Figure 2). The left part of the panel shows (top to bottom): (i) the distribution of growth phase duration, that is much longer for A types than for B or C type roots; (ii) the graphs of transitions with probabilities associated with transitions states; and (iii) the linear trend models estimated for each state. With this model, each root can be tagged and assigned to a given type (lower right panel).

changed the proportion of roots in each type, but not the definition of types. This suggests that environmental or genetic effects could be captured directly through effects on subsets of statistical parameters [72,73]. For instance, environmental effects could be formalized through a parameterized response curve between a transition probability, as depicted in Figure 2, and an environmental variable. These parameters can then be considered as genotype-dependent, as in the case of models accounting for genetic and environmental effect on shoot growth [80,81].

Table 1. Structural Functional Plant Models Able to Generate Lateral Roots Random Diversity

Model name	Growth stochasticity[a]	Various lateral root types[b]	Lateral root types/proportions modified by environment[c]	Refs
AMAPsim	Yes	No	No	[109]
ArchiSimple	Yes	Yes (continuum)	No	[72]
CRootBox	Yes	Yes	No	[73]
DigR	Yes	Yes	No	[74]
OpenSimRoot	Yes	Yes	No	[75]
RootMap	No	No	No	[110]
RootTyp	Yes	Yes	No	[76]

[a]Growth stochasticity means that growth parameters are not fixed, but chosen randomly within a given distribution.
[b]Various lateral root types refers to the possibility, for the user, to explicitly input several lateral root types for each mother root.
[c]Lateral root types/proportions modified by environment refers to the ability of the model to modulate the types and proportions of lateral roots based on environmental clues.

Lateral Root Random Diversity for Efficiency in Adversity

Addressing the functional significance of lateral root random diversity means dealing with several levels of complexity: (i) environmental clues are perceived locally (e.g., local patches of nitrate associated with intense mineralization) but heritable benefits are seen at the whole plant level and on the long term (fitness); (ii) developmental decisions leading to lateral root diversity are taken during short time windows (Figure 2) with only a partial knowledge of the future whole plant context and soil conditions; (iii) benefits are (soil) context-dependent, few long lateral roots are better to capture the mobile nitrate while many short ones are preferable to capture the immobile phosphate [18,82]; (iv) benefits need to be evaluated in reference to carbon costs; (v) lateral roots and their environment are part of the same system and they influence each other; and (vi) root developmental patterns or responses are most often, if not always, described through the filter of averaging while distributions would be certainly more insightful. Nevertheless, in the following, we attempt to connect the available results (either from rare studies or most often from simulations) around five different, yet overlapping, aspects of the functional significance of lateral root random diversity, which are sketched in Figure 5.

Functional Complementarity

Several examples indicate that the functions of the root system are, at least in part, distributed between the different types of roots. A first example is the ratio of radial-to-axial hydraulic conductance, which is predicted to affect the distribution of root water uptake along a lateral root [83]. Specifically, in thin lateral roots with a large ratio [84], the water influx is expected to be biased towards the root base, while thick lateral roots with a small ratio (mainly because axial conductance is much larger in thick than in thin roots) would distribute a larger influx on their entire length (Figure 5A). In this context, a random diversity of lateral roots allows the plant to optimize the route of water from the bulk soil to the shoot and to avoid localized hotspots of uptake that are prone to cause localized soil drying and drop of rhizosphere conductivity [85]. The coexistence of lateral roots with different hydraulic properties, and which do not take up water equally even when they are exposed to the same rhizosphere moisture, is also expected to smooth out the distribution of water uptake through the soil profile.

The specificity of lateral root responses to phosphorus, nitrogen, and water shortage, is also an indication of functional complementarity. This functional complementarity is a cornerstone of multifunctional root system ideotypes (e.g., drought- and low nitrogen-tolerant) that are proposed to rely on a diversity of lateral root growth types optimized to the distribution of water and nitrogen in

LR random diversity

high   low

(A)

(B)

(C)

(D)

(E)

(F)

(G)

FUNCTIONAL
COMPLEMENTARITY

FORAGING
EFFICIENCY

RISK
MANAGEMENT
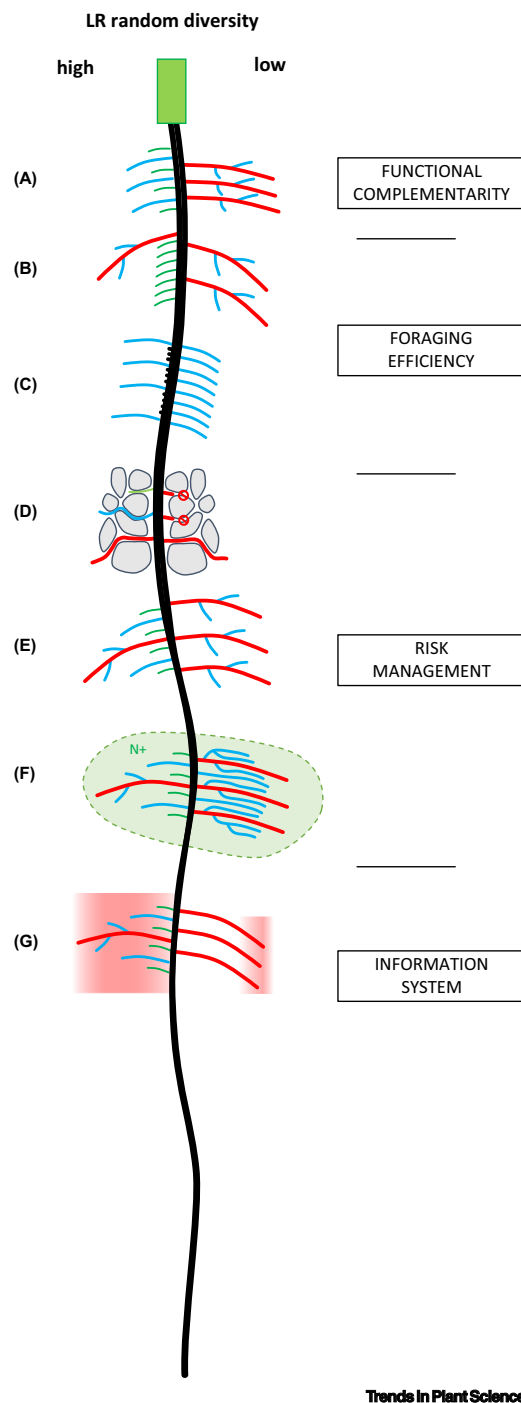
INFORMATION
SYSTEM

Trends in Plant Science

Figure 5. Proposed Contributions of Lateral Root (LR) Random Diversity to Efficiency. (A) LR with different sizes and hydraulic properties (left) complement each other to smooth the spatial distribution of root water uptake. (B,C) Diverse sets of lateral roots (left) explore a given soil volume and acquire a limiting resource at a reduced cost. (D) An intrinsic diversity (left) increases the likelihood for lateral roots to better seek out cracks and pores and to minimize the likelihood of buckling. (E) Low cost–low gain foraging units (left) are risk averse in stochastic environments. (F) In rich environments, plants can afford high cost–high gain foraging units (right). (G) A set of lateral roots with diverse growth rates (left) sense soil properties with a better coverage of the soil volume than if they had the same growth pattern (right).

the soil profile [86,87]. In addition to the different lengths of lateral roots, this functional diversity can be due to the position of the roots relative to their neighbor, and to the extent of secondary branching that is often exacerbated in long laterals [61]. Finally, it can be due to the anatomy and molecular arsenal of each lateral root (cluster roots being an extreme case of functional specificity [88]).

Foraging Efficiency

The diversity of lateral roots discussed in this paper essentially focuses on length and thickness. As these are tightly correlated with construction and maintenance costs, one can expect lateral root diversity to be an important lever to adjust the foraging efficiency (i.e., soil volume explored per unit carbohydrates invested into roots) (Figure 5B,C). This foraging efficiency has been predicted to increase with the diversity of lateral root growth patterns [89].

Beyond its effect on the volume of soil explored, the way carbon is invested among different root types (including lateral root types) also affects how resources flow in the soil–plant system, in a resource-dependent manner. For example, S-type lateral roots in rice root system may act as long-lived super root hairs (Figure 5B,C), increasing the root surface area and nutrient uptake, while at the same time being carbon cost-efficient compared with the large L-type lateral roots [90]. Mimicking root hairs at high density, these fine S-type roots will further improve soil exploration at minimal cost [91]. Moreover, the overlap between the rhizosphere of neighbor lateral roots (meaning an inefficient carbon investment) is expected to decrease with alternating diverse roots types [89]. Consistent with this, rice exhibits a decrease of lateral root density with crown root rank that also shows some genotypic differences [92].

More generally, it has been suggested that root system foraging efficiency could be cast in a more general context of behavioral ecology, where behavior classically refers to the action or reaction of a foraging unit (e.g., an individual root) to an event or stimulus [93]. For instance, as pointed out by Forde [13], diversity of individual root trajectories resembles random walk strategy used by animals to find resource-rich patches when they have no *a priori* knowledge of the location of their target. In that perspective, selection should favor a diversity of lateral root behaviors that are recruited to enhance whole plant fitness, rather than the performance of each and every foraging unit. In agreement with this view, using the auxin insensitive mutant *axr-4*, it was shown that diversity and responsiveness to nutrient patches (responsiveness being lost in the mutant) are particularly important for plant fitness to better capture the immobile phosphorus and much less to capture the highly mobile nitrate [94].

Risk Management

The optimal carbon investment in lateral roots is largely context dependent. For example, when the spatial and temporal distribution of resources is known, plants can afford a low-cost strategy and develop lateral roots preferentially into resource-rich patches (Figure 5F) or layers [1]. However, in stochastic environments where local conditions change over time, such strategy is inherently risk prone, while plants that invest in many foraging units with lower resource gains might be considered risk averse [93]. It was recently shown that plants are capable of risk-sensitive behaviors, by which they adjust their relative allocation to stable versus variable soil compartments, depending on the average nutrient availability [95]. The role of lateral root diversity in that context remains to be addressed. However, the observation that the distribution of lateral root growth rate is modified according to assimilate availability [11] suggests that lateral root diversity contributes to some form of risk management.

The context in which decisions concerning lateral root development and growth are taken extends beyond resource availability and carbon allocation. In particular, cavity expansion pressure and bending stiffness, which influence root penetration and likelihood of buckling, are largely dependent on the root shape, on its rate of penetration, and on the soil mechanical properties ahead of and around the tip [96]. Their importance may be revealed by the evolution of developmental responses such as **hydropatterning** [32] and xerobranching [22], which repress the initiation of lateral roots that would otherwise emerge in air (dry soil macropore), and with limited lateral

mechanical support in the elongation zone, which may prevent them re-entering the bulk soil [97]. Since the shape and growth rate of emerging lateral roots are determined very early (Figure 2), potentially before the lateral roots can be informed of the soil structure (pore size, deformability), an intrinsic lateral root diversity should increase the chances for a lateral root to better seek out cracks and pores (Figure 5D) and to minimize the likelihood of buckling when it enters the soil [98].

Unleashed Phenotypic Plasticity

The abundant literature on lateral root plasticity, certainly biased towards *Arabidopsis* seedlings, implicitly assumes the existence of a unique lateral root type which responds to environmental cues, leading to a range of lateral roots phenotypes (reaction norms). However, careful observations have shown that different lateral root types do not respond similarly to the same variation of their substrate [99,100] and that their responses are affected by genotype-by-environment interactions [19]. From an evolutionary perspective, a root system comprising different types of lateral roots, whose proportions and behavior can be modulated in type-specific manners, benefits from many more degrees of freedom than a root system made of lateral roots that all respond in the same way (Figure 5E,F).

Information System

Since root tips provide the plant with a variety of signals [101], some being transported throughout the plant [102,103], a root system can be seen as a distributed network of sensors. In such distributed systems, decisions at the local level (for a lateral root, to grow or not to grow) need to be taken considering both the local environment as well as some integrated control by the whole plant. In this context, lateral root diversity, leading to a random spatial distribution of lateral root tips (Figure 5G), avoiding clusters of root tips in the same area, may better contribute to providing the plant with a balanced level of signals and, in turn, set-up the right decision after integrating both the local and whole plant information.

Concluding Remarks and Future Perspectives

Most of the characterizations of lateral roots in plants rely on cumulative or averaged variables (e.g., total length, average diameter, specific root length). Moreover, a vast majority of studies on lateral root primordia have focused on the identification of standard patterns of development. Here, we defend the idea that consideration of the diversity of lateral roots and primordia is essential because it is probably at the basis of the huge phenotypic plasticity of the root system exposed to a variable and unpredictable soil environment. We therefore suggest that diversity of lateral roots (and primordia) should be more often (if not systematically whenever possible) quantified through appropriate traits such as probabilities, or intra-plant distributions of length/diameter (see simple methods for measuring intra-plant root diameter distribution in [14,15]). We also urge the root community to discuss and adopt standards for capturing and sharing this information. Recently, the Root System Markup Language (RSML) [104] format was proposed. It has the virtue (among others) to store detailed variables at the lateral root scale. Given the large number of groups evaluating root plasticity in response to the environment in a variety of phenotyping displays [105–108] the recourse to a common data format should multiply the possibilities of meta-analyses.

How the many molecular signals involved at some point in lateral root development interfere with diversity is essentially not known, although auxin certainly plays one of the first roles. In this regard, the lateral root primordium sounds like an ideal organ to explore the role of stochastic processes in development. Incorporating the concept of entropy in plant biology is likely to be an important step in line with the advances it allowed in animal embryogenesis.

Outstanding Questions

Can the plant root community agree on a metric to account for the diversity of lateral root growth patterns and/or lateral root length?

More generally, can the community agree on a place (database) and format (e.g., RSML) to share enriched root system architecture information, together with soil and climate metadata?

How large is the genetic variability of intrinsic lateral root random diversity within crop species and how large are the responses of this diversity to various environmental stresses?

How can we improve the root architecture models to incorporate the impact of the environment on lateral root random diversity?

What is the functional importance of more or less lateral root random diversity for the whole plant?

Do the several signals involved at some point in primordia and lateral root development promote or attenuate lateral root random diversity?

Can methods and tools be developed to evaluate the entropy of primordia while they develop, such as cell to cell variation in gene expression?

A lot must now be done to explore the genetic variability of intrinsic and environmentally driven lateral root diversity in crops. In parallel, models are essential to predict the consequences of more or less intrinsic diversity or more or less environment-induced plasticity. With this information in hand, one could provide (pre)breeding schemes with new traits (diversity), allowing the selection of efficient cultivars in conditions where resource fluctuations in time and space are particularly high, as in poor soils and/or under low-input agriculture conditions.

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