Quelques effets des températures élevées sur le développement des fruits
Jean-Luc Regnard

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Qq effets des températures élevées sur le développement des fruits

Some responses of fruit development to high temperatures

J.L. REGNARD

9 avril 2015 – Journée Fruits et Semences, Paris
Foreword

- Context of global climate change: periods of high $T^\circ$, 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
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)

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” ...

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).
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

\[
\Delta S = R_n + H + \lambda E + G + M
\]

$\Delta S$: heat storage
$R_n$: net radiation (absorbed)
$H$: heat sensible heat flux (convection $\to$ air)
$\lambda E$: latent heat flux (due to transpiration) $\lambda E$: very limited for the fruit
$G$: conduction fluxes (from soil to plant $\to$ 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

Temperature gradients within the crop

Temperature gradients measured in a sunflower crop


Capitules: more hot

Leaf $T^\circ$ depends on position within the plant cover

Height of the plant cover

Temperature (°C)

Journées Fruits et Semences
Paris, 09 April 2015

Some responses of fruit development to high temperatures
Jean-Luc REGNARD (Montpellier SupAgro – UMR AGAP)
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

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

But: heterogeneity of internal fruit quality traits not correlated with the internal T° gradients.
Heat avoidance

- Mitigation of incoming/intercepted energy
  - e.g. hail nets
- Leaf pubescence: \(\uparrow\) 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 $T^\circ$ constraint, duration, period of the cycle!)
• Scientific consensus in cereals (?) based on the observation of plant response

- $15^\circ < T < 32^\circ \text{C : moderate } T^\circ$
  $T^\circ$ modifies existing processes: through their speed and duration

- $32^\circ < T < 50^\circ \text{C : very high } T^\circ$
  high $T^\circ$ impedes or disrupts some metabolic processes
  new metabolic activity are induced

- $50^\circ \text{C < T : lethal temperatures}$


• 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.

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. Guiliioni)
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)
“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)

<table>
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<tr>
<th>Tissue and organ type (DFCI Apple Gene Index)</th>
<th>Gene name</th>
<th>Leaf</th>
<th>Root</th>
<th>Flower</th>
<th>Fruit</th>
<th>Shoot</th>
<th>Phloem</th>
<th>Xylem</th>
<th>Seed</th>
<th>Bud</th>
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<td>MdHsfA5b</td>
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<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
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</tr>
</tbody>
</table>

25 full length HSFs identified in apple.

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 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).

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.

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

Some effects of temperature rise on fruit development

Journées Fruits et Semences
Paris, 09 April 2015

Some responses of fruit development to high temperatures
Jean-Luc REGNARD (Montpellier SupAgro – UMR AGAP)
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
  - Plum

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Some responses of fruit development to high temperatures
Jean-Luc REGNARD (Montpellier SupAgro – UMR AGAP)
Temperature, respiration costs and carbon balance

\[ R = a e^{kT^\circ} \]

\((T^\circ \text{ range: } 0^\circ-42^\circ\text{C})\)

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

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°


<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Sampled years (n)</th>
<th>Average FDP (days)</th>
<th>c.v.</th>
<th>Average error (± days)</th>
<th>DD*</th>
<th>c.v.</th>
<th>Average error (± days)</th>
<th>GDH**</th>
<th>c.v.</th>
<th>Average error (± days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maycrest</td>
<td>7</td>
<td>72</td>
<td>11.3</td>
<td>6.5</td>
<td>639.3</td>
<td>4.8</td>
<td>2.1</td>
<td>22779.1</td>
<td>3.1</td>
<td>1.4</td>
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<td>Mayglo</td>
<td>3</td>
<td>90</td>
<td>5.6</td>
<td>3.6</td>
<td>803.7</td>
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<td>E. Lady</td>
<td>7</td>
<td>123</td>
<td>7.2</td>
<td>6.1</td>
<td>1437.2</td>
<td>6.5</td>
<td>4.4</td>
<td>44592.0</td>
<td>4.2</td>
<td>3.3</td>
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<td>137</td>
<td>5.3</td>
<td>6.1</td>
<td>1691.7</td>
<td>6.1</td>
<td>4.6</td>
<td>49625.4</td>
<td>3.7</td>
<td>3.2</td>
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<tr>
<td>O’Henry</td>
<td>9</td>
<td>150</td>
<td>6.3</td>
<td>7.8</td>
<td>1977.4</td>
<td>6.2</td>
<td>4.7</td>
<td>56893.4</td>
<td>4.9</td>
<td>4.0</td>
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<tr>
<td>Mean</td>
<td>7.1</td>
<td>6.03</td>
<td>6.6</td>
<td>4.24</td>
<td>1964.8</td>
<td>6.4</td>
<td>4.2</td>
<td>40506.3</td>
<td>4.1</td>
<td>2.96</td>
</tr>
</tbody>
</table>

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)


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 "

Journées Fruits et Semences
Paris, 09 April 2015

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Jean-Luc REGNARD (Montpellier SupAgro – UMR AGAP)
Fruit shape : apple

‘Golden Delicious’ apple
Provence lowlands

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

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.

<table>
<thead>
<tr>
<th>Location</th>
<th>Santa Paula (CA)</th>
<th>Tustin (CA)</th>
<th>Lindsay (OK)</th>
<th>Thermal (CA)</th>
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<tr>
<td>lat.</td>
<td>34°31’N</td>
<td>33°74’N</td>
<td>34°83’N</td>
<td>33°64’N</td>
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<td>alt.</td>
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<td>4m</td>
<td>32m</td>
<td>4m</td>
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<tr>
<td>côte à</td>
<td>15km</td>
<td>5km</td>
<td>560km</td>
<td>60km</td>
</tr>
<tr>
<td>climat</td>
<td>frais et sec, T° contrastées</td>
<td>frais et humide</td>
<td>chaud et sec</td>
<td>très chaud et très sec</td>
</tr>
</tbody>
</table>

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

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 $T^\circ$ effects on cell organisation at harvest stage? Other fruit models could also be used (cf. Baldazzi et al., 2012)
Fruit quality: sugar / acid balance & polyphenols

T°C > 10°C are necessary for grape maturation

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

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

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

Pigments: peel chlorophyll and carotenoids

Sharp decrease of acidity in more hot locations
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)

<table>
<thead>
<tr>
<th>% color</th>
<th>Night temp.</th>
<th>Days after full bloom</th>
<th>Days after full bloom</th>
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<tr>
<td></td>
<td></td>
<td>86</td>
<td>93</td>
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<tr>
<td>0-25</td>
<td>Warm</td>
<td>100.0</td>
<td>96.2</td>
</tr>
<tr>
<td></td>
<td>Cool</td>
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<td>0.0</td>
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<tr>
<td></td>
<td>Cool</td>
<td>0.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>

$\chi^2$ significance at 5% level = 9.49

NS\textsuperscript{1} NS NS NS 11.9 36.7 22.5 27.7 86.6 50.0

\textsuperscript{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 $T^\circ \rightarrow$ lack of red colour (e.g. Pink Lady ®) $ightarrow$ Fruit growers are wrong if waiting for colour: too late fruit picking!

Apple skin anthocyanin content ($\pm$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.

<table>
<thead>
<tr>
<th>DAFB</th>
<th>Anthocyanin (nmol cm$^{-2}$)</th>
<th>DAFB</th>
<th>Anthocyanin (nmol cm$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>86</td>
<td>27.0±2.1</td>
<td>75</td>
<td>9.9±0.3</td>
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<tr>
<td>100</td>
<td>40.1±1.0</td>
<td>96</td>
<td>9.2±0.1</td>
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<tr>
<td>114</td>
<td>59.4±2.3</td>
<td>110</td>
<td>10.0±0.1</td>
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<tr>
<td>128</td>
<td>99.0±3.2</td>
<td>124</td>
<td>22.5±0.4</td>
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<tr>
<td>141</td>
<td>107.0±2.8</td>
<td>138</td>
<td>26.9±0.6</td>
</tr>
</tbody>
</table>

Apple skin anthocyanin content ($\pm$SE) of ‘Gala’ apples grown in Nelson (NZ), with and without warm air heating over 7 days

<table>
<thead>
<tr>
<th>Time</th>
<th>Unheated Anthocyanin (nmol cm$^{-2}$)</th>
<th>Time (d)</th>
<th>Heated Anthocyanin (nmol cm$^{-2}$)</th>
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</thead>
<tbody>
<tr>
<td>0</td>
<td>18.2±1.95</td>
<td>0</td>
<td>21.4±1.95</td>
</tr>
<tr>
<td>1</td>
<td>37.7±6.03</td>
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<td>27.1±6.03</td>
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<tr>
<td>2</td>
<td>45.1±5.67</td>
<td>2</td>
<td>26.2±5.67</td>
</tr>
<tr>
<td>5</td>
<td>33.4±5.35</td>
<td>5</td>
<td>13.8±5.35</td>
</tr>
<tr>
<td>7</td>
<td>42.3±6.40</td>
<td>7</td>
<td>25.7±6.40</td>
</tr>
</tbody>
</table>

(Heated fruit)

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 \( \text{watercore} \) occurrence (Sugiura et al., 2013)
Fruit sunburn

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

- 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 β-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
Literature cited (1)


