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<u>Current work: Root-rhizosphere-soil interactions</u>

- Implications of root demographics, root traits, and rhizosphere composition for plant growth, physiology, and yield
- Climate, soils, water
- Impact of management on root systems & rhizosphere
  - Tree production (rootstock-scion interactions)
  - Irrigation
  - Canopy management (pruning, heading, staking)
  - Cover cropping, intercropping, tillage
  - Fertilization (timing, type, amount)
  - Soil modifications (amendments, WOR)









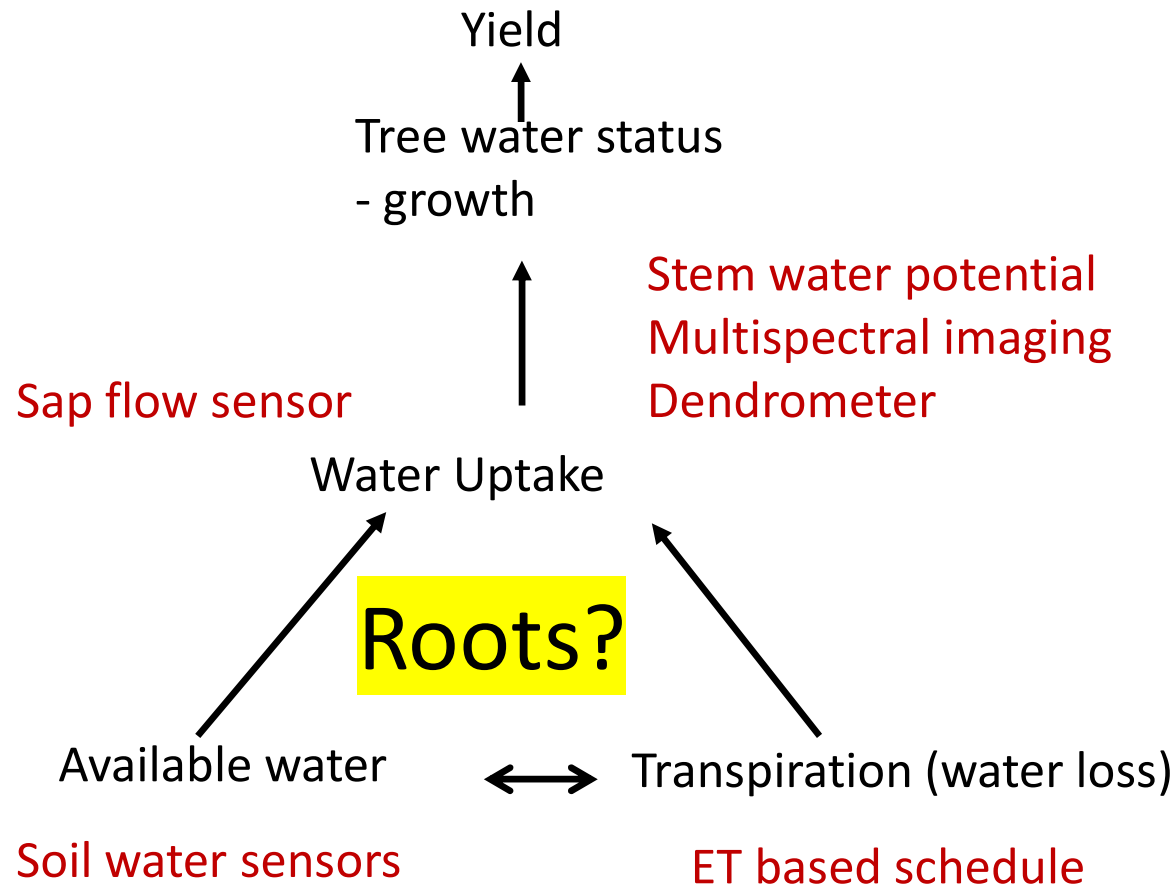
Fine roots are similar to leaves in that they occupy a space briefly but are collectively responsible for providing vital resources (water and nutrients) to the plant.

This presentation will describe the spatial and temporal dynamics of root growth as affected by orchard management practices such as irrigation and pruning.

Do roots matter when irrigating?



Yes – they are the entry point for both water and nutrients. If they are not there, extraction of water and nutrients cannot take place.



Ways to determine irrigation needs

More complicated than just "measuring around roots" — water can affect the health and water uptake ability of your roots

- **Water management challenge** how to ensure you have **active roots in the right place** for continued water and nutrient uptake







Yield

Tree water status &
carbohydrate availability for
growth

Canopy size/light interception

Water Uptake

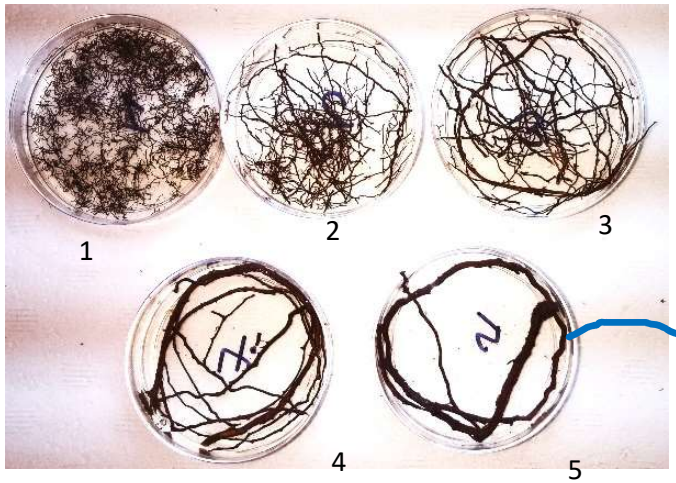
Fine root growth
and distribution
- Space
- Time

Available
water

Transpiration

We need to know more about (fine) root system growth and function!

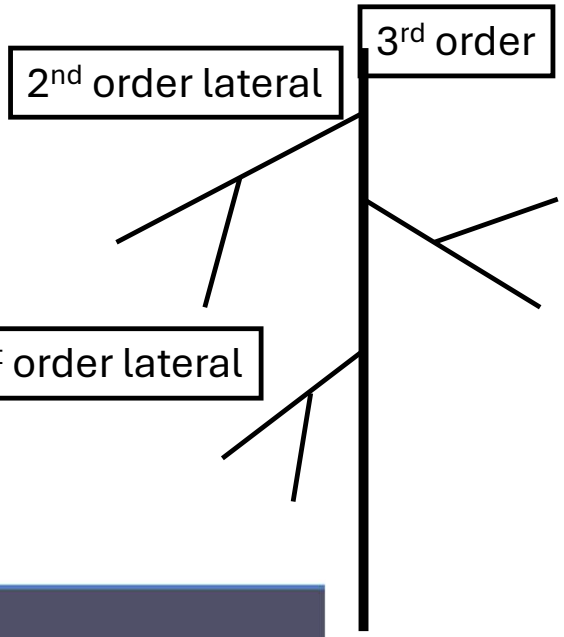
Fine absorptive roots

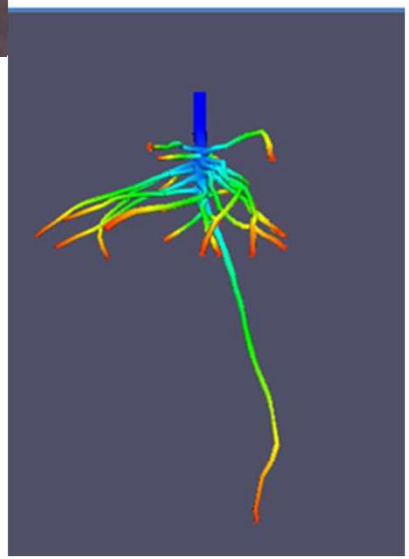


Functional classification



0.5 mm, 0.02 inch diameter



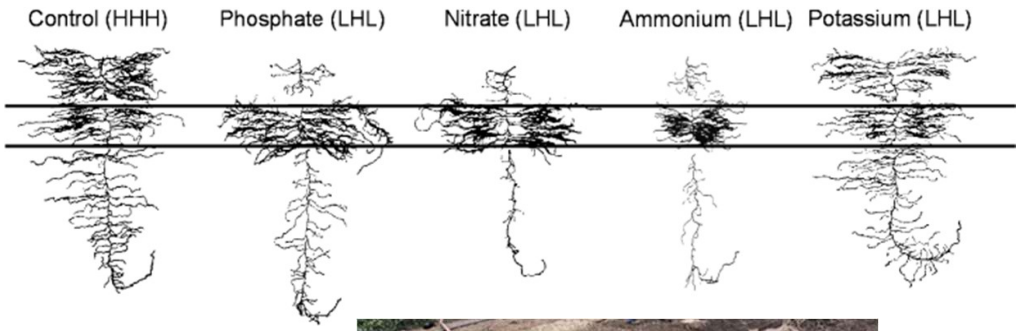


Tip (red) = youngest & most active water transporters

Most fine roots are not white! Fine roots turn brown within weeks, and live a few months

Thinking of roots short term versus long term

- Short term (fine root dynamics)
  - Water and nutrient uptake
  - Length extension and branching is very responsive to fluctuations in local environmental conditions
- Long term (scaffold root placement)
  - Tree stability
  - Long distance transport of water & nutrients -– provides "scaffolding" for fine root placement and soil exploration (depth, extent)
  - Responsive to climate, site management (e.g., soil characteristics, irrigation depth, young tree training/pruning, propagation)





Root – soil interactions in perennial systems

- There are some predictable seasonal & diurnal gradients that affect root growth & function
  - Light – daily total & distribution affects phenology (availability of carbohydrates from canopy) is seasonal
  - Temperature
    - Seasonal patterns – AND - reverse temperature gradient with soil depth winter vs summer
    - Diurnal patterns – greater fluctuations in topsoil temperature, stable deeper in the soil
  - Rainfall (wet winter/dry summer in a Mediterranean climate)
- Interactions with soil parameters (depth, texture, structure, toxicity)
- Understanding the impacts of these gradients and interactions will help manage root systems for optimal performance

Towards a model of orchard management that takes roots into account

- What do we need to know?
  - Factors that affect long term structural root placement – "scaffolding" for fine root placement
  - Factors that affect short term fine root dynamics – responsible for water & nutrient uptake
- Starting *assumption* for building a model:

  "Root systems will maintain optimal distribution of absorptive surface area to maximize uptake of water & nutrients"

  Optimal distribution of permanent roots for long term water uptake and transport is different from opportunistic short-term response to availability of water & nutrients in the topsoil

  We should manage the young tree root system to develop a structural root system that ensures long-term viability and productivity of the whole tree

Some "simple" things we need to know to make a good model

- When are roots produced (fine root phenology)? And, when do they die?
- How does water, nutrient, temperature, soil texture/structure affect root phenology?
  - And spatial distribution (long term)
  - And function?
- What root traits do the "best" rootstocks have in common?
- What factors decide whether a root dies or becomes a long term (structural) root?

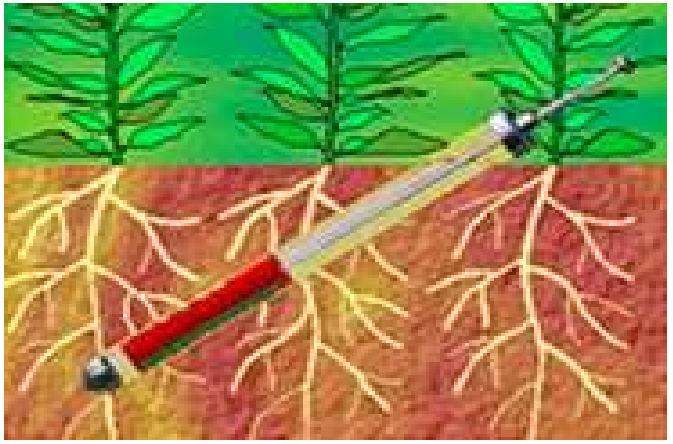




Phenology

- Minirhizotron method
- Allows for measurements of production and mortality
- Images collected at 1-3 week intervals
- Great at capturing temporal dynamics of fine roots in one location











Roots are born white, but turn brown as walls of external cells become suberized and water impermeable.

Roots have to continually explore new soil volumes to extract water and nutrients.

Most first order roots have a finite length growth and then die – measured in weeks, not years!

Exploratory roots have indefinite growth and give rise to new lateral roots. They function to explore new soil volumes and are part of the transportation infrastructure to move water and nutrients to the shoot

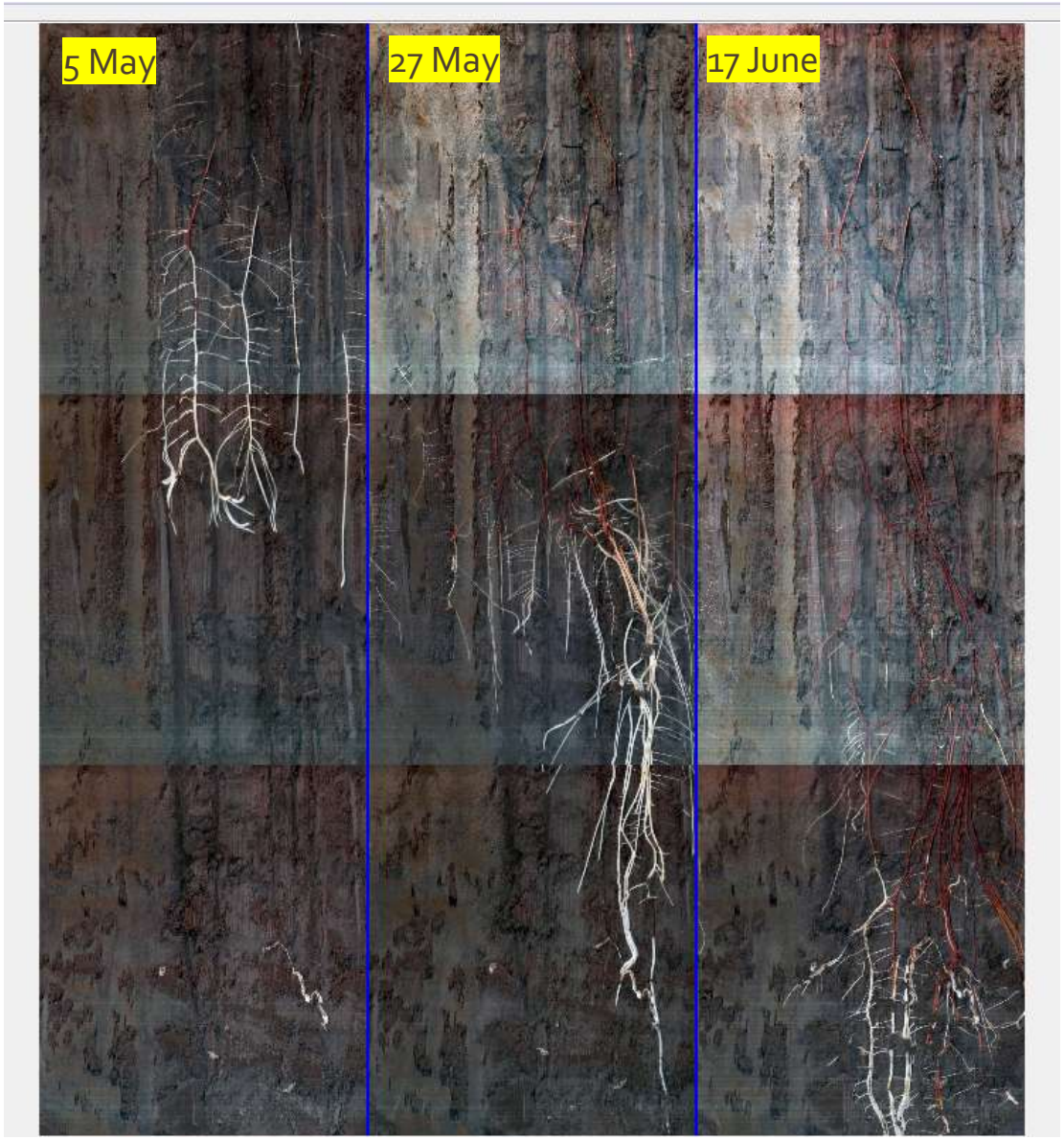
One week interval

- fine laterals appear and disappear
- higher order root turns brown

0-20 cm

20-40 cm

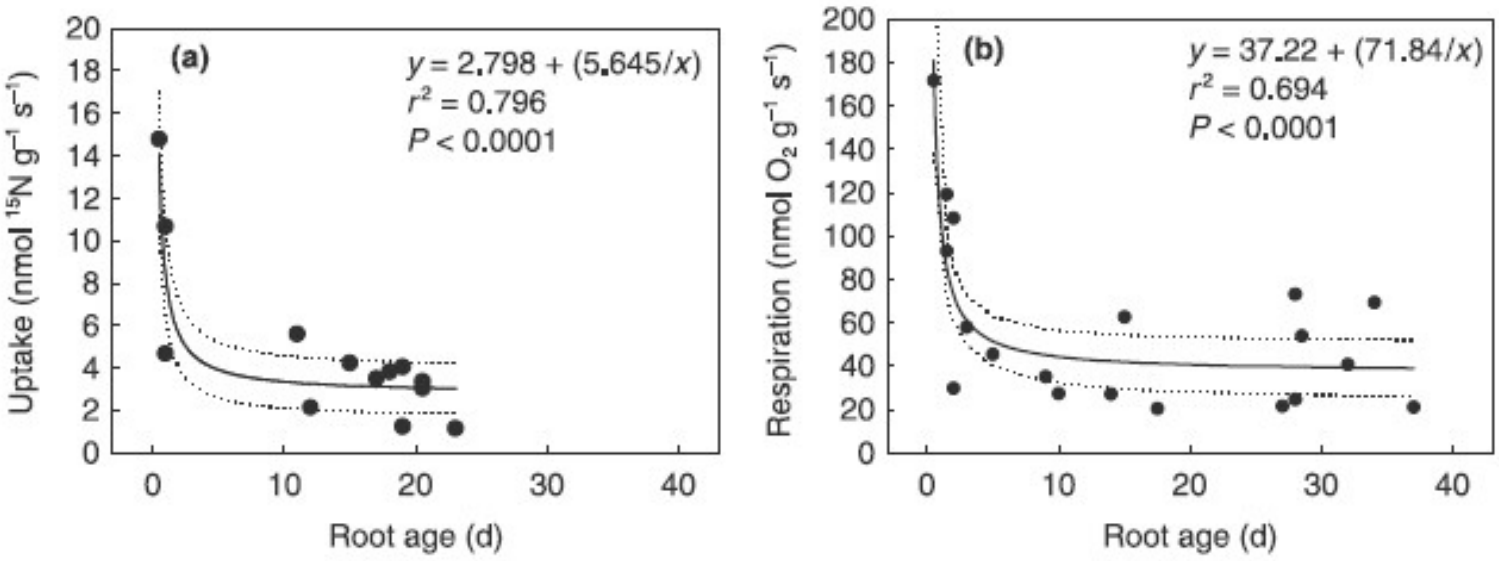
40-60 cm



Why is it important to keep making new roots?

Benefit (N uptake)

Cost (respiration)

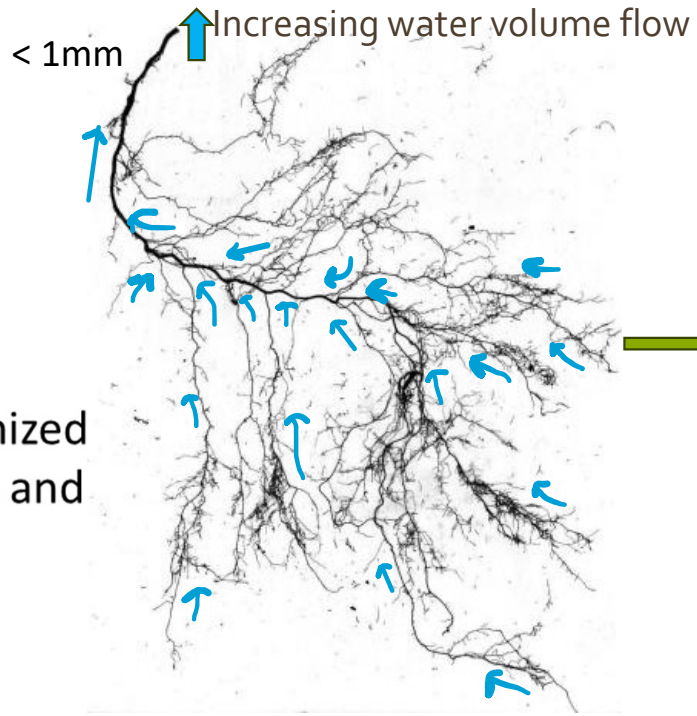


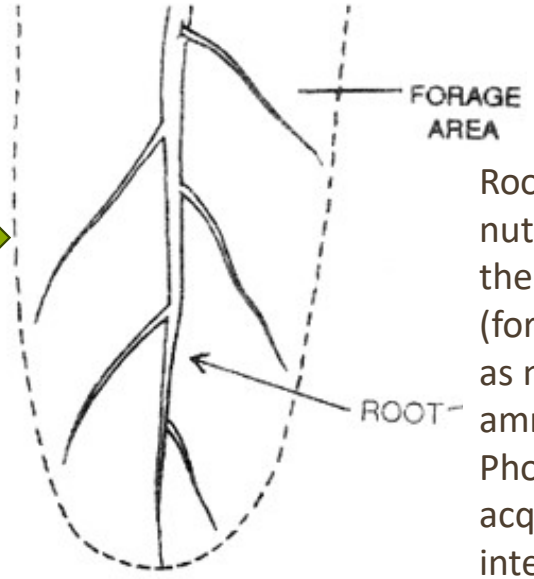


- Nitrate uptake capacity declines rapidly as the root ages (days!)
- It requires generating new roots to take up new nutrients
- Why this decline in capacity?

Nutrient depletion zones

- Roots have a zone of influence where the nutrients are extracted and depleted within days – akin to mining
- Formation of nutrient depletion zones requires <u>new root growth for soil exploration</u>





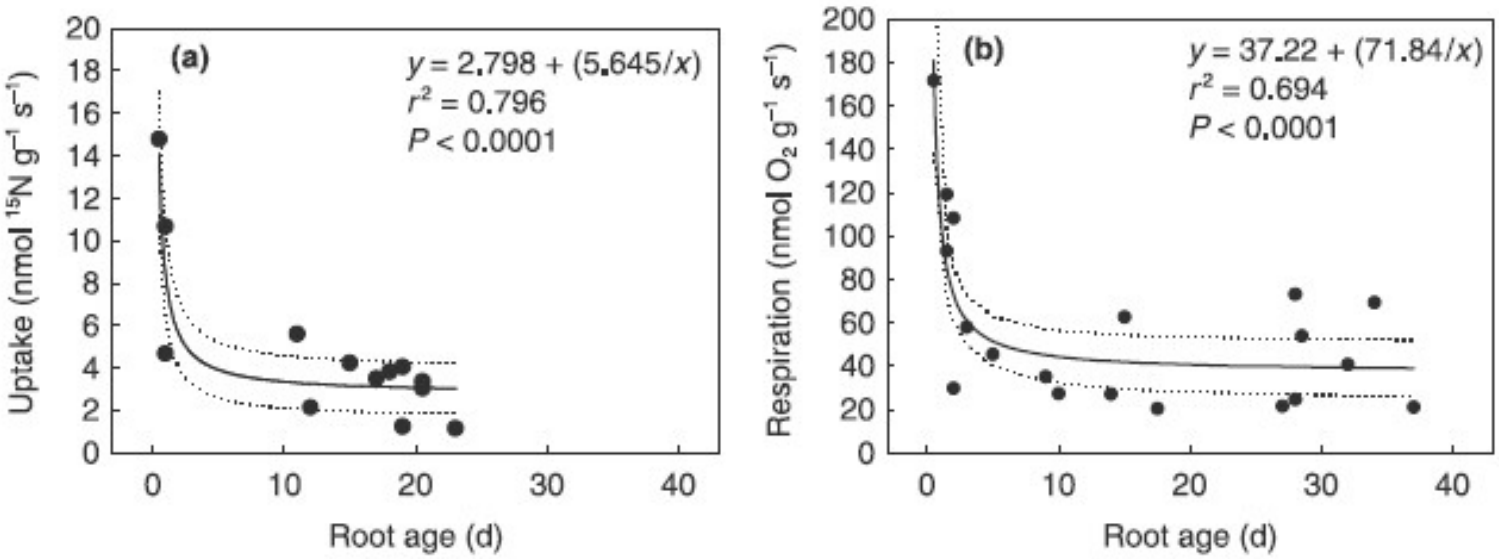
Root systems are optimized for efficient acquisition and transport of water and nutrients

Root acquires all nutrients available to the root via diffusion (for mobile ions such as nitrate or ammonium). Phosphorus is acquired by direct interception. The zone is then depleted

You might think that depletion zones don't form when you fertigate multiple times per day…….but that does not matter

Benefit (N uptake)

Cost (respiration)

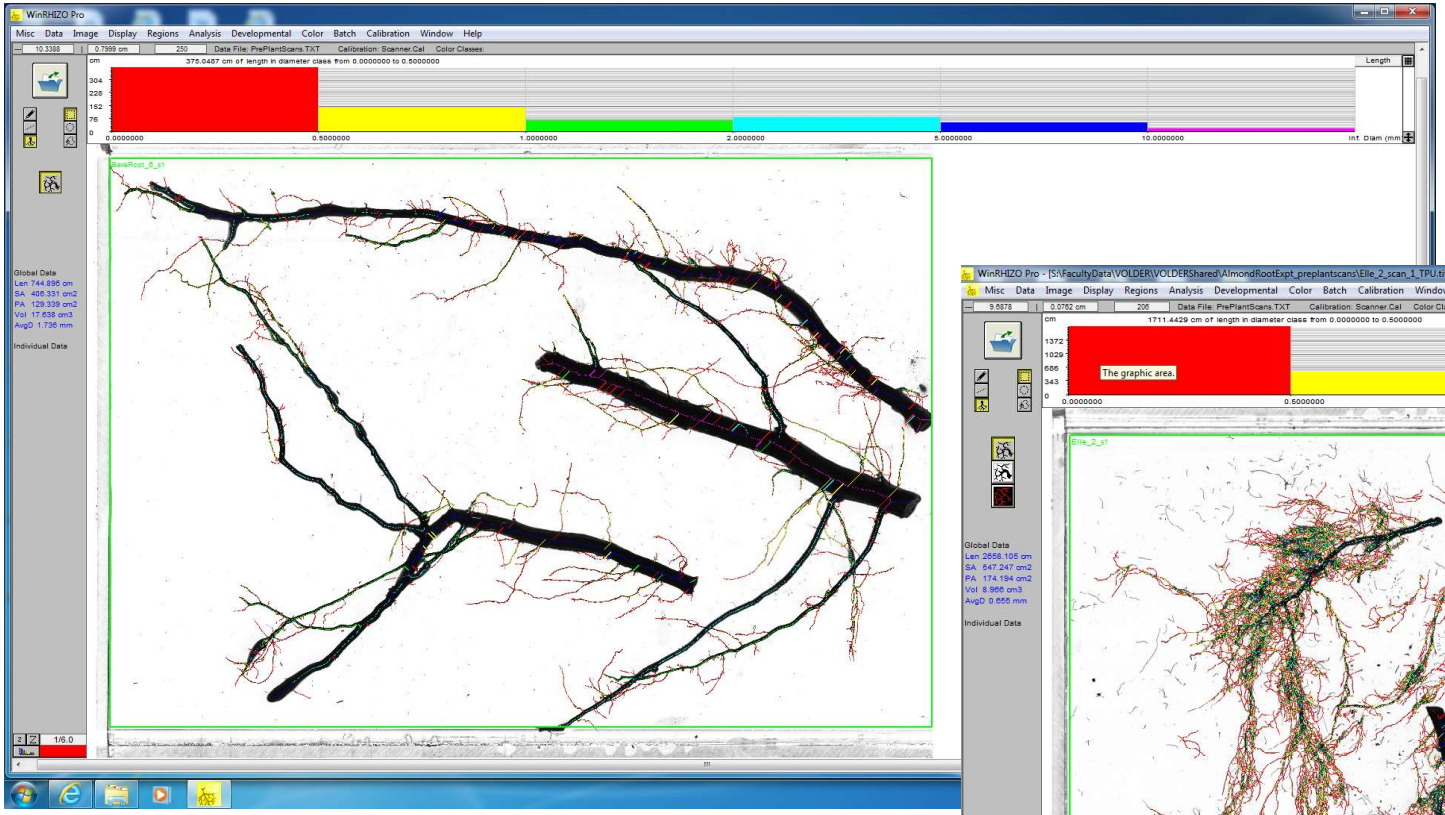


- Nitrate uptake **capacity** declines rapidly as the root ages (days!) even when exposed to high nutrient concentrations
- In nature, it would be an evolutionary disadvantage to maintain high uptake capacity with associated high respiration as nutrients are not replenished on a daily basis
- Thus it requires generating new root to take up new nutrients

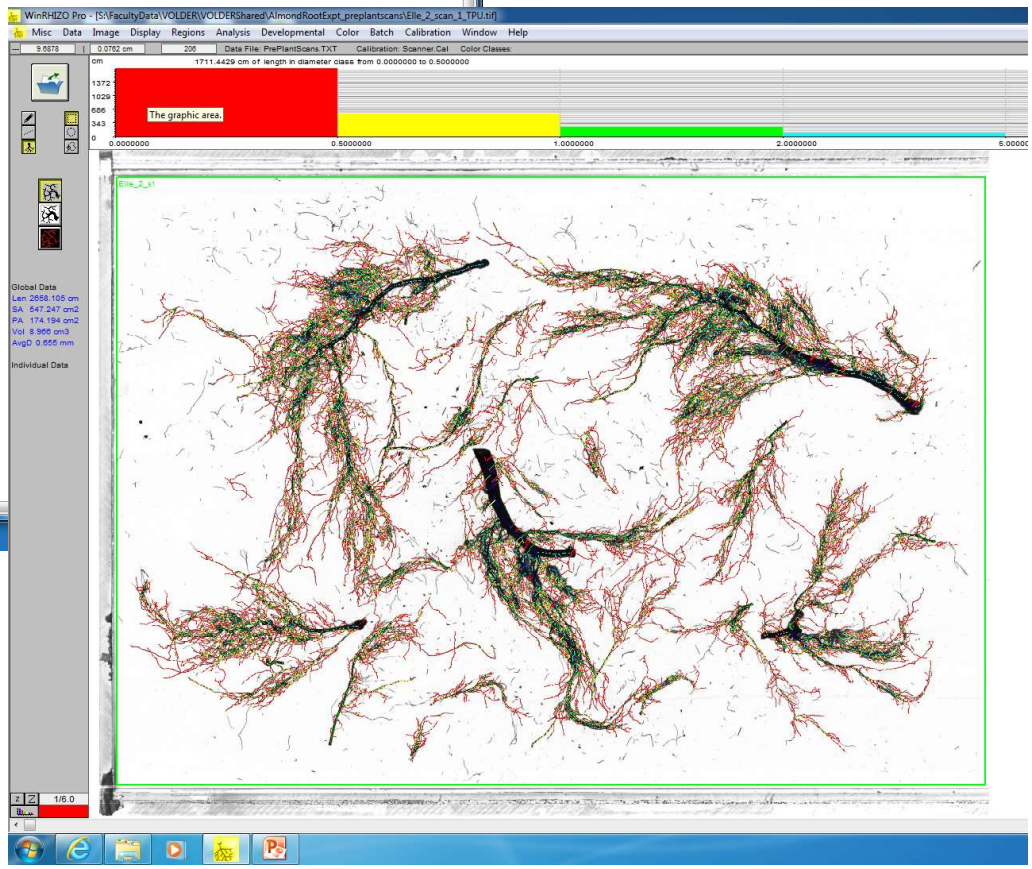




Comparing production patterns of bare root versus pot grown trees



Bare root
Red = 380 cm in 0-0.5 diameter class

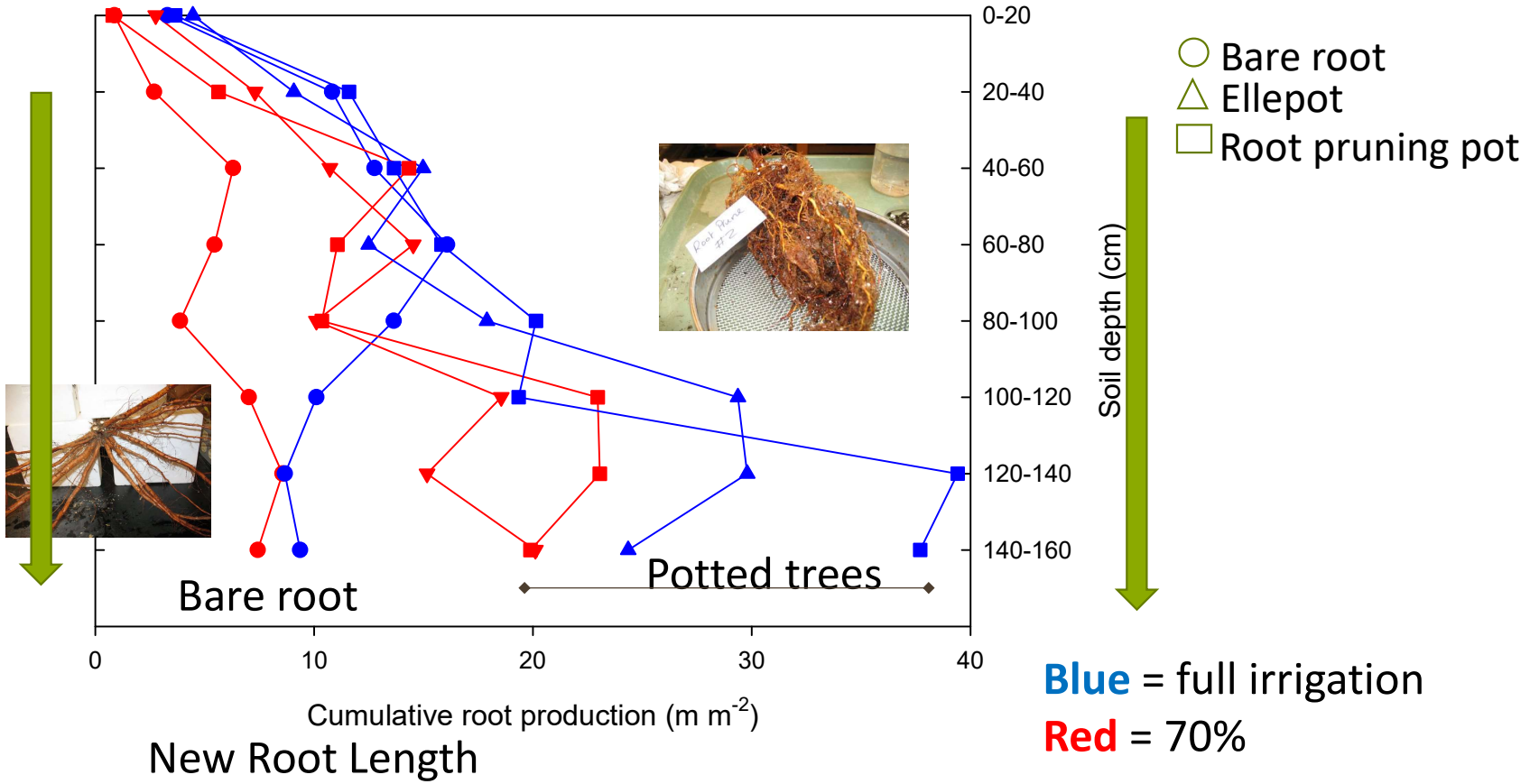


Pot grown
Red = 1711 cm in 0-0.5 mm diameter class

Bare root versus pot grown root systems – both Krymsk 86.

Cumulative fine root length production after two years

- shallow roots of potted trees responded less negative to reducing irrigation than bare root trees
- potted trees produced much more root length at depth than bare root trees



New Root Length

Stem area increase (cm^2) from Feb 2015 to April 2019

			Area increase (cm2) <u>full irrigation</u>		**Area increase (cm2) <u>70% irrigation</u>**	
Scion	Pot type	Initial area (cm2)	Unpruned	Pruned	Unpruned	Pruned
Nonpareil	Bare root	2.12	130.4	117.4 **- 10%**	128.1	109.4 **- 15%**
	RP pot	0.26	124.5	105.2 **- 15%**	117.9	96.41 **- 18%**
	Ellepot	0.23	132.4	109.3 **- 17%**	112.6	95.38 **- 15%**

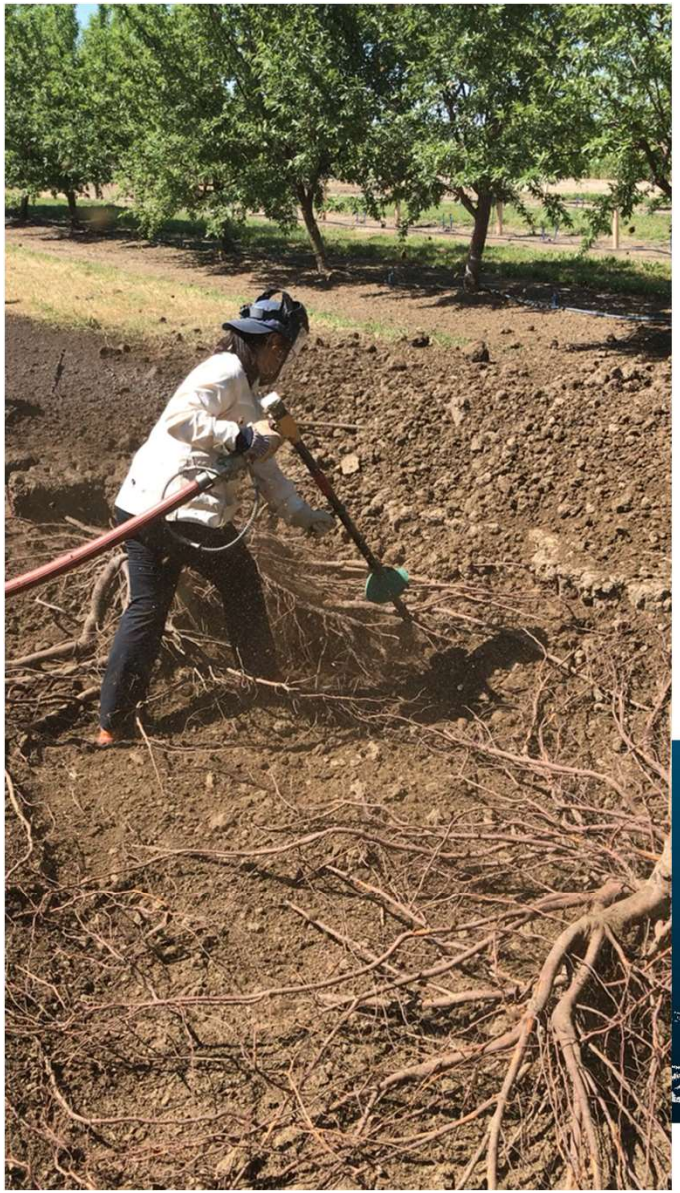
Average effect of pruning in the first three years: -15% stem area increase

Reducing irrigation led to average 8.5% decrease in stem area after 4 years vs 15% decrease from pruning

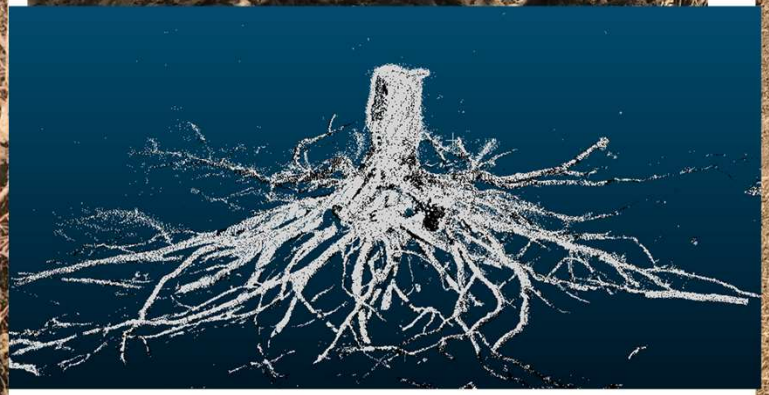
			Area increase (cm2) <u>full irrigation</u>		**Area increase (cm2) <u>70% irrigation</u>**	
Scion	Pot type	Initial area (cm2)	Unpruned	Pruned	Unpruned	Pruned
Nonpareil	Bare root	2.12	130.4	117.4	128.1 **- 2%**	109.4 **- 7%**
	RP pot	0.26	124.5	105.2	117.9 **- 6%**	96.41 **- 8%**
	Ellepot	0.23	132.4	109.3	112.6 **-15%**	95.38 **- 13%**

Average effect of pruning: -15%, Average effect of -30% irrigation: -8.5%
Unpruned Nonpareil bare root trees had least impact of reducing irrigation

Ellepot trees responded more negatively to reducing irrigation than those in the root pruning pot









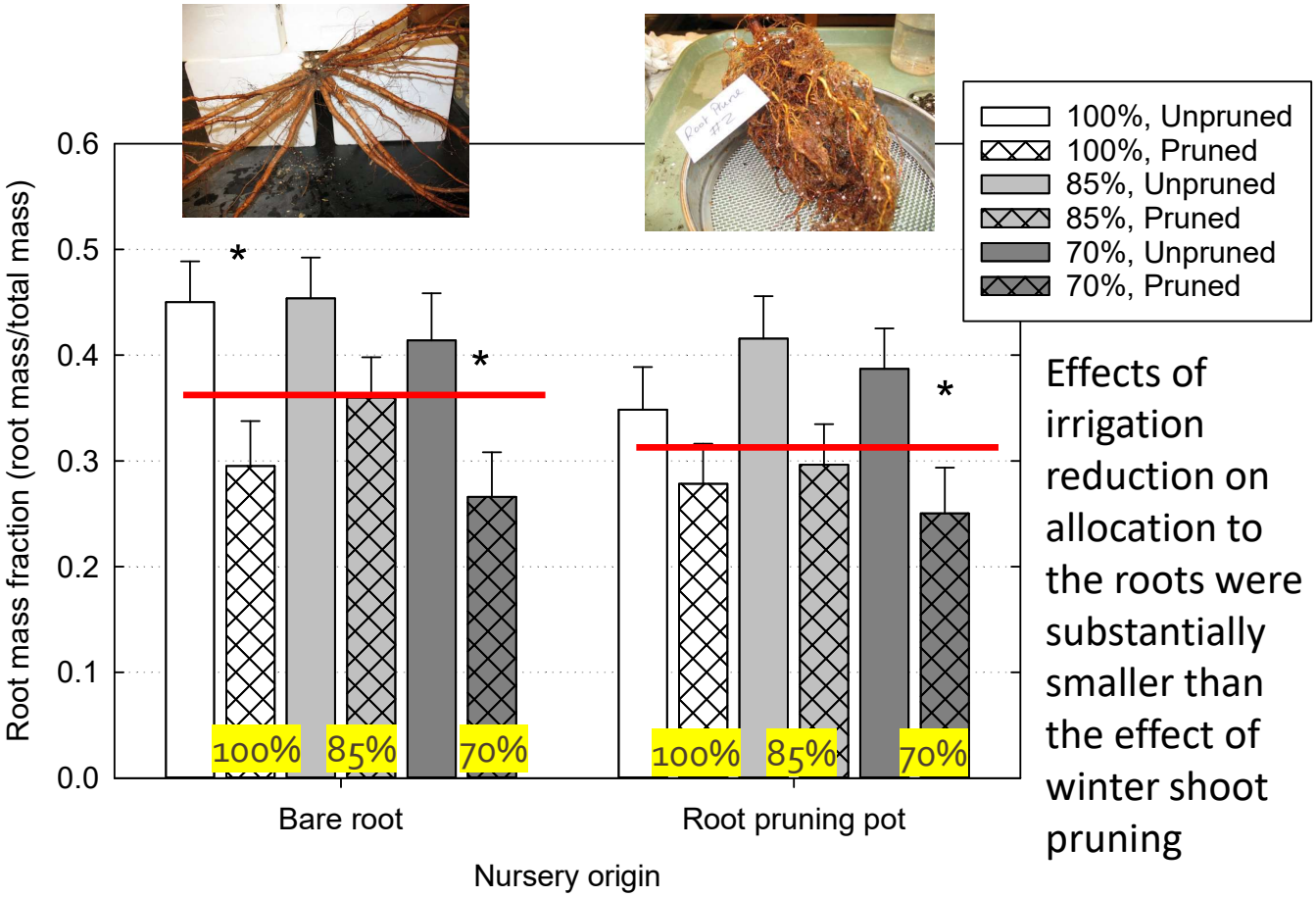
The roots were more negatively affected by winter pruning than the shoots

	Shoot mass (kg)	Root mass (kg)	Total mass (kg)	RMF
Unpruned	52.3	28.8	81.1	0.40
Pruned	36.0	17.5	53.4	0.30
	-31%	-39%	-34%	



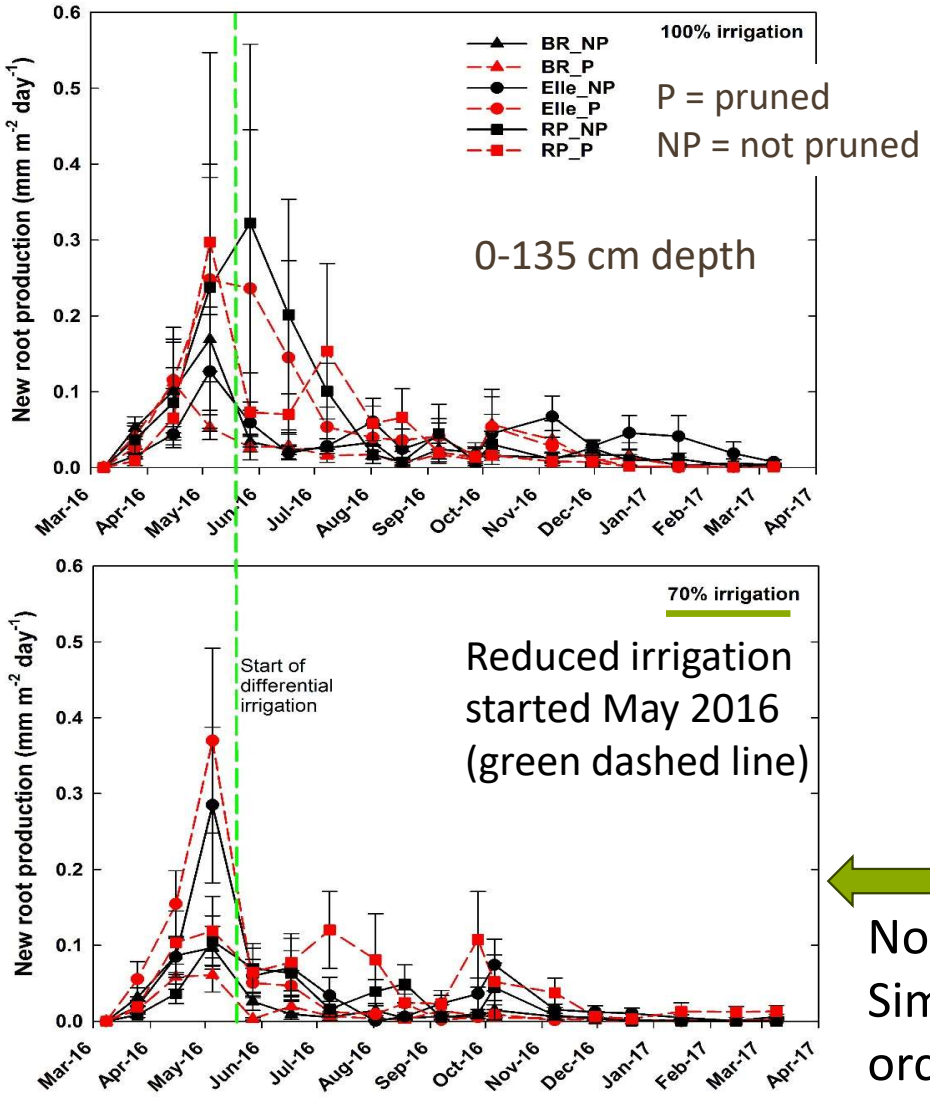
Pruning has a greater negative effect on root mass than shoot mass

Average effect of pruning on **stem area increase** from 2015 to 2019: -15%
Reducing irrigation by 30% : -8.5 %



Effects of irrigation reduction on allocation to the roots were substantially smaller than the effect of winter shoot pruning

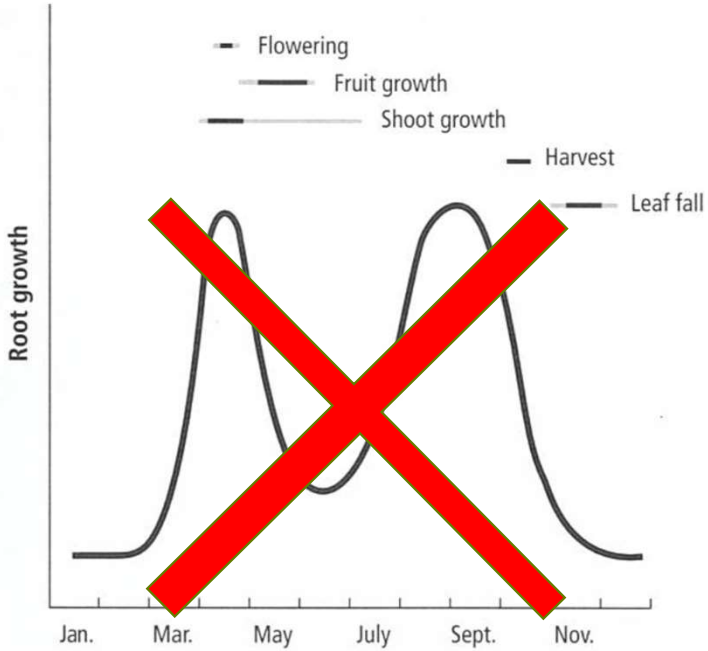
Nonpareil on Krymsk 86 rootstock, planted Feb 2015



P = pruned

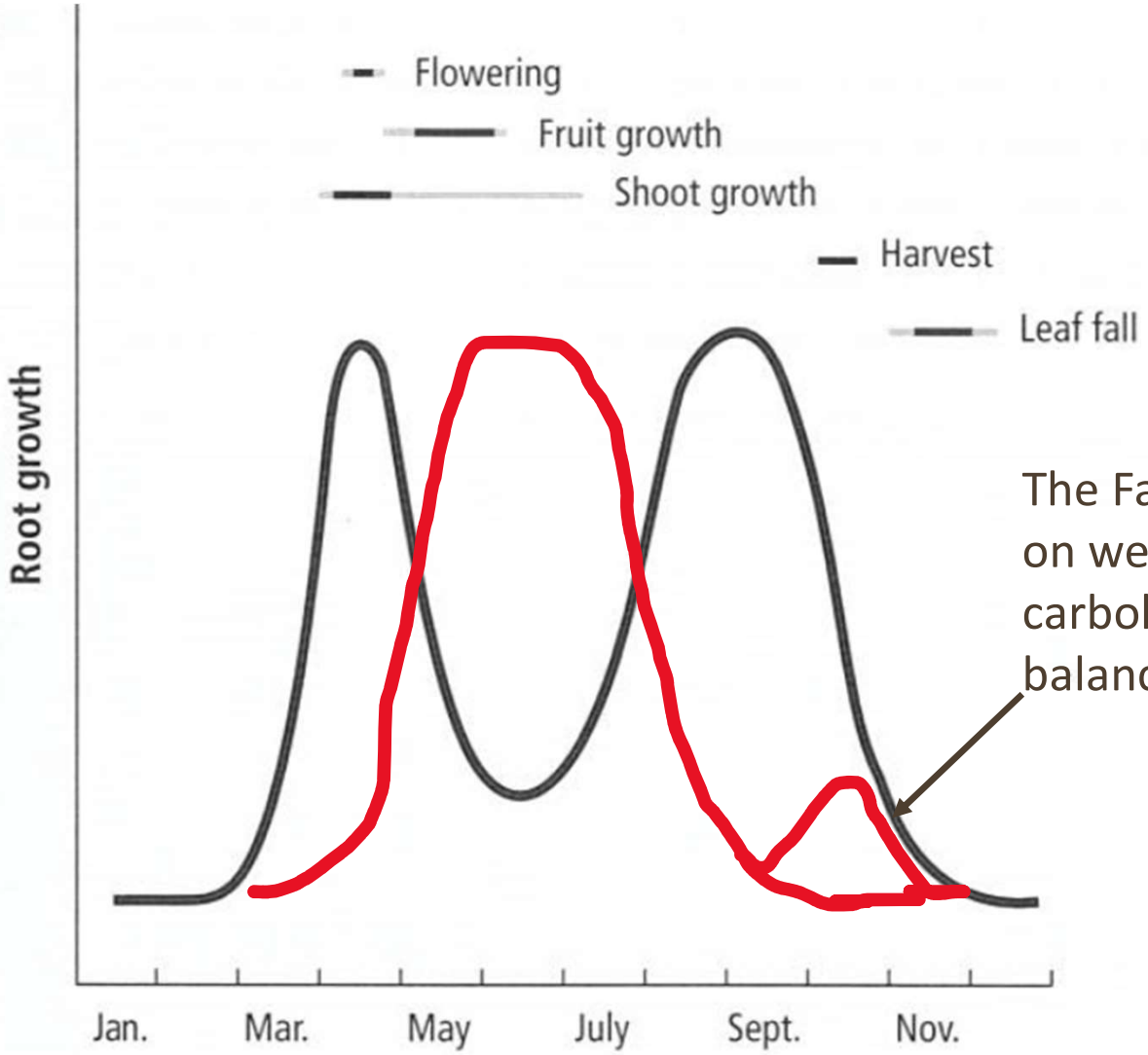
NP = not pruned

When are new fine roots produced?

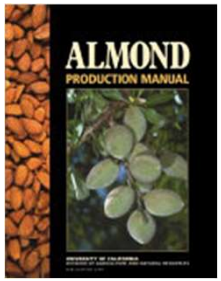


Note absence of Fall peak

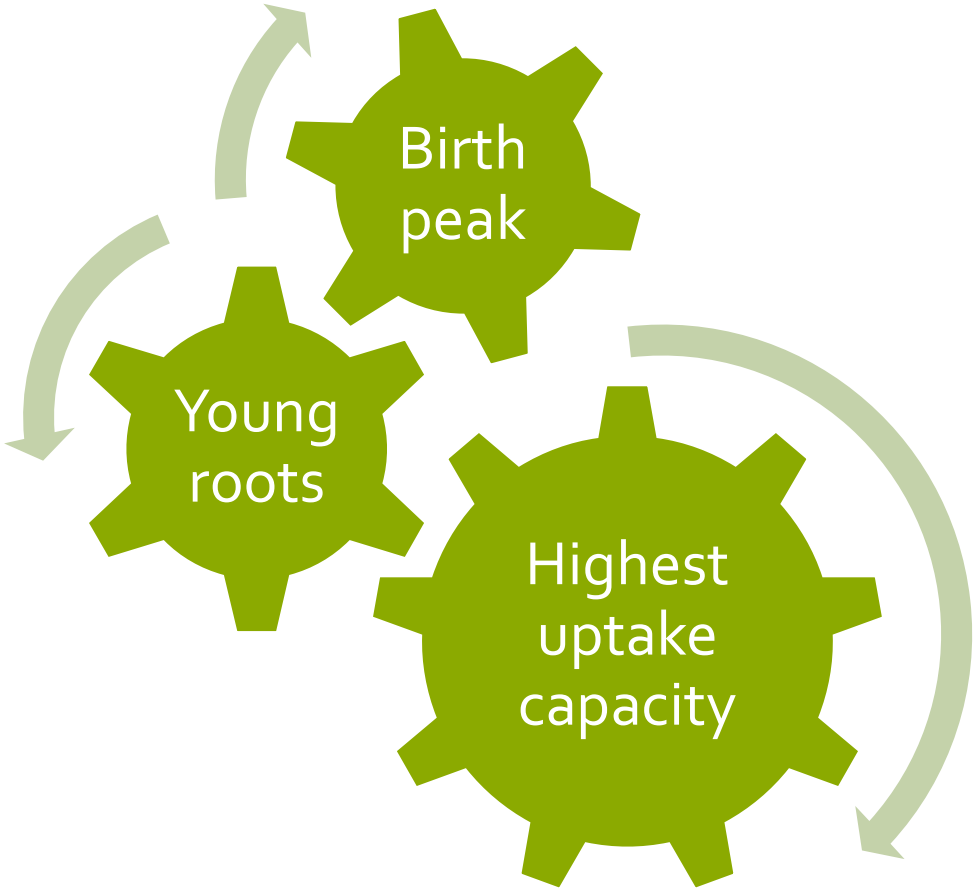
Similar patterns in multiple almond, walnut orchards (CA), as well as pecan (TX)



The Fall root flush depends on weather and carbohydrate reserve balance in the tree.

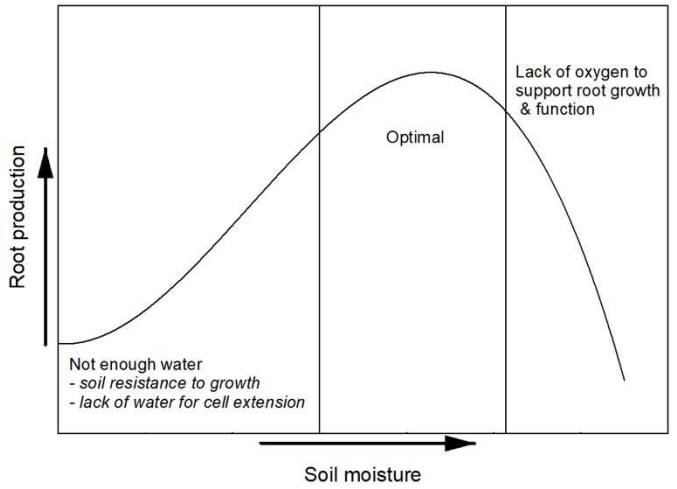


When should you fertilize?



How does water availability affect root depth distribution?

- Accidental discoveries of >70 m (> 200 ft) deep roots in wells and >20 m (>60 ft) roots in caves show enormous plasticity in rooting depth response to the environment
- Typical in deficit irrigation studies: more water applied annually –> deeper and more extensive root system
- Typical in flooding studies - keeping the top-soil close to field capacity –> more water leads smaller and more shallow root system
- Modified by soil characteristics (drainage rate, oxygen availability), Timing of water applications



Roots “chase” deep water

Accidental discoveries of >70 m (> 200 ft) deep roots in wells and >20 m (>60 ft) roots in caves show enormous plasticity in rooting depth response to the environment

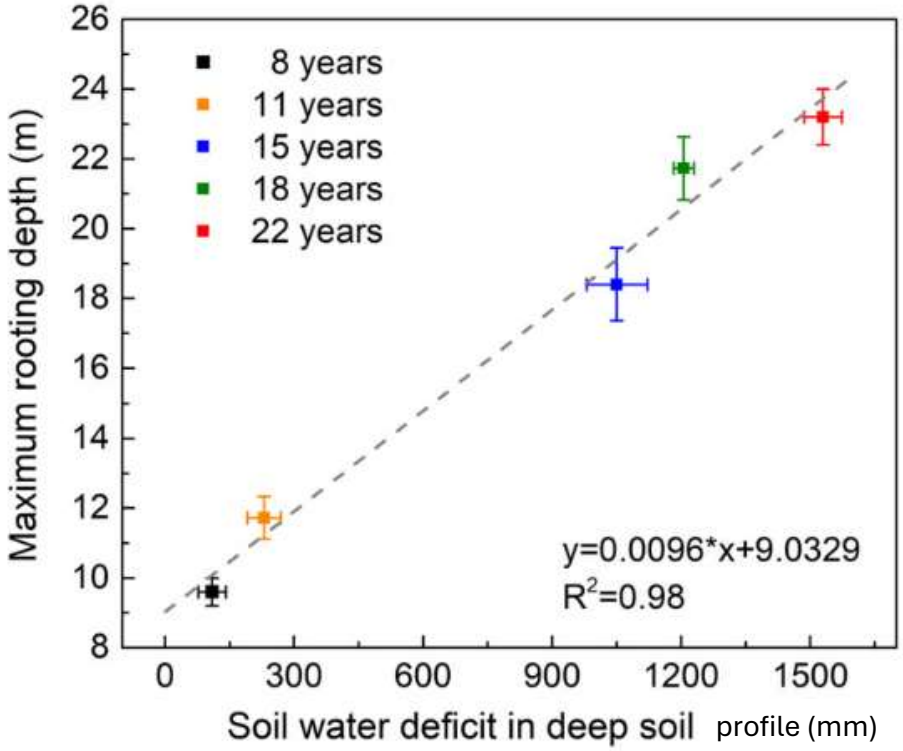


FIGURE 5 The relationship between soil water deficit in deep soil (below 1 m) and maximum rooting depth of fine roots (diameter <2 mm)

(Loess = excessively drained)

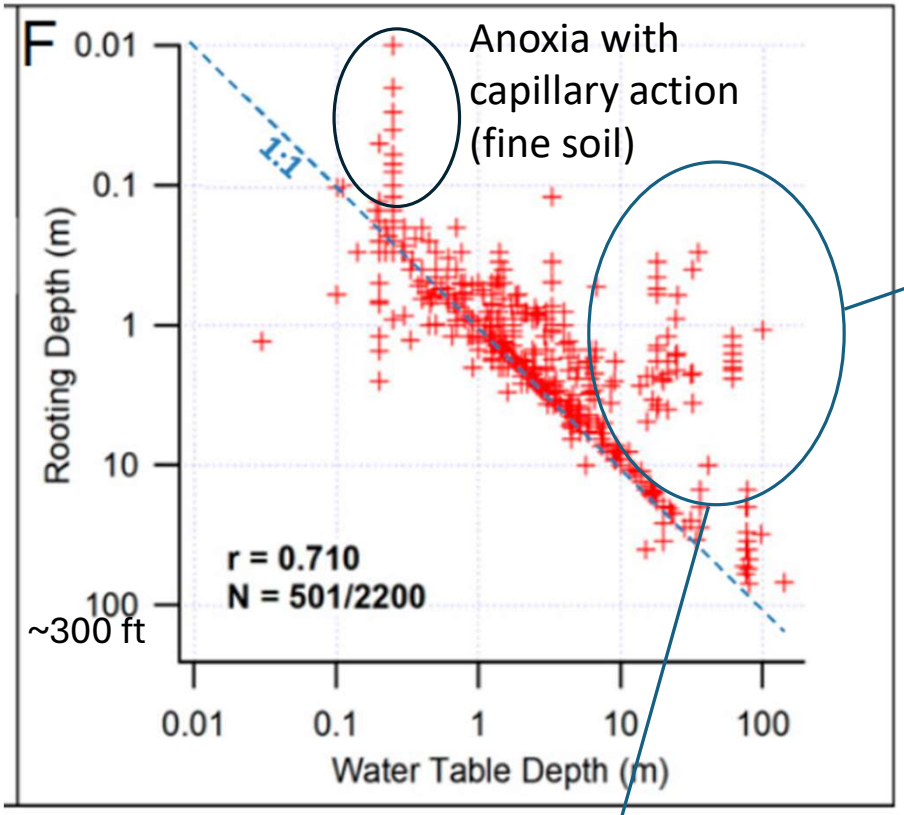
SCIENTIFIC BRIEFING

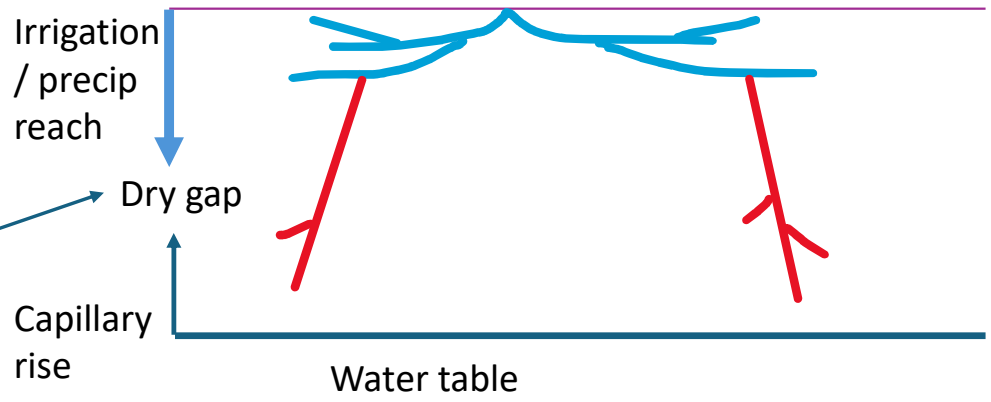
WILEY

Water mining from the deep critical zone by apple trees growing on loess

Huijie Li[1] | Bingcheng Si[1,2] | Pute Wu[1] | Jeffrey J. McDonnell[3,4]

As the soil profile is drying out as trees age (no irrigation applied), roots grow deeper





RESEARCH ARTICLE | ECOLOGY

Hydrologic regulation of plant rooting depth

Ying Fan, Gonzalo Miguez-Macho, Esteban G. Jobbágy, +1, and Carlos Otero-Casal Authors Info & Affiliations

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In natural systems, rooting depth is found to be limited by water table depth

Roots do not reach water table because either:
- Dry gap is too large / hard pan
- Topsoil remains too wet all year (frequent rain/irrigation)

How do we get roots to go deep?
- Allow the soil profile to dry in Spring
- Guide trees to grow deep roots when establishing

Why can’t we easily measure root depth?



Small portion of extreme vertical roots, deep anchoring – water uptake (would never hit with random soil coring)



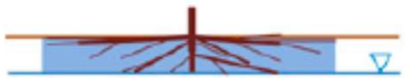
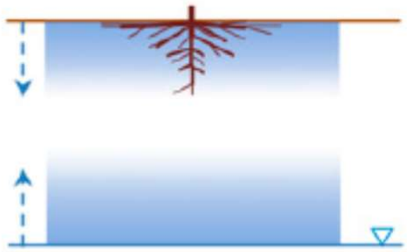
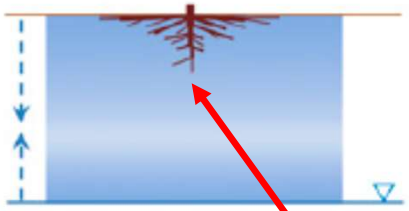
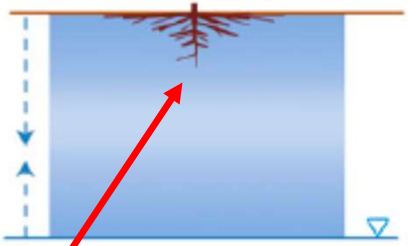

Hydrologic regulation of plant rooting depth

Mediterranean or

Infrequent large events

High rainfall spread across the year or

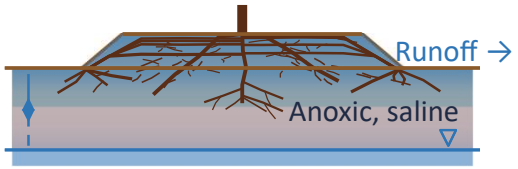
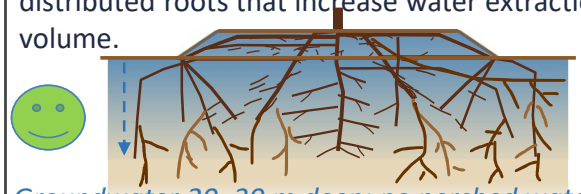
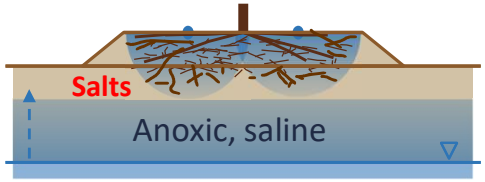
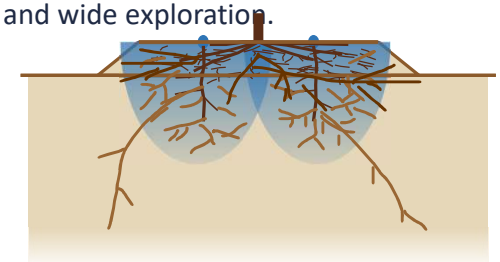
Frequent smaller events

Case-6: Roots shallow and wide, above water table  Anoxic	**Case-5:** Roots tap ground-water in dry season; dimorphic or deep roots 	**Case-4:** Roots follow deep wet-season infiltration 
Case-9: Roots shallow and wide; buttress, stilt, and other above-ground roots in lowland species  Anoxic	**Case-8:** Roots have no need to grow deeper; frequent and abundant top wetting 	**Case-7:** Roots have no need to grow deeper; frequent and abundant top wetting 
Valley Bottom, Poor Drainage	**Mid Slope, Good Drainage**	**Hill Top, Excellent Drainage**

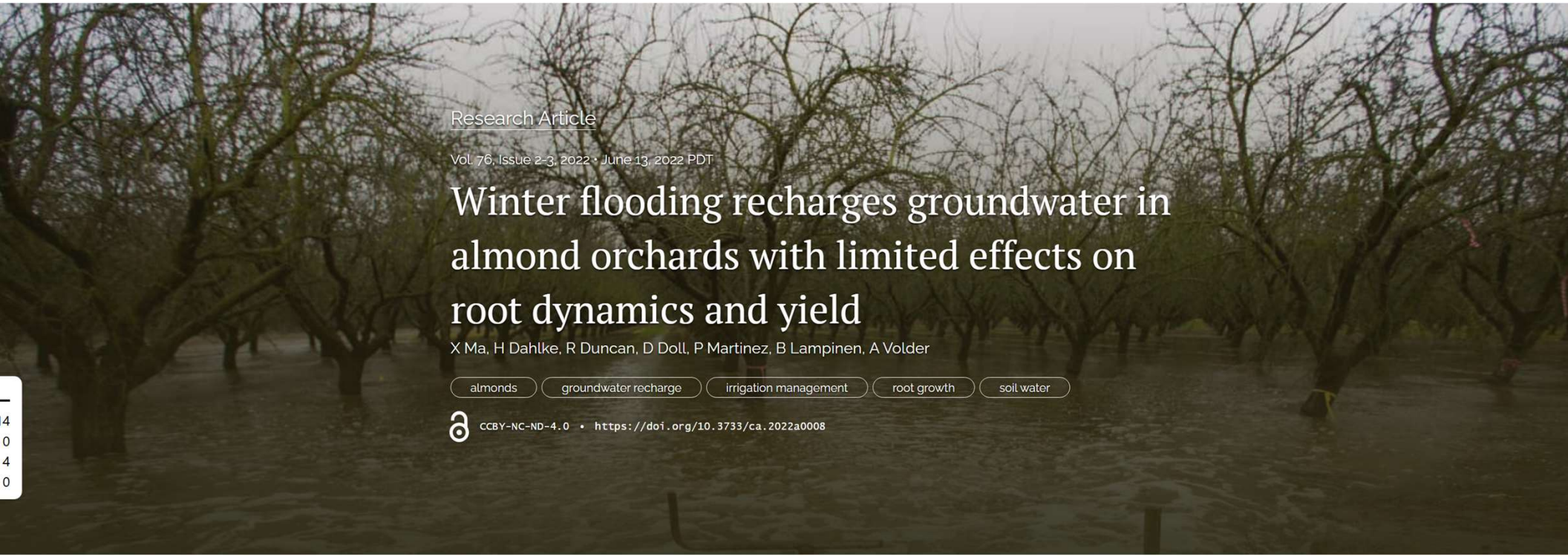
Left to Right is drainage gradient – from poor to excellent. The greater the drainage, the greater the potential dry gap.

Note the effect of frequent and abundant top wetting on root distribution

California (Brentwood, Davis & Delhi) — soil texture, water storage & water table; winter-dominant rainfall

	Fine texture (low drainage)	**Medium texture** (moderate drainage)	**Coarse texture** (excellent drainage)
	Delta margin, Brentwood (Contra Costa Co.): WT 1.5 m, saline shallow groundwater	*Davis (Yolo Co.): Deep soils, moderate to good drainage, high water storage*	*Delhi (Merced Co.): Delhi sand, rapid permeability; WT ≥ 40 ft (12 m)*
Few events, deep irrigation (flood, sprinkler)	Large events leaches salts, but water draining below the roots cannot move sideways fast so the water table rises and causes anoxic and saline conditions in the root zone. 	Roots follow the deep wetting front; the profile drains and re-aerates between events; deep, well-distributed roots that increase water extraction volume.  *Groundwater 20–30 m deep; no perched water table*	Shallow roots, a few may follow the deep wetting front down; water passing below them drains toward deep groundwater (nitrate leaching). Drought stress  *Drains toward water table ≥ 12 m (nitrate leaching)*
Frequent irrigation, drip	Irrigation reaches the capillary zone, leaving the subsoil anoxic; the berm keeps fine roots above the anoxic zone and daily irrigation leaches salts out of the berm and shallow root zone; salt builds at wetted-zone edges limiting root volume 	Berm with double-line drip; dense fine roots in the berm and wetted zones; conditions limit extensive deep and wide exploration.  *Groundwater 20–30 m deep; no perched water table*	Little storage, double-line drip; well-branched roots fill the narrow wetted columns; leaching below. Works if you have guaranteed water access  *Water table ≥ 40 ft (12 m); negligible capillary rise*
Practical	Berm and, drip or microsprinklers; short sets; tile drains **Rootstock tolerance needed:** Salinity, boron, waterlogging, hypoxia	Berm keeps crown dry in winter; fewer, longer sets possible **Rootstock tolerance needed:** Phytophthora / winter wet soils; drought between sets	Frequent, short sets (low storage); more emitters or lines **Rootstock tolerance needed:** Drought between sets

. After Fan et al. 2017, PNAS 114:10572.



No impact on root production, IF flooding takes place in late Jan (Winter), when trees are dormant. Only tested on soils with good to excellent drainage – below field capacity in 48 hours.

What happens when it is too wet – June 2017
Walnut – but link to Monterey failure story





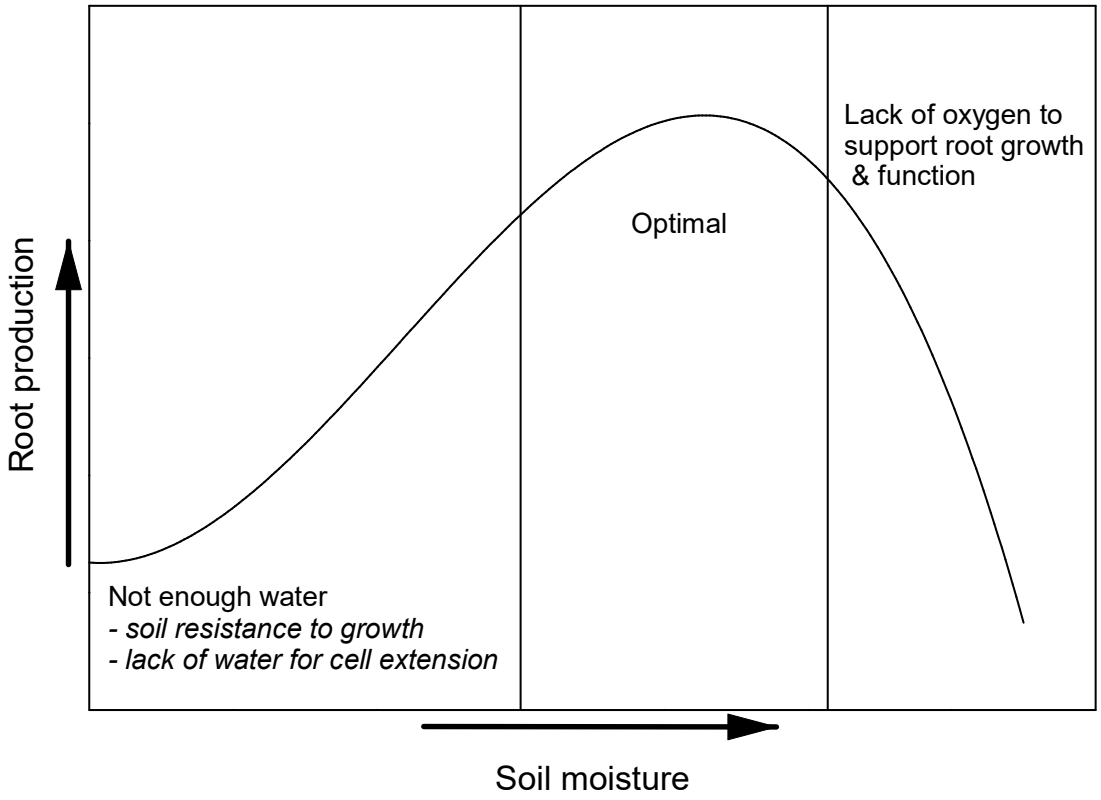
Standing water was only 50 cm below the soil surface – walnut trees not leafing out

Interactions between nutrient uptake, water, and rootstock-scion

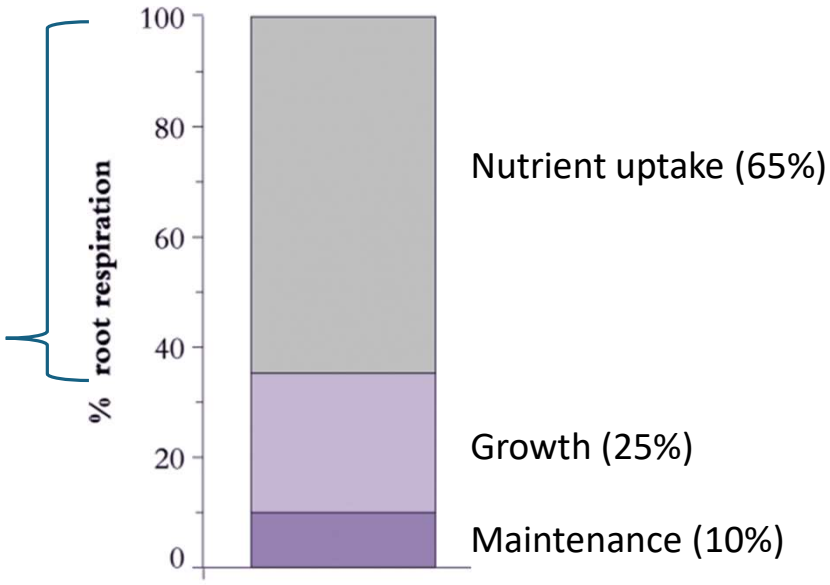
Low oxygen conditions lead to:

- Cellular respiration efficiency is reduced by 96% in the absence of oxygen
- Lack of respiratory energy stops new root growth & stops active nutrient uptake
- Reduced membrane permeability to water
  - Roots stop taking up water – stomates close - **drought symptoms** on shoot
  - Roots stop taking up nutrients – **nutrient deficiency symptoms** on shoot
- Prolonged conditions could cause carbohydrate starvation, reduced defense to herbivores/pathogens and root death





- A gradual negative effect on root production when soil moisture is below optimal, but a sharp decline in root production when the soil gets too wet
- The “optimum” depends on soil characteristics and tolerance of your rootstock
- Balance between enough water to reduce soil friction, support evapotranspiration, and still having enough oxygen to support root respiration for nutrient uptake and root growth



This is why anoxic conditions cause nutrient deficiency symptoms – but fertilizer is not the answer – getting oxygen to the roots (reducing water) is



Walnut



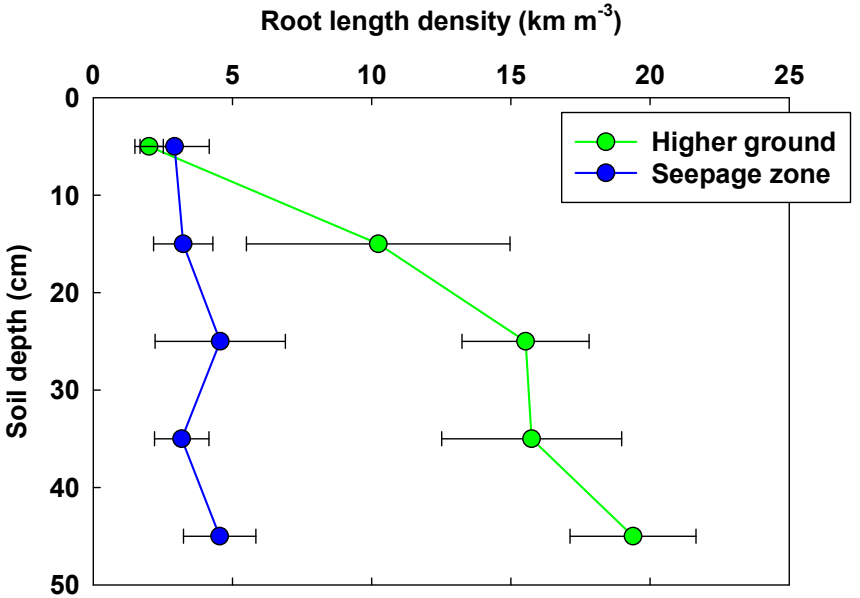
Trees located on higher ground (control)



Trees failing to push in the seepage zone



Chandler on RX1 (4th leaf) – soil cores collected on June 29, 2017 (early summer). Standing water at 50 cm (20”) soil depth.

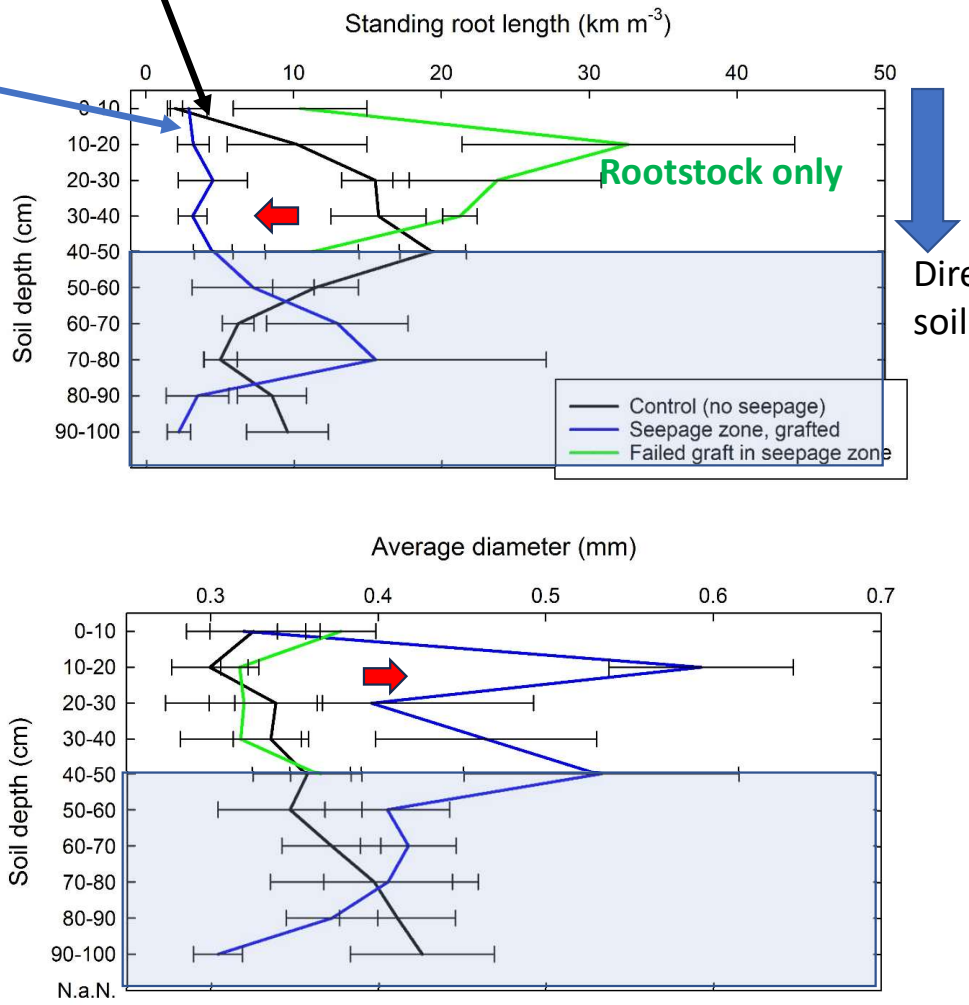


Standing water at ~50 cm – water moves up via capillary movement and lack of oxygen significantly reduces new root production in the top soil (except nearest the surface)

Graft survived

No recovery of fine root growth in top soil as soil dries

Grafted, never flooded



Direction of soil drying

Black line – grafted trees on higher ground

Blue line – grafted trees in seepage zone

Green line – rootstock only in seepage zone

Comparing the two sets of trees in the seepage zone (grafted, **blue**, versus rootstock only, **green**)

- Rootstock only trees had much greater standing root length and comparable root diameters to roots of grafted trees on higher ground. (**black** line)
- No new fine diameter roots were produced in the grafted trees in the seepage zone (**blue** line).

What could be happening?

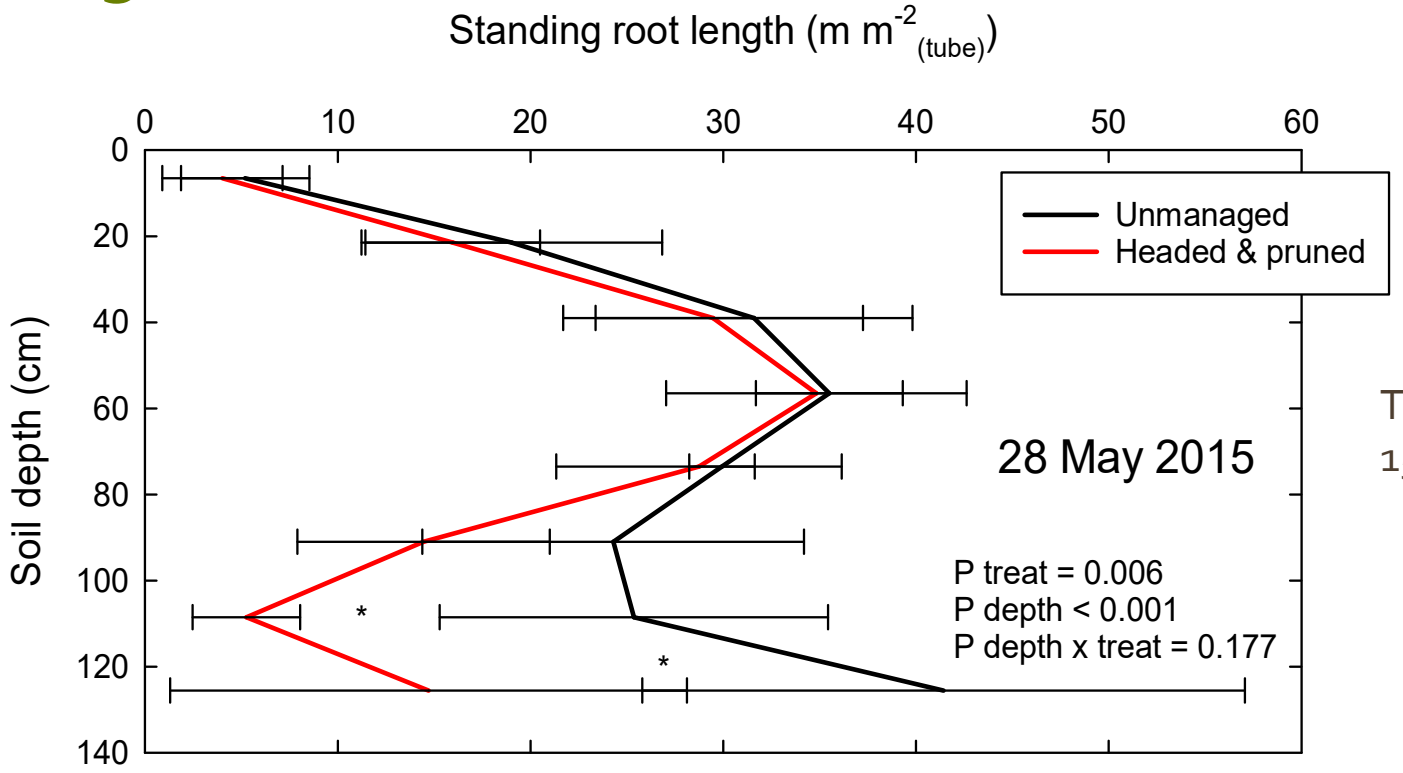
- Grafted trees did not fully push buds and had reduced standing root length, whereas rootstock only trees were able to recover from the flooded conditions as topsoil dried
- Hypothesis: Bud push failure is the result of impaired water delivery to the pushing buds of the grafted scion
  - New roots are necessary for sufficient water delivery to the buds to support full leaf out
  - Graft union restriction and/or greater scion vigor may prevent the necessary carbohydrate flow from storage to the roots that enables new root growth



Shoot management impacts on the roots

- Carbohydrate assimilation and transport to the roots is directly related to root production
  - Pruning, clipping, defoliation, all reduce leaf area available for photosynthesis → reduced assimilation
  - Environmental – light interception, temperature, soil water, humidity, wind (all affect photosynthesis through stomatal opening)
- Signaling (hormones, hydraulic, other signaling molecules)
  - Developmental stage
  - Environmental factors
  - Biotic interactions
  - Scion choice

Heading at planting reduced deep root production in the next 3 months

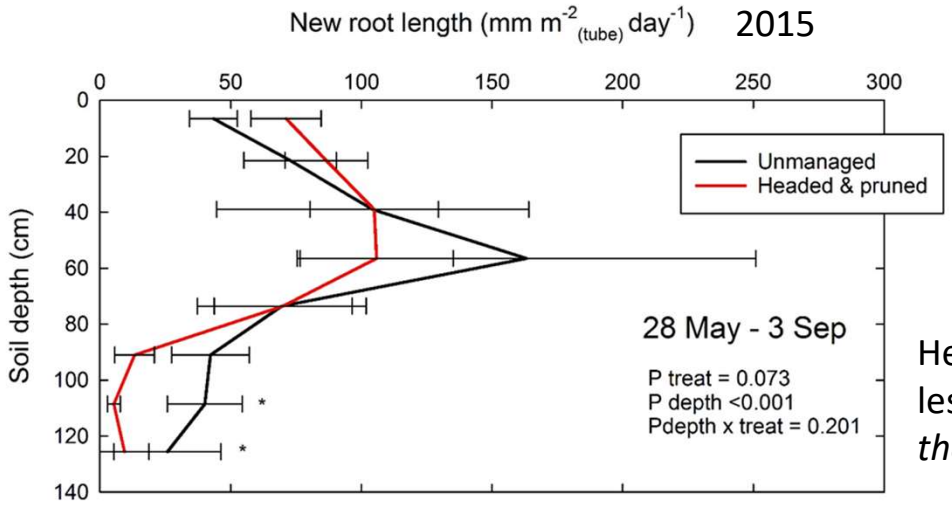


Trees were planted 15 Feb 2015

Those deep roots may be particularly important in non-irrigated or low irrigated planting sites – they may keep trees alive through the summer

Bare root trees

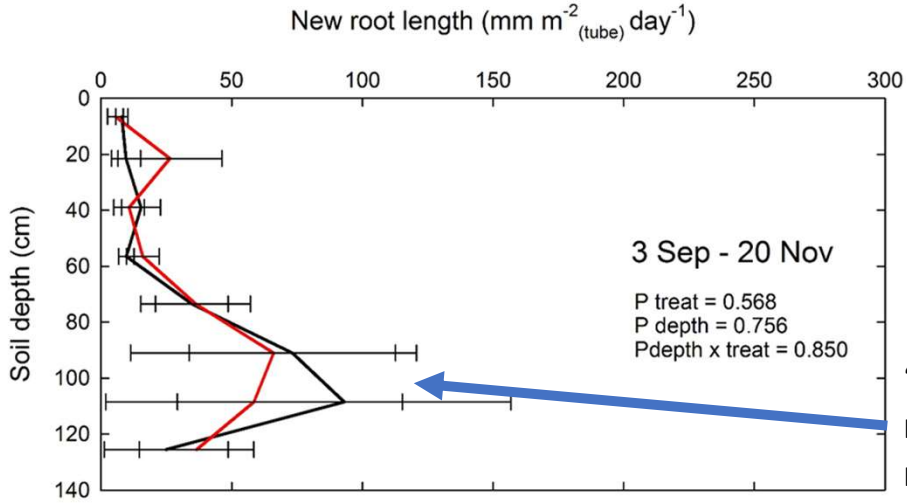
Summer



Red lines are headed and pruned at planting (Feb 2015)

Headed and pruned trees produced less roots over the summer, *mostly in the deeper soil layers*

Fall



"Bump" in Fall root production mostly deeper than 60 cm, not very relevant for nutrition

Investigations of large structural roots

Provide "framework" for dynamic fine root system

- Placement of absorptive surface area (temporal, spatial)
- Transport of water & nutrients from the most external fine roots via the structural root system to the leaves



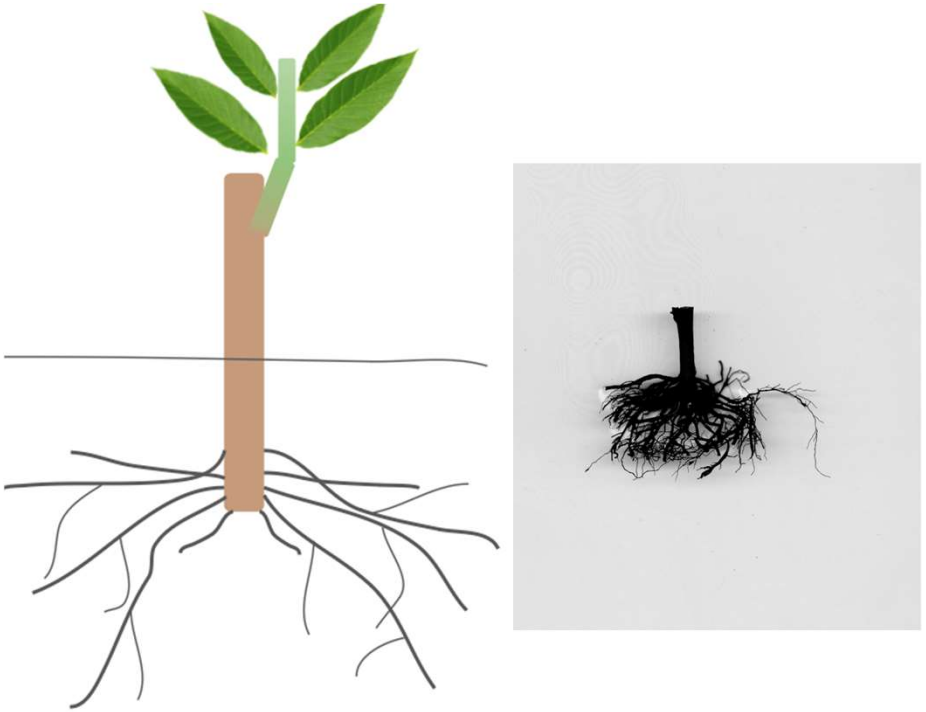




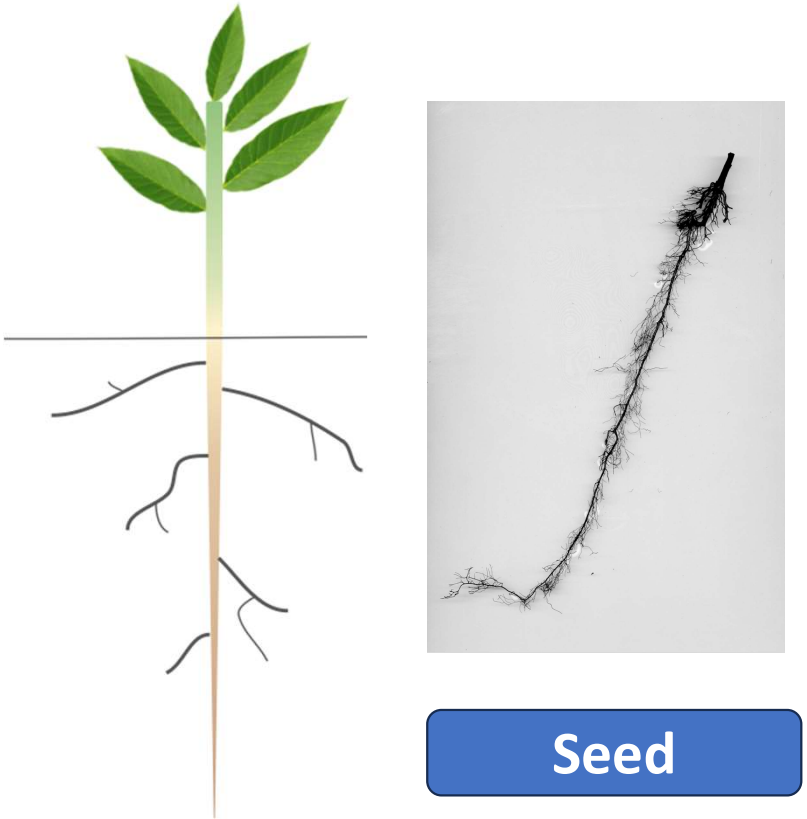



Upside down view

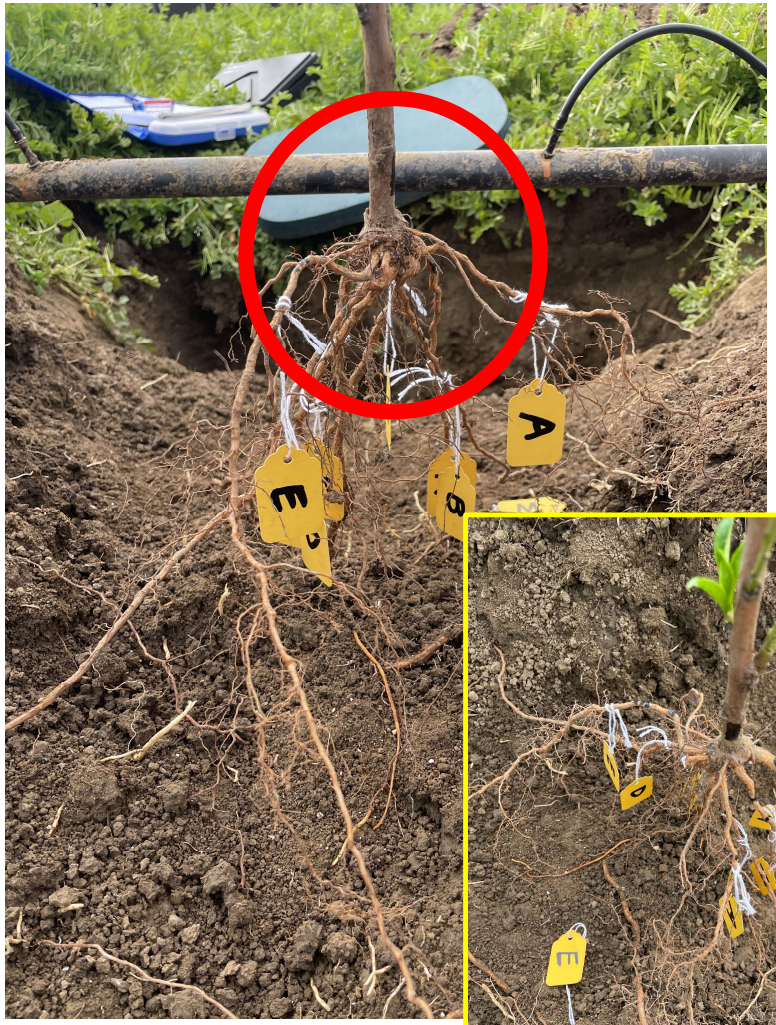
Clonal (cuttings) versus seed generated trees



Clonal



Seed



Clonal (Lovell)

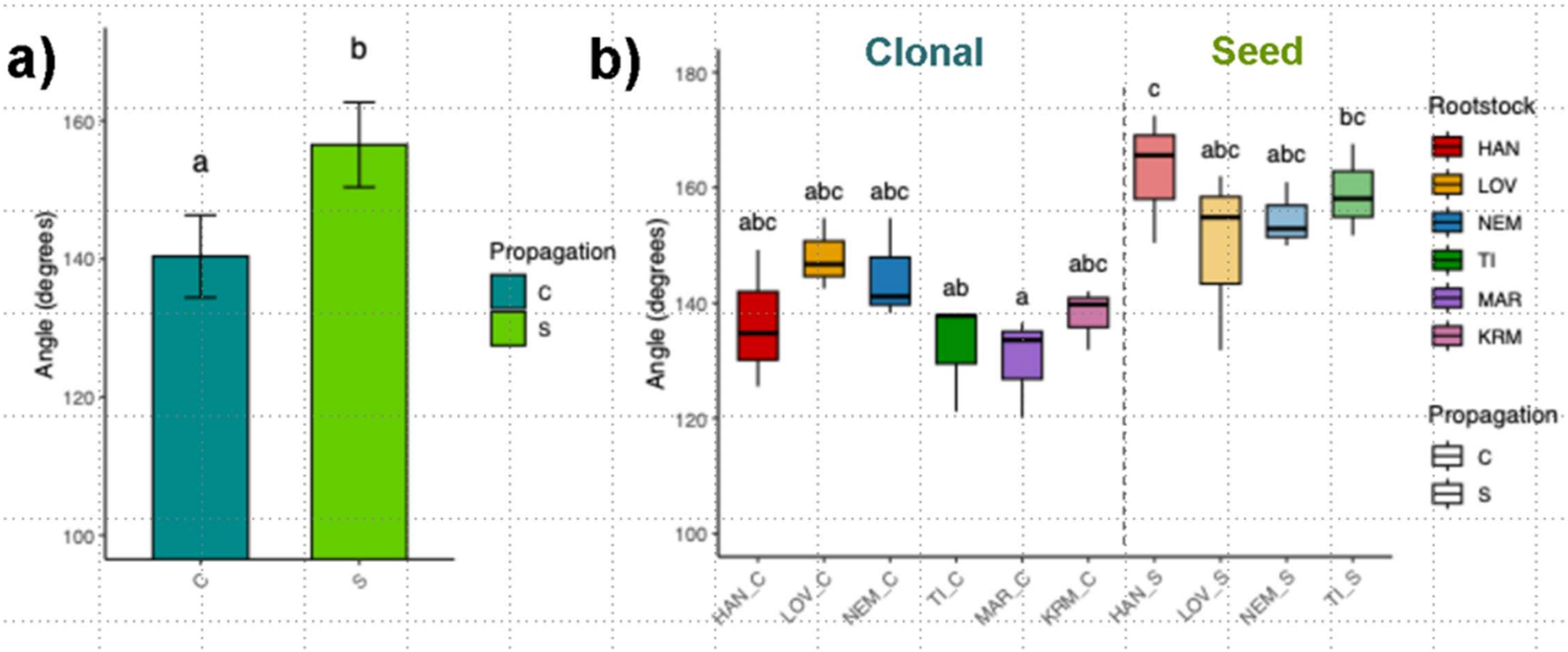


Seed (Lovell)



Planted in June 2024, extracted October 2024

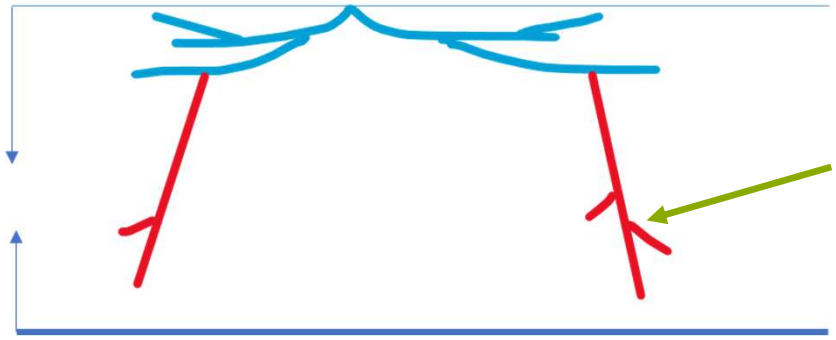
Seed generated trees had steeper scaffold root angles



= 180

In shallow soil you need roots to spread sideways, so clonal may be better.

Management of young trees for proper long term root development is key



Cannot have fine root production in zones where coarse roots have not developed – so, ***young trees must be encouraged to develop a deep and/or wide scaffold root system*** early



As with canopy structure, characteristics of the structural coarse root system are set early in tree development



Roots reached 1 m depth in October after planting in May

Summary

- Fine roots (< 0.5 mm) are responsible for water and nutrient uptake
- Produced throughout the year, with a large peak Spring - Mid Summer; if any, the Fall peak is much smaller
- Active fine roots are very sensitive to overwatering (low oxygen) as their activity requires high respiration rates
- Young tree management is key – properly developing the early root system will get the scaffold roots where they need to be (initial angle, spatial exploration) so that they can produce fine roots in the right place.
- Practices that affect scaffold and deep root growth include
  - Heavy pruning of young trees – reduces carbon allocation to (deep) root growth and reduces overall tree growth
  - Frequency and depth of water applications, particularly in Spring
  - Clonal vs seed propagation. But likely substantially modified by genetics and potting system

Acknowledgements

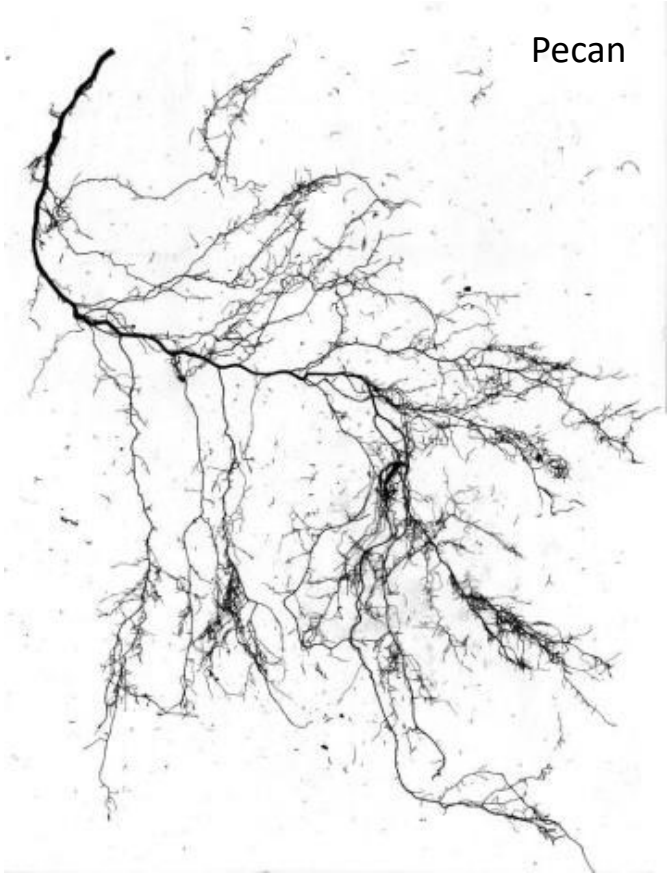
Grad students:

- Bhavana Viswanathan (MS), Andrew Cartmill (PhD), Donita Cartmill (PhD), Jose Franco (PhD), Catherine Simpson (PhD), Hayley Hannah (MS), Paige Graves (MS), Oana Popescu, Kirk Laminack (MS), Sat Pal Sharma (PhD), *Tamara McClung (MS), Hana You (PhD), Xinyu Yao (MS), Courtney Nichols (MS), Juliana Wu (MS), Paul Martinez (MS), Rachel Noone (PhD)*
- Numerous undergraduate helpers…….. digging, washing, sorting, scanning, cataloging, weighing, extracting, analyzing
- Funding: California Dept of Agriculture, Almond Board of California, USDA-NIFA

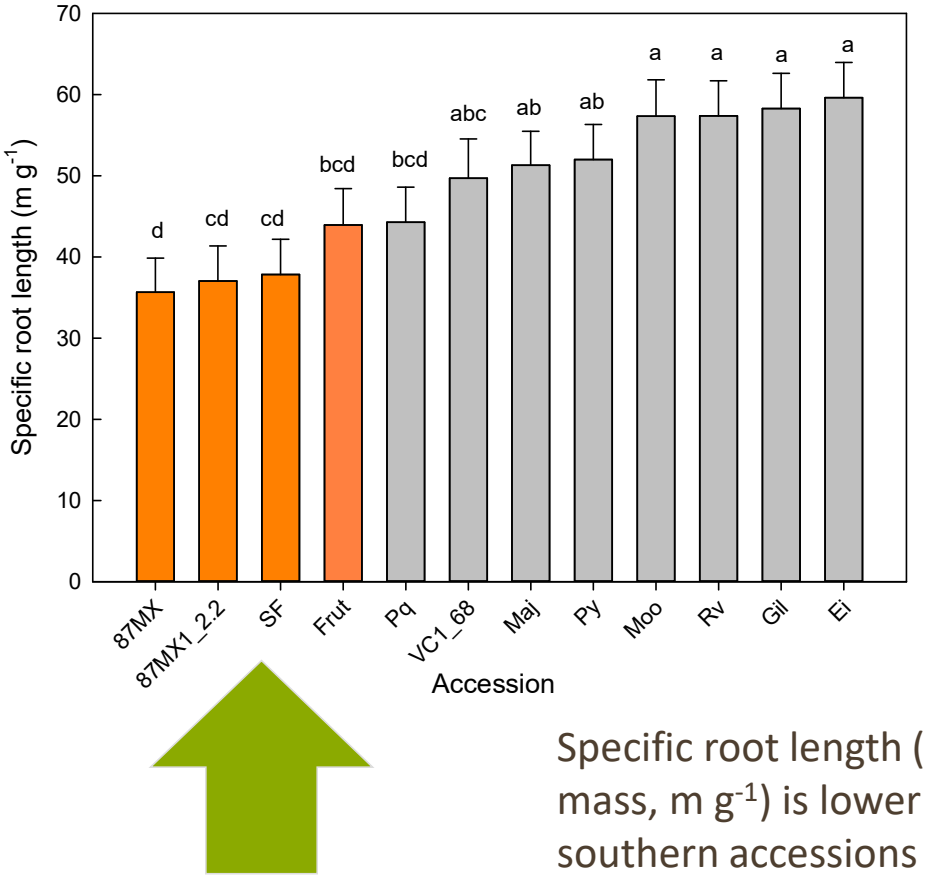
Discussions with:
Bruce Lampinen, Brian Bailey, Maciej Zwieniecki, Kate Scow, Amelie Gaudin, Mae Culumber, Sandipan Samaddar (all UC Davis / UC ANR), Leo Lombardini (Univ. of Georgia), David Eissenstat (PSU) and many others along the way



Root traits adapt to local conditions -genetics



Volder & Grauke, unpublished



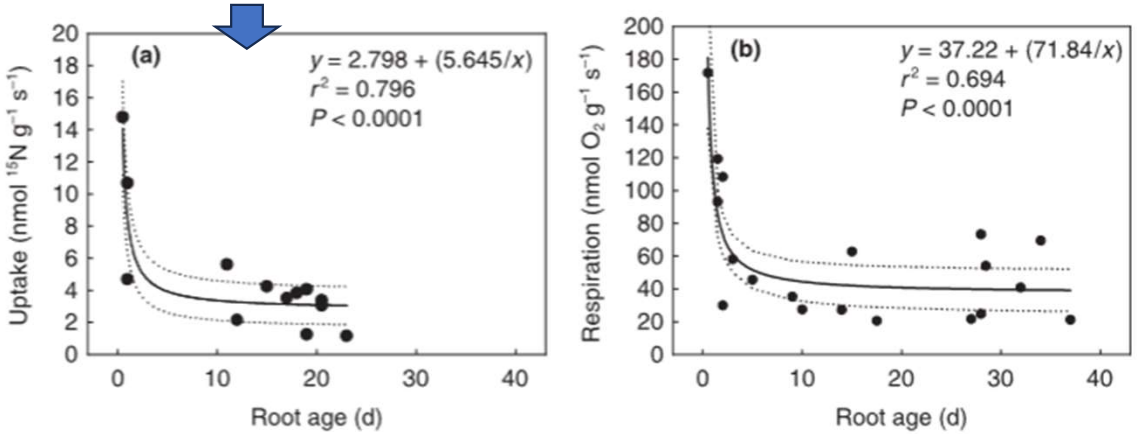
Pecan fine roots harvested from **common garden** in Burlington, Tx

Specific root length (length per mass, m g^{-1}) is lower in more southern accessions

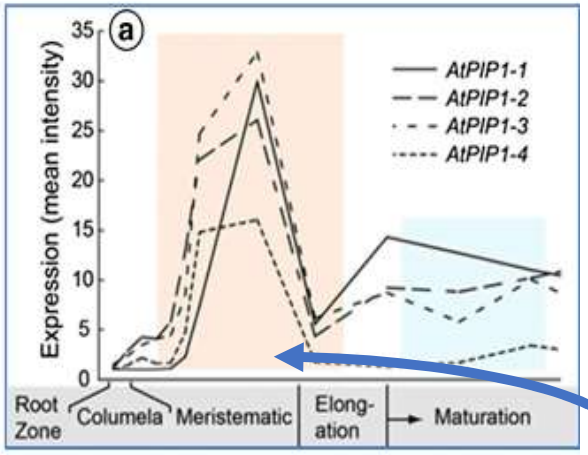
Orange = southern accessions with lowest natural precipitation

No change in diameter – this means fine roots were **denser** for cultivars from a drier origin

Nitrogen uptake capacity decreases rapidly as a root tip ages in place (turns brown) – grape roots



Water and nutrient uptake is proportional to the number of young root tips –i.e., fine root branching



Aquaporins (PIP) allow water to move freely across cell membranes. They are highly expressed in root tips

