How Does an Almond Tree Grow?

December 8, 2015

growing ADVANTAGE
The Almond Conference

Gabriele Ludwig, Almond Board

growing ADVANTAGE
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Speakers

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Reviewing Fundamentals: Focusing on Spurs

The Fundamentals:

The overall objective of all cropping systems is **to maximize resource capture** and **optimize resource use** to achieve sustainable economic yields.

What Resources are We Mainly Interested in?

- light energy
- carbon
- oxygen
- water
- nutrients



What are the three most prominent chemical elements in dry plant parts?

Carbon C
Hydrogen H
Oxygen O
(Roughly in a ratio of 40:7:53)

Where does all that C H O come from?

PHOTOSYNTHESIS!

The basic photosynthesis/respiration reactions

(the most important processes for supporting life on the planet)

Solar energy absorbed by chlorophyll

Photosynthesis →

$$\underset{(H_2O)}{\text{Water}} + \underset{(CO_2)}{\text{Carbon dioxide}} \rightleftharpoons \underset{(CH_2O)_n}{\text{Carbohydrates}} + \underset{(O_2)}{\text{Oxygen}}$$

← Respiration

Chemical energy
To build and repair

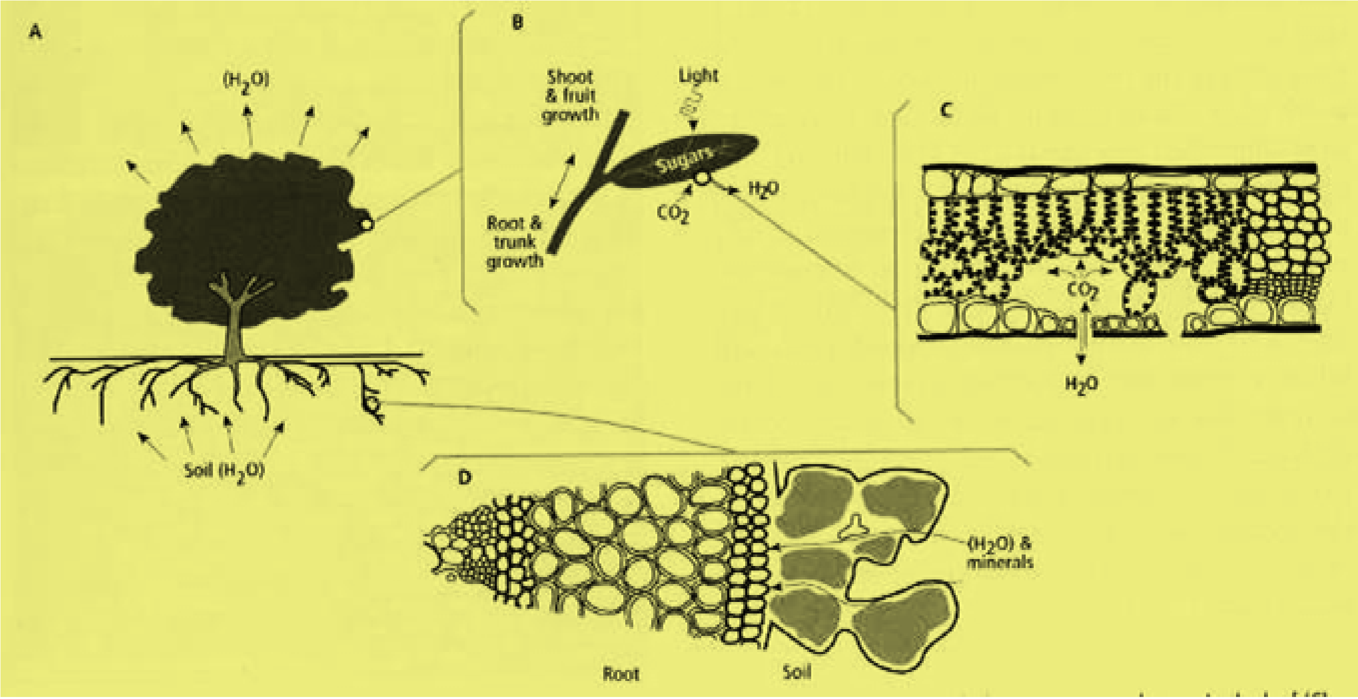
Plants, nature's original solar energy collectors

- What are nature's natural solar energy cells?
- Chloroplasts

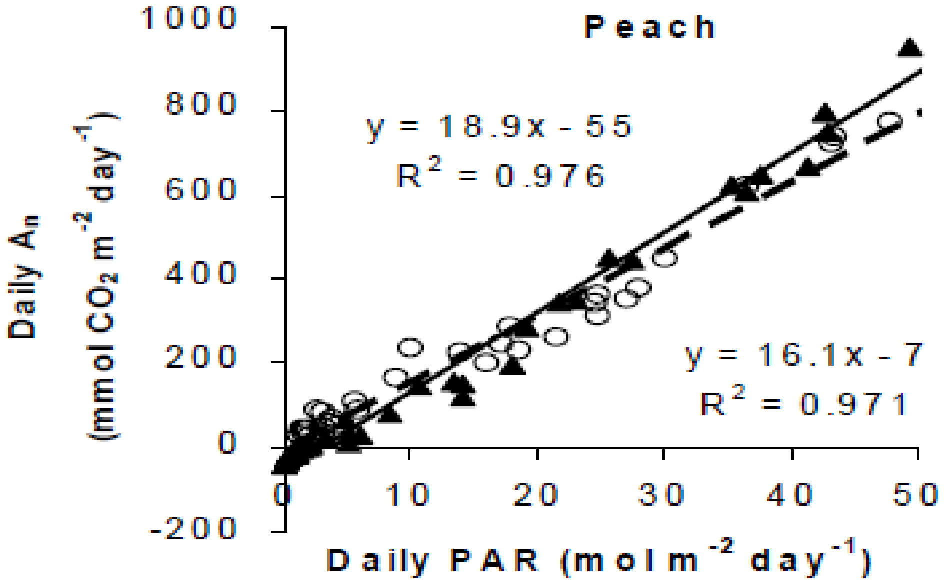
The primary function of tree structure is **to support and display leaves** and the sole function of leaves is **to house and display leaves for solar energy collection**.

- Problem: chloroplasts need an aqueous environment to function, air is dry and CO_2 from air is required for photosynthesis.
- Solution: leaves with waxy cuticle to prevent dehydration and air control vents called stomates.

Carrying out photosynthesis is always a compromise between taking up CO_2 and losing H_20.

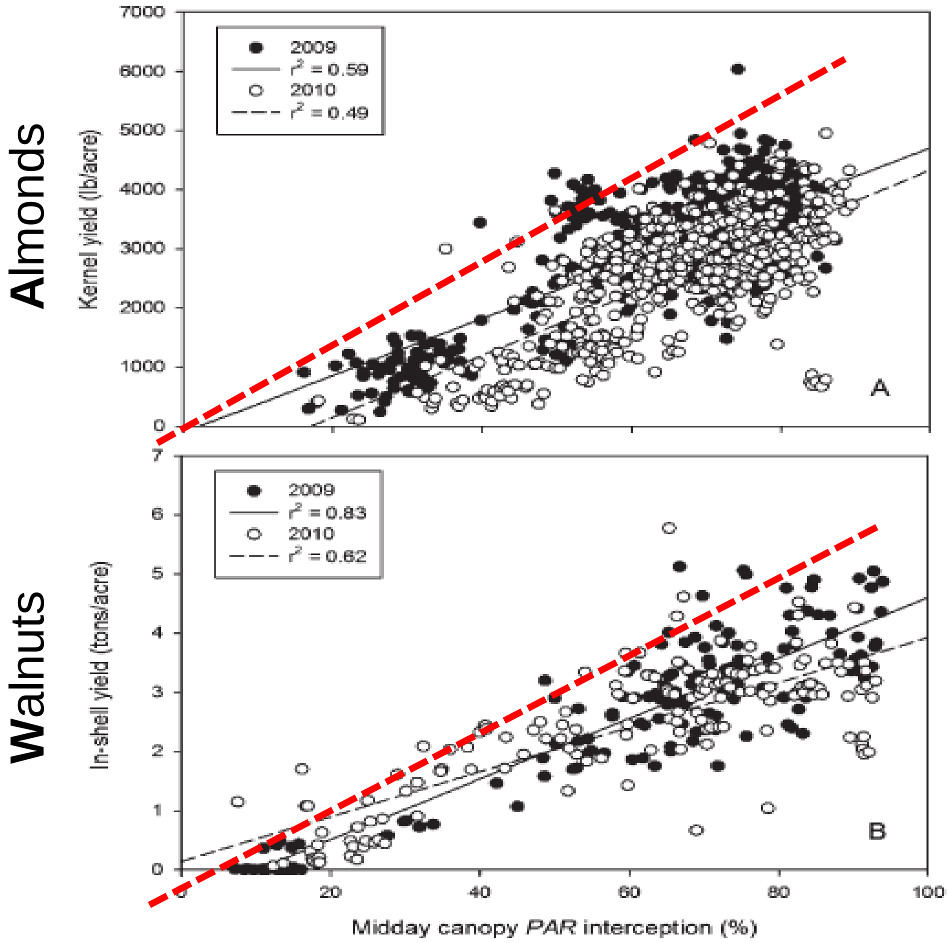


Under non-stress conditions, canopy photosynthesis is a direct function of the light intercepted by the canopy during a day.



Rosati, et al. 2002. Acta Hort. 584: 89-94

Light interception (that drives photosynthesis) is related to crop yield but why then is there so much scatter in all of these points?

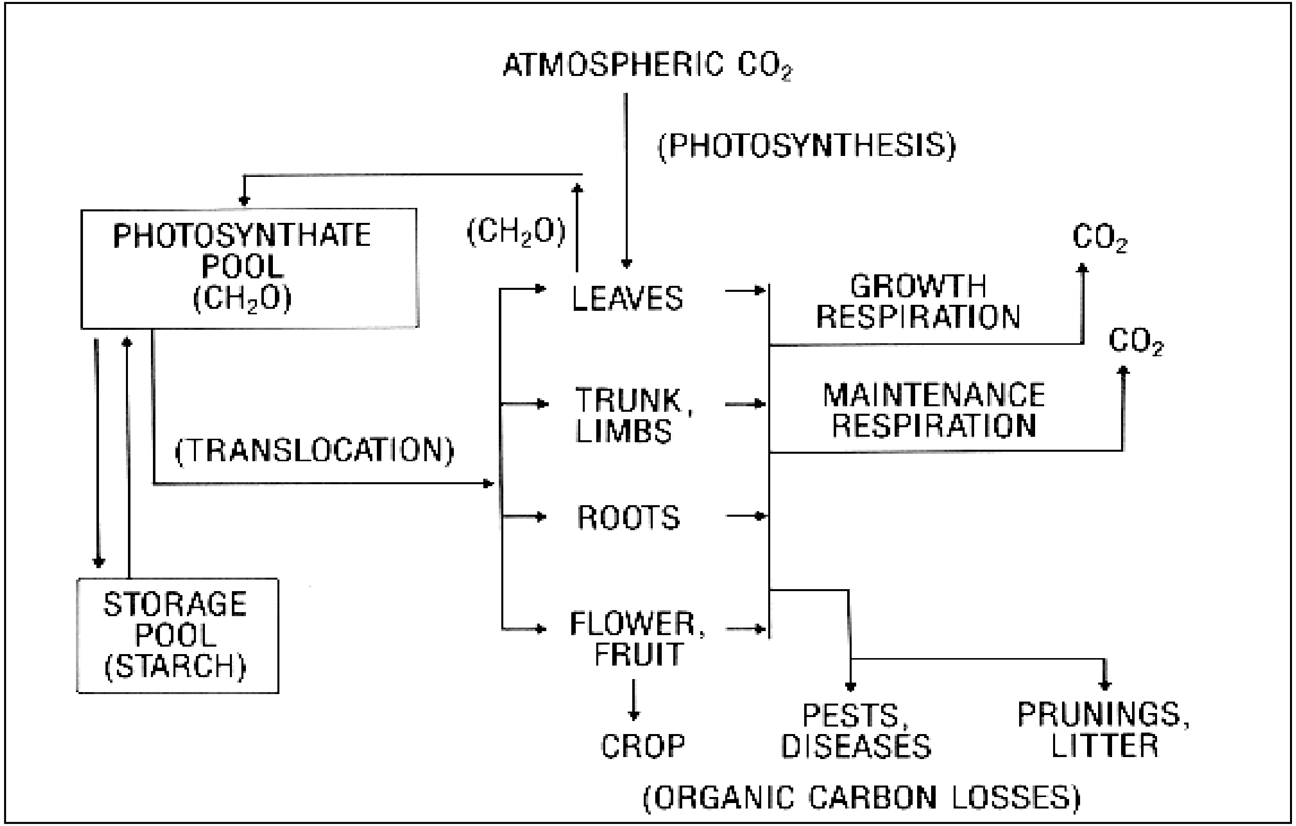


Lampinen, et al.,2012

Carbon Distribution within the Tree

The translocated CH_2O's are mainly sorbitol, sucrose and glucose in almond trees.

(This is a conceptual diagram of where the CH_2O's go but how does that happen?)



What determines how and where CHO’s are used within the tree?

This is a question that has received much attention over the past 50 years and scientists still disagree about it.

However, I believe it is relatively simple.

Carbon distribution is mainly controlled by the development and growth patterns of individual organs and their ability to compete for CH_2O's.

- A tree is a collection of semi-autonomous organs and each organ type has an organ- specific developmental pattern and growth potential.
- Organ growth is activated by endogenous and/or environmental signals.
- Once activated, environmental conditions and genetics determine conditional organ growth capacity.
- Realized organ growth for a given time interval is a consequence of organ growth capacity, resource availability, and inter-organ competition for resources.
- Inter-organ competition for CH_2Os is a function of location relative to sources and sinks of CH_2Os, transport resistances, organ sink efficiency and organ microenvironment.

Bottom line: ***The tree does not allocate CH_2Os to organs, organ growth and respiration takes it from the tree.***

One of the most practical examples of this concept at work is this type of tree.

Five cultivars on one tree

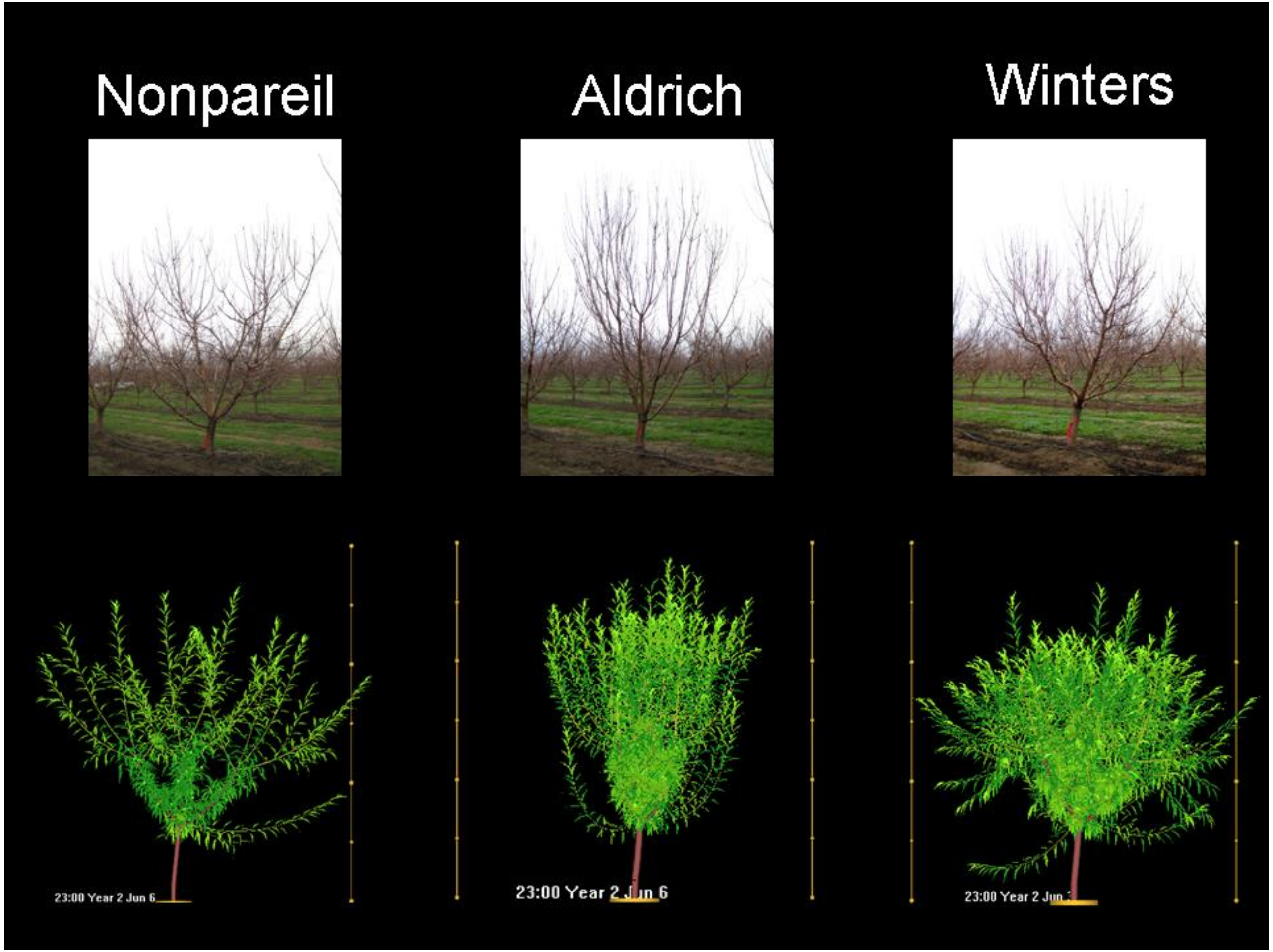
Five cultivars on one tree.

Using these principles to simulate tree growth and productivity over time.

Results from a 3-dimensional computer graphics based simulation model called L-Almond

This model calculates the photosynthesis of each leaf and the uptake of water by the tree, then these resources are distributed around the tree using the previously stated organ development and growth principles.

The growth of three almond cultivars simulated with the L-Almond model.



The tree provides resources (CH_2O, H_2O, nutrients), tree organs use them.

- ***Organ use of resources*** is dictated by ***organ growth and development***.
- ***Organ development and growth*** dictate tree growth and fruit production (**not *vice versa***).

Why does this matter? You need to ***manage trees to optimize resource capture*** and you need to ***manage organs to optimize organ growth to attain high crop yields***.

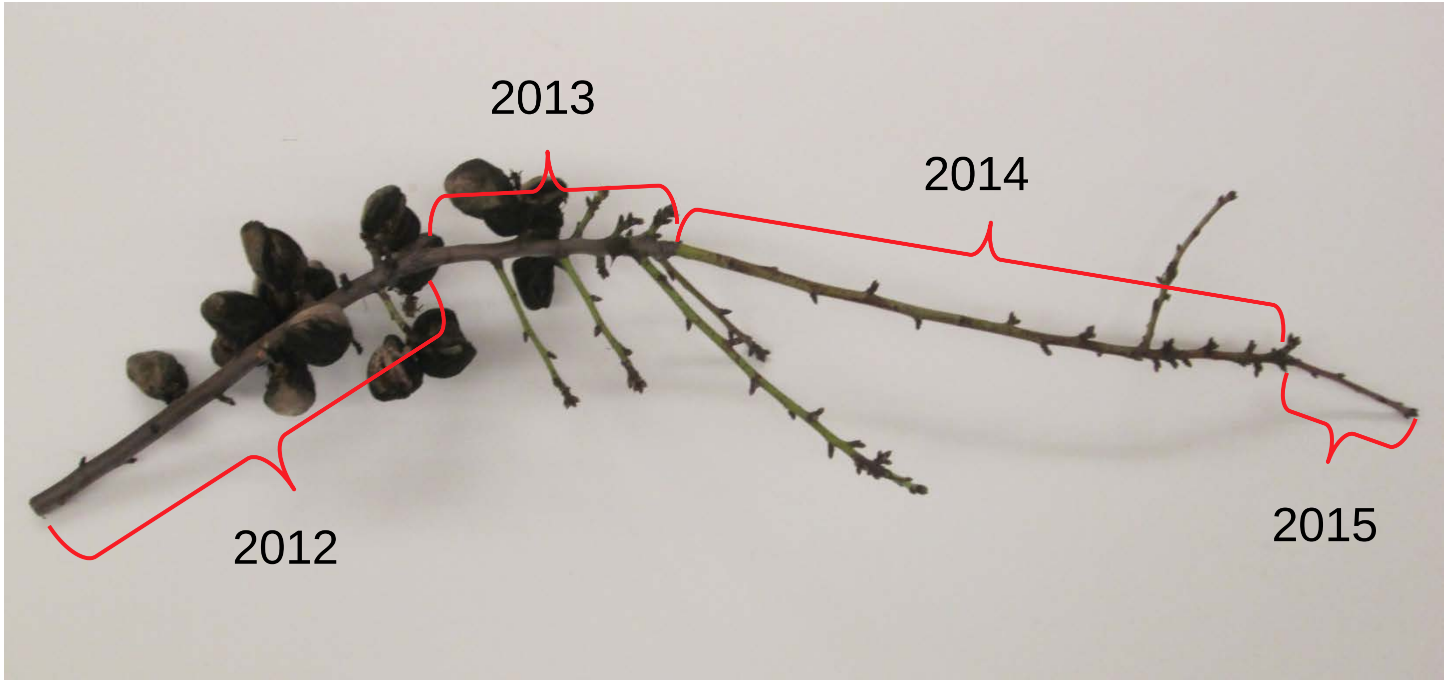
Spurs – the Organ of Interest
Almond spur population dynamics

- Most of you probably think about growing almonds as managing orchards or trees but I would like to emphasize that growing almonds is really about managing productive spur populations. At orchard maturity most almonds are produced on spurs. So **maintaining healthy spur populations is the key to high yields.**

Bearing Habit of Almond Shoots.

4-year-old almond branch.

Nuts are primarily produced on spurs on older wood.



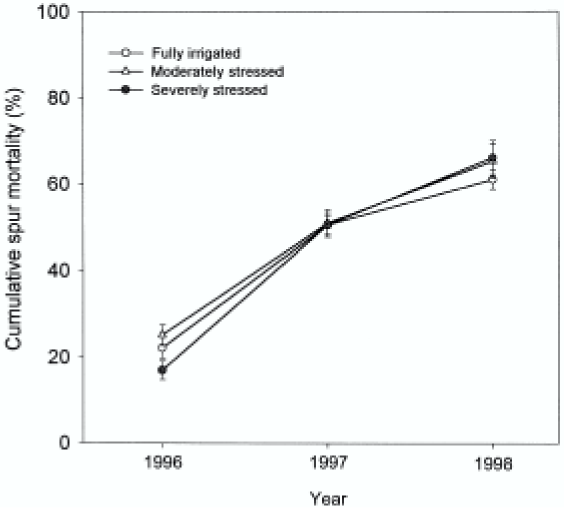
Effects of irrigation deprivation during the harvest period on yield determinants in mature almond trees.

Esparza, DeJong, Weinbaum and Klein (2001)
Tree Physiology 21: 1073-1079

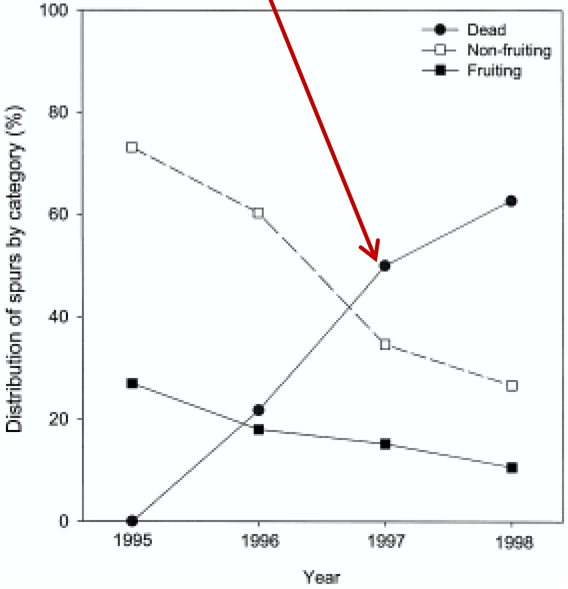
Tagged 2185 spurs in 1995 and followed for 3 yrs. Deficit irrigation treatments had little effect on spur mortality but **an average of 15-20% of tagged spurs died each year.**

Tree yields were only affected after 3 years of deficit irrigation during harvest.

Largest effect of deficit irrigation was reduced shoot growth in next year.



Dead spurs

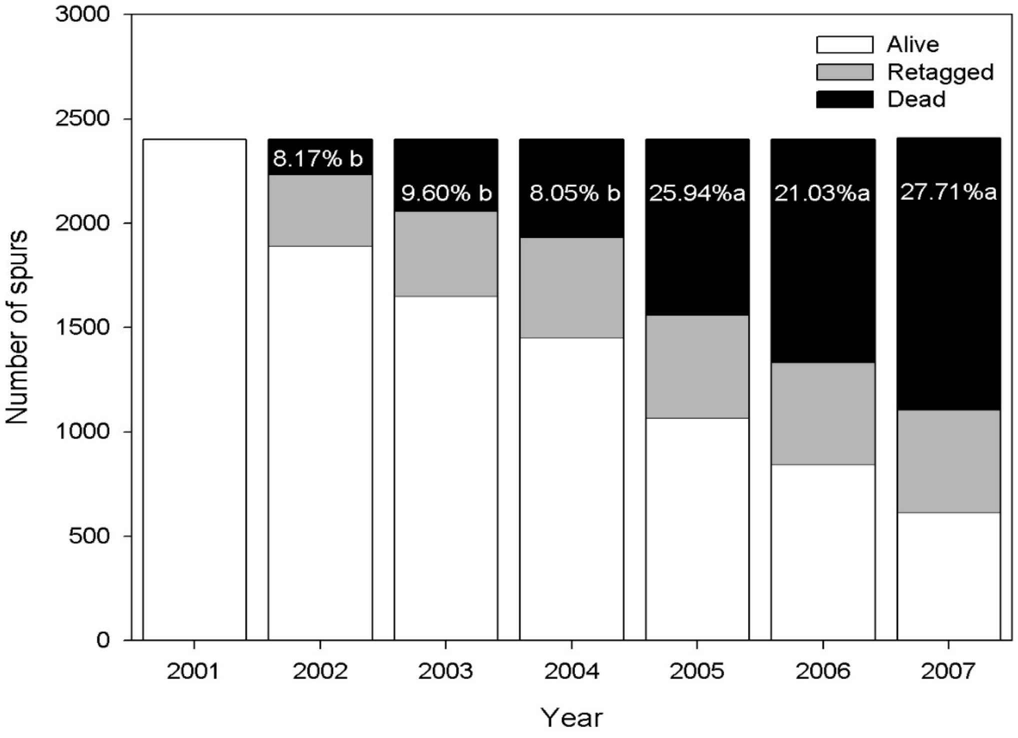


Spur Dynamics Study

- In 2001 Bruce Lampinen's lab initiated the Spur Dynamics study. They tagged 2,400 spurs (50 spurs /tree in 48 trees) and followed the behavior of those spurs for 7 years (retagging new spurs in similar locations when spurs were lost or dead for the first 3 years).

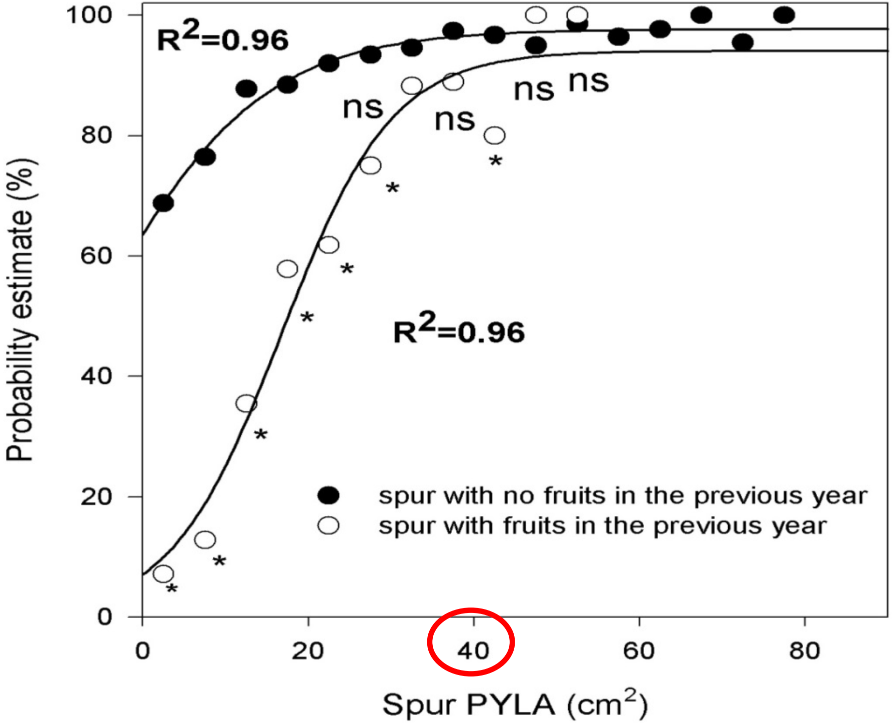
Number of living, dead and retagged almond spurs tagged in 2001 (total 2,400). Percentages reflect the number of dead spurs in relation to the number of spurs alive in the previous year in each year. Black bars indicate cumulative number of dead spurs.

In the first 4 years spur mortality was ~ 8 – 10% but during the last 3 years it was > 20%.



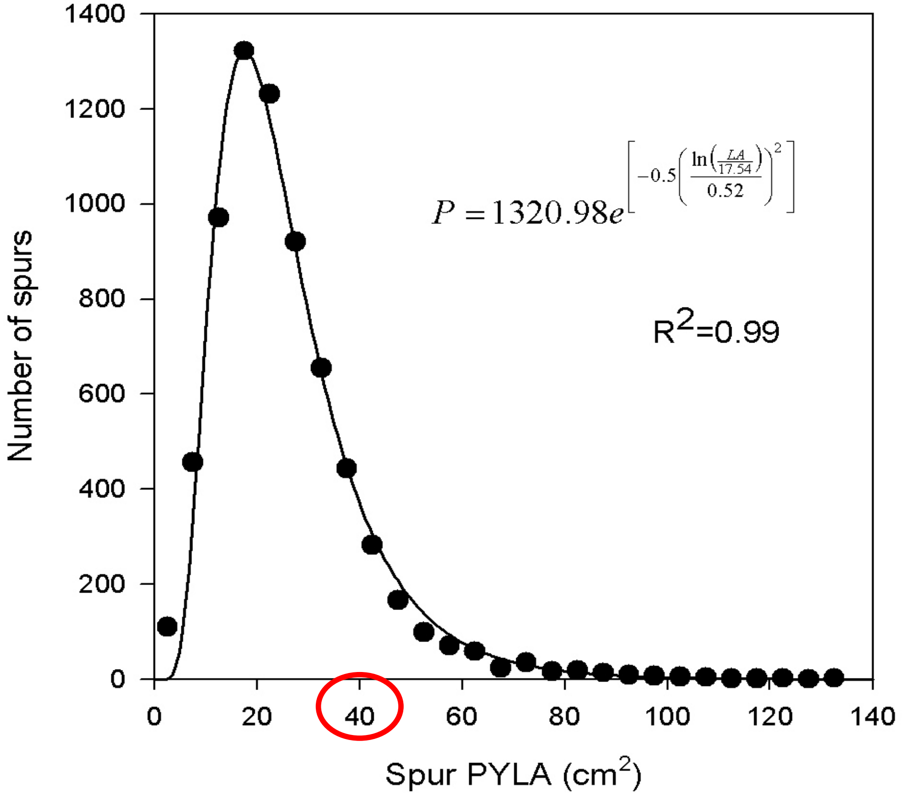
Probability estimation (%) of **spur survival** after bearing and not bearing fruit in the previous year in relation to previous year spur leaf area (PYLA, cm^2)

Bearing spurs were more likely to die in subsequent year than non-bearing spurs, and spur death was strongly related to previous year spur leaf area.



Spur distributions with respect to their previous year leaf area (PYLA, cm^2)

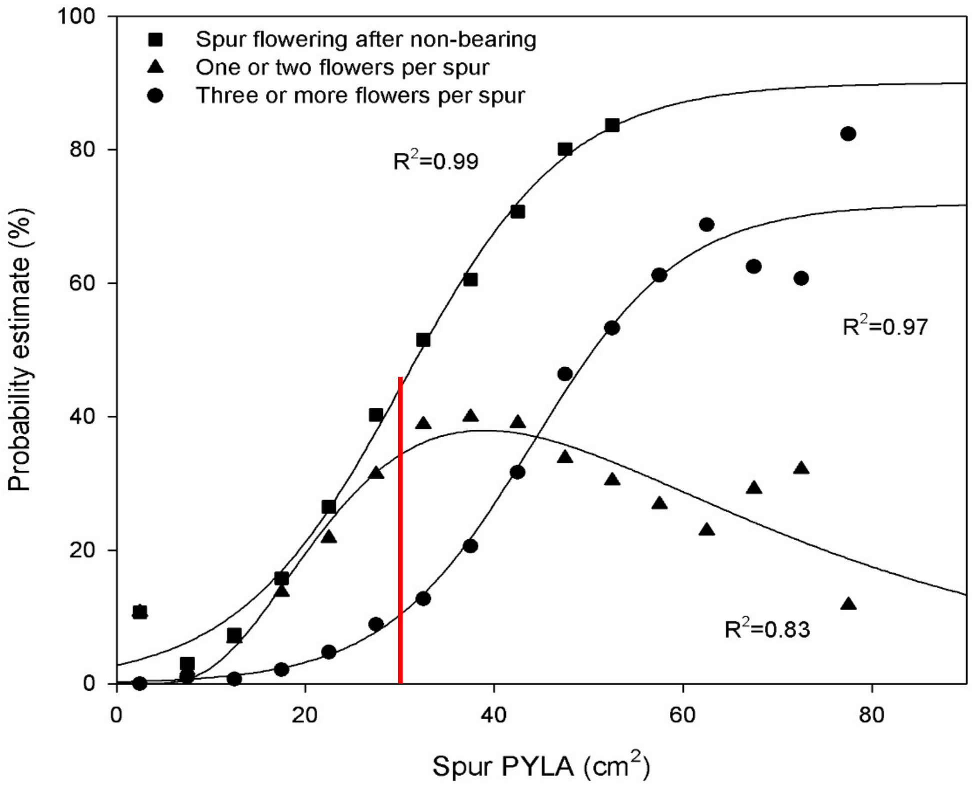
Most spurs have previous year leaf areas of < $40cm^2$.



Probability estimation (%) for spur flowering and spur bearing fewer than 2 flowers or more than 2 flowers after not bearing in the previous year in relation to frequency classes of spur previous year leaf area (PYLA, cm^2)

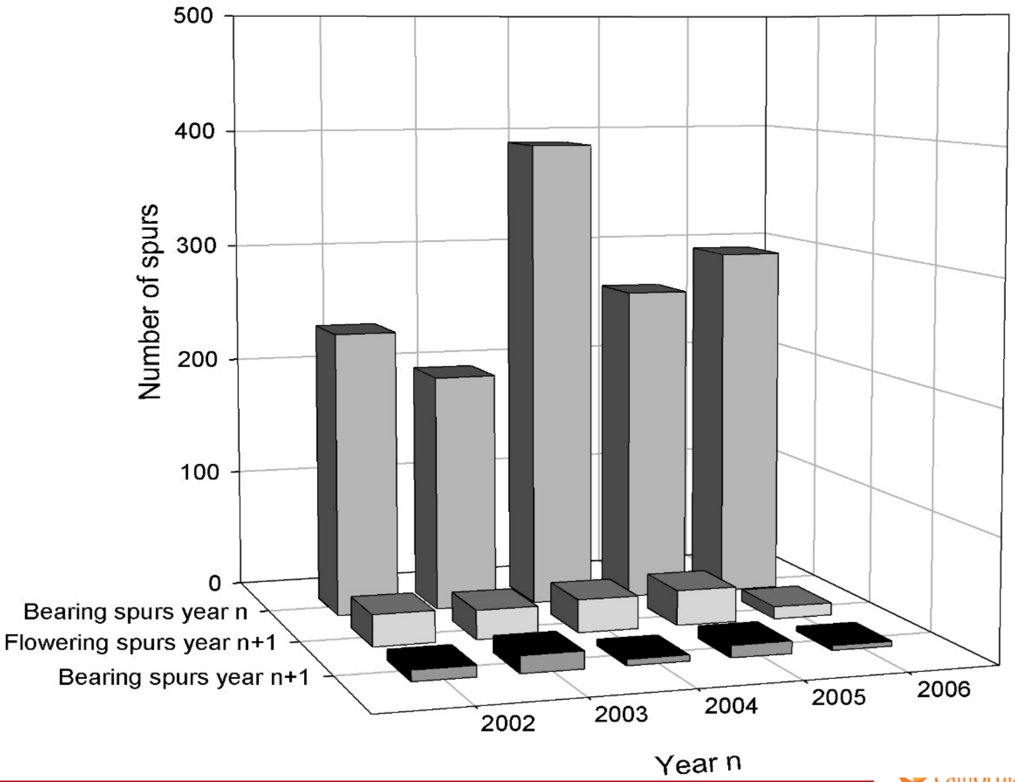
Spurs with PYLA of < 30 cm^2 have < a 50% chance of flowering.

Spur probability of flowering and bearing multiple flowers increases with PYLA.



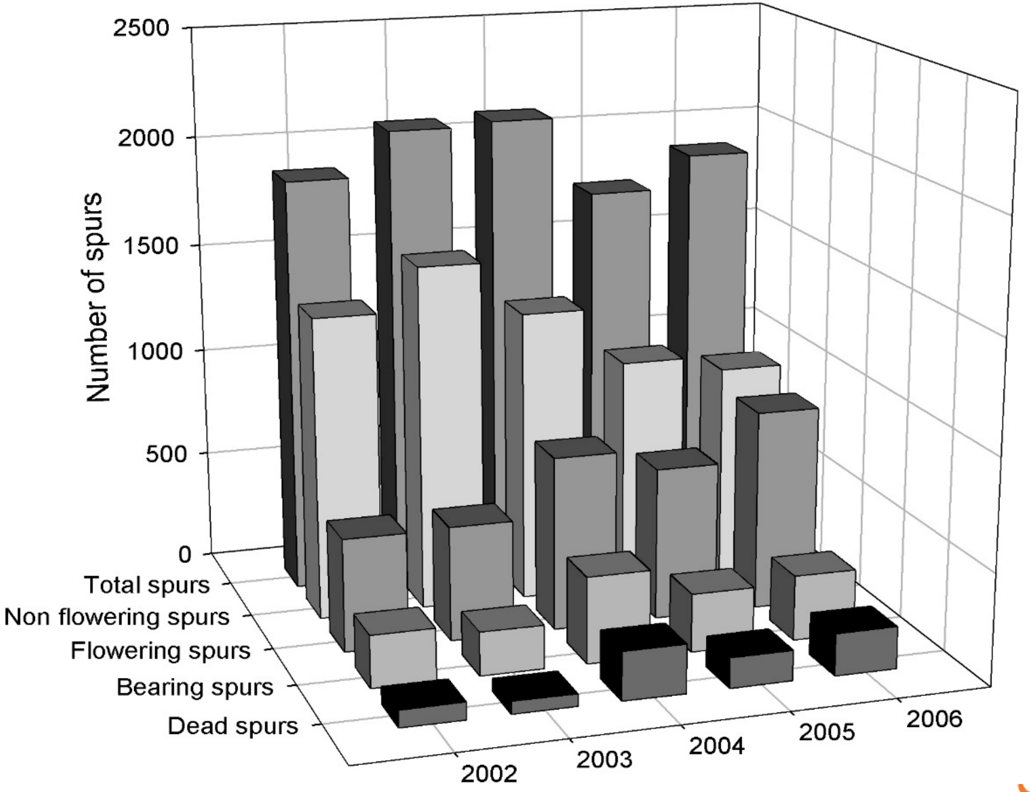
Number of bearing spurs in the year n and return bloom and fruit bearing in the subsequent year.

There was a strong tendency for a spur not to bear fruit in two sequential years.



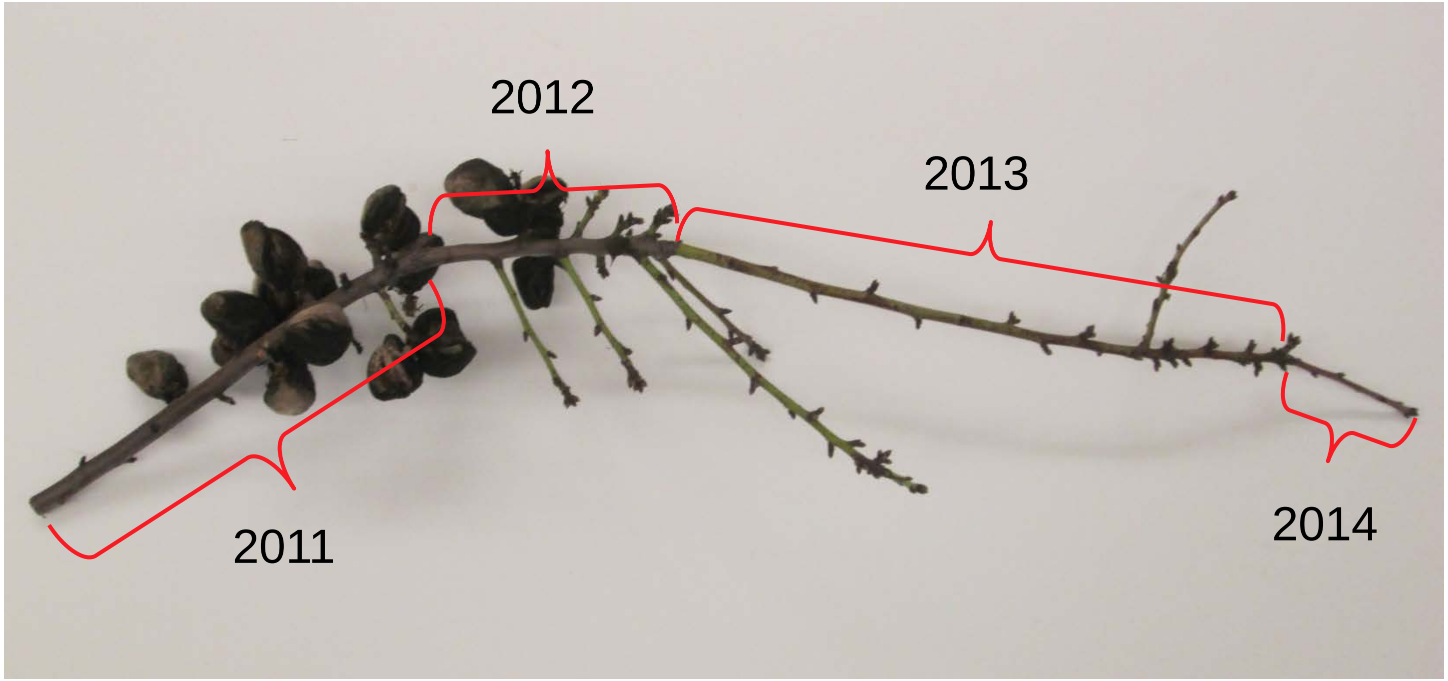
Spur population description over 5 years (including retagged spurs). Number of total spurs, non flowering spurs, flowering spurs, bearing spurs and dead spurs in the following year after bearing.

Spur population is very dynamic.



Renewing fruiting sites and developing new spurs

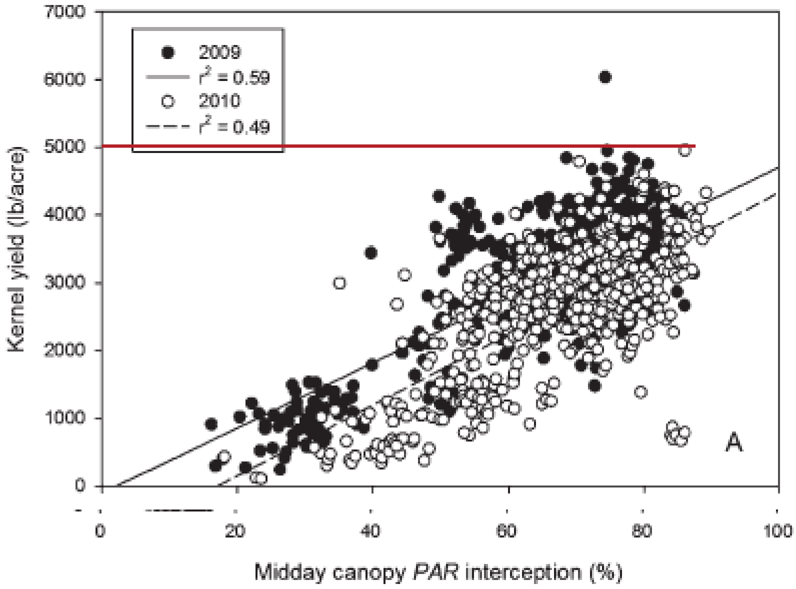
The new growth in 2014 and 2015 provides new fruiting sites as old spurs die.



New shoots on the top of trees provide new spurs over time.

If an orchard kernel yield is ~3,000 lbs per acre, what does the spur population of that orchard look like?

- 3,000 lbs with 454 nuts per lb = 1,362,000 nuts per acre
- With average of ~1.25 nuts per bearing spur then there were ~1,089,600 bearing spurs per acre.
- If there are 121 trees/acre (18x20 ft) then there were ~9,000 bearing spurs per tree. If that represents 14.25% of the spur population then there were ~63,000 active spurs per tree.
- Of those 63,000 spurs
  - ~15% are resting (bore previous year)
  - ~15% bear fruit
  - ~20% flowered but did not bear fruit
  - ~25-40% are resting (not sure why, probably low LA)
  - ~10-25% die **(must be replaced)**



Bottom Line

- **Almond orchard yields are dependent on maintaining a healthy population of spurs. Spur mortality and productivity is a function of previous year leaf area.**
- **Spur death is a given, so annual replacement of spurs is essential for future production.**
- **Spur extension growth and spur leaf growth occurs in early spring, right after bloom; and shoot extension growth (providing new sites for renewing the spur population) occurs during the “grand period of growth” in the two months after bloom.**

Spring mobilization and transport of stored CH_2O are critical for SPUR FLOWERING, FRUITING AND RENEWAL but we know relatively little about these processes.

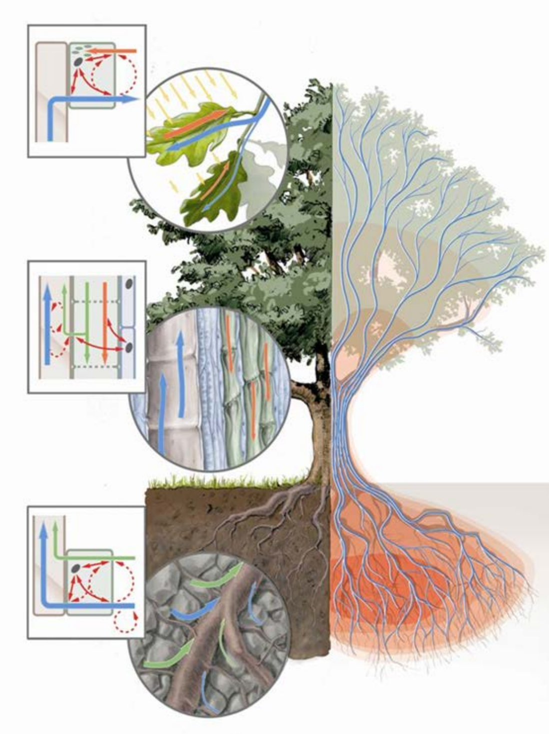
Dr Zwieniecki will describe new research on these topics.

Similarly, while we know that root development, growth and activity are essential for providing NUTRIENT AND WATER RESOURCES to the tree, we know relatively little about the seasonal development, growth and activity of the ROOT SINK.

Dr. Volder will describe new research on these topics.

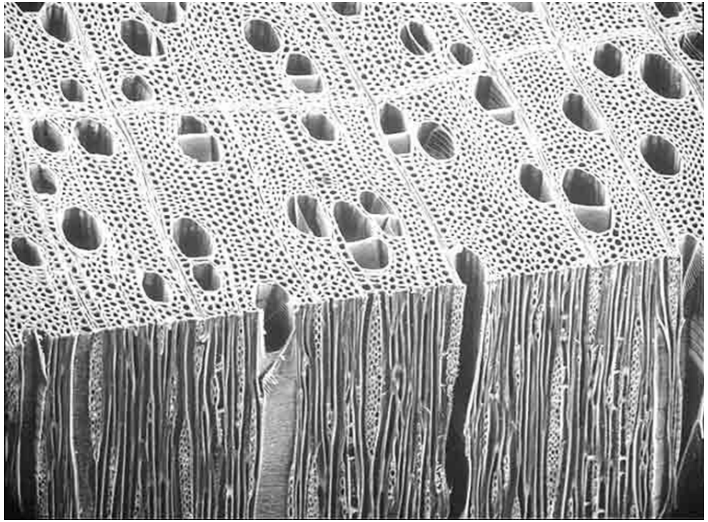
Life without debt – carbohydrate management

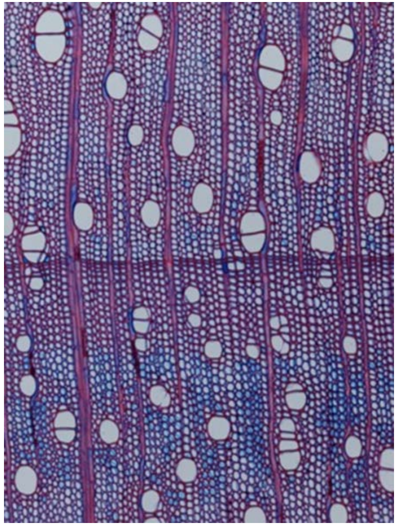
- Carbohydrates provides energy for growth, defense, and reproduction (yield)
- Carbohydrates are the tree's liquid assets - 'currency'.
- Soluble carbohydrates can be considered as 'cash' that flows around the tree and is used to pay for services.
- Trees continuously measure soluble sugar levels
- Starch is the 'currency' savings account.
- Starch is invisible to tree i.e. there is no 'bank statement', nor interest on savings. The tree cannot get a sugar loan.
- Capacity for starch storage has developed over evolutionary time to allow for tree survival in particular climate conditions.
- Starch content is highly dynamic – controlled by enzymatic activity (degradation and synthesis).
- Enzymatic activity is ultimately controlled by internal factors (gene expression, substrate availability), and environment (temperature).

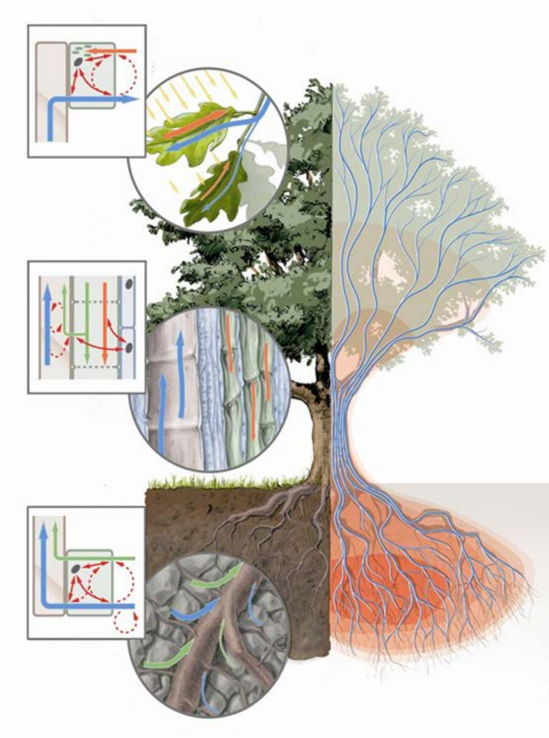


Life without debt – carbohydrate management

- Soluble carbohydrates are distributed via phloem and xylem
- They are stored in living cells (special organelles called plastids)
- Living cells in xylem tissue are called xylem parenchyma cells, they are located in xylem rays – connected to phloem and extending deep into the xylem tissue (wood).

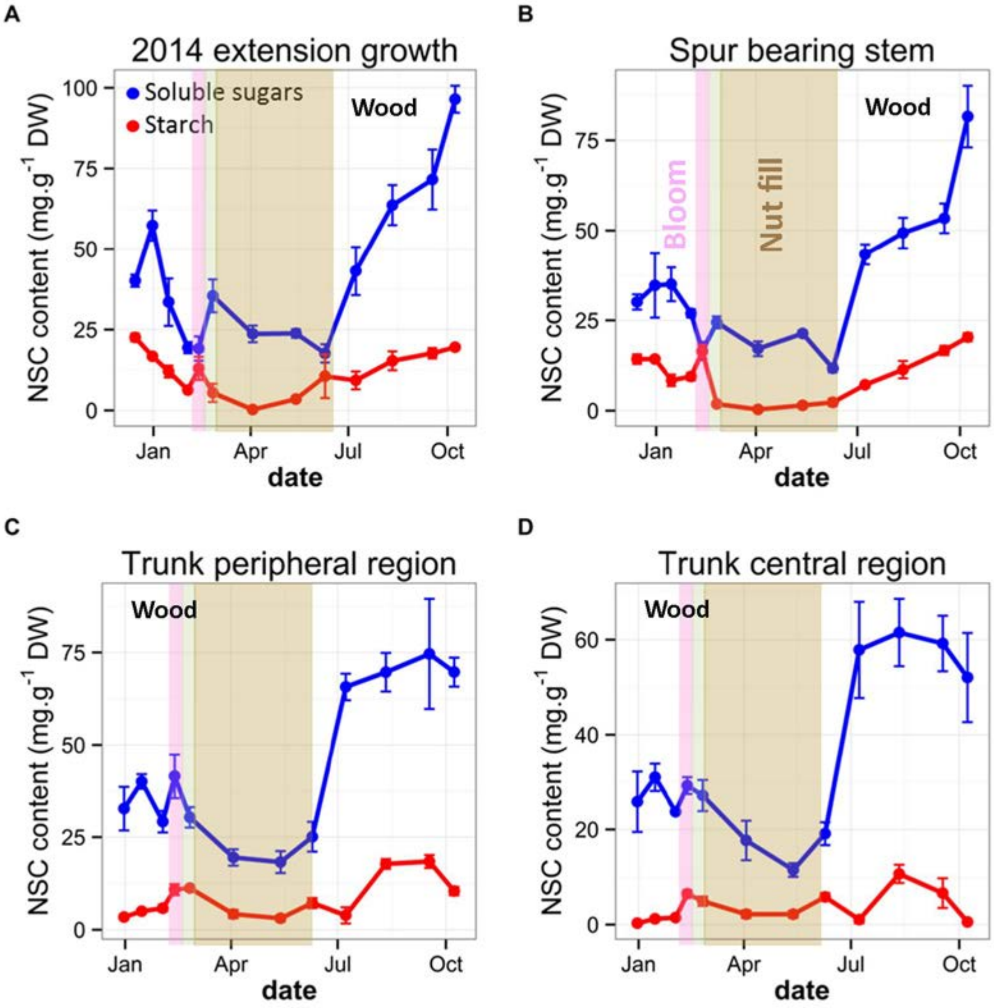






Life without debt

- Starch and soluble sugar concentrations in wood undergo significant changes during a year.
- Dormancy period is marked by significant loss of carbohydrates in branches from December till flower bud-break.
- During flower development starch reserves are depleted.
- Nut fill period further depletes starch reserves to near zero throughout the entire tree.
- Recovery of reserves occurs in summer and fall and most likely post harvest.

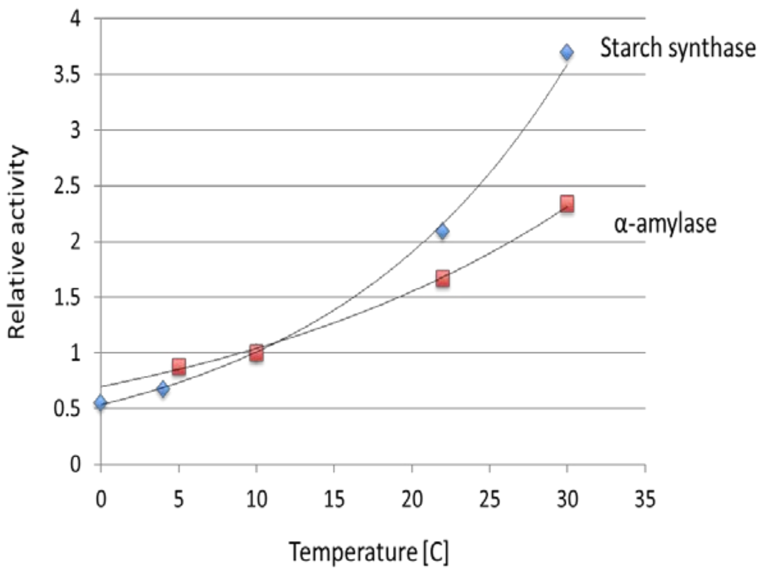


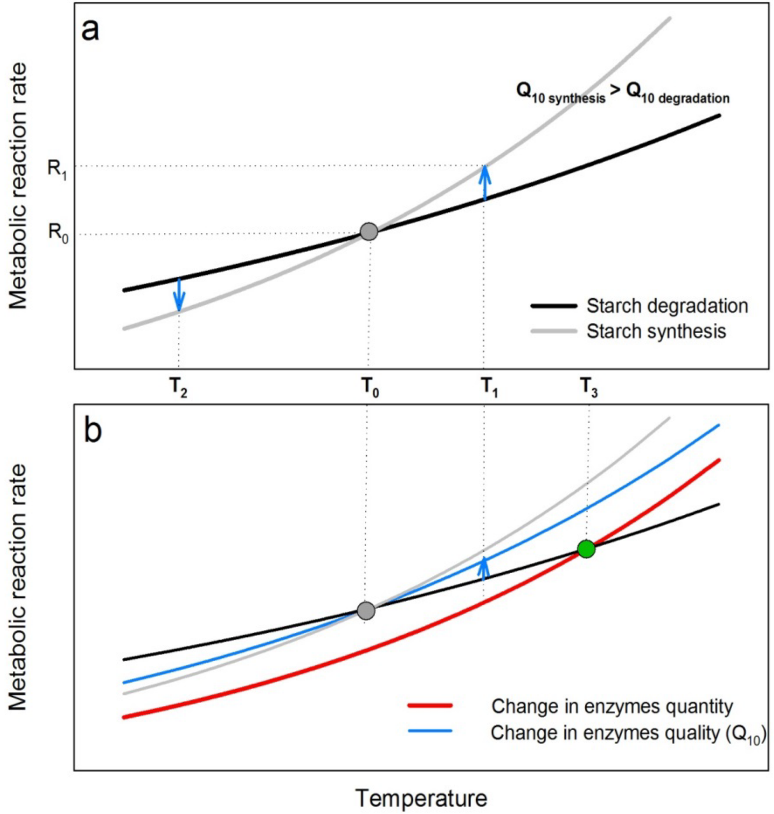
Z Lab

california almonds
Almond Board of California

Role of temperature in carbohydrate management

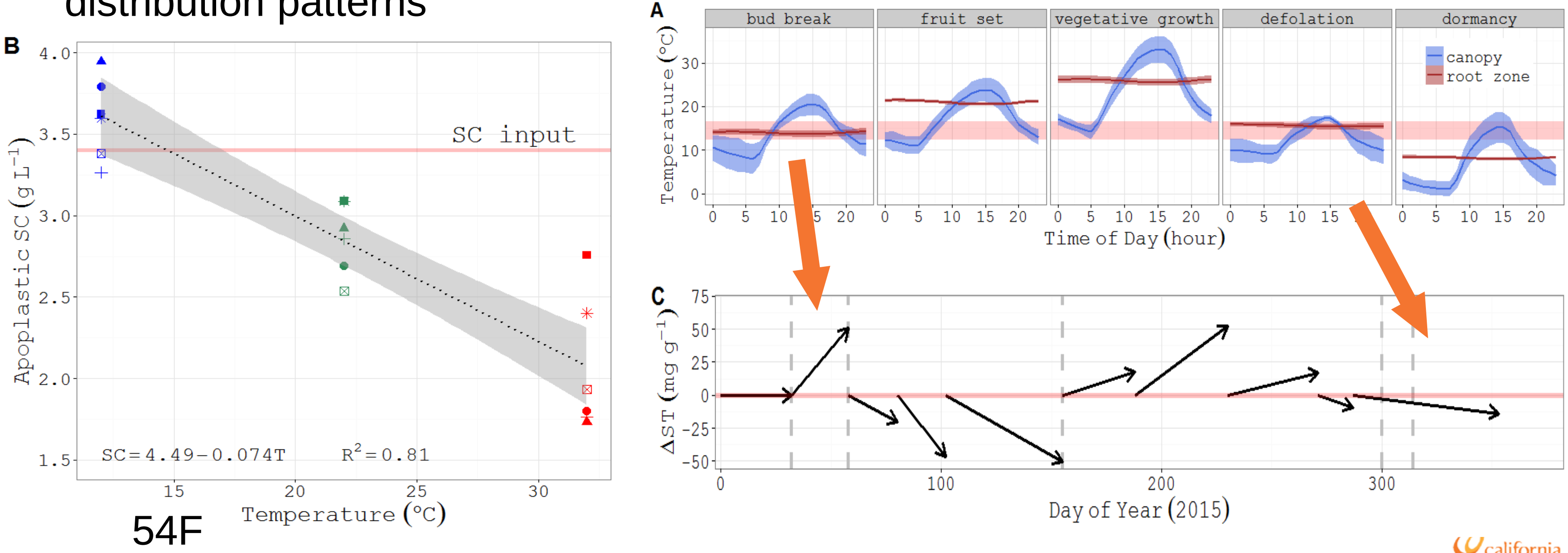
- Differential responses of enzymes to temperature leads to temperature dependent carbohydrate metabolism.





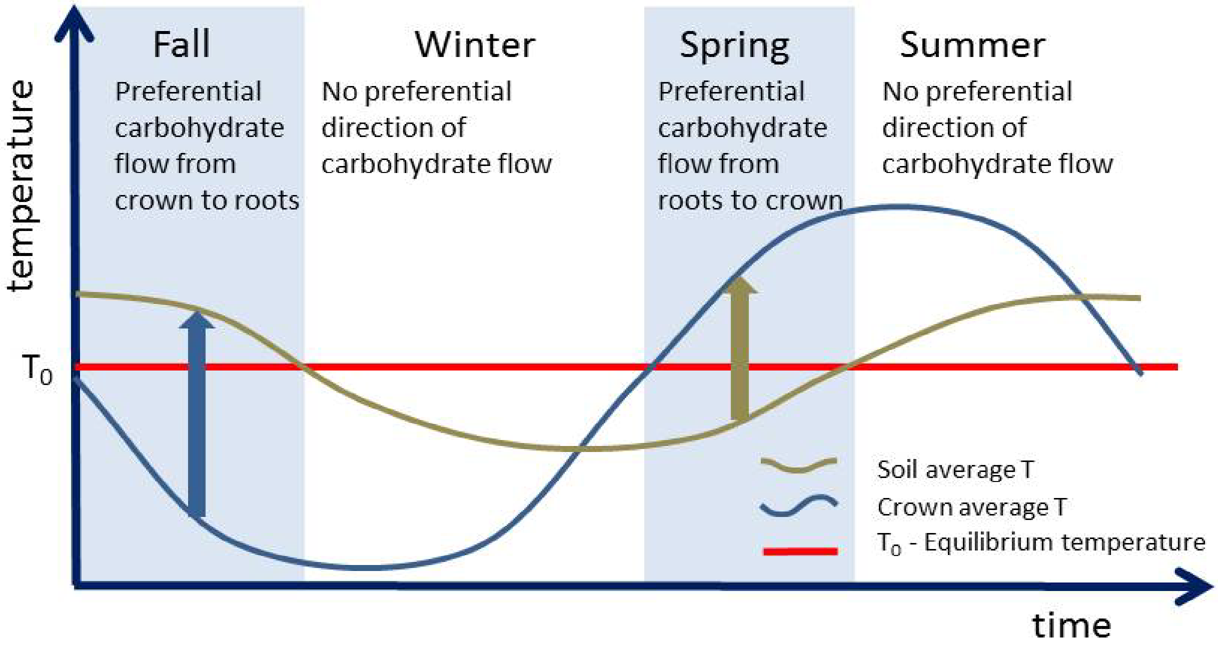
Role of temperature in carbohydrate management

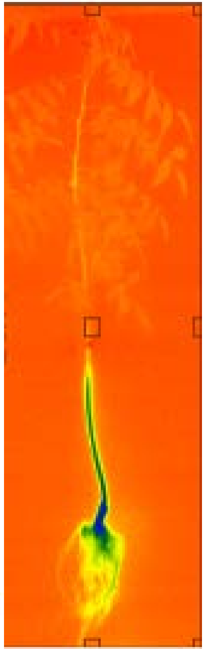
- Temperature determines equilibrium level of soluble carbohydrates in branches
- Soluble carbohydrates are mobile and can be moved to sites of growth or storage
- Diurnal and seasonal temperature swings may guide tree carbohydrate distribution patterns



Role of temperature in trees' carbohydrate management

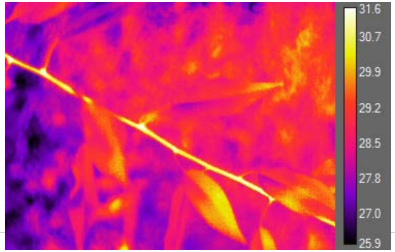
- Temperature dependence of starch metabolism may have significant implications for seasonal movement of carbohydrates at the tree level

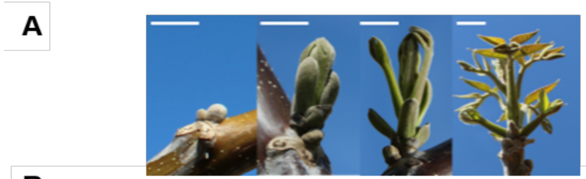


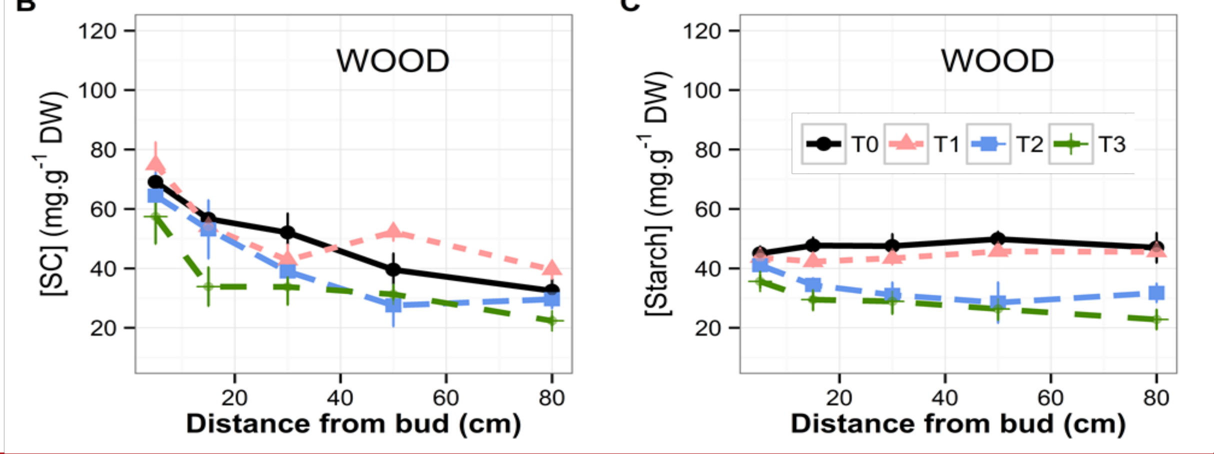


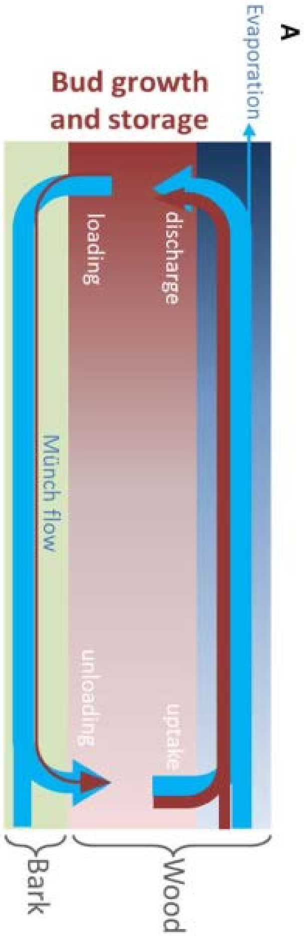
Role of temperature in tree carbohydrate management

- Temperature dependence of starch metabolism may have significant implications for diurnal movements of carbohydrates at the branch level



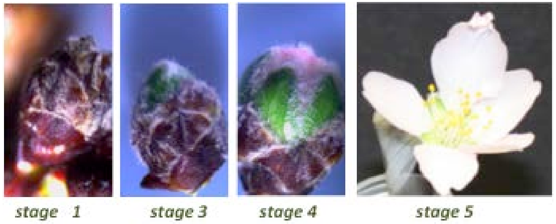


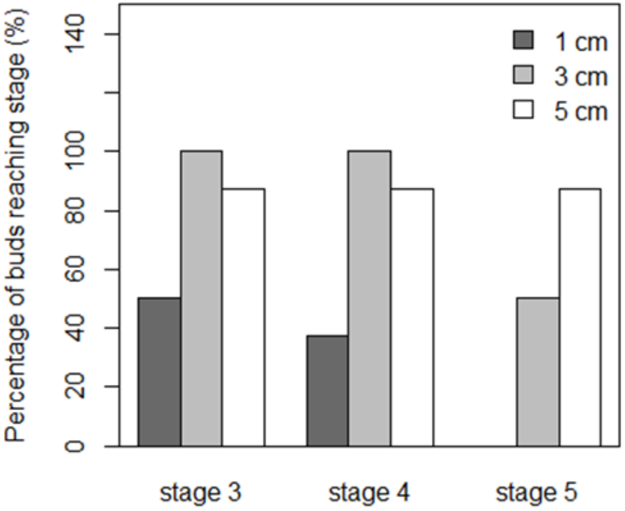


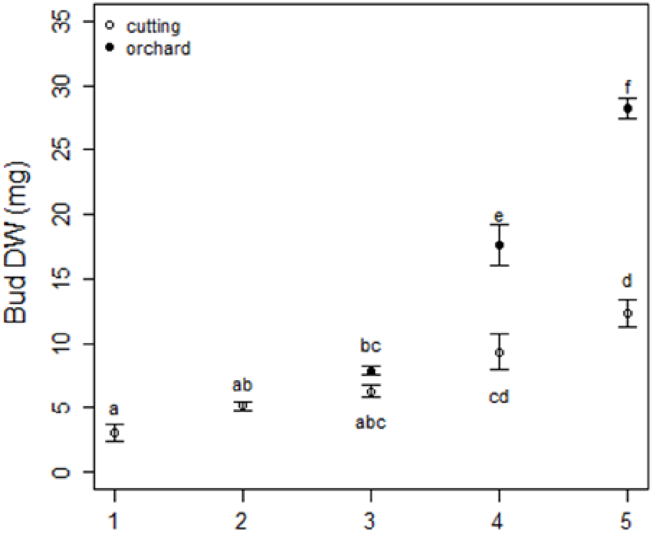


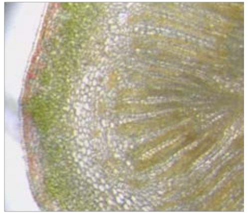
Flowering and carbohydrate management

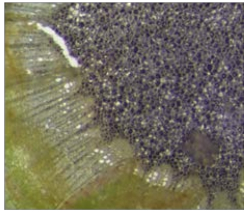
- The spring redistribution of the carbohydrates toward the branch tips, and spurs is crucial for flowering success of the almond trees







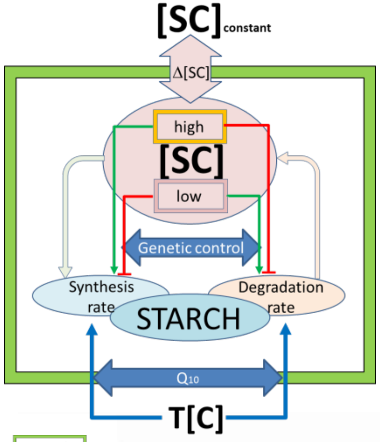


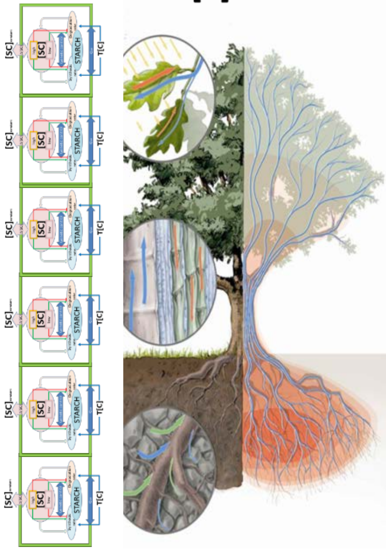


Role of temperature in tree carbohydrate management

Take home message

- Currently we do not manage orchards for carbohydrates or use carbohydrate analysis to inform management practices.
- Diurnal variation of temperature in spring and fall might be a key factor determining yield as it primes trees for surviving winter (dormancy) and spring flowering.
- There is no true dormancy in CA – during winter trees still distribute carbohydrates, respire, protect from environment, or grow roots.
- Slow shift in winter thermal conditions due to climate change (especially related to warm days) might negatively affect a tree’s ability to prime for spring bloom.
- Cell/branch carbohydrate equilibrium temperature thresholds might provide insight into chilling requirements, and provide breeding targets for development of trees for different climatic conditions.





Astrid Volder,
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The Black Box – Root Growth

growing ADVANTAGE
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Types of roots

Longer lived, “permanent” roots

- Large diameter (> 50 mm) structural roots, close to trunk – anchorage, transport
  - ➢ Majority of root biomass
- Transport framework roots (5-50 mm) – transport of water & nutrients, anchorage
- Exploratory roots (0.5 – 5 mm) – soil exploration, transport & anchorage
- Fine diameter (0.05 – 0.5 mm), short-lived roots – water uptake, nutrient absorption
  - ➢ Majority of root length

Root system diversity

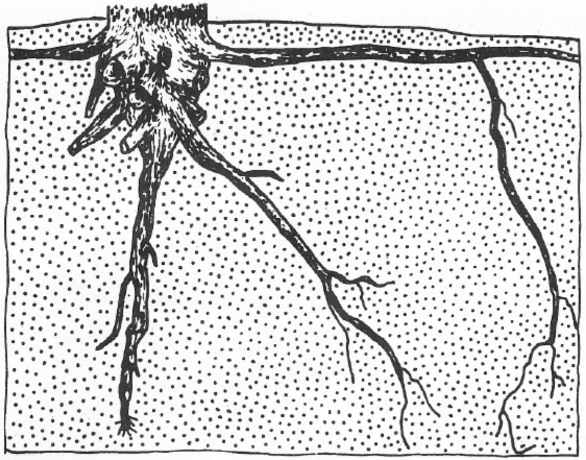
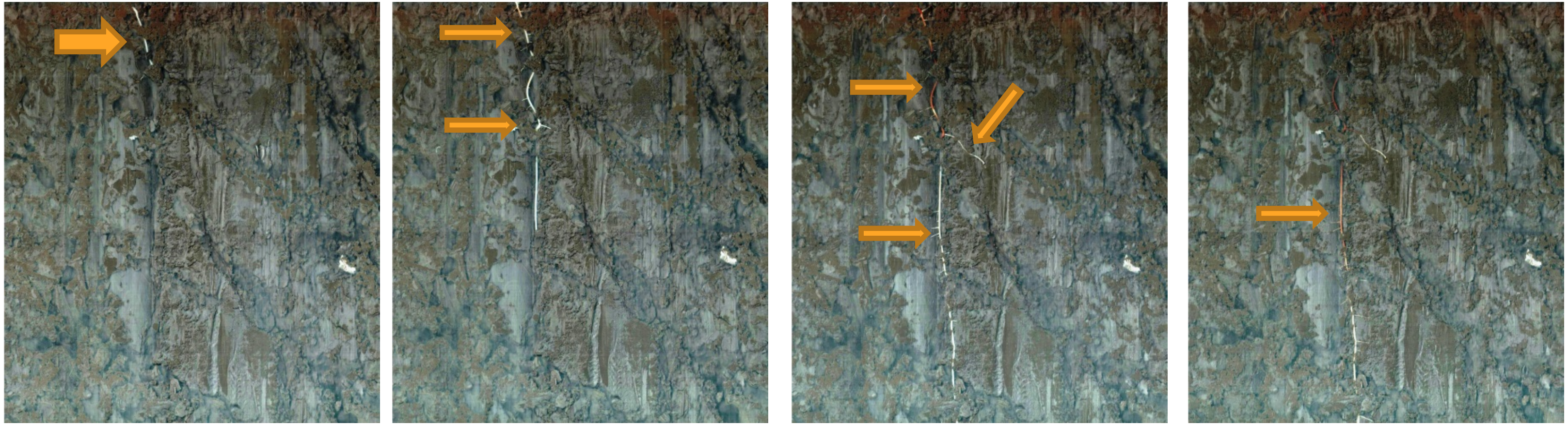


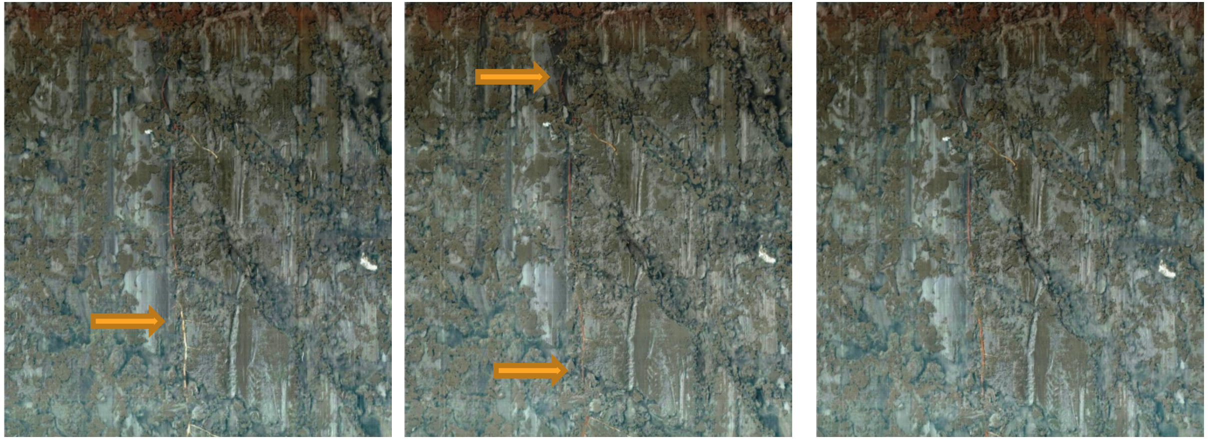
FIGURE 2-18 Types of roots that may occur on a mature tree. The vertical taproot is usually choked out by roots above. The heart root grows at an angle from the buttress of the trunk (root collar). Horizontal lateral roots are usually near the surface. Sinker (striker) roots grow downward from lateral roots. *(Adapted from Fayle, 1968.)*

Types of growth

- Determinate
  - Growth stops when a maximum size/length is reached
  - 1st order roots (functional classification)
- Indeterminate
  - Growth does not have a pre-set stopping point
  - “Pioneer” roots



3rd week of July

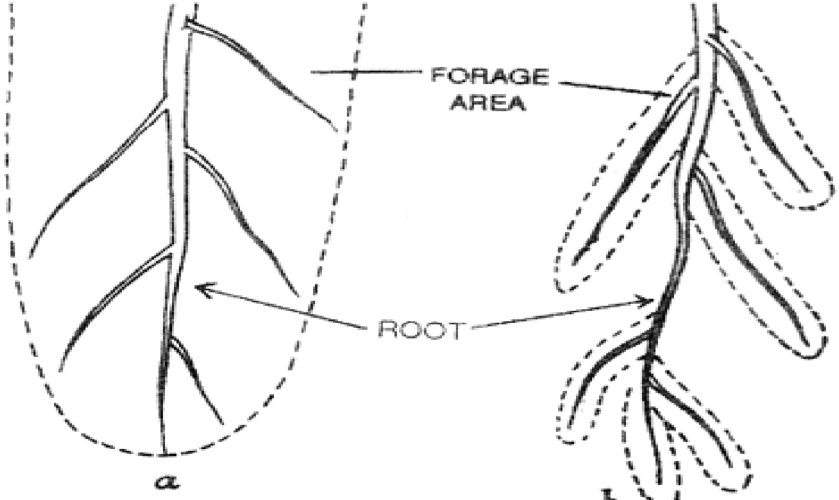


One week interval

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

Function of fine lateral roots

- Acquisition of water & nutrients → expand soil volume explored
- Formation of nutrient depletion zones requires constant new growth & exploration
- Anchorage?



Forage area for (a) mobile and (b) immobile nutrients

Once roots encounter a nutrient-rich patch fine roots and hairs proliferate

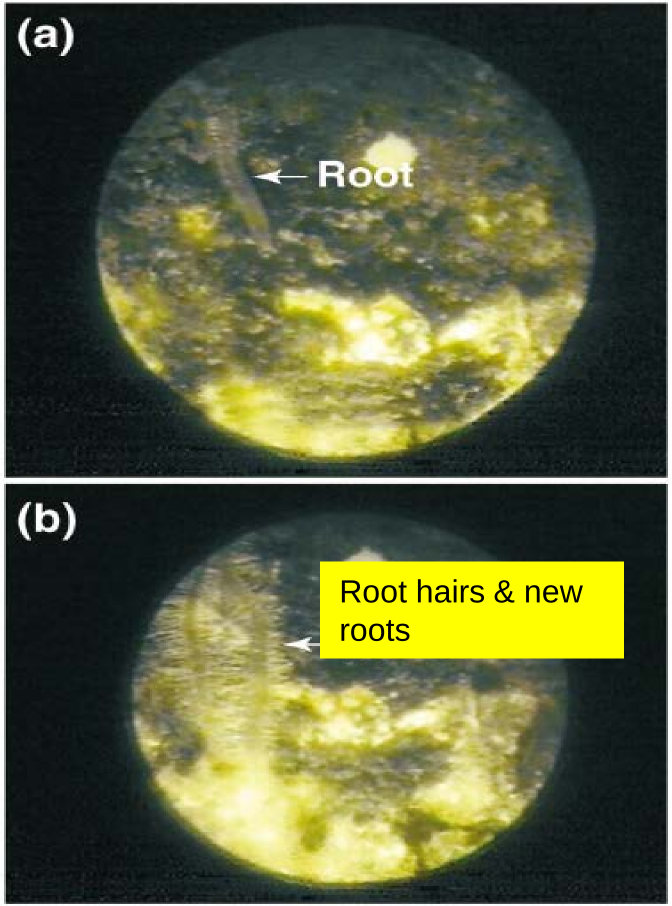


Fig. 3. Root growth into an N-rich organic patch composed of lyophilized algal cells viewed using a minirhizotron tube and a borescope camera. Each image is ~7 mm in diameter. (a) 21 days after the patch has been added, a single root is seen growing into the nitrogen-rich zone. (b) The same image four days later shows increased root production and root-hair development in the nitrogen-rich zone.

Hodge, Robinson and Fitter (2000). Trends in Plant Science 5:304-308

Locally enriched zone with nitrate - N

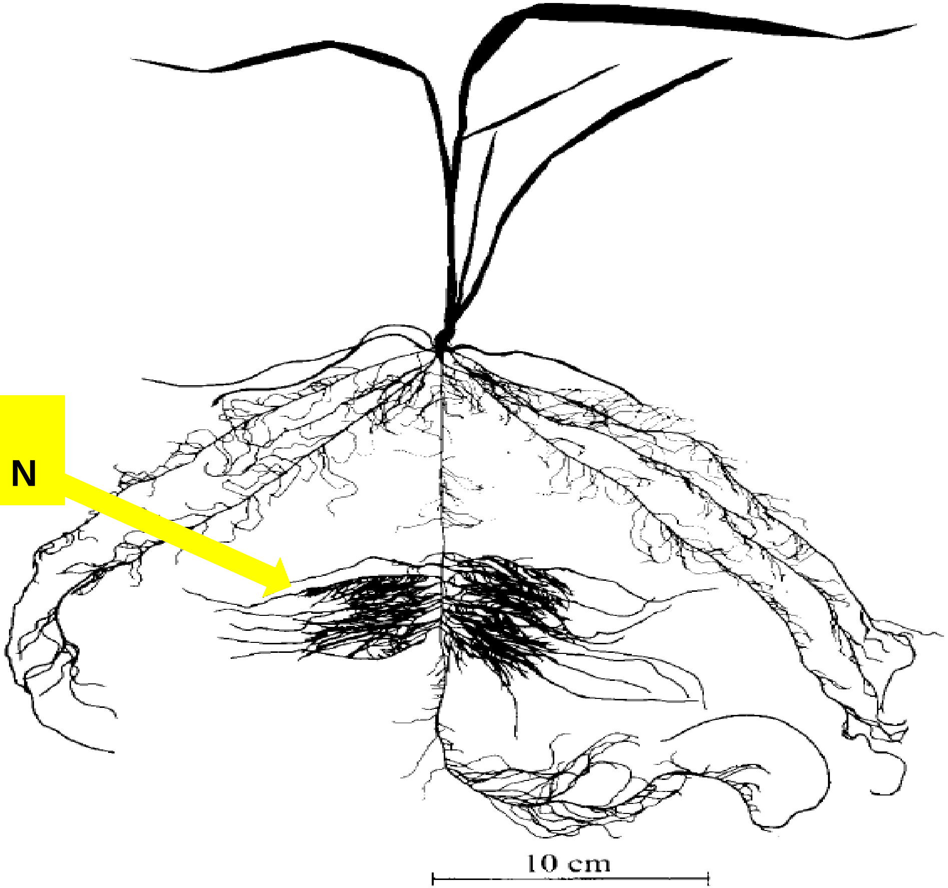


FIG. 1. Effects of a localized supply of 1·0 mM nitrate on root growth in barley. The middle zone of one seminal axis was supplied with nutrient solution containing 1·0 mM nitrate while the remainder received 0·01 mM nitrate. The plant was grown for 20d at 16–18 °C.

Drew and Saker 1975

Not all root length is used for nutrient uptake

Table 3. Effective root length, L_V^*/L_V (%), where L_V^* is the root length per unit volume of soil at which diffusion-driven uptake equals measured uptake (see Table 1 and Fig. 2), and L_V is that measured in the experiment

Time (d)	Nitrogen treatment	
	Unfertilized	Fertilized
13	21.8	4.9
29	10.2	2.9
47	7.5	2.4
72	7.8	2.9
84	9.0	3.5
97	11.0	4.4
Mean	11.2	3.5
(SE mean)	(2.19)	(0.40)

Percent of root length active in nitrate uptake

Plant, Cell and Environment (1991) **14**, 77–85

What limits nitrate uptake from soil?

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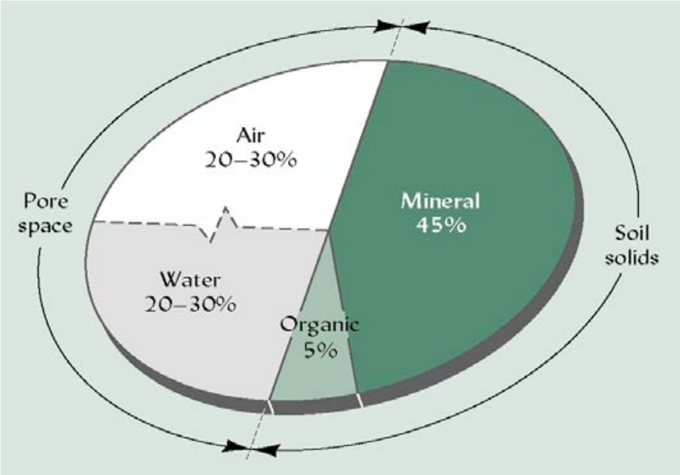
Soil structure

For satisfactory plant growth, it is essential that the soil provides a favorable physical environment for root development to provide the plant's needs for water, nutrients, and anchorage

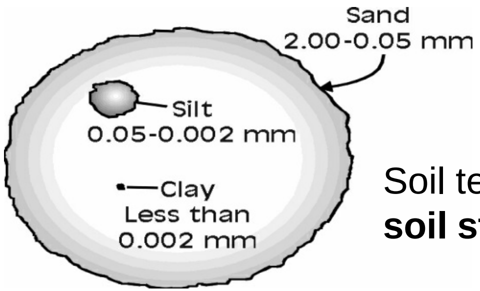
Factors essential for good root development

- Pore space
- Water
- Air / oxygen

Oxygen diffuses 10,000 times slower through water than through air. Too much water → not enough oxygen to support new root growth and root function



Mineral solids



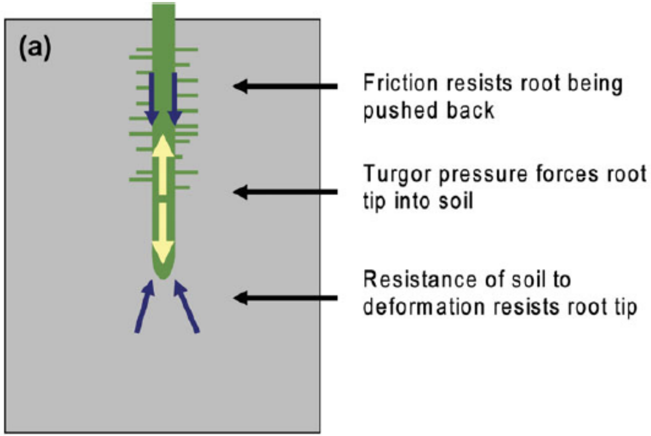
Soil texture affects **soil structure**

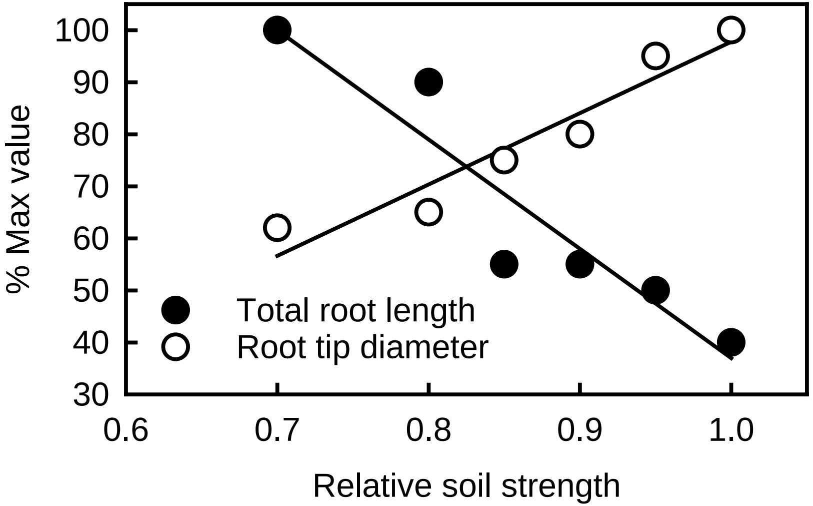
Soil pores (core part of soil structure)

- Volume of soil not filled with solids – spaces between the “dirt”
- Vary considerably in size depending on soil texture
- Macro-pores (>50 μm) – drain easily by gravity, allow rapid oxygen diffusion
- Micro-pores (<0.2 μm) – filled with plant unavailable water, very slow oxygen diffusion

- *Root hairs generally need pores >10 μm*
- *Most fine roots are >50 μm (really >100 μm) in diameter and thus fine roots need to grow through macro-pores or create their own macro-pores*

Increasing soil strength (penetration resistance) reduces root length production

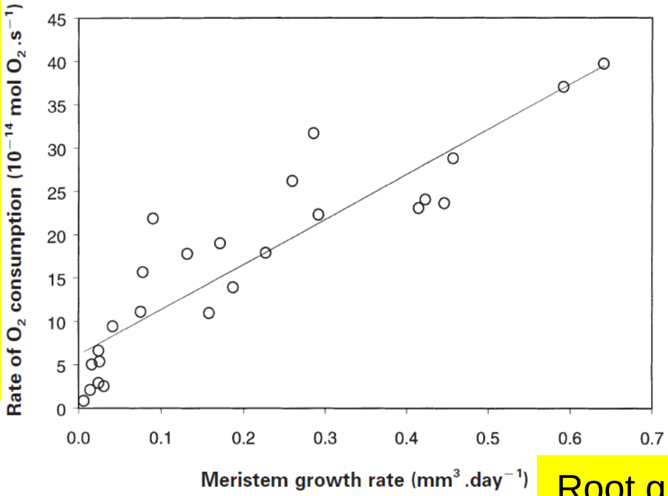




Soil strength is the combined effect of soil bulk density and soil water content. Both compaction (increases bulk density and decreases macro-pores) and low water content increase penetration resistance.

Oxygen is essential for root growth

Oxygen uptake



Root growth

Fig. 5. Relationship between meristem growth, expressed as the volumic rate of tissue production ($mm^3\ d^{-1}$), and O_2 consumption of the meristem (mol $O_2\ s^{-1}$) ($r^2 = 0.90$). The efficiency in root respiration was close to 6.62×10^{-4} mol $O_2\ g^{-1}$ dry matter.

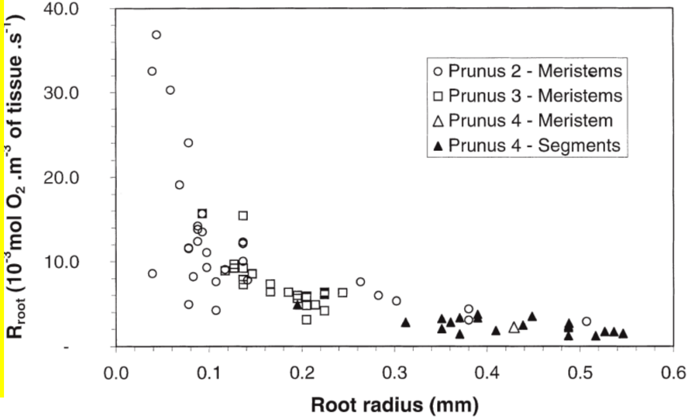
Journal of Experimental Botany, Vol. 51, No. 345, pp. 755–768, April 2000

Journal of Experimental Botany

Mapping meristem respiration of *Prunus persica* (L.) Batsch seedlings: potential respiration of the meristems, O_2 diffusional constraints and combined effects on root growth

L.P.R. Bidel[1], P. Renault[2,4], L. Pagès[3] and L.M. Rivière[1]

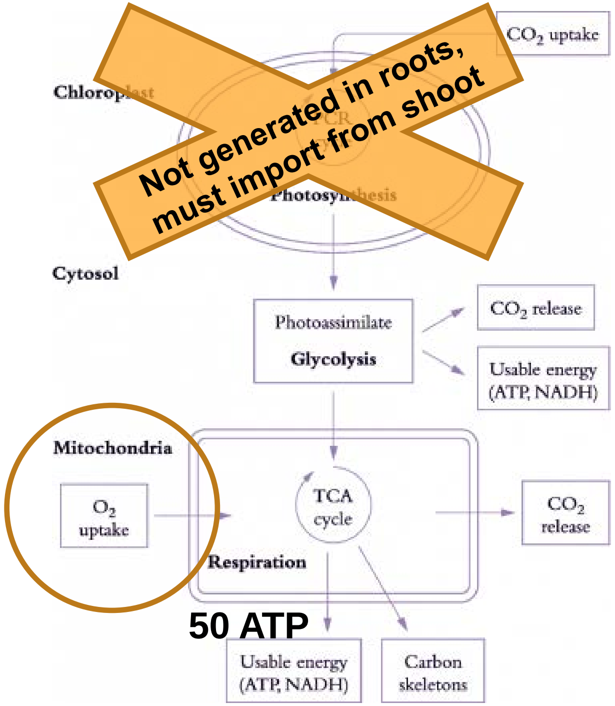
Oxygen uptake



Very fine --------------------→fine

- A greater root growth rate requires more oxygen
- The finest roots (those with the most surface area per unit mass) require most oxygen

Oxygen is essential to generate energy (ATP) in roots



4-10 ATP

Converting to ATP requires O_2

TABLE 11.2
The maximum yield of cytosolic ATP from the complete oxidation of sucrose to CO_2 via aerobic glycolysis and the citric acid cycle

Part reaction	ATP per sucrose[a]
Glycolysis	
4 substrate-level phosphorylations	4
4 NADH	4 × 1.5 = 6
Citric acid cycle	
4 substrate-level phosphorylations	4
4 $FADH_2$	4 × 1.5 = 6
16 NADH	16 × 2.5 = 40
Total	60

Source: Adapted from Brand 1994.
Note: Cytosolic NADH is assumed oxidized by the external NADH dehydrogenase. The nonphosphorylating pathways are assumed not to be engaged.
[a]Calculated using the theoretical ADP/O values from Table 11.1.

***PLANT PHYSIOLOGY*, 5e, Table 11.2** Taiz and Zeiger Plant Physiology

Without O_2, the total ATP yield from one sucrose is 4 ATP instead of 60 ATP → a loss in efficiency of 93%

Reproduced from Plants in Action, http://plantsinaction.science.uq.edu.au, published by the Australian Society of Plant Scientists. Chapter 6

Most respiratory energy is used for nutrient uptake & assimilation

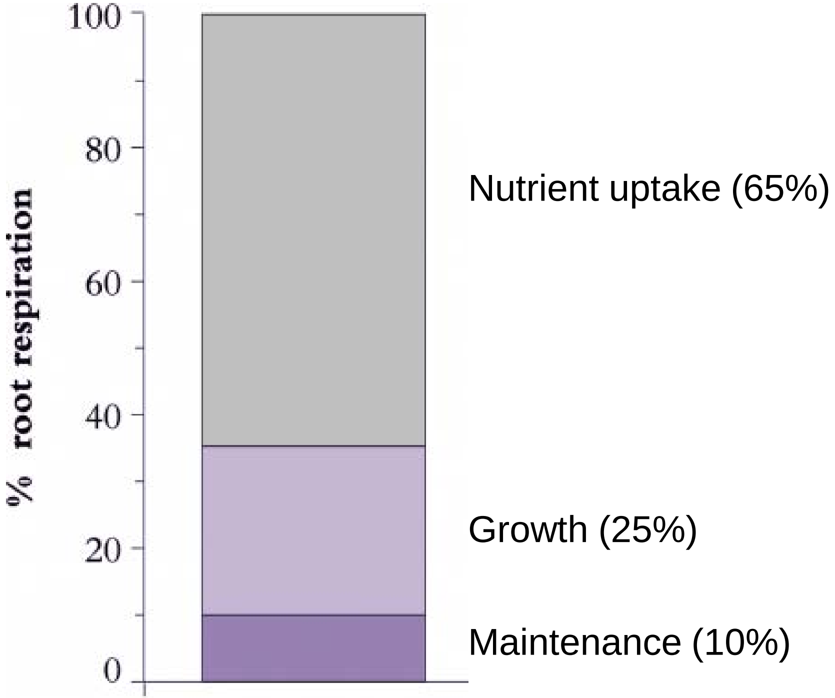


Table 6.7

Construction costs of synthesis of compounds in plant tissues (g glucose needed per g of organic compound) in plant tissues. Non-structural carbohydrate includes sucrose and starch.

Compound	Glucose needed (g per g)
Lipids	3.03
Lignin	2.12
Protein (using NO_3^-)	2.45
Protein using NH_4^+	1.62
Cellulose	1.22
Non-structural carbohydrate	1.09
Organic acids	0.91

Based on Poorter 1994; Penning de Vries et al. 1974

Reproduced from Plants in Action, http://plantsinaction.science.uq.edu.au, published by the Australian Society of Plant Scientists. Chapter 6

Favorable Physical Environment for Root Functioning

Water (requires smaller pores to hold water against gravity)

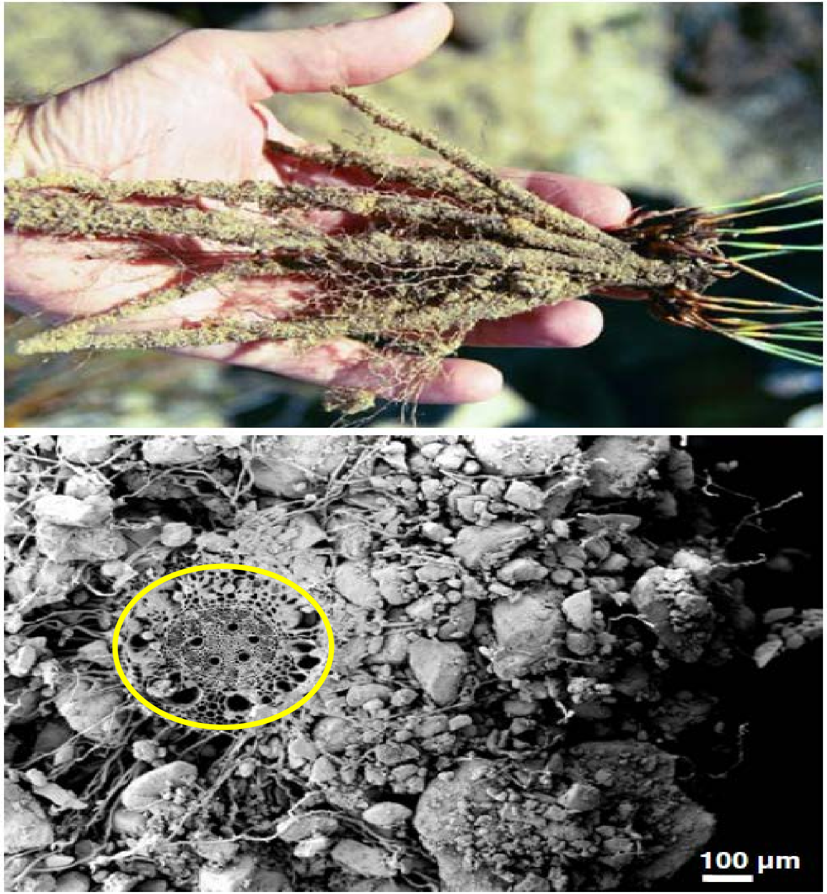
- Reduces resistance to root growth
- Essential for cell elongation as well as leaf gas exchange and overall plant growth

Oxygen (requires air filled pores – macro-pores)

- Energy is used for cellular maintenance, root growth AND nutrient uptake
- Respiration ***in the presence of oxygen*** yields 15 times more energy (ATP)

Nutrients

- Stimulates fine root proliferation and overall plant growth



Fine root ~0.5 mm in diameter

Fig. 2 Rhizosheaths formed around roots of *Lyginia barbata* R.Br. (top photograph) and barley (*Hordeum vulgare* L., bottom micrograph). Micrograph obtained by cryoscanning electron microscopy of the rhizosheath sampled in situ in field-grown barley plants. Development of long root hairs and their role in aggregating the soil thereby forming the rhizosheath is clearly visible (Reproduced by kind permission of Philippe Hinsinger (top photograph) and Margaret E. McCully)

Roots and their surrounding soil and soil microbiota have an intimate connection and a strong impact on each other

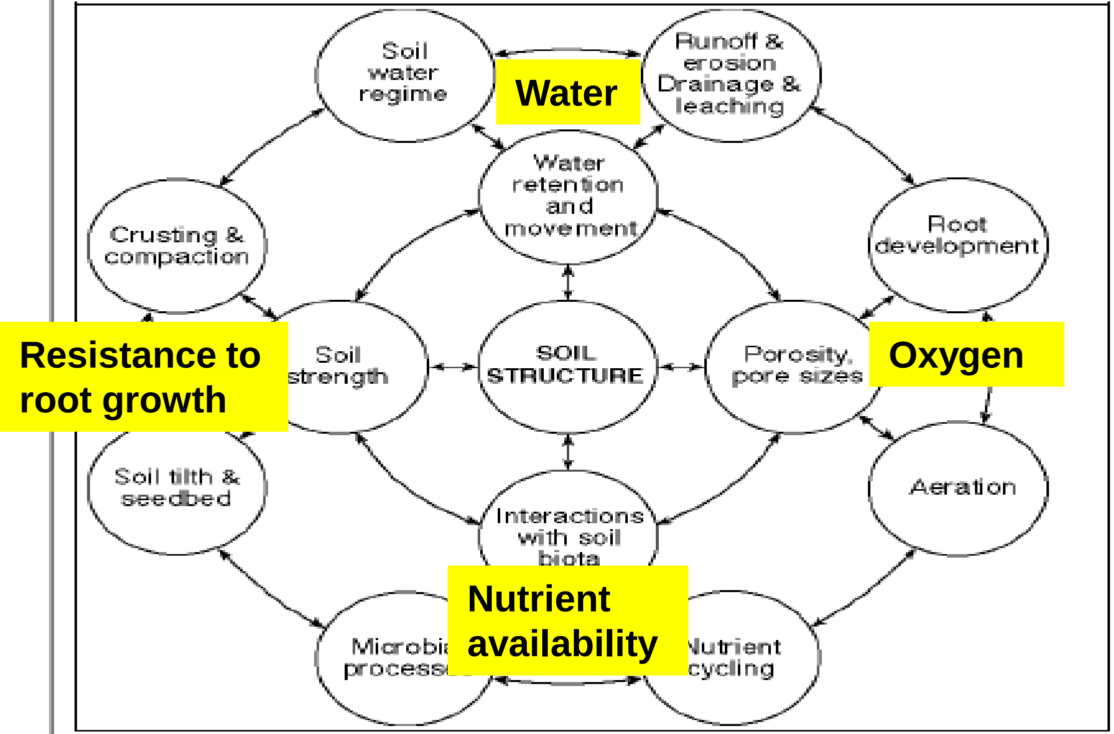
Plant Soil (2009) 321:117–152
DOI 10.1007/s11104-008-9885-9

REVIEW ARTICLE

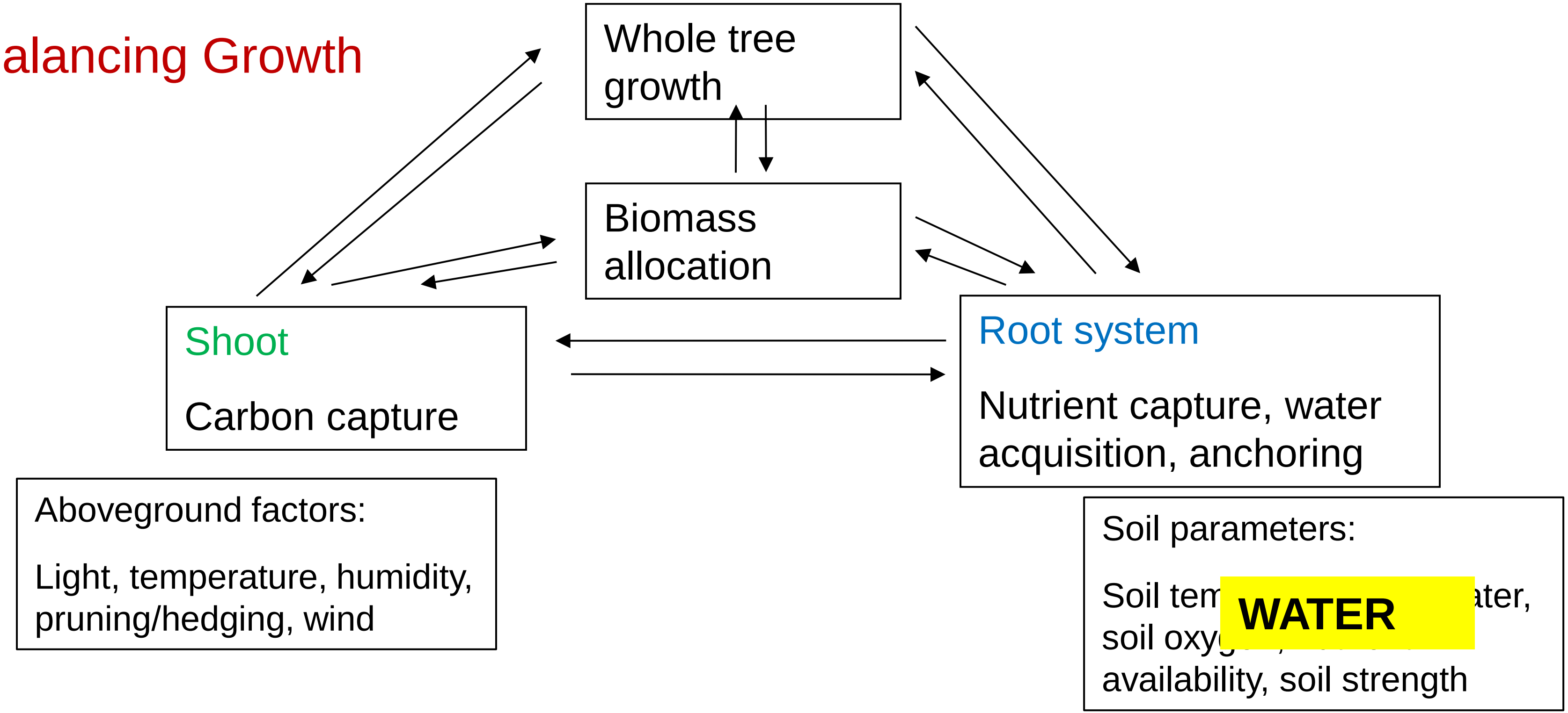
Rhizosphere: biophysics, biogeochemistry and ecological relevance

Philippe Hinsinger · A. Glyn Bengough ·
Doris Vetterlein · Iain M. Young

FIGURE 1
The central importance of soil structure (after Lal, 1994)



Balancing Growth



Canopy management

Root system management

Questions?