Qq effets des températures élevées sur le développement des fruits

Some responses of fruit development to high temperatures

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9 avril 2015 – Journée Fruits et Semences, Paris

Foreword

- *Context of global climate change: periods of high T°, drought, flooding, …*
- *« Some » responses: this presentation does not pretend to be exhaustive!*
- *Increasing nr. of scientific papers (e.g. grapevine)*
- *« Echoes » to found in Zhamwu Dai & Marc Saudreau presentations*

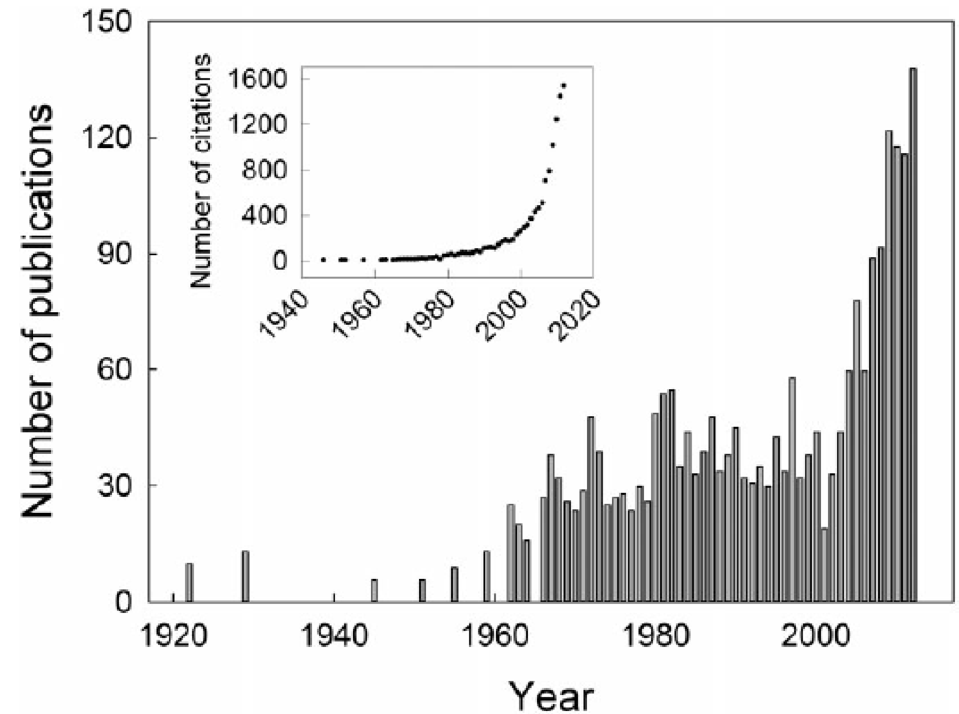


Figure 1. Yearly distribution of indexed publications containing the key words 'temperature' and 'grapevine' between 1909 and 2012. Inset shows the historical evolution in the number of citations of publications related to these key words. Data were obtained in November 2012 from the Web of Science (Thomson Reuters 2013).

Authors point out what follows:

"comparisons of thermally contrasting locations (and vintages) can be inconclusive as the effect of temperature is often confounded with other weather and climate factors" …

A rising interest to temperature effects on perennial plants
(e.g. grapevine : Bonada and Sadras, 2014. Aust. J. Grape & Wine Res. doi: 10.1111/ajgw.12102)

What are « high » temperatures?
What are we really measuring / considering?

- Air temperature?
- Organ temperature?

Determinants of temperature rise in plant organs

- Intensity of solar radiation
- Air temperature
- Wind speed (boundary layer is limiting the convective heat transfer)
- Limitation due to transpiration

$$\boxed{\Delta S = Rn + H + \boxed{\lambda E} + G + \cancel{M}}$$

ΔS: heat storage

Rn: net radiation (absorbed)

H: heat sensible heat flux (convection → air)

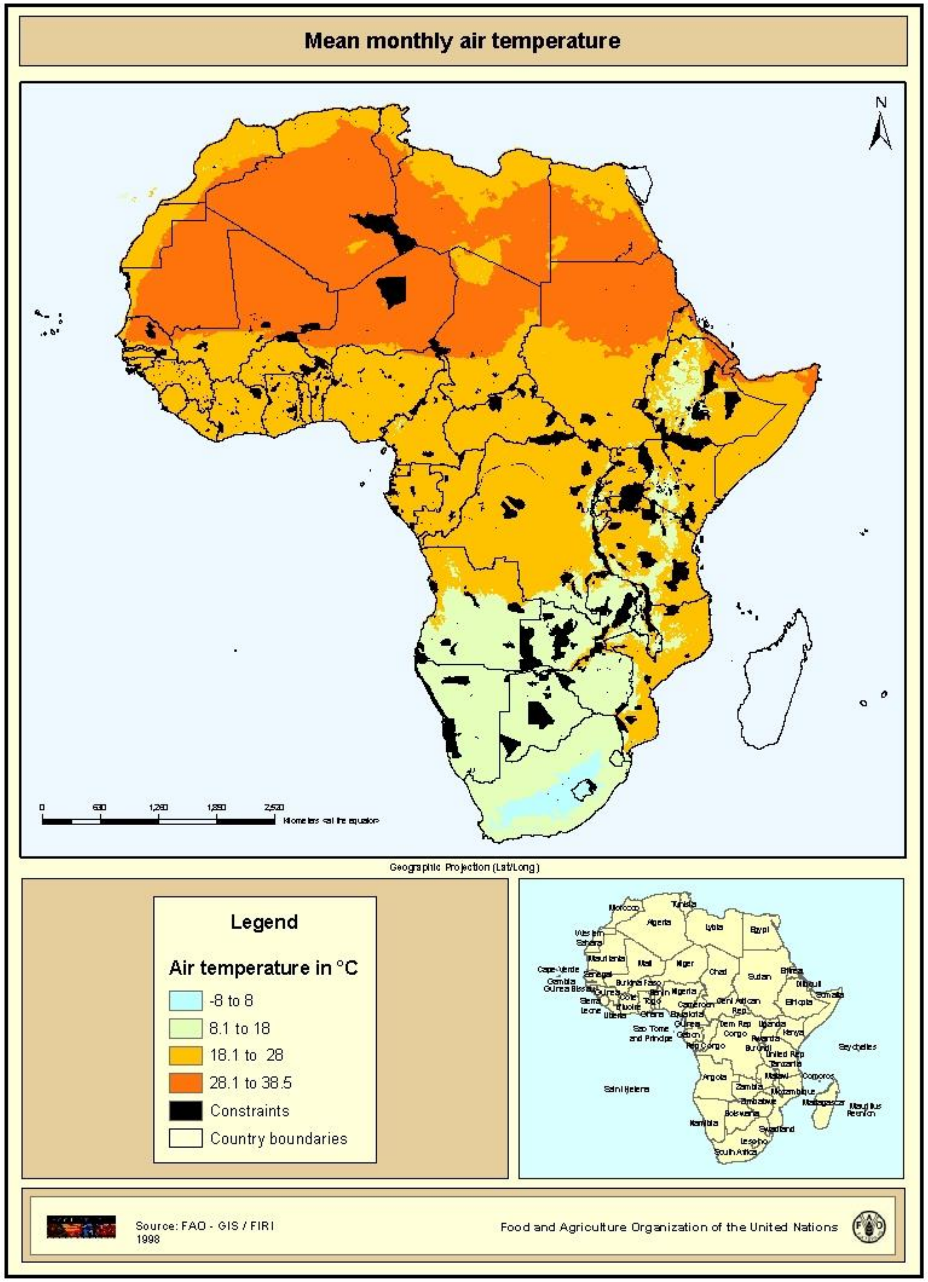
λE : latent heat flux (due to transpiration) λE: very limited for the fruit

G: conduction fluxes (from soil to plant → organ)

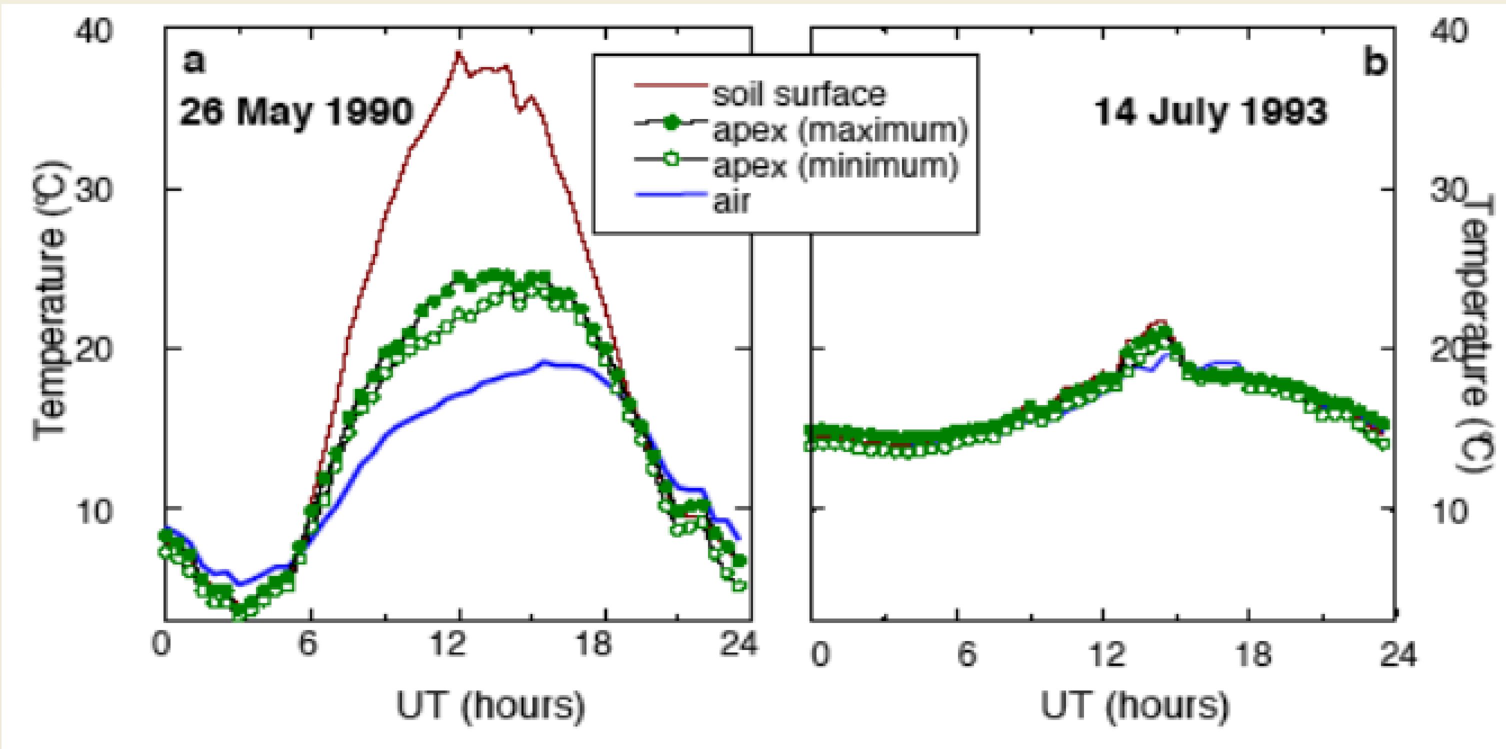
M: energy absorbed by biochemical reactions

Can we measure the sole temperature effects?

In many places, the heat effects are superimposed to that of drought :
e.g. the African continent (source FAO)



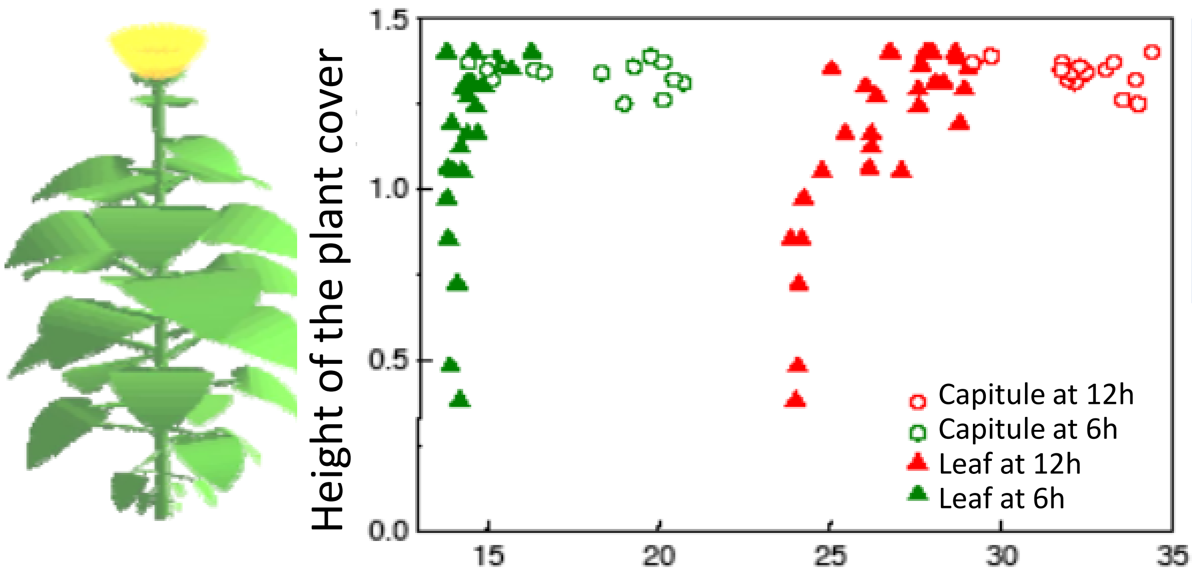
Discrepancies between air / plant temperature



a. Sunny days **b. Overcast sky**

(Guilioni et al., 2000. Agric. For. Meteorol. 100: 213–230)

Temperature gradients within the crop



Temperature (°C)

Temperature gradients measured in a sunflower crop

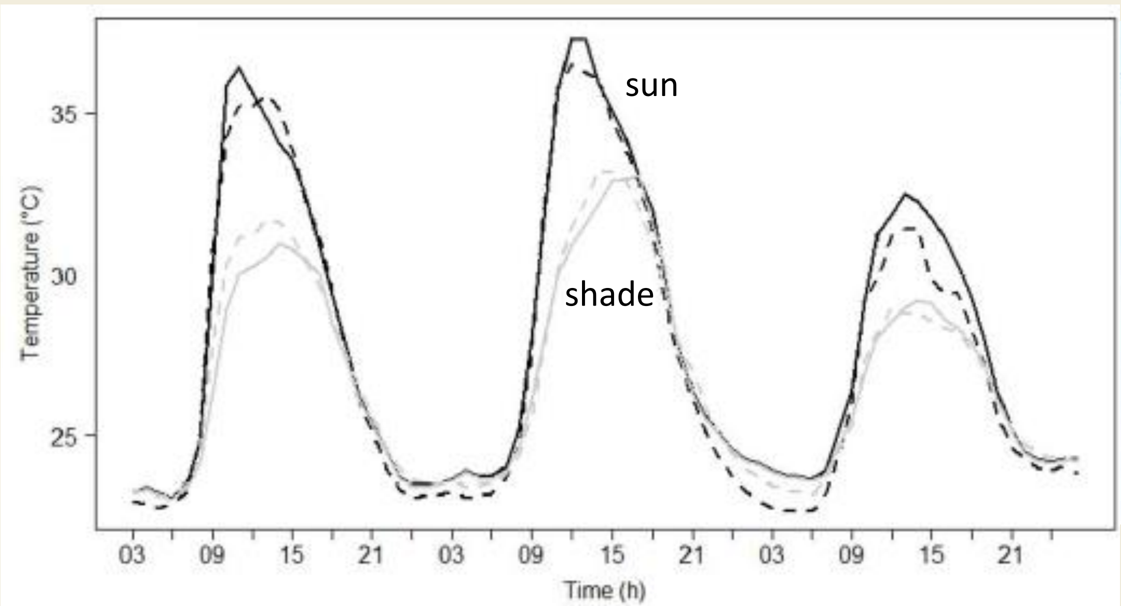
(Guilioni & Lhomme, 2006. Agric. For. Meteorol. 138: 258-272)

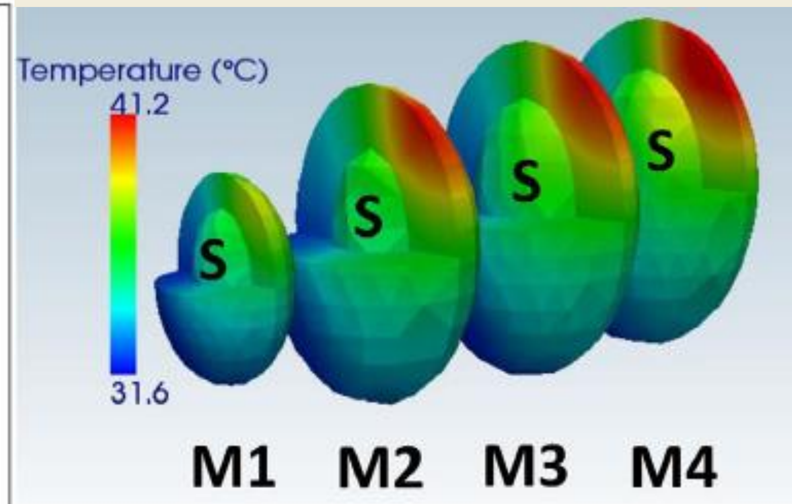
Capitules: more hot

Leaf T° depends on position within the plant cover

Variation of organ temperature according to sun exposure

For the same mango fruit, the strongest T° differences (sun vs shade) can reach 5° to 10°C





→ Successive maturity stages →

Variation of fruit T° (dashed line: measured ; solid line: modelled)
(grey : shaded side of mango peel ; black: sun-exposed side)

(Nordey et al., 2014. PlosOne 9: e92532).

But: heterogeneity of internal fruit quality traits not correlated with the internal T° gradients.
(Nordey et al., 2014. J. Plant Physiol. 171: 1555–1563).

Heat avoidance

- **Mitigation of incoming/intercepted energy**
  - **e.g. hail nets**
- **Leaf pubescence : ↗ leaf reflectance**
- **Leaf inclination**
  - **e.g. Eucalyptus**
- **Transpiration maintained / increased**
  - **e.g. Cotton**

Heat escape (?) Perennial plants can hardly escape main abiotic constraints; this is the case for the heat stress

- **Reflective spray / evaporative cooling**
  - **e.g. Apple** (Gindaba & Wand, 2007)

Definition of temperature thresholds?

- A complex question (effects depend on the intensity of T° constraint, duration, period of the cycle!)
- Scientific consensus in cereals (?) based on the observation of plant response

15° < T < 32°C : moderate T°

T° modifies existing processes: through their speed and duration

32° < T < 50°C : very high T°

high T° impedes or disrupts some metabolic processes

new metabolic activity are induced

50° C < T : lethal temperatures

Stone P. (2001) .The effects of heat stress on cereal yield and quality. In Crop Responses and Adaptations to Temperature Stress (A.S. Basra, ed.), pp. 243–291. Food Products Press, Binghamton, NY, USA.

- Accurate assessment of temperature threshold is lacking on fruits

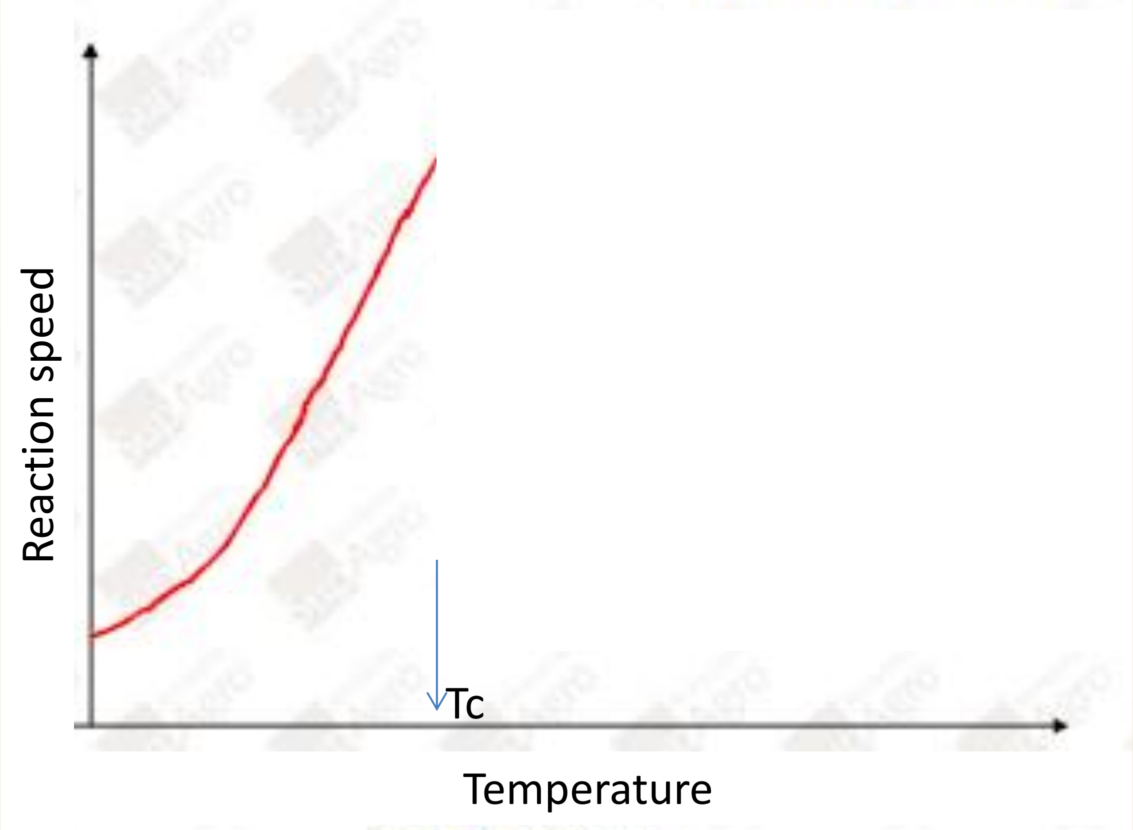
General effects of temperatures

General effects of temperatures

- « The effects of temperature on growth and productivity is the most complex topic in environmental physiology since it integrates all processes » (Lakso, 1994; *).
- A comprehensive coverage of this topic is beyond the scope of this presentation (e.g. pressure of pests and diseases not included ; cf. presentation M. Saudreau).
- Before addressing the effect of high temperature extremes, some general effects of temperatures need to be presented

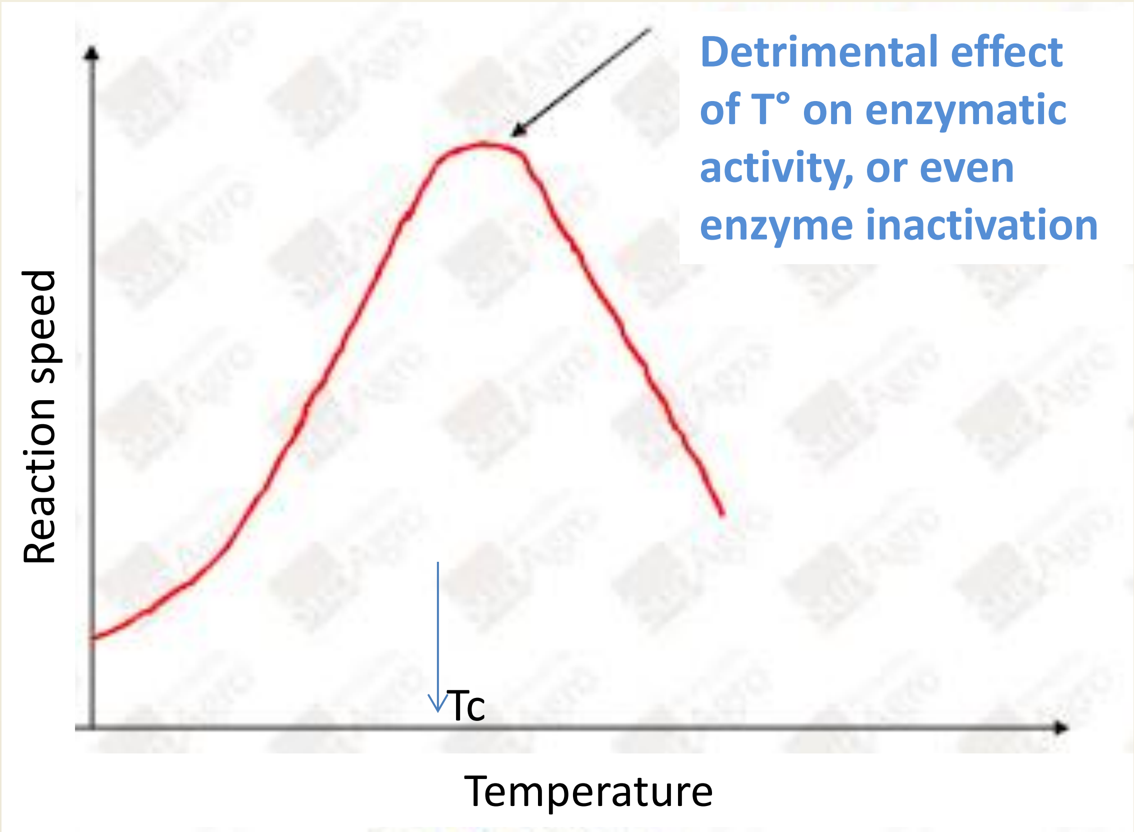
* Lakso A.N., 1994. Apple. Handbook of environmental physiology of fruit crops. Vol. 1. pp. 3-35. (Schaffer, B. & Andersen, P. C., eds). CRC Press Inc. – Univ. of Florida

Numerous enzymatic reactions are temperature driven



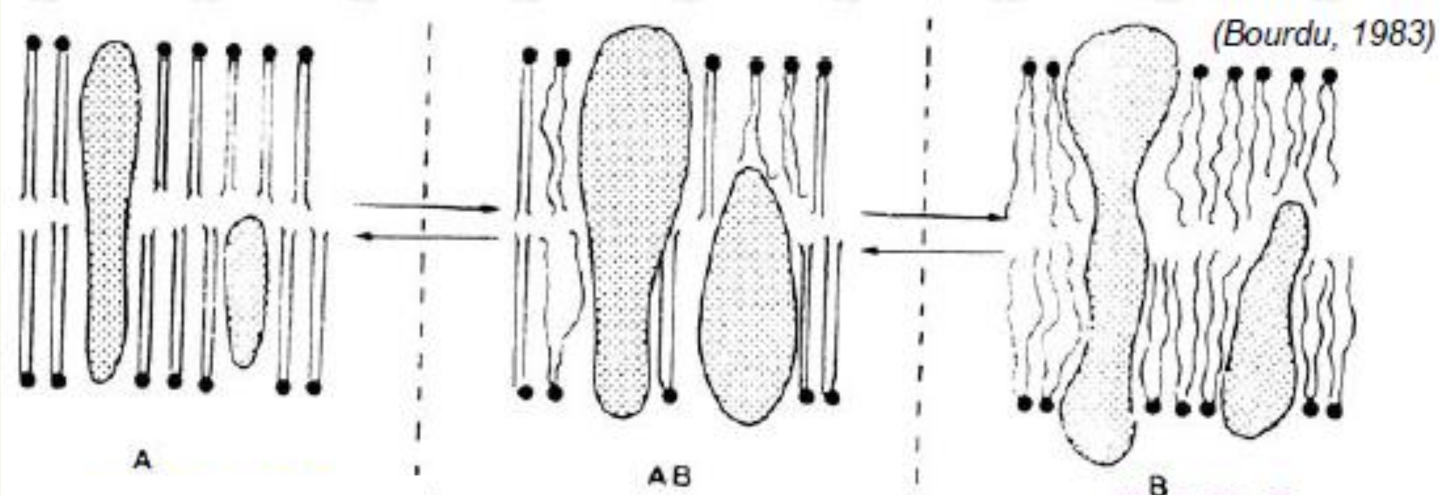
The crop functioning is a complex combination of multiple processes that all depend on particular temperature dependence
(source: L. Guilioni)

Numerous enzymatic reactions are temperature driven



The crop functioning is a complex combination of multiple processes that all depend on particular temperature dependence
(source: L. Guilioni)

Effect of temperature on the cell membranes



Low fluid cell membrane: Contracted protein structure ; P-lipidic chains rigorously organized

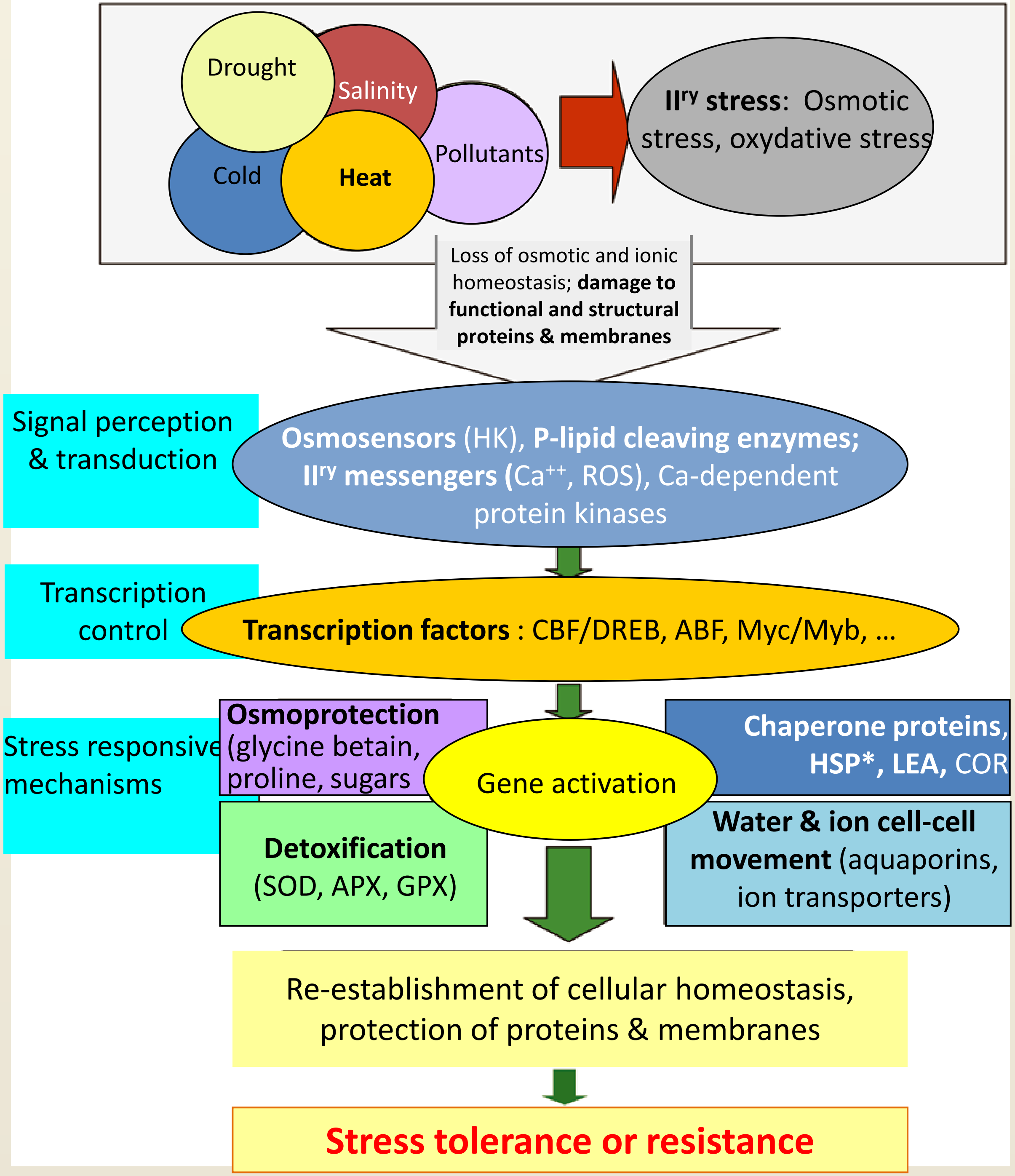
Semi-permeability (medium T°).

Optimal fluidity

Excessive cell membrane fluidity
More hydrophilic links; disorganized lipidic chains ; electrolytes leak

General scheme of cellular response to abiotic stress (incl. heat)

(Wang et al., 2003. Planta 218: 1-14



* Heat shock proteins

Heat shock transcriptional factor (HSFs)

"Trees are organisms with long lifespans that regularly experience climatic fluctuations. Survival and reproduction is dependent upon an array of protective mechanisms that involve the activation of a wide range of transcriptional factors, and their products are considered to play a central role in response to extreme physiological conditions.
There is evidence that heat shock transcriptional factors (HSFs) are important regulators in sensing and signaling of different environmental stresses ».

(Giorno et al., 2012. BMC Genomics, 13: 639)

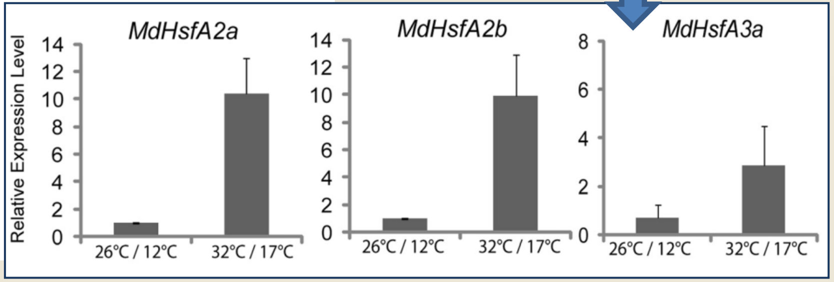
25 full length HSFs identified in apple.

Tissue and organ type (DFCI Apple Gene Index)

Gene name	Leaf	Root	Flower	Fruit	Shoot	Phloem	Xylem	Seed	Bud
MdHsfA1a	+		+	+	+	+			
MdHsfA1b				+					
MdHsfA1c				+					
MdHsfA1d	+		+	+	+	+			
MdHsfA2a		+	+		+				
MdHsfA2b		+							
MdHsfA3a					+				
MdHsfA3b					+				
MdHsfA3c					+				
MdHsfA4a		+	+						
MdHsfA5a		+	+	+					
MdHsfA5b		+	+	+					
MdHsfA8a				+					
MdHsfA8b				+					
MdHsfA9a	+								

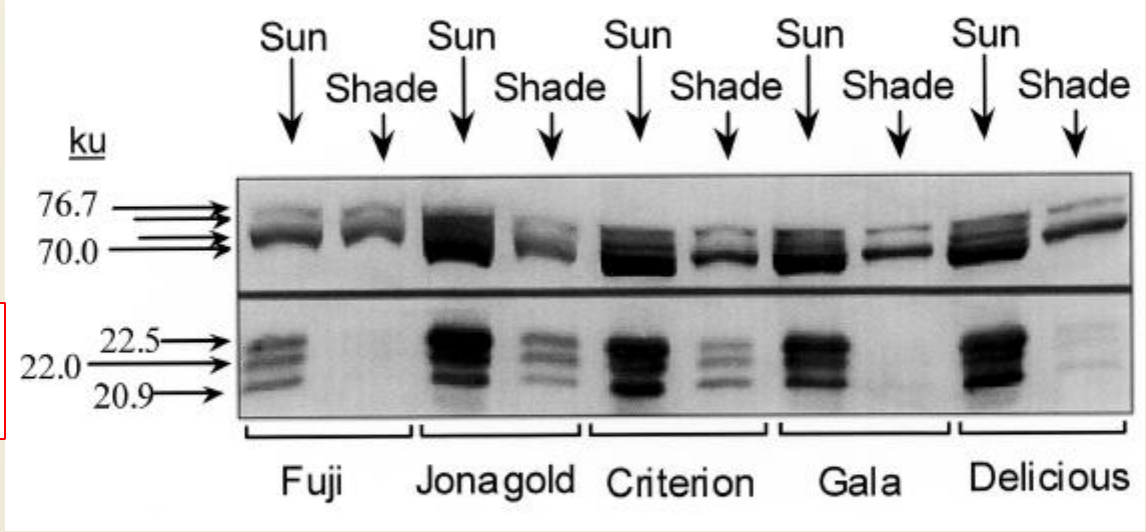
Expression of HSFs in ≠ Malus tissues.

Transcriptomic analysis of 3 HSFs under high T°



Heat shock proteins (HSP) are synthesized in response to heat stress and prevent disruption of cell biochemical processes

Small HSPs



- Small molecular weight HSPs rapidly produced in full sun- exposed apple peel
- Accumulation detected 48 hours after a 4-hour heat treatment

Immunoblots of total proteins (35 µg/lane); apples sampled on Aug. 17.
Blots probed with antibodies against human HSP70 and pea HSP18.1.
Arrows indicate approx. mol. weights in unified atomic mass units (u)

(Ritenour et al., 2001. J. Amer. Soc. Hort. Sci. 126: 564–570).

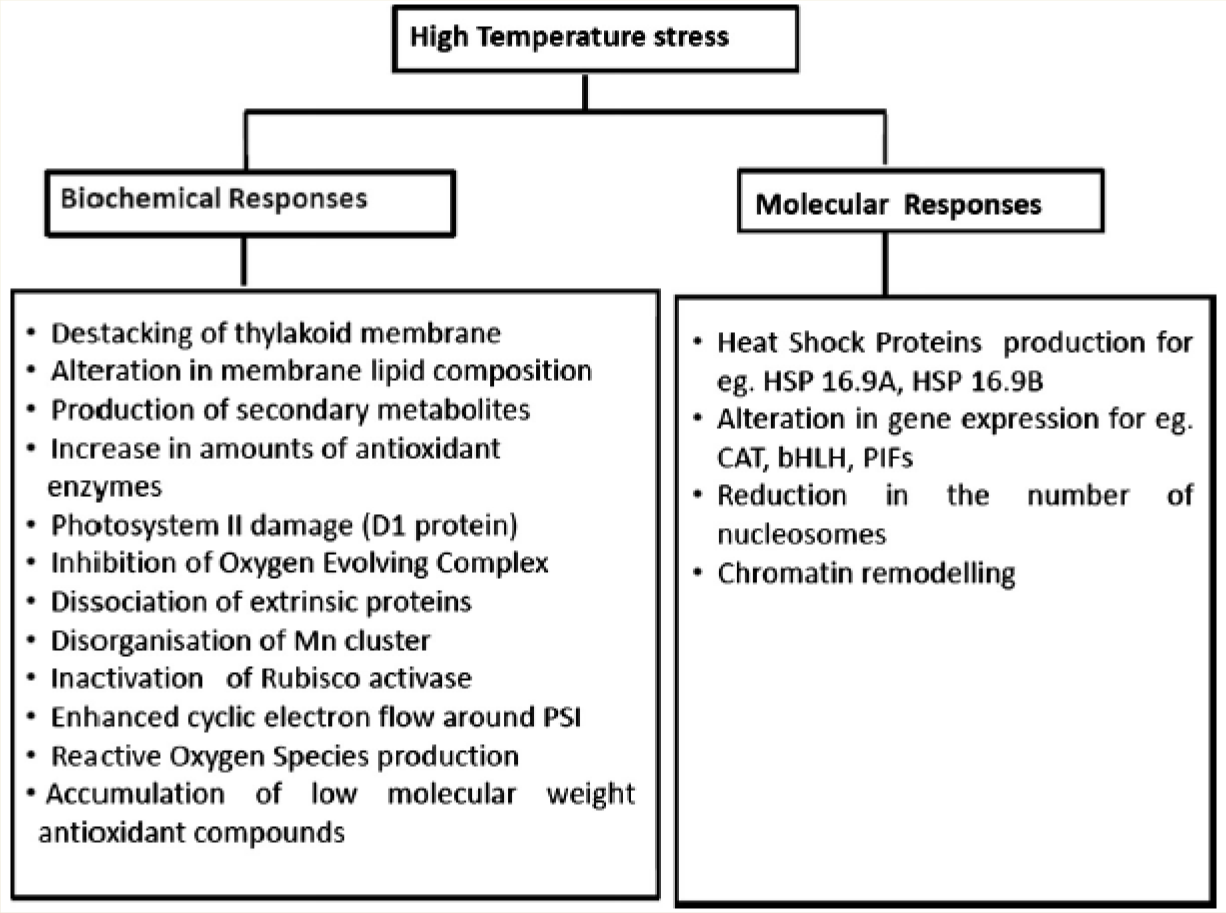
Proteomic approches

(Mediterranean woody sp. in response to abiotic stress)

- With regard to abiotic stress, a recent review on proteomic methodologies (covering 15 papers) enabled the identification and quantification of 395 stress-responsive proteins.
- These results revealed metabolic adjustments to stress, with major alterations in C, N, and amino acid metabolisms.
- The most consistently represented stress-responsive proteins are: RuBisCO, RuBisCO activase, heat shock proteins, chlorophyll a/b binding protein, and proteins from the oxygen-evolving complex.

(Pinheiro et al. 2014. Envir. Exp. Botany. 103: 117-127)

Cellular avoidance and tolerance mechanisms of plant in response to high temperature stress



(Mathur et al. 2014. J. Photochem. and Photobiol. B: Biology, 137: 116–126).

Some effects of temperature rise on fruit developemt

Effects of temperature on fruit trees

- « The effects of temperature on growth and productivity is the most complex topic in environmental physiology, since it integrates all processes » (Lakso, 1994).

- Many fruit tree processes are impacted by temperature:

  Respiration costs (as a whole)

  Blooming duration, ovule fertilization, fruit set,

  Vegetative growth rate, duration; Canopy net photosynthesis

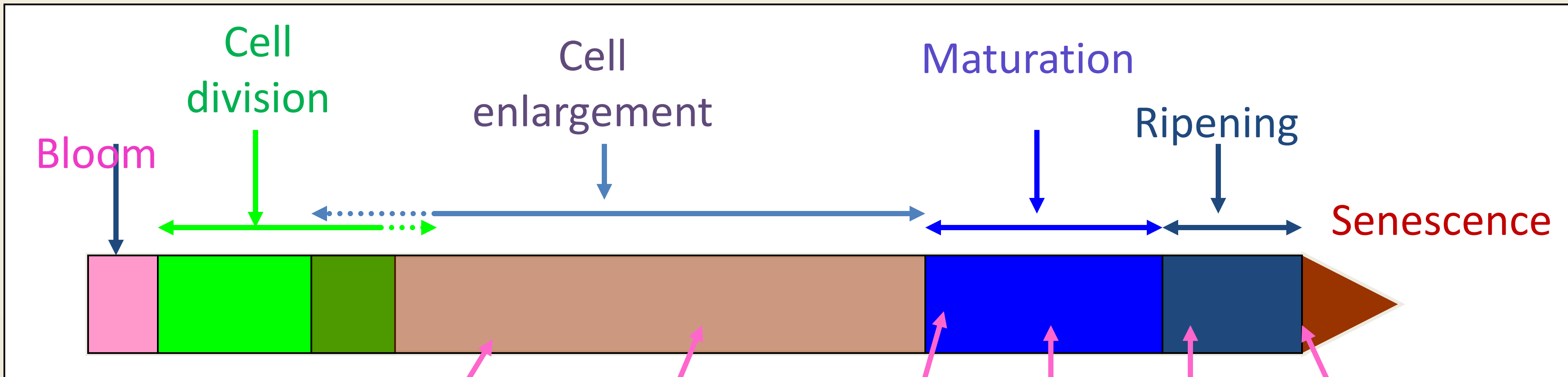
  Fruit growth rate; maturity processes

  Fruit quality (& disorders)

→ Resulting yield = a combination of these processes

General framework of fruit development

- Development stages (by courtesy of J.J. Kelner)



- Harvest stages:

Zucchini
French beans

Gooseberry
Cucumber

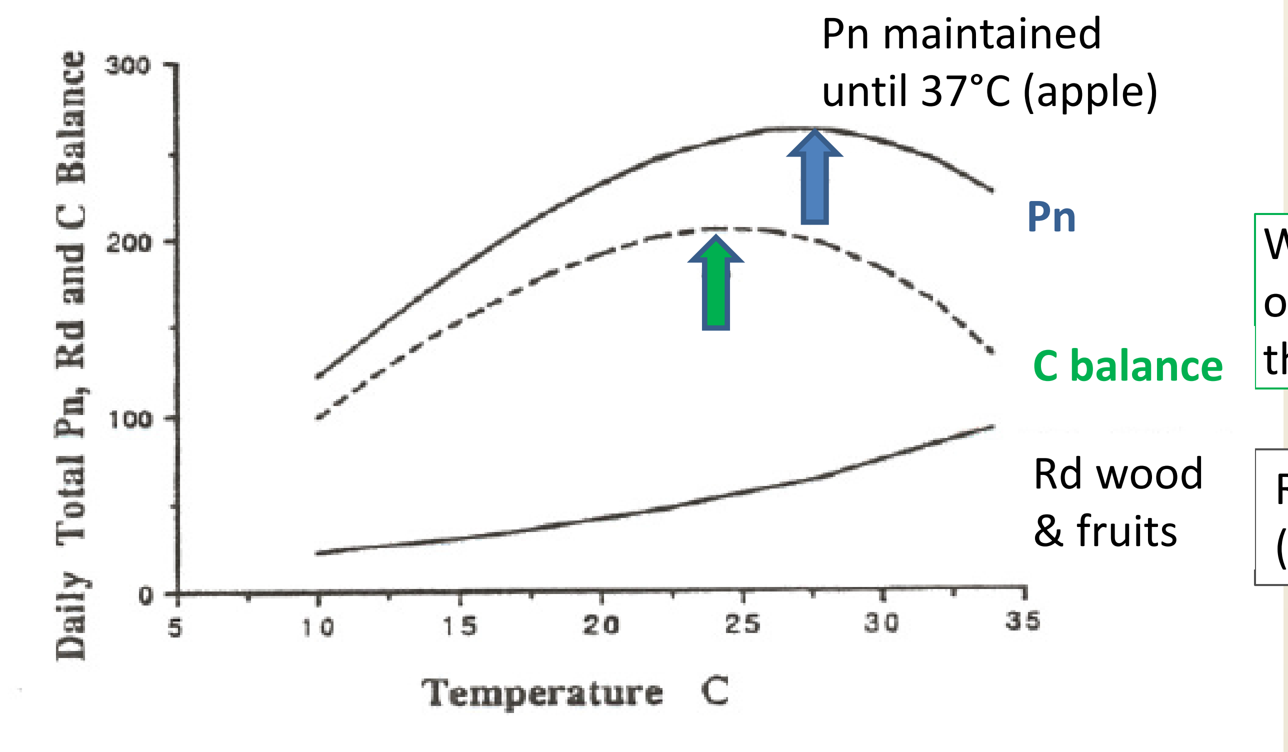
Apple
Pear

Peach
Apricot

Grape
Cherry
Tomato

D'Agen
Plum

Temperature, respiration costs and carbon balance



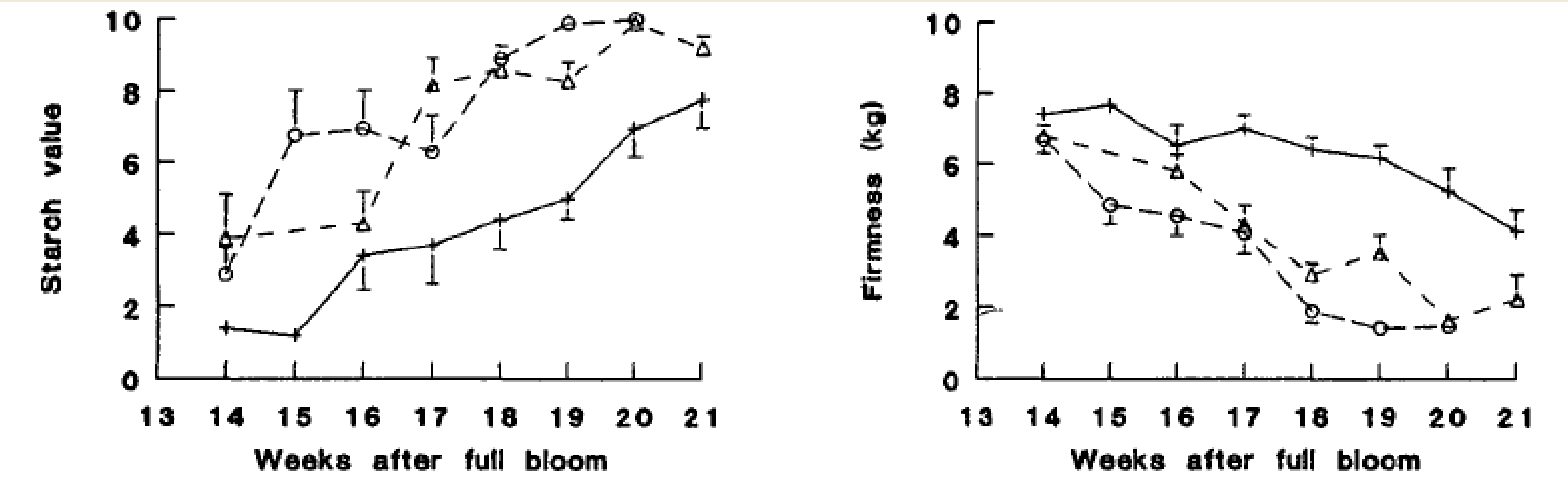
Whole tree C gain: the optimum T° is lower than that of Pn

$R = a\ e^{kT°}$
(T° range: 0°-42°C)

Lakso A.N., 1994. Apple. Handbook of environmental physiology of fruit crops. Vol. 1. pp. 3-35. (Schaffer, B. &Andersen, P. C., eds, CRC Press Inc. – Univ. of Florida)

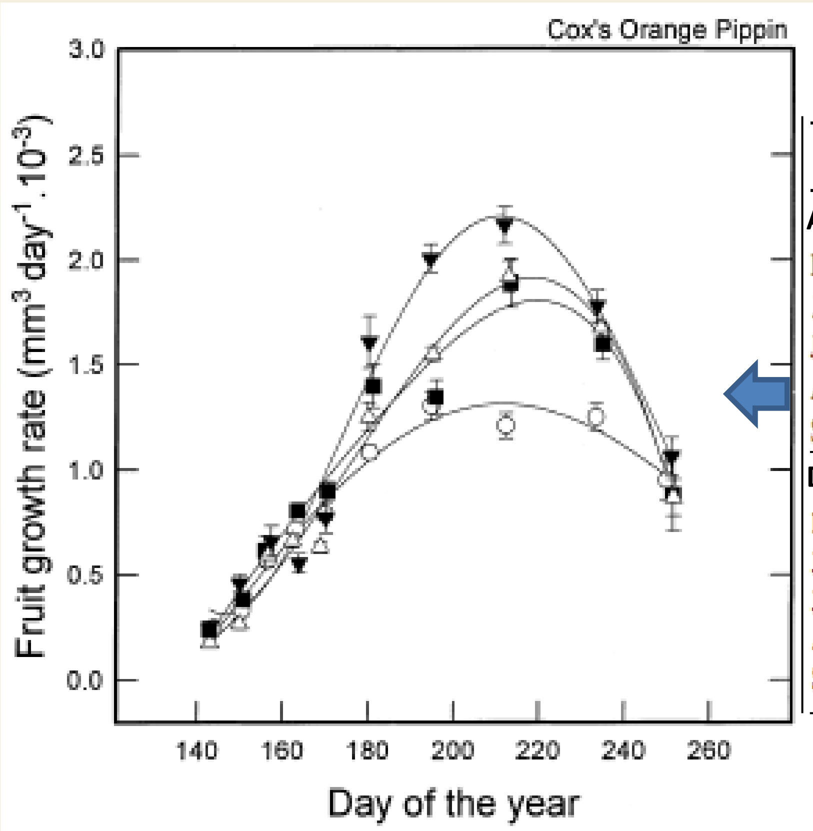
After fruit set : at cell division stage

- **T° occurring in the month following bloom** in apple are crucial.
  « During this 3-4 weeks period **carbon balance may be critical**, and high temperatures especially at night have been found to cause fruit abscission » (e.g. Dennis F.G. Jr, 1979. Hortic. Rev., 1: 395 ; cited by Lakso, 1994)
- **Maturity** of 'Elstar' apple **is hastened by a more elevated T°** during 6 wks after bloom, without change after this period. (Tromp, 1997).



'Elstar' apples grown at 16 (+), 20 (△) or 24°C (○) for six weeks following bloom.

Fruit growth rate



Mean 24 h average air and soil T° and calculated degree-days from 3 positions in the tree canopy

	PT		HP		Outside	
Air temperatures						
May	15.4[a]		13.8		13.8	
June	17.7		16.5		16.4	
July	17.5		16.6		16.7	
August	17.0		16.0		16.2	
September	14.5		13.7		13.7	
Degree-days	PT	cumul.	HP	cumul.	Outside	cumul.
May	271		220		220	
June	419	690	370	590	370	590
July	426	1116	395	981	395	985
August	411	1527	381	1372	381	1365
September	236	1764	204	1575	210	1576

Fruit growth rate in 'Cox's Orange Pippin' apple hastened by tunnel forcing (Atkinson et al., 1998)

Closed triangle: polytunnel (**PT**)
Open triangle: partial polytunnel (**HP**)
Closed square: **Outside** in the orchard, with irrigation
Open circle: **Outside** in the orchard, without irrigation

Modelling duration of fruit development / air T°

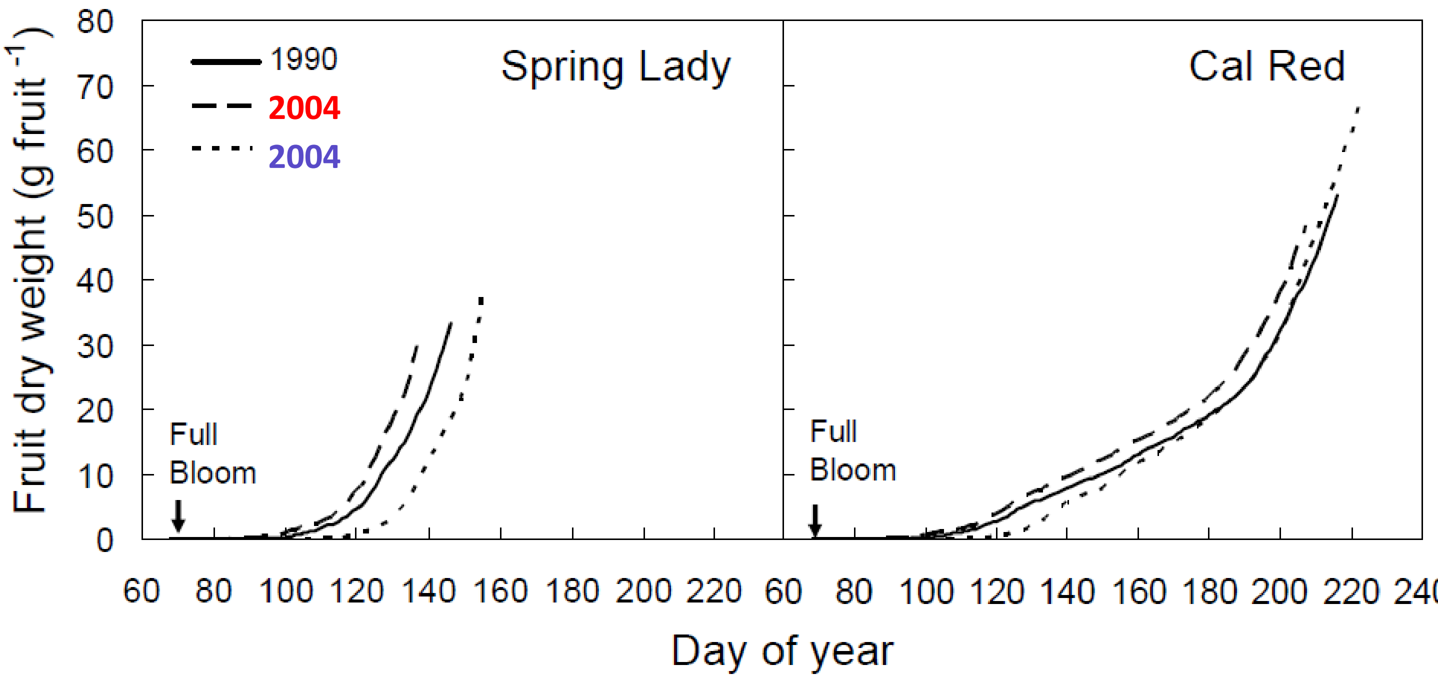
(Marra et al., 2002. Acta Hort. 592: 523-529).

Cultivar	Sampled years (n)	Average FDP (days)	c.v.	Average error (± days)	DD*	c.v.	Average error (± days)	GDH**	c.v.	Average error (± days)
Maycrest	7	72	11.3	6,5	639,3	4.8	2,1	22779,1	3.1	1,4
Mayglo	3	90	5.6	3,6	803,7	8.6	4,9	28505,7	4.1	2,3
E. Lady	7	123	7.2	6,1	1437,2	6.5	4,4	44592,0	4.2	3,3
Fantasia	8	137	5.3	6,1	1691,7	6.1	4,6	49625,4	3.7	3,2
O'Henry	9	150	6.3	7,8	1977,4	6.2	4,7	56893,4	4.9	4,0
Mean			7.1	6,03		6.6	4,24		4.1	2,96

Thermal time calculated in terms of degree days (DD) (base T° : 7 °C, critical T° : 35 °C) or GDH (base T° : 7.5 °C, opt. T° : 26 °C , critical T° : 38.5 °C).
GDH showed a lower coefficient of variation and a higher predictive capacity, in terms of days, than DD for all of the cultivars tested.

Modelling duration of fruit development / air T° (2)

(Lopez et al. 2011. Acta Hort. 903: 1055-1062).



Simulated patterns of potential fruit weight of early-maturing ('Spring Lady') and late-maturing ('Cal Red') peaches during 3 yrs contrasting by spring T°.

2006 : one of the coolest springs on record, with a GDH30 of 3000.

1990 : representative normal year with a GDH30 of 5400.

2004 : warmest spring on record, with a GDH30 of 8500.

Hot springs → the earliest & smallest fruits.

Fresh springs → the latest and largest fruits

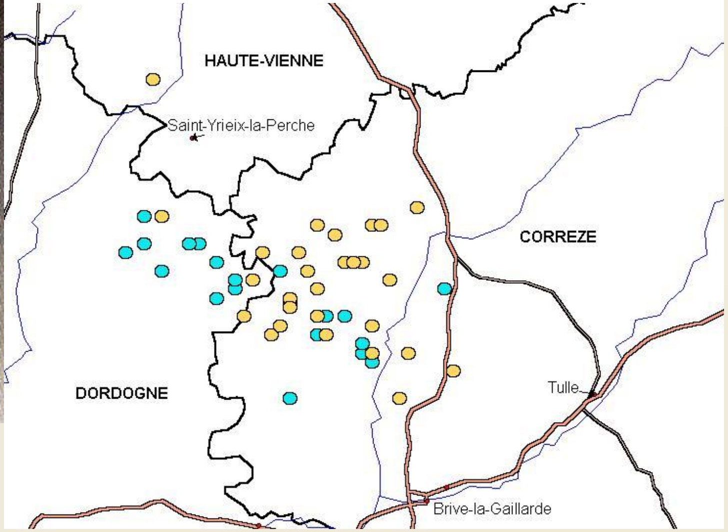
" fruit growth potential that is not realized within a given time interval is lost and cannot be made up "

Fruit shape : apple

'Golden Delicious' apple
Provence lowlands

'Golden Delicious apple'
hill + elevation (300-500m)

Pomme du Limousin (DOP / AOP)



Climate effects of fruit cell division phase and axial vs. equatorial growth rates are scarce.

Mean cell volume → effect on texture

Fruit shape : Citrus

Variations of ‘Valencia’ Orange and ‘Dancy’ tangerine fruit morphology as influenced by climate : coastal locations (less hot, less varying T°, less VPD) → more thin fruit rind, flatter shape.

	Santa Paula (CA)	Tustin (CA)	Lindsay (OK)	Thermal (CA)
lat.	34°31'N	33°74'N	34°83'N	33°64'N
alt.	86m	4m	32m	4m
côte à	15km	5km	560km	60km
climat	frais et sec, T° contrastées	frais et humide	chaud et sec	très chaud et très sec
Orange 'Valencia'	aplatie, petit calibre, écorce mince et lisse		sphérique, gros calibre, écorce épaisse et rugueuse	
Mandarine 'Dancy'	aplatie, petit calibre, écorce mince et lisse		sub-sphérique, assez gros	
			légèrement boursouflée	boursouflée, mamelon net

In The Citrus industry, vol II. (ed. Reuther W., Batchelor L.D. and Webber H.J., 1968).

Fruit texture

Food Bioprocess Technol (2013) 6:859–869
DOI 10.1007/s11947-011-0775-4

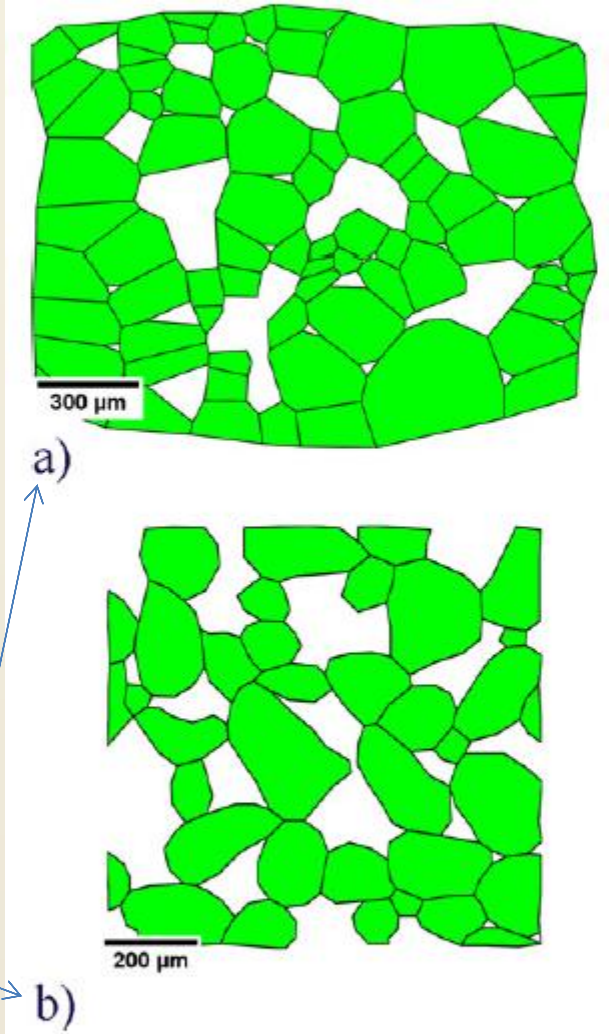
ORIGINAL PAPER

Virtual Fruit Tissue Generation Based on Cell Growth Modelling

Metadel K. Abera · Solomon Workneh Fanta · Pieter Verboven · Quang T. Ho · Jan Carmeliet · Bart M. Nicolai

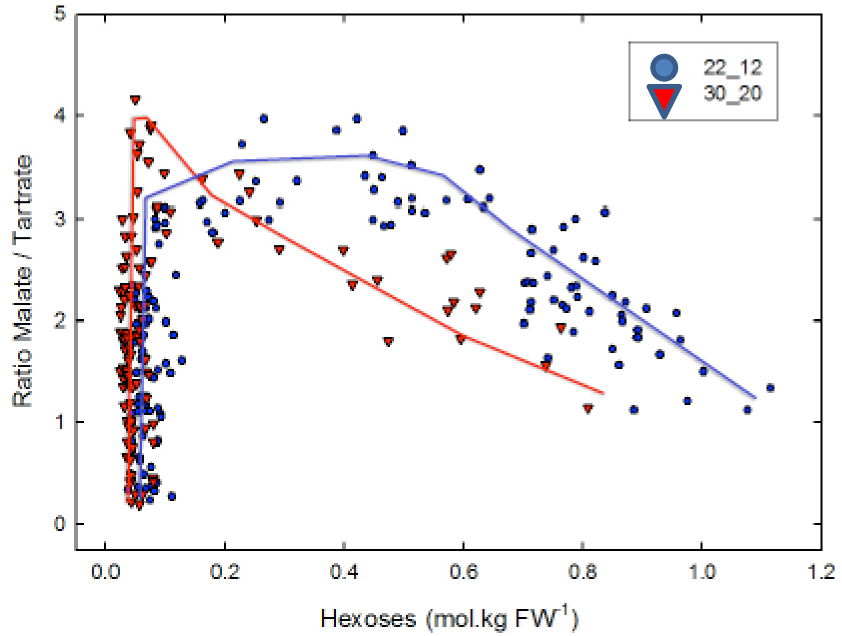
Illustration of tissue growth with intercellular air spaces of lysigenous origin and a small proportions of schizogenous origin:

a) tissue obtained using the growth model
b) digitised synchrotron radiation tomography image of apple cortex



Can such a 2D-model allow representation of T° effects on cell organisation at harvest stage? Other fruit models cou;d also be used (cf. Baldazzi et al., 2012)

Fruit quality : sugar / acid balance & polyphenols

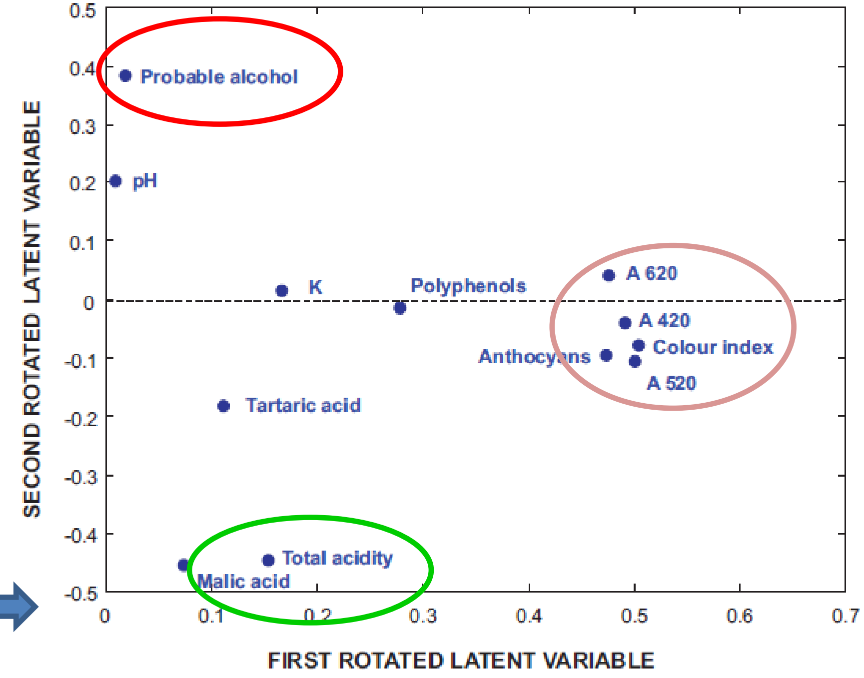


Malate/Tartrate ratio according to a sugar concentration scale (whole bunch) (M. Rienth, unpublished)

T°> 10°C are necessary for grape maturation

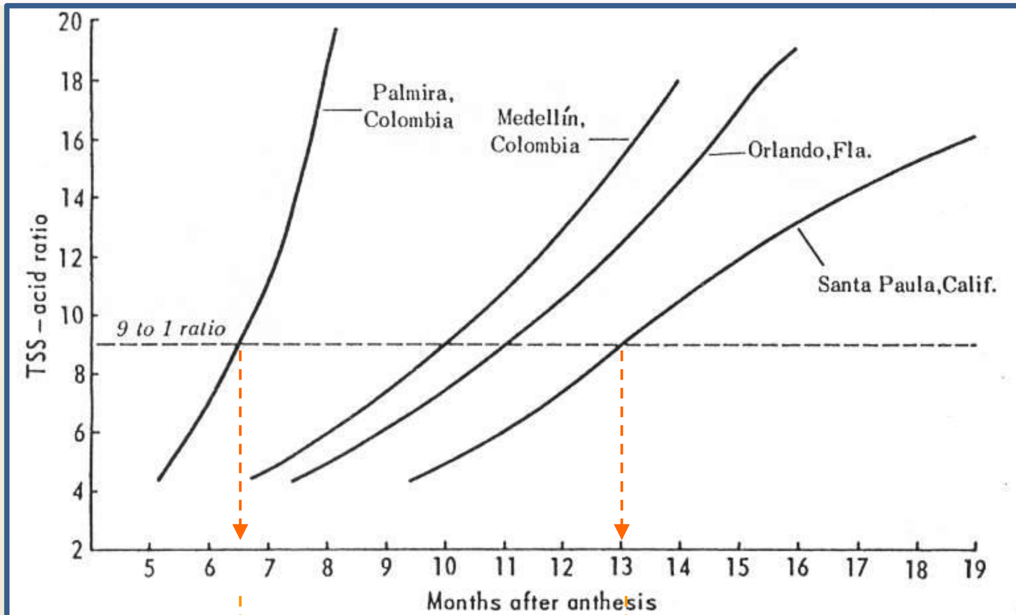
But high T° in grapevine:

- **Stimulates the malic respiration**, and lowers the M/T ratio (malic enzyme activity increases between 10° and 46°C)
- **Lowers the berry acidity** at maturity
- **Delays the phenolic maturity**

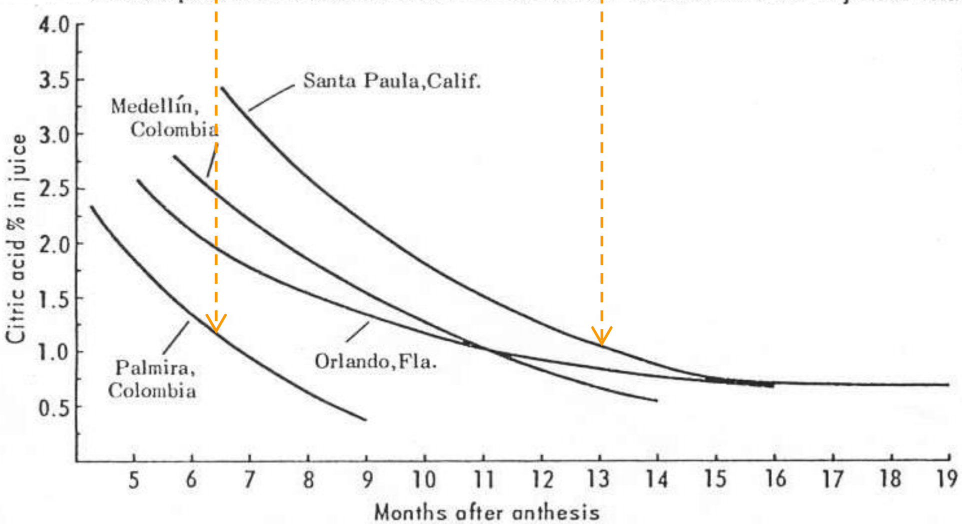


Different solutes accumulation does not respond to the same factors. Climate change increases separation of technologic and phenolic maturity (Meléndez et al., 2013. Anal. Chim. Acta 761: 53-61).

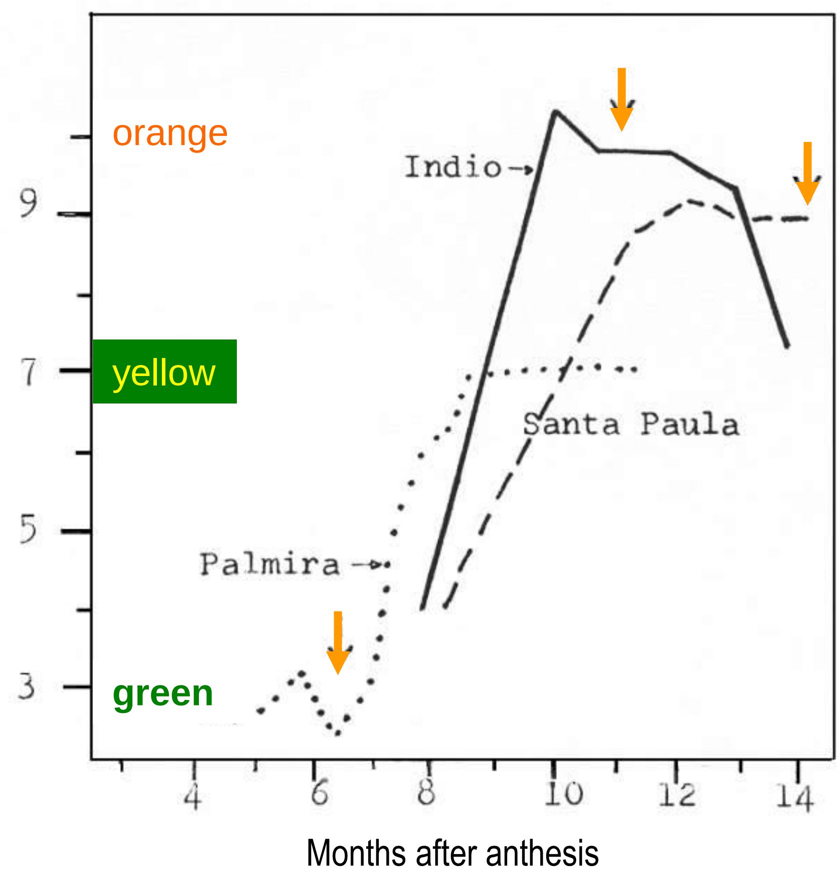
Pigments : peel chlorophyll and carotenoids



Schematic presentation of seasonal trends in the ratio of total soluble solids to acid in juice of Valencia



Sharp decrease of acidity in more hot locations



Evolution of 'Valencia' fruit colour for 3 climates.
Yellow arrows = beginning of harvest
→ No carotenoid synthesis in Palmira at harvest

Pigments : peel anthocyanin synthesis (1)

Warm nights delay onset of red colour (e.g. Red Chief).

Warm : 26° (day) / 22° (night) ; Cool : 26° (day) / 11° (night)

% color	Night temp.	Days after full bloom								
		86	93	100	107	114	121	128	135	142
0-25	Warm	100.0	96.2	89.5	63.0	37.0	23.5	11.5	0.0	0.0
	Cool	100.0	96.4	81.9	52.7	17.5	3.1	0.0	0.0	0.0
26-40	Warm	0.0	3.8	4.5	14.8	21.7	17.6	34.6	53.8	25.0
	Cool	0.0	3.6	13.9	32.7	35.0	34.4	26.3	0.0	0.0
41-66	Warm	0.0	0.0	6.0	18.5	37.0	35.4	30.8	7.7	25.0
	Cool	0.0	0.0	4.2	14.4	45.0	43.8	42.1	12.5	25.0
67-89	Warm	0.0	0.0	0.0	3.7	4.3	23.5	15.4	30.8	0.0
	Cool	0.0	0.0	0.0	0.0	2.5	18.8	31.6	37.5	25.0
90-100	Warm	0.0	0.0	0.0	0.0	0.0	0.0	7.1	7.7	50.0
	Cool	0.0	0.0	0.0	0.0	0.0	0.0	0.0	50.0	50.0
χ^2 significance at 5% level=9.49		NS[1]	NS	NS	11.9	36.7	22.5	27.7	86.6	50.0

[1]Not significant.

(Blankenship et al., 1987). In this trial, there was no shift in fruit maturity

Pigments : peel anthocyanin synthesis (2)

Warm autumn, lack of fresh night T° → lack of red colour (e.g. Pink Lady ®)
→ Fruit growers are wrong if waiting for colour: too late fruit picking !

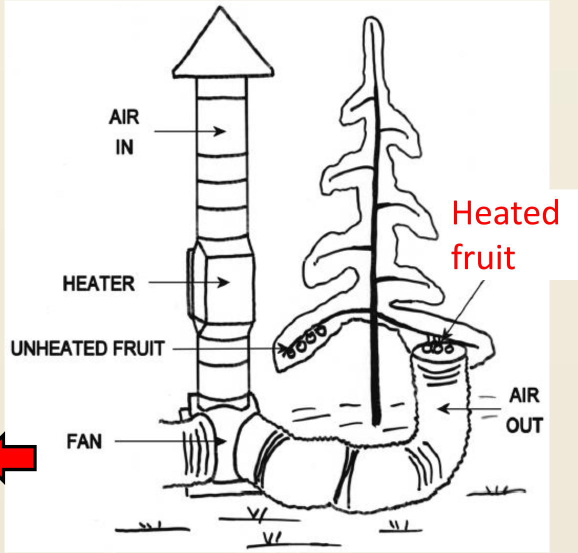
Apple skin anthocyanin content (±SE) of 'Gala' apples grown in Havelock North (N-Z) and Lleida (Cat., Spain), over the 9 wks before eating ripe. DAFB = days after full bloom.

New Zealand		Spain	
DAFB	Anthocyanin (nmol cm^{-2})	DAFB	Anthocyanin (nmol cm^{-2})
86	27.0±2.1	75	9.9±0.3
100	40.1±1.0	96	9.2±0.1
114	59.4±2.3	110	10.0±0.1
128	99.0±3.2	124	22.5±0.4
141	107.0±2.8	138	26.9±0.6

(Palmer et al., 2012.
Acta Hort. 929: 81-87).

Apple skin anthocyanin content (±SE) of 'Gala' apples grown in Nelson (NZ), with and without warm air heating over 7 days

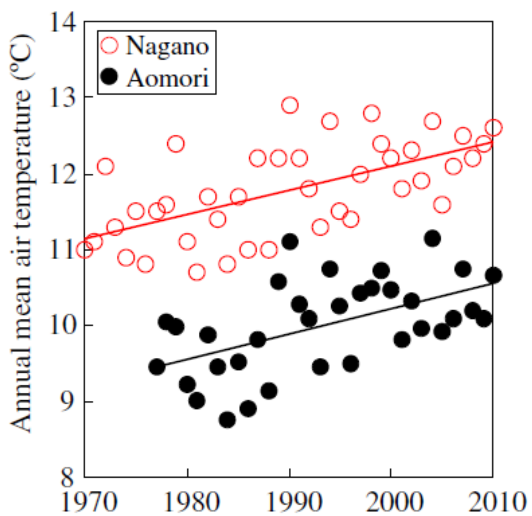
Unheated		Heated	
Time	Anthocyanin (nmol cm^{-2})	Time (d)	Anthocyanin (nmol cm^{-2})
0	18.2±1.95	0	21.4±1.95
1	37.7±6.03	1	27.1±6.03
2	45.1±5.67	2	26.2±5.67
5	33.4±5.35	5	13.8±5.35
7	42.3±6.40	7	25.7±6.40

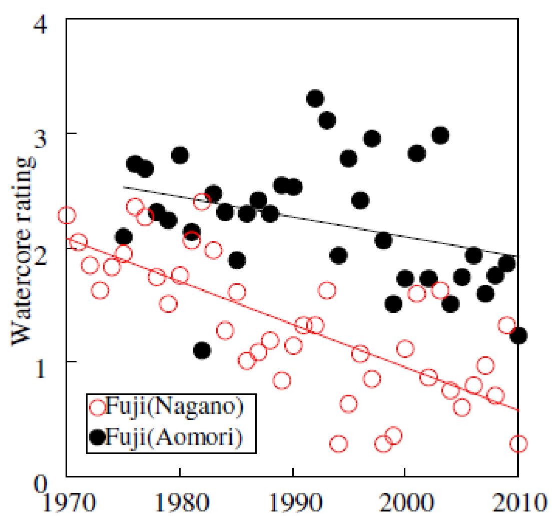


Fruit heating rapidly reduces expression of the R2R3 *MYB* transcription factor (*MYB10*) responsible for regulation of red skin colour (Lin-Wang et al., 2011).

Post-harvest diseases

- **Scald** occurrence on 'Cortland' and 'Delicious' apples (1 orchard, 6 years) negatively correlated with preharvest hours below 10°C (Bramlage & Watkins, 1994)
- **Watercore** occurrence of in 'Himekami' and 'Fuji' apples: greater at 13°/5° and 23°/15°C than at 33°/25°C. No relation with sorbitol metabolism (Yamada et al., 1994).



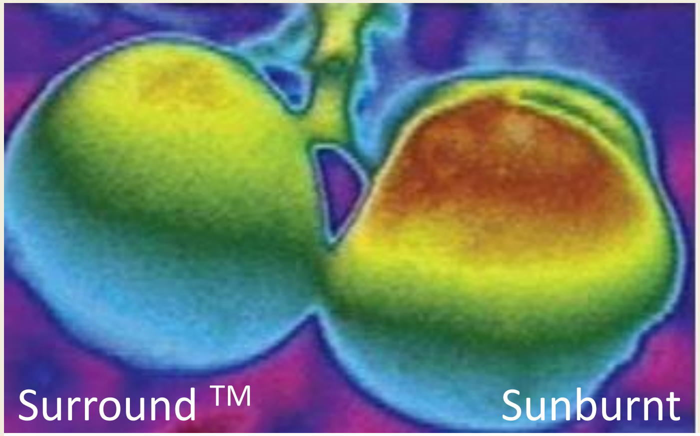


A 40-yrs survey on apple quality variations across climate change shows ↘ watercore occurrence (Sugiura et al., 2013)

Fruit sunburn

(Wünsche et al., 2004.
Acta Hort. 636: 631-636)

Sunburn browning on Fuji apple. Schrader et al., 2001. Two types of sunburn in apple caused by high fruit surface (peel) temperature. Plant Health Progress (on line) doi:10.1094/PHP-2001-1004-01-RS.



Infrared photography showing the sun-protection effect of a SurroundTM spray.
Orange/red indicates the hottest area
See also http://www.fatcow.com.au/c/agnova-technologies/surround-sunburn-protection-from-agnova-technologies-n869389#aQYGTzYujCstjTEI.99

- Local over-heating of the fruit surface due to excessive levels of incoming solar radiation in combination with high ambient air temperatures.
- Underlying physiological mechanisms of this skin blemish not fully understood.
- Hypothesis: sunburn damage may be an expression of plant defense mechanisms involved in the response to oxidative stress.
  - In the damaged zone, some photobleaching of chlorophylls a/b is noted.
  - Pigments with radical scavenging ability such as ß-carotene and chlorogenic acid also increase substantially with greater sunburn damage.

Conclusions

- Pay attention to the organ T°
- Cellular and molecular effects of high temperature stress are progressively better understood
- Fruit trees, as perennials, cannot escape; high T° avoidance depends on morphological adaptations and transpiration; fruit possibilities are limited
- Fruit themselves are submitted to sharp T° variations
- Fruit vulnerability of to high T° notably results from effects on growth and maturation …) that threaten quality at harvest & post-harvest
- Modelling approaches are required: (i) fruit temperature combined with (ii) T° effects on the fruit and (iii) fruit growth
- Some cropping practices mitigating / alleviating the effects of high T° are currently / need to be / developed

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