Unveiling Fine Root Dynamics: Functional Insights and Applications in Fruit Crops

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Introduction

Although the sun provides plants with energy through their leaves, this energy is useless without the other necessary elements that plants need for survival. Plants obtain the remaining nutrients from the soil through their root systems. In fruiting trees, these roots must gather sufficient moisture and nutrients to thrive. Different fruit trees produce roots with different structures and behaviors.

Fine roots perform a host of critical functions, including water and nutrient uptake, synthesis of growth regulators and secondary metabolites, and maintenance of belowground symbioses. Fine root activity is a crucial determinant of plant productivity, ecosystem nutrient cycling, and global carbon sequestration. However, their underground growth limits our ability to observe fine roots under natural conditions. Questions such as when fine roots are produced, how they age, and why they die remain unanswered for most species and ecosystems. In recent years, the use of minirhizotrons (root observation tubes) and miniaturized camera equipment has opened a new world of belowground plant biology. The active growth of fine roots in woody perennials is not continuous throughout the growing season, especially in the case of fruit-bearing trees.

Concept of fine roots

Fine roots are often defined as roots with diameters of < 2 mm, and they are primarily responsible for nutrient and water uptake. Fine roots are naturally subject to rapid decay and renewal (turnover) over time, thus contributing to the carbon and nutrient balance at the ecosystem level. Fine roots account for almost 50 % of net primary annual below-ground production, and several environmental factors and diseases can modify the dynamics of this process. Root turnover is a key process in plant adaptation to unfavorable conditions. Fine roots adapt to local conditions, and their characteristics are expected to change to maximize their functionality. In water- and nutrient-rich environments, trees are expected to produce a network of relatively thin roots and a high specific root length (SRL) to enhance resource acquisition, whereas in resource-poor stands, trees may favor roots with a greater diameter and a lower SRL to deliver a longer functional lifespan and reduced loss of resources through turnover (Mosca et al., 2017).

Recent studies on the morphological characteristics of root systems have provided insight into the relationship between root architecture and the resulting increased efficiency in the use of important resources, such as water and nutrients, and improved productivity of cultivated crop species. The importance of root architecture for plant productivity relies on the fact that soil resources, such as water and nutrients, are unevenly distributed or are subjected to localized depletion. Thus, knowledge of the root system of a plant species is essential for exploiting these resources (Fassio et al., 2016).

McCormack et *al.* (2015) redefined fine roots for better understanding of below-ground contribution:

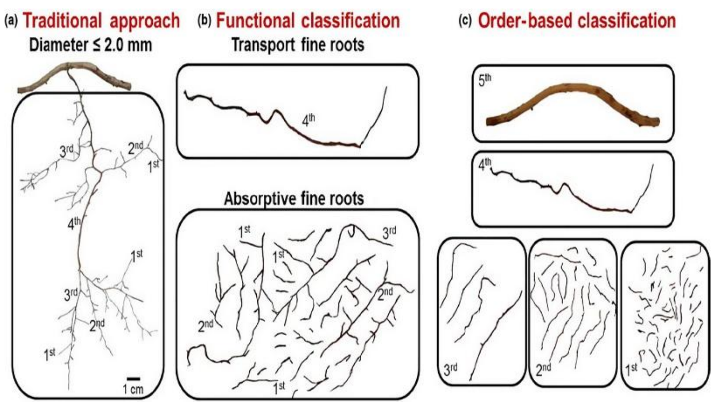

Fig. 1: Approaches of fine roots classification (root branch of *Liriodendron tulipifera*)

Table 1: Pros and cons of different classification

Approach	Traditional classification	Functional classification	Order-based classification
Description	Roots ≤ 2 mm in diameter grouped together	Roots ≤ 2 mm in diameter separated into absorptive and transport fine roots	Roots ≤ 2 mm in diameter separated into individual root orders
Processing time	Fast	Moderately fast	Slow
Advantage	Requires no prior knowledge of site or species	Enables comparisons among functionally similar	Consistent and accurate comparisons of root

		roots, faster than order-based	traits across species and site
Disadvantage	Root trait and biomass data are difficult to interpret and compare across species and sites	Might require a prior assessment of root traits to determine functional divisions	Labor-intensive and time-consuming

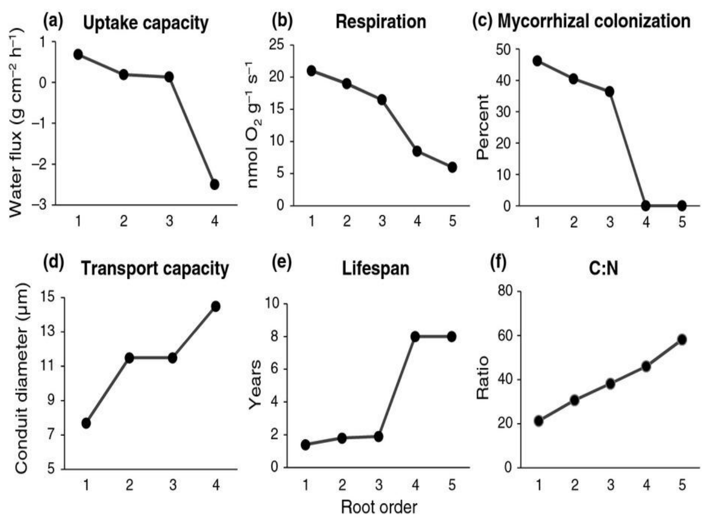

Fig. 2: Common patterns of root trait variation across distal fine-root orders

(McCormack *et al*., 2015)

Traits associated with fine root function

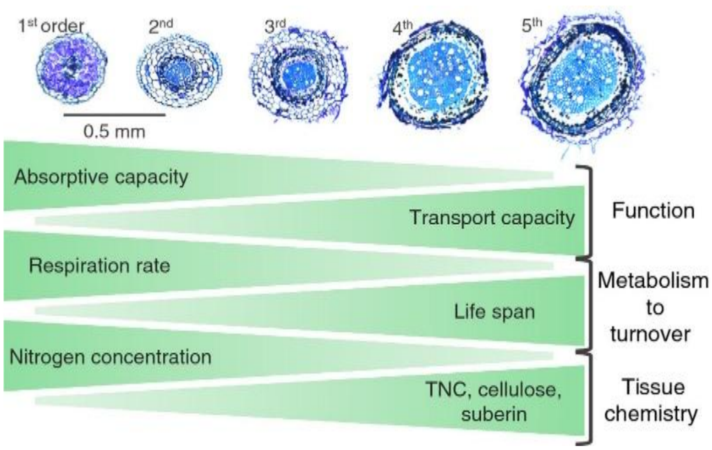

Fig. 3: Pattern of increasing root diameter and secondary development with increasing root order

(McCormack *et al*., 2015)

Drivers of fine root dynamics

However, the timing of fine root growth in woody perennials does not follow a particular phenological pattern and is therefore often difficult to predict (Rogers and Head, 1969). Therefore, understanding the factors controlling root growth is important.

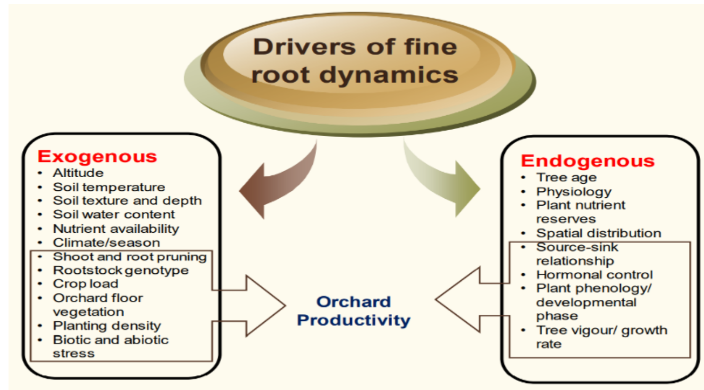

Fig. 4: Factors affecting fine root dynamics

Fine root life span

Pathway 1 represents a potential increase in lifespan with increased plant productivity, carbohydrate synthesis, and subsequent resource allocation to fine roots under favorable growing conditions. In Pathway 2, colonization by mycorrhizal fungi and root endophytes increases root lifespan by protecting against desiccation and pathogen attack or by benefiting plant growth by providing nutrients and water resources. Increased pressure from pathogen attack, saprophytic fungi, and herbivores decreases lifespan in pathway 3, while increased root respiration, excessive production of reactive oxygen species (ROS) and reactive nitrogen species (RNS), and eventual tissue damage under stressful growing conditions decrease lifespan in pathway 4.

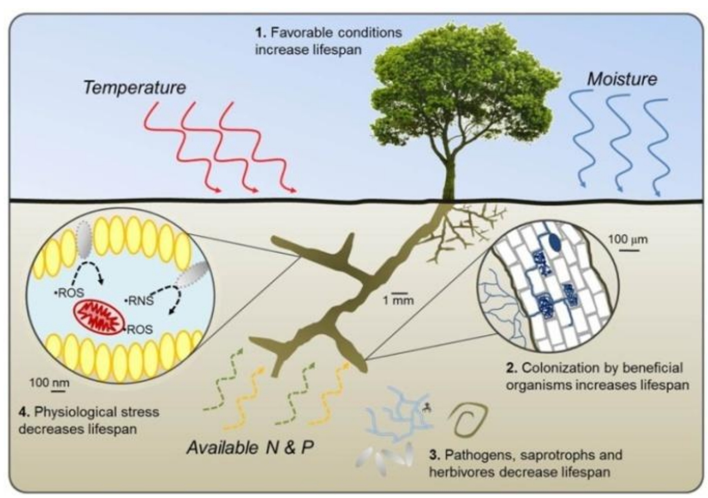

Fig. 5: Impacts of extrinsic factors on fine root lifespan.

Chen and Brassard, 2013

Fine root dynamics: applications in fruit crops

- ✓ Nutrient management
- ✓ Water relations
- ✓ Abiotic stress resilience
- ✓ Biotic stress resilience
- ✓ Carbon sequestration
- ✓ Propagation and establishment
- ✓ Tree vigor management
- ✓ Soil reinforcment

Nutrient management

- Living fine roots C: N:P ratio is 450:11:1 (Jackson *et al.*, 1997)
- Fine roots are a substantial sink for plant carbon: 22% to 33% of the total allocation of photosynthate (McCormack et *al.*, 2015).
- The soil core technique was used to determine fine root biomass (FRB) in standing orchards of mango, litchi, kinnow mandarin, aonla, guava, and sweet orange at 1m & 2 m from the trunk (Raizada *et al.*, 2013).
- Nearly 43% of FRB in all species were in the 0-10 cm layer, except in mango (52%), and 78% of FRB were confined to the 0-20 cm layer.
- Fine root production: decline d by 50% at stem distance of 2m.
- Fine root turnover: 0.580 to 0.852 yr -1, the highest in kinnow and lowest in guava.
- Application of 10t of biochar/ha increased fine root biomass in grapevines (Amendola et *al.*, 2017).
- Four 'R' stewardship of nutrient management: right time, right place, right method, and right dose.

Water relations

- Rewald et *al.* (2011) studied different root orders of 4-year-old Citrus *volkameriana trees* with respect to water flux.
- First-order roots showed a significantly higher rate of water uptake than second - and third-order roots, whereas fourth and fifth-order roots showed excess water.
- Plants may utilize hydraulic redistribution to prevent coarse root desiccation and increase nutrient acquisition.
- The first root order accounted for 50% of the surface area (SA).

Abiotic stress resilience

- Abiotic stresses such as drought, waterlogging, salinity, extreme temperature, low illumination, nutrient deficiency or excess, heavy metals, elevated atmospheric CO 2 , and mechanical restrictions
- Dehydration of fine roots may promote the production of signals that alter plant growth under drought conditions (Franco et *al.*, 2011).
- Root traits that maintain plant productivity under drought conditions include small fine root diameters, long specific root lengths, high root length density, and xylem diameter (Comas *et al.*, 2013).
- Fine roots are most sensitive organ to salinity and continuous root production is related to salinity tolerance trait
- It plays an important role in Na stress tolerance via indirect ion exclusion through turnover, blocking Na transfer to shoot tissues, and/or accumulating the highest concentrations of this ion.

Biotic stress

The effects of belowground herbivory do not manifest aboveground until a significant portion of the root system has been removed. The 'damage threshold' for root loss, defined as the percentage of the root system that can be removed without measurable reduction in above-ground production

- Defense compounds were differentially allocated across root branching orders, whereas defense induction or stress response was only detected in first-order roots.
- Soil insects in peach (Wells et *al.*, 2002) and Phytophthora in Citrus *spp.* (Kosola et *al.*, 1995) altered fine root demographics.
- Resistance RS provides a robust root system for rapid establishment and early production.

Carbon sequestration

- The proportion of photosynthate allocated for fine root construction could account for 30–50% of the total photosynthate.
- Global fine root carbon is more than 5% of all carbon contained in the atmosphere (Jackson *et al.*, 1997)
- Annual fine root turnover was 7.7, 6.8 and 1.5 for the 5,18- & 22-year-old apple trees.

- Role of fine roots in C sequestration is still controversial as considerable portion of photosynthate used to support fruit production.

Propagation and establishment

- Shallow root systems with more fine roots developed by clonal trees of avacado could provide a more absorptive surface area than deeper root systems developed by seedlings trees (Fassio *et al*., 2016).
- Cuttings exhibited a root system mostly composed of fibrous roots and rapidly increased in size after planting in Valencia orange (Castle and Youtsey, 1977).
- Albrecht *et al.* (2017) compared root architecture and growth of different rootstock plants, generated from seed, stem cuttings, or TC, during the early weeks of growth in the greenhouse.
- It is suggested that the larger number and length of fine roots on rootstock plants propagated through vegetative methods may be better suited for resource acquisition as compared with seed propagated plants.
- Citrus RS propagated by cuttings and TC are superior in resource acquisition compared to seedlings.

Tree vigor management

- Basile *et al*. (2007) compared growth patterns and morphology of fine roots of size-controlling and invigorating peach (*Prunus persica* (L.) Batsch) rootstocks. Peach trees were grafted on five rootstocks: a vigorous control (Nemaguard), three intermediate vigor rootstocks (K119-50, P30-135 and Hiawatha), and a semi-dwarfing rootstock (K146-43).
- They reported evidence that in peach trees, dwarfing rootstocks produce a larger amount of fine roots per unit canopy size than more vigorous rootstocks.
- He suggested that a greater allocation of carbohydrates to the size-controlling rootstocks may limit carbon allocation to the shoots, thereby restricting growth.

Soil reinforcement

- Plant roots support soil, which stabilizes sloped landscape and limit soil erosion. Root size properties, including root diameter influence the mechanical reinforcement of slope.
- Soil stability depends on the root tensile strength. Root tensile strength increases with decreasing root diameter so fine roots are stronger than coarse roots. Fine roots are important to soil fixation than coarse roots.
- During slope failure, fine roots tend to break but stay in position, while coarse roots can slip out of the soil.

Future line of work

- Proper technique for studying fine roots.
- Fine root dynamics in fruit plants are poorly understood especially under tropical, subtropical and arid conditions.
- Advancing molecular and imaging tools may deliver rapid assessment of fine roots.
- Deeper understanding of fine root traits at species, rootstock genotype, stock-scion combination under different orchard management practices is needed for sustainable fruit production.

Conclusion

The study of root growth dynamics remains limited due to the complexity of root systems and the challenges involved in examining them compared to aboveground organs. To develop a cohesive understanding, it is essential to classify fine roots based on their functions and root orders. Beyond their primary role in water and nutrient uptake, fine root traits are closely linked to scion vigour, stress tolerance, propagation efficiency, and soil erosion control. Moreover, robust fine roots with high turnover rates and greater dry matter allocation represent desirable attributes in fruit breeding programs.

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