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Root Tragedy of the Commons:
What is it and Where Might it Occur?

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Summary

Understanding how plants change their root foraging strategy in the presence of neighbors is of paramount importance for plant ecology and agriculture. The root tragedy of the common (RToC) is a plant behavior predicted by game theory models in which competing plants forage for soil resources inefficiently. The RToC is generally assumed to be induced by non-self root recognition, and researchers consider root overproliferation and reduced fitness with respect to a plant growing solo as the trace left by plants engaging in an RToC in experiments and model results. Herein, I first challenge both notions, and argue that the RToC is a suboptimal phenotypically plastic response of plants that is based in soil resource information exclusively. Second, I discuss how this new perspective carries important implications for the design of experiments investigating the physiological mechanisms underlying observable plant root responses. Finally, I discuss why placing the RToC theory in the context of more general root research is fundamental: The RToC represents a mechanistic foundation for understanding the belowground behavior of plants interacting with neighbors, and a spatially explicit approach to RToC may produce more comprehensive results.

Keywords

Game theory; Plant behavioral ecology; Plant competition; Plant interaction mechanisms; Root foraging strategies; Root methods.

1 Introduction

As a response to the presence of non-self roots in the soil, plants can invest more, the same, or less biomass into their roots (Belter & Cahill, 2015; Postma *et al.*, 2021). Understanding how plants allocate resources belowground in response to competition is of paramount importance for several areas in plant ecology and agriculture. Forecasting the dynamics of belowground carbon, largely driven by root production, is key for decision making in the context of mitigating climate change (Xia *et al.*, 2017; Qi *et al.*, 2019). Further, predicting how plants will distribute their biomass in crops as a function of plant density is fundamental to maximize yield in agricultural sciences (Anten & Vermeulen, 2016; Fréville *et al.*, 2019).

The seminal paper "Tragedy of the Commons as a Result of Root Competition" (Gersani *et al.*, 2001) presented both the first game theory model of plant root proliferation as a response to competition and the first experimental validation of the model's prediction. The authors observed that plants overallocated biomass to their roots in response to the interaction with other plants as compared to the root allocation maximizing resource net gain. This foraging behavior follows the definition of a tragedy of the commons (Hardin, 1968), i.e., the over-exploitation and depletion of a shared resource by several stakeholders. Shortly after its publication, many researchers aimed to corroborate Gersani *et al.* (2001)'s results. Most of the follow-ups focused on discussing the limitations of the experimental design (Schenk, 2006; Chen *et al.*, 2012, 2015; McNickle & Brown, 2014) and, more recently, on how different ways of analyzing the data serve to test hypotheses based on disparate mechanisms (Chen *et al.*, 2020; McNickle, 2020). This methodological debate can be considered to have drawn attention to the finger, rather than to the moon that the finger was pointing to.

Clarifying theoretically which mechanisms lead plants to forage inefficiently by growing more roots than what is optimal is crucial to point empirical studies to the right designs and data interpretations. In this context, I aim to challenge here some of the current axioms of the field. First, I ask what the actual definition of the root tragedy of the commons (RToC) is, and question three major assumption: (*i*) that the RToC is an evolutionary problem necessarily involving plant fitness, (*ii*) that the RToC requires self/non-self root discrimination mechanisms, and (*iii*) that competing plants engaging in a RToC must overproliferate roots as compared to plants growing solo. Second, I discuss some of its repercussions in experimental designs and show that the controversial experiment by Gersani et al. (2001) was actually well designed. Third, I highlight the need to integrate the game theoretical approach to root foraging strategies with other approaches, and stress the particular implications of accounting for explicit space, which can be crucial for understanding the root foraging strategies of plants in natural and agricultural scenarios.

2 Defining the RToC

2.1 The RToC is a plastic response

In evolutionary ecology, the tragedy of the commons is typically linked to a loss of fitness (Rankin *et al.*, 2007). For instance, trunks that trees develop to compete with each other for light is an inefficient trait fixed by evolution that limits the fecundity of trees (Falster & Westoby, 2003). As a result of being evolutionary fixed, trees grow a trunk even if planted in an open landscape. Plants could have a fixed genetic plan for root development too. Contrastingly, as behaving organisms (McNickle *et al.*, 2009) plants display a large phenotypic plasticity in root growth (Callaway *et al.*, 2003; Kembel & Cahill, 2005) and will typically adjust the proliferation of roots in soil based in both abiotic environmental information (Hodge, 2004) and the presence of competing neighbors (Craine, 2006).

The RToC has been linked to fitness repeatedly in the scientific literature, leading researchers to assume that reduced fertility is a necessary condition to prove it occurs (Gersani *et al.*, 2001; O'Brien *et al.*, 2005; Chen *et al.*, 2021). This is an inaccurate expectation if we stick to Hardin (1968)'s definition, and consider soil resources to be the commons. The RToC occurs if competing plants invest too much biomass in growing their roots and overexploit soil resources in their self-detriment (Rankin *et al.*, 2007). In other words, competing plants engage in an RToC when their resource net gain (i.e., the benefits of the resources uptaken by roots minus the cost of growing such roots) is suboptimal due to an excessive root growth (Zea-Cabrera *et al.*, 2006). While it is reasonable to expect that plants engaging in an RToC will produce less offspring, proving a significant reduction in the fecundity of competing plants is not a requisite to conclude that the RToC is taking place.

2.2 The mechanisms underlying the RToC

Plants adjust root growth in a soil patch based in four mechanisms: (*i*) resource depletion; (*ii*) growth inhibition and allelopathy; (*iii*) plant root recognition, and (*iv*) the involvement of soil microbes (Chen *et al.*, 2020). These could be classified as resource (*i*) and non-resource (*ii*, *iii*, and *iv*) mechanisms. The resource mechanism is obligatory and ubiquitous, and sets the baseline plastic response of every plant to competitors. Indeed, neighbor presence modifies the resource dynamics in soil, and focal plants responding to nutrient availability must adjust their root production accordingly (Pierik *et al.*, 2013). Adventitious non-resource mechanisms may or may not inform decision-making algorithms to tune the exploitative response of plants, leading to a spectrum of possible responses in terms of root growth (Belter & Cahill, 2015; Postma *et al.*, 2021). Both the facts that plant behavioral responses to non-self roots are diverse and species-specific, and that different non-resource mechanisms may operate in each case, are not under question. Nevertheless, disentangling theoretically what is a plant's baseline response to neighbor-induced changes in nutrient dynamics is fundamental to understand mechanistically plant competition for soil resources (Tilman, 1988; Craine, 2005).

Plants are generally accepted to engage in an RToC based on non-resource mechanisms—concretely plant root recognition (Gersani *et al.*, 2001; Falik *et al.*, 2003; Hodge, 2012; McNickle & Brown, 2014; Chen *et al.*, 2020; McNickle, 2020). Nevertheless, the RToC is actually the baseline response of plants to competition that one should expect based on the resource mechanism of competition (see O'Brien & Brown, 2008). In root-foraging models that mechanistically predict an RToC, there is no explicit mechanism accounting for self/non-self discrimination, and such mechanisms are not necessary. For instance, in their model Gersani *et al.* (2001) wrote the resource net gain (G) for a focal plant (*i*) as:

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$$G_i(u_i, x) = \frac{u_i}{x} H(x) - C(u_i) \qquad [1]$$

where u_i is the root density of each individual plant, x is the total root density so that $x = \sum_{i=1}^{n} u_i$, H is a saturating function that yields the total amount of resources uptaken by all n plants in soil (hence the first term in the equation yields the resources uptaken by the focal plant), and C is a cost function. Because each plant optimizes its own net gain selfishly ($\partial G / \partial u_i = 0$), plants in the model adjust their root proliferation to the resource uptake exclusively, engaging in an RToC.

A more recent game theory model of root foraging by Cabal *et al.* (2020) incorporates simple but explicit resource dynamics. In this model, the *H(x)* function from Gersani *et al.* (2001) is replaced by resource dynamics, including a root uptake rate (α), a resource input (I), and an abiotic leach rate (δ) in the resource net gain equation:

$$G_i(u_i, x) = \frac{I\, \alpha\, u_i}{\delta + \alpha x} - C(u_i) \qquad [2]$$

This version of the model allows the tuning of resource dynamics with some degree of freedom. Evidently, any change in αx driven by x is equivalent to a change in δ. In further model analyses, Cabal *et al.* (2021a) demonstrated that plants in this model responded to neighbor effects engaging in a RToC in the same qualitative manner they responded to increases in the abiotic resource leach rate. By overproliferating roots, plants can uptake the resources faster, and when these resources are leached quickly, higher root densities can become advantageous.

On the other hand, it is generally accepted in other fields that, in order to avoid the tragedy of the commons, active recognition of other stakeholders and the implementation of complex mechanisms is necessary (He *et al.*, 2015; Murase & Baek, 2018). Likewise, competing plants need to gather information about each other to eschew the RToC. This is conspicuous when assessing the cooperative solution conditions in Cabal *et al.* (2020)'s model, which needs to satisfy $\partial G_T / \partial u_i = 0$ with $G_T = \sum_{i=1}^{n} G_i$. Accordingly, plants must not only be able to actively recognize non-self roots in soil, but they also need to measure the resource net gain of such non-self roots. This represents a challenge for agricultural scientists that aim to optimize the collective yield of crops by means of controlling root growth (Schneider & Lynch, 2020), because even human selected or engineered cultivars may not be able to avoid engaging in an RToC if they lack the physiological capacity to gather complex information about nearby plants, such as how efficient they are foraging resources in each patch of soil.

2.3 Trace of the RToC in experimental pots and model outputs

Another axiom of the field is to assume that the RToC occurs when plants overproliferate roots relative to the setting where they own a patch of soil (Maina *et al.*, 2002; O'Brien *et al.*, 2005; Apaloo *et al.*, 2014; Chen *et al.*, 2021). However, this notion is not always true. For instance, plants engaging in an RToC may overproduce or underproduce roots, or may not significantly change their root production compared to plants growing alone depending on the optimization approach used (Kim *et al.*, 2021).

Game theory, originally developed to study the interaction among rational decision-makers, became a powerful tool to investigate evolutionary questions toward the end of the twentieth century (Maynard Smith, 1982). Game theory revolutionized the field of evolutionary ecology as it demonstrated that non-optimal traits might evolve when the net reward of a resource-allocation strategy is evaluated in the presence of interacting individuals (Parker & Maynard Smith, 1990). Plants could optimize their individual net gain when growing free of neighbors, reaching an 'individual optimal.' They could optimize their collective net gain when growing in a community, reaching a 'collective optimal.' Finally, they could optimize their individual net gain when growing in a community, reaching an 'evolutionary stable strategy' (ESS). Note that the term ESS is used here as a formalism, but the RToC is a phenotypic plasticity response rather than an evolving trait.

The RToC occurs when plants sharing soil resources invest suboptimally into their roots by proliferating fine roots excessively with respect to the collective optimum. Unlike the individual optimum, collective optima are not always solved in models *(but see Cabal et al.*, 2020; O'Brien & Brown, 2008; also see Mcnickle & Brown, 2014 whose 'ideal free distribution' response curve is equivalent to a collective optimal). Furthermore, it is impossible to experimentally control for collective optima in empirical studies testing for an RToC, given that plants in a community will either engage in a RToC or cooperate, but researchers can estimate such optima based in the respective individual optima (for instance, see section 3.2).

Despite falling in the same trap as most recent studies owing to a comparison of the ESS results to the individual optimal, Cabal *et al.* (2020) presented an alternative collective optimum solution. Based on their interpretation of their results, plants engaged in an RToC when they overallocated resources to their roots compared to conditions when plants were growing alone, which occurred in crowded communities only. Revisiting their results, and comparing the ESS to the collective optimum rather than to the individual optimum, plants following the ESS are actually recognized to overallocate resources to roots compared to the collective optimum in all cases (**Fig 1**). In their model results, the RToC is actually ubiquitous, occurring even when interacting plants underallocated resources to the roots with respect to solitary plants. This insinuates that the RToC may be markedly more widespread than previously thought.

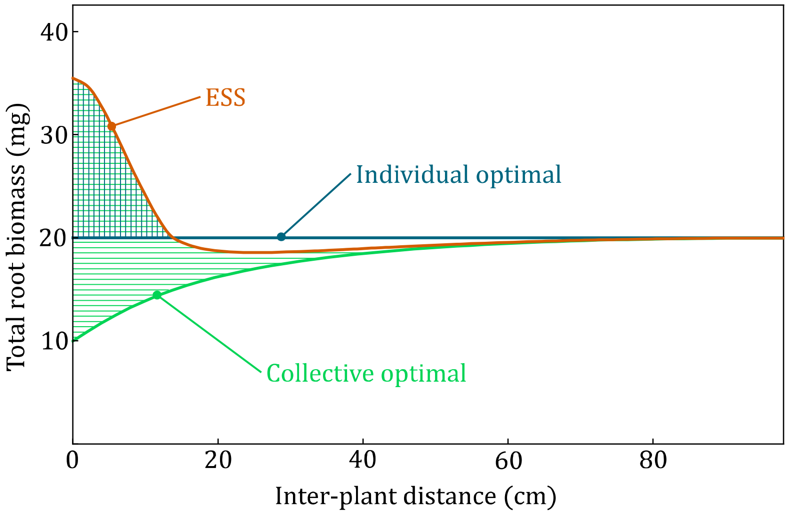

Figure 1: Allocation to roots in plants based on the model and parametrization of Cabal *et al.*, (2020). Optimal root biomass is presented for a plant growing alone (blue), following an ESS (orange), and following the Pareto optimum (green), as a function of the distance separating both plants. Shaded area with vertical lines represent overproliferation as a response to competition, and horizontal lines represent the actual RToC.

3 Identifying an RToC

3.1 Experimental design to test the RToC

Two decades had passed since the publication of the seminal paper by Gersani *et al.* (2001), a time where researchers largely debated the pros and cons of possible experimental designs to test the RToC. From a general point of view, we can classify the traditional experimental designs into two categories: owned/shared systems, where competing plant roots are intermingled in the interaction treatment, and mesh divider systems, where competing plant roots are separated by a mesh that is permeable to water, solutes, and other desired soil elements, but not to root growth. More recently, a spatially explicit approach was proposed (**Fig. 2**), which will be discussed in **Section 4.2**.

Owned/shared systems were used by Gersani *et al.* (2001) to produce control and interaction setups with constant total soil volume and nutrients available at the community level. Because their model was based on resource mechanisms and was not spatially explicit, they were assuming that the resource is an ideal common pool (i.e., a unit of resource that a root tip absorbs will immediately reduce the resource availability for all roots). In owned/shared experimental designs, the roots of the plants are highly intermingled across the container, which may be considered a sufficiently good approximation to the ideal common pool assumption.

The first limitation of this experimental design was identified by Laird & Aarssen (2005), who noticed that, because the intermingled roots in the shared container are weighted in bulk, owned/shared experimental designs can identify a spurious relationship between the shoot to root biomass ratio and the RToC due to size inequalities leading to an aggregation bias. The confounding effects of changing volume and nutrients available to the plant with neighbor presence were highlighted shortly after. Hess & De Kroon (2007) replicated the original study modifying the size of the pots and the concentration of fertilizer applied to them. Semchenko, Hutchings, & John (2007) used, for the first time, a mesh divider system to test for the RToC. Neither of the two studies found the overproliferation of roots.

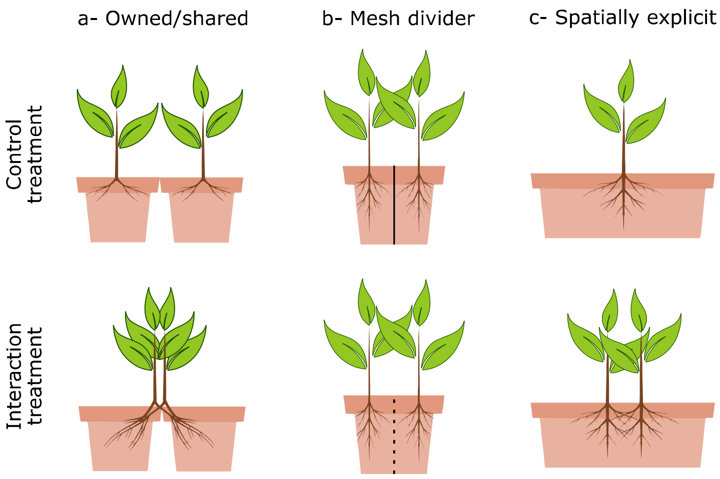

Figure 2: Three methods to study root allocation responses to plant-plant interactions. **a-** The owned/shared experimental design represented by the split-root system of Gersani *et al.* (2001). **b-** The mesh divider experimental design represented by some of the container partition systems by Semchenko *et al.* (2007) (solid line represents an impermeable barrier, slashed line represents a permeable mesh but a barrier to root growth). **c-** The spatially explicit experimental design represented by the gutter system of Cabal *et al.* (2020).

The mesh divider experimental design has become popular (McNickle, 2020) and is often used today to test for the RToC (Zhu *et al.*, 2019, 2020; Chen *et al.*, 2021). Nevertheless, owing to the resource-based nature of the RToC, mesh divider systems are largely constrained. In mesh divider systems roots do not intermingle, failing to meet the ideal common pool assumption, and each plant owns a container compartment and can preemptively absorb all resources in it. If interacting plants growing in compartments separated by a permeable mesh are of similar sizes and the same species, there will be no resource mixing, even if the mesh and the substrate are ideal resource conductors. Resources would only flow across the mesh if diffusion is driven by a nutrient concentration or a water potential gradient (Kirkham, 2014). Because plants in each compartment are typically identical, both compartments are symmetrical in resource concentration distribution and no force will trigger resource mixing. Hence, in terms of resource mechanisms, the interaction treatment does not differ from the control treatment (**Fig. 3a**).

Mesh divider systems can be used to test the effect of non-resource mechanisms controlling for resource mechanisms; this is because microorganisms, plant signals, and allelochemical substances exuded by plants can diffuse across the mesh divider (Kong *et al.*, 2018) (**Fig. 3b**). We can reinterpret accordingly some results from the literature. For instance, Gersani *et al.* (2001) found root overallocation in their split-root experiment with soybean plants (*Glycine max*), while Chen *et al.* (2021) found no response in a mesh divider experiment and interpreted their result as a denial of the RToC in the species. Owing to their mesh divider experimental setup, it is difficult to accept the conclusion of the latter study. As soybean plants were not found to respond to the presence of a neighbor in terms of root proliferation, we can conclude that mechanisms such as root communication through root exudates (Baluška & Mancuso, 2021; Wang *et al.*, 2021), or self/non-self root discrimination by sensing chemical or electrical signals (Sharifi & Ryu, 2021) is not functioning. Such notion indicates that soybean plants may not be able to engage efficiently in cooperative behaviors. Nevertheless, soybean plants may still engage in an RToC, detectable only if the response to the resource mechanism is investigated.

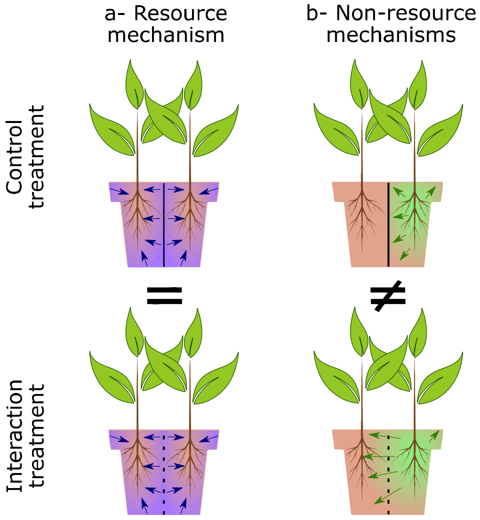

Figure 3: Effects of the mesh divider experimental design on the two main mechanisms of plant interaction **a-** Resource competition: Although the mesh is permeable, there will be no *de facto* flow of resources through the mesh divider, and both the control and the interaction treatments are exactly the same. **b-** Plant signaling: chemical signals reach the neighboring plant compartment when a permeable mesh is used.

3.2 Soybean plants engage in an RToC

As discussed previously, criticisms of the experiments performed by Gersani *et al.* (2001) with soybeans were centered in their lack of control for the volume and nutrients available per plant in their experiment. Owing to an improved understanding of the RToC, we can see that their experiment was meticulously designed. The RToC being an exploitative competition response questions the generalized concern for controlling for nutrient availability per plant. Adding supplementary nutrients in the interaction treatment of owned/shared systems to compensate for the neighbor-induced resource depletion is not only unrealistic, but would override any possible evidence for an RToC. Additionally, the concerns regarding rooting volume, based on the idea that each plant has access to twice the rooting volume in the interacting treatment, are not justified, because in owned/shared experiments testing for an RToC the rooting volume is kept constant across treatments at the community level.

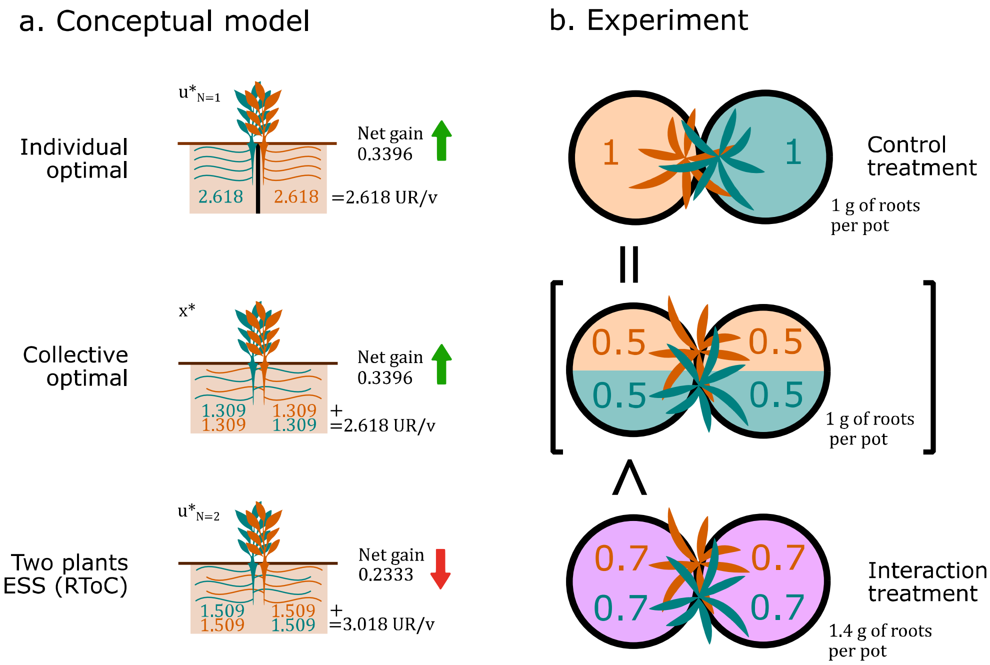

Figure 4: Schematic interpreting the results from Gersani *et al.* (2001) **a-** conceptual model (values based on numerical results shown in **Supporting Information**) and **b-** experimental results (approximated values from the original paper's results), depicting how the individual

optimal is analogous to the collective optimal of two plants sharing two soil volumes in their approach.

Gersani *et al.* (2001)'s experiment, and similar owned/shared designs, have been criticized because researchers have interpreted that the root allocation of a plant growing alone in one pot was compared to the root allocation of a plant sharing two pots with a neighbor. The key to understand this type of experimental design relies on correctly interpreting how their model was constructed (see **Supporting Information**), and realizing that their control treatment is a proxy for collective optimal root densities. The fundamental assumption of this design is that non-competing plants forage optimally, hence one can calculate the optimal root density (root biomass per unit volume or pot) that maximizes net gain, whether one or several plants share the pot. This root density can be interpreted as a base to estimate collective optimal in the two-pot system: If the root density in shared pots is higher, researchers can deduce that competing plants engage in an RToC (**Fig 4**).

4 Popping the bubble

4.1 There is much life outside the RToC!

Over the last two decades, the field of RToC has grown within a bubble, seemingly immiscible to the rest of root knowledge developed by ecologists. Unfortunately, the RToC—and more generally, game theory—are still not pervading across plant ecology disciplines (Mcnickle & Dybzinski, 2013) and might be restricted to a few closed research lines and groups. Popping that bubble and allowing game theoretical tools to inform other root ecology areas of research would markedly improve our understanding of plants. The ecology of plant interactions is currently moving toward an approach centered on individual plants and their phenotypical plasticity (Bakker *et al.*, 2021; Escudero *et al.*, 2021) but there is very little we know about how plant interactions affect the plastic response of plants to abiotic conditions (Wang & Callaway, 2021). In this context, accounting for RToC would be a remarkable way for studying phenotypically plastic responses of plants to the presence of neighbors, because game theory produces mechanistically-informed dynamic predictions.

4.2 The spatially explicit approach to RToC

Studies investigating the RToC also need to consider broader root ecology principles. The spatial aspect of plant belowground competition might be the weakest point of classic RToC studies. Spatially explicit studies of belowground plant competition have attracted the attention of ecologists probably since the illustrated book of Muller (1946) on root distribution profiles, triggering the interest for root territoriality (Schmid *et al.*, 2015), and local root responses to competition in soil patches (Mcnickle *et al.*, 2016; Garlick *et al.*, 2021; Lepik *et al.*, 2021). Spatial studies of root competition often found that plants segregate their roots horizontally in the direction of their neighbors (Schenk *et al.*, 1999) and in the vertical soil profile (Ward *et al.*, 2013). This segregation has often been interpreted as opposed to root overproliferation and hence to the RToC (Maina *et al.*, 2002; McNickle, 2020).

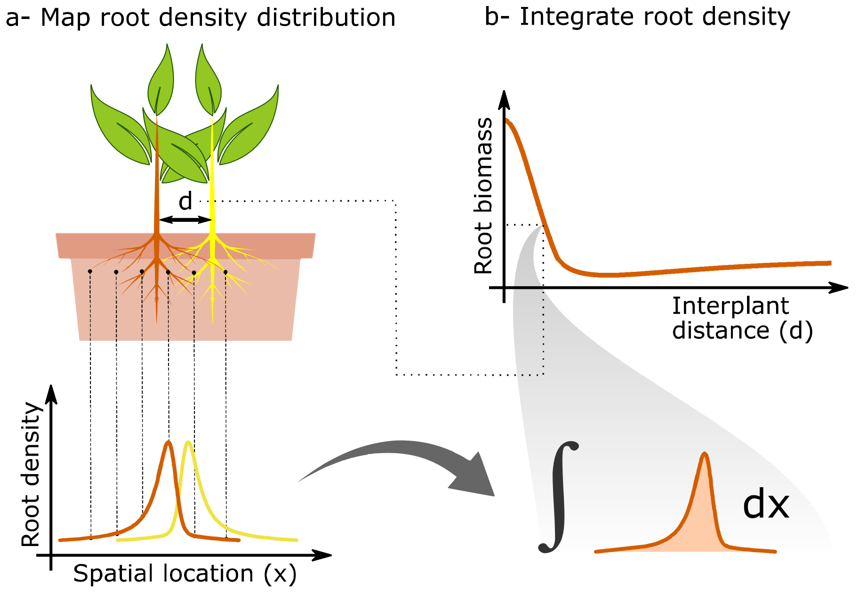

Figure 5: The spatially explicit method to determine plant root allocation strategy. **a-** Individual plant root density distribution in the container must be mapped across soil space (x) (orange represents an interacting focal plant and yellow represents its neighbor). **b-** Integrating the root densities for a given inter-plant distance (d) yields the total biomass allocated by the focal plant to roots for such distance.

Game theory models of root foraging behavior have rarely accounted for explicit space. However, the earliest attempt may be the model developed by Novoplansky & Cohen (1997). O'Brien *et al.* (2007) later developed a similar model of root competition for space as an evolutionary game. Both focused on the spatial ranges of plant roots in space and the root range overlap between neighboring pairs of plants. Although these papers represent a great contribution to spatial root competition theory, they did not have a remarkable impact on the RToC debate because they did not measure how competition affected the overall plant allocation of biomass into their roots when plant root systems overlapped. More recently, Cabal *et al.* (2020) developed another spatially-explicit game theory model of root foraging behavior. Based on the integration of root densities across space, these authors presented predictions of total root biomass of plants growing at different inter-plant distances (**Fig 5**). This approach yields information about the root foraging range of the plants, the local responses of plants in soil patches, and the total root allocation. The model predicted divergent root responses at different distances from the focal plants' stem, and hence proved that competing plants could segregate their root systems and simultaneously engage in a RToC.

5 Conclusions

What is it? - The RToC is currently viewed as a rather uncommon plant response in which plants, actively detecting their neighbors, overallocate resources into their roots and produce less seeds compared to conditions where they are growing alone. Nevertheless, the RToC is a phenomenon by which plants, based on information about the resource that can be taken up from the soil, invest more in their roots than the community-level foraging optimal.

Where might it occur? - The RToC may be much more widespread than previously thought. First, because contrary to general belief resource mechanisms are ubiquitous and unavoidable, but, to engage in collective optimal strategies, plants must resort to information about the presence and net gains of non-self roots. Hence, even cultivar species subjected to human selection may be unable to avoid the RToC. Second, because only empirical results which show that plants overallocated to their roots with respect to their solo strategy have been considered as evidence of an RToC to date. However, researchers that reported no response or even underallocation of biomass into roots may have observed an RToC too.

Empirical caveats - Mesh-divider experimental designs neglect resource mechanisms of interaction and hence neutralize the potential RToC behavior of plants. Although largely criticized, owned/shared experimental designs may have be better suited to test for the RToC. However, the game theoretical study of belowground plant interactions will display improved reliability and comprehensiveness if a spatially explicit approach is adopted.

Future directions - The concept of the RToC has grown relatively isolated from the other root ecology sub-disciplines. However, root ecology can markedly benefit from incorporating the game theoretical perspective by gaining a tool to make mechanistically-informed predictions. Hopefully, by integrating the concept of the RToC into the broader field of plant ecology, the scientific study of belowground plastic responses of plants to interactions with neighbors will further advance in the right direction.

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