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Internal Lower Oxygen Limits of Apple Fruit

A thesis presented in partial fulfilment
of the requirements

for the degree of

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at

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**Christopher William Yearsley
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*In memory of my mother
and
to Kathryn, Tim, Daniel, Elissa and Andrew*

Abstract

The optimum atmosphere for a crop, with respect to oxygen, lies just above the lower oxygen limit (*LOL*), at which maximum benefits in relation to fruit quality are achieved and below which fruit quality is compromised by fermentation. In contrast to previous work, *LOL*s in this study were estimated on the basis of steady-state internal atmospheres (*LOL*'s) as well as external atmospheres (*LOL*^es) as it is the internal O₂ partial pressure ($p_{O_2}^i$, Pa), close to equilibrium with the cytosol, that mediates important physiological processes. The study tested whether *LOL*'s of 'Cox's Orange Pippin' and 'Braeburn' apples were affected by temperature, elevated CO₂, and physiological age.

Two types of *LOL*s were identified: the anaerobic compensation point (*ACP*) and the fermentation threshold (*FT*). *ACP* was described in terms of plots of the internal CO₂ ($p_{CO_2}^i$) versus internal ($p_{O_2}^i$) and external ($p_{O_2}^e$) O₂, and *FT* in terms of plots of both a measure of the respiratory quotient (RQ_{ia}) and ethanol (EtOH) concentration versus $p_{O_2}^i$ and $p_{O_2}^e$. Mathematical solutions for estimating *ACP* and *FT* based on the RQ_{ia} (FT_{RQ}), and a statistical 'bootstrap' procedure suitable for estimating all *LOL*s and their bias-corrected 95% confidence intervals, are described.

LOL's of postclimacteric fruit of both cultivars tended to increase slightly between 0° and 28°C and sharply at 32°C. *LOL*'s ranged between 0.5 kPa and 2.2 kPa $p_{O_2}^i$; values for FT_{RQ}^i and FT_{EtOH}^i tended to be higher than for ACP^i . Elevated $p_{CO_2}^e$ (0 to 8 kPa at 0° and 20°C) did not significantly affect *LOL*'s at 20°C, but increases in FT_{RQ}^i and FT_{EtOH}^i occurred for fruit at 0°C. A small decrease in O₂ uptake and RQ_{ia} was measured for fruit in 2 to 8 kPa $p_{CO_2}^e$ at 20°C. No consistent changes in *LOL*'s were observed for either cultivar in relation to physiological age (preclimacteric, climacteric, or postclimacteric fruit at 0° or 20°C).

In contrast to ACP^i , ACP^e increased markedly with temperature, resulting from its dependence on both skin permeance and respiration rate (both of which change with time fruit are in storage). Consequently, use of *LOL*'s, rather than *LOL*^es is recommended for optimising atmospheres for both sealed packages and controlled atmosphere storage, to minimise risk of fermentation.

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List of Symbols and Abbreviations

A	=	fruit surface area (m^2)
AAT	=	alcohol acyltransferase
ACC	=	l-aminocyclopropane-l-carboxylic acid
Acet	=	acetaldehyde
ACP	=	anaerobic compensation point
ACP^e	=	external anaerobic compensation point
ACP^i	=	internal anaerobic compensation point
ADP	=	adenosine diphosphate
ADH	=	alcohol dehydrogenase
AMP	=	adenosine monophosphate
ANOVA	=	analysis of variance
ATP	=	adenosine triphosphate
ATP-PFK	=	ATP phosphofructokinase
b	=	number of bootstrap samples
BBD	=	'Braeburn' browning disorder
BBD^i	=	internal 'Braeburn' browning disorder
BCa	=	bootstrap bias corrected 95% confidence interval
Ca	=	calcium
CA	=	controlled-atmosphere
cDNA	=	complementary deoxyribonucleic acid
C_2H_4	=	ethylene
C_2H_6	=	ethane
CI	=	confidence interval
CN^-	=	cyanide ion
CO_2	=	carbon dioxide
c_{O_2, H_2O}^i	=	concentration of O_2 in water (mol m^{-3})
c_{j, H_2O}^T	=	concentration of gas j in water at temperature T (mol m^{-3})
c_{O_2, H_2O}^T	=	concentration of O_2 in H_2O at a given temperature, T (mol m^{-3})

CoA	=	coenzyme A
'COP'	=	'Cox's Orange Pippin'
CV	=	coefficient of variation
$dp_{C_2H_6} / dt$	=	rate of change of ethane partial pressure (Pa s^{-1})
$\Delta p_{C_2H_4}^{\Delta t}$	=	difference in partial pressure of C_2H_4 between initial and final measurements over time Δt (Pa)
$\Delta p_{CO_2}^{\Delta t}$	=	difference in partial pressure of CO_2 between initial and final measurements over time Δt (Pa)
Δp_j	=	difference in partial pressures of gas j between internal and external atmospheres (Pa)
$\Delta p_{O_2}^{\Delta t}$	=	difference in partial pressure of O_2 between initial and final measurements over time Δt (Pa)
Δt	=	difference in time between initial and final sampling (s)
ε	=	cortical tissue porosity ($\text{m}^3 \text{m}^{-3}$)
EC	=	energy charge
EFE	=	ethylene forming enzyme
EP	=	extinction point
$error_{wvp}^{sat,T}$	=	percentage error (%) due to the dilution effect of water vapour pressure at temperature T
EtAc	=	ethyl acetate
EtOH	=	ethanol
ETS	=	electron transport system
Eq(s).	=	equation(s)
F	=	fruit firmness (N)
F1,6-P ₂	=	fructose 1,6-bisphosphate
F2,6-P ₂	=	fructose 2,6-bisphosphate
F6P	=	fructose 6-phosphate
f_{CO_2}	=	flow rate of CO_2 ($\text{mm}^3 \text{s}^{-1}$)
FF	=	fruit firmness (N)
Fig(s).	=	figure(s)
f_{N_2}	=	flow rate of N_2 ($\text{mm}^3 \text{s}^{-1}$)

f_{O_2}	=	flow rate of O_2 ($\text{mm}^3 \text{ s}^{-1}$)
FT	=	fermentation threshold
FT^e	=	external fermentation threshold
FT^i	=	internal fermentation threshold
FT_{Acet}	=	fermentation threshold based on acetaldehyde accumulation
FT_{EtAc}	=	fermentation threshold based on ethyl acetate accumulation
FT_{EtOH}	=	fermentation threshold based on ethanol accumulation
FT_{EtOH}^e	=	external fermentation threshold based on ethanol accumulation
FT_{EtOH}^i	=	internal fermentation threshold based on ethanol accumulation
FT_{RQ}	=	fermentation threshold based on respiratory quotient
FT_{RQ}^e	=	external fermentation threshold based on respiratory quotient
FT_{RQ}^i	=	internal fermentation threshold based on respiratory quotient
gas	=	gas phase
g	=	gram
$init p_{C_2H_6}$	=	initial partial pressure of ethane in the fruit's internal atmosphere (Pa)
h	=	hour
H°	=	background skin colour hue angle
H_2O_2	=	hydrogen peroxide
IA	=	internal atmosphere
K	=	potassium
k_I	=	$p_{O_2}^t$ at which $r_{O_2}^f$ is half maximal (Pa)
k_f	=	a fruit constant ($\text{mol kg}^{-1} \text{ s}^{-1} \text{ Pa}^{-1}$)
k_x	=	constant with number x
kg	=	kilogram
kgf	=	kilogram force
K_m	=	Michaelis-Menten constant (units of substrate eg. Pa)
kPa	=	kilopascal
L	=	background skin colour lightness
l	=	liter

LDH	=	lactate dehydrogenase
<i>liq</i>	=	liquid phase
<i>LOLs</i>	=	lower oxygen limits
<i>LOL^es</i>	=	external lower oxygen limits
<i>LOLⁱs</i>	=	internal lower oxygen limits
<i>M</i>	=	fruit mass (kg)
m	=	metre
<i>M_a</i>	=	mass of non-infiltrated wedge in air (kg)
MA	=	modified-atmosphere
MAP	=	modified-atmosphere packaging
Mg	=	magnesium
<i>M_i</i>	=	apparent mass of infiltrated wedge submerged in water (kg)
μl	=	microliter
μmol	=	micromole
mm	=	millimetre
mmol	=	millimole
<i>M_n</i>	=	apparent mass of non-infiltrated wedge submerged in water (kg)
mol	=	mole
<i>M_R</i>	=	relative molecular mass
mRNA	=	messenger ribonucleic acid
n	=	number of fruit or items in a sample
N	=	newton
N ₂	=	nitrogen
N ₃ ⁻	=	azide ion
NAD ⁺	=	adenine dinucleotide (oxidised form)
NADH	=	adenine dinucleotide (reduced form)
NADPH	=	nicotinamide adenine dinucleotide phosphate
nmol	=	nanomole
<i>N_j</i>	=	mole fraction of gas species <i>j</i> (% , mol mol ⁻¹ , μl l ⁻¹)
<i>N_{CO₂}</i>	=	mole fraction of CO ₂ (mol mol ⁻¹)

$N_{\text{CO}_2,\text{core}}$	=	mole fraction of CO_2 in the core cavity (mol mol^{-1})
$N_{\text{CO}_2,\text{room}}$	=	mole fraction of CO_2 in the room (mol mol^{-1})
N_{O_2}	=	mole fraction of O_2 required (mol mol^{-1})
$N_{\text{O}_2,\text{core}}$	=	mole fraction of O_2 in the core cavity (mol mol^{-1})
$N_{\text{O}_2,\text{room}}$	=	mole fraction of O_2 in the room (mol mol^{-1})
NR	=	nitrogen respiration
NS	=	not significant
N_{std}	=	mole fraction of gas or vapour in the standard ($\mu\text{l l}^{-1}$)
N_{stock}	=	mole fraction of stock standard ($\mu\text{l l}^{-1}$)
O_2	=	oxygen
O_2^\cdot	=	super oxide free-radicals
p	=	probability or level of significance of a statistical test
P	=	phosphorus
Pa	=	pascal
PCK	=	pyruvate carboxykinase
PDC	=	pyruvate decarboxylase
PEPC	=	phosphoenol pyruvate carboxylase
PDH	=	pyruvate dehydrogenase
pH	=	measure of a solutions concentration of hydrogen ions
P_i	=	inorganic orthophosphate
PK	=	pyruvate kinase
PP_i	=	inorganic pyrophosphate
$p_{\text{H}_2\text{O}}^{\text{sat},T}$	=	saturated water vapour partial pressure at temperature T (Pa)
p_j^e	=	partial pressure of gas j in the external atmosphere (Pa)
$P_{\text{C}_2\text{H}_6}$	=	fruit permeance to ethane ($\text{mol s}^{-1} \text{m}^{-2} \text{Pa}^{-1}$)
P_{CO_2}	=	fruit permeance to CO_2 ($\text{mol s}^{-1} \text{m}^{-2} \text{Pa}^{-1}$)
p_{CO_2}	=	partial pressure of CO_2 (Pa)
$p_{\text{CO}_2}^e$	=	external (or package) partial pressure of CO_2 (Pa)
$p_{\text{CO}_2}^i$	=	internal partial pressure of CO_2 (Pa)

P_j	=	skin or fruit permeability to gas j ($\text{mol s}^{-1} \text{m m}^{-2} \text{Pa}^{-1}$)
P_j'	=	skin or fruit permeance to gas j ($\text{mol s}^{-1} \text{m}^{-2} \text{Pa}^{-1}$)
p_{O_2}	=	partial pressure of O_2 in the intercellular air space (Pa)
$p_{\text{O}_2}^e$	=	external (or package) partial pressure of O_2 (Pa)
$p_{\text{O}_2}^i$	=	internal partial pressure of O_2 (Pa)
p_{tot}	=	total system partial pressure (Pa)
P_{O_2}'	=	fruit permeance to O_2 ($\text{mol s}^{-1} \text{m}^{-2} \text{Pa}^{-1}$)
PPi-PFK	=	pyrophosphate phosphofructokinase
Q_{10}	=	temperature coefficient (= [rate of O_2 uptake at $(T+10^\circ\text{C})$] / [rate of O_2 uptake at T])
r^2	=	square of the correlation coefficient (r), or proportion of the total variability in the y -values that can be accounted for by the independent variable x .
R	=	gas constant ($8.3143 \text{ m}^3 \text{ Pa mol}^{-1} \text{ K}^{-1}$)
r_{CO_2}	=	specific rate of transfer of CO_2 between internal and external atmospheres ($\text{mol kg}^{-1} \text{ s}^{-1}$)
$r_{\text{C}_2\text{H}_4}$	=	specific rate of transfer of C_2H_4 between internal and external atmospheres ($\text{mol kg}^{-1} \text{ s}^{-1}$)
ρ_{juice}^{20}	=	density of fruit juice at 20°C (kg m^{-3})
ρ_{fruit}^{20}	=	density of cortical tissue of fruit at 20°C (kg m^{-3})
$\rho_{\text{H}_2\text{O}}^{20}$	=	density of water at 20°C (kg m^{-3})
r_j	=	specific rate of transfer of gas j between internal and external atmospheres ($\text{mol kg}^{-1} \text{ s}^{-1}$)
r_{O_2}	=	specific rate of transfer of O_2 between internal and external atmospheres ($\text{mol kg}^{-1} \text{ s}^{-1}$)
$r_{\text{O}_2}^{ACP^i}$	=	rate of transfer of O_2 for the system at the ACP^i (mol s^{-1})
$r_{\text{O}_2}^{\text{air}, T}$	=	specific rate of transfer of O_2 in air at temperature T ($\text{mol kg}^{-1} \text{ s}^{-1}$)
$r_{\text{O}_2}^{\text{air}, 0}$	=	specific rate of transfer of O_2 in fruit in air at 0°C ($\text{mol kg}^{-1} \text{ s}^{-1}$)

$\dot{r}_{O_2}^{air}$	=	rate of transfer of O ₂ for the system in air (mol s ⁻¹)
$\dot{r}_{O_2}^T$	=	rate of transfer of O ₂ for the system at temperature T (mol s ⁻¹)
$r_{O_2}^T$	=	specific rate of transfer of O ₂ at temperature T (mol kg ⁻¹ s ⁻¹)
$r_{O_2}^{max,T}$	=	specific maximum rate of O ₂ uptake when p'_{O_2} is non-limiting, at temperature T (mol kg ⁻¹ s ⁻¹)
$\dot{r}_{O_2}^{max,T}$	=	rate of transfer of O ₂ for the system when p'_{O_2} is non-limiting at temperature T (mol s ⁻¹)
RQ	=	respiratory quotient
RQB	=	respiratory quotient breakpoint
RQ_{ia}	=	respiratory quotient based on internal atmospheres
s	=	second
SAM	=	S-adenosylmethionine
SDH	=	succinate dehydrogenase
se	=	standard error
sed	=	standard error of the difference between means
sem	=	standard error of the mean
s_{O_2,H_2O}^T	=	solubility of O ₂ in H ₂ O at a given temperature, T (mol m ⁻³ Pa ⁻¹)
SSC	=	total soluble solids content (% , ° Brix)
t	=	time (s)
T	=	fruit temperature (°C)
TCA	=	tricarboxylic acid cycle or Krebs cycle
V_h	=	volume of submerged portion of hook (m ³)
V_{jar}	=	volume of respiration jar (m ³)
V_{net}	=	net volume, [jar volume - fruit volume] (m ³)
V_{stock}	=	volume of stock gas (m ³)
V_{std}	=	total volume of combined standard (m ³)
V_w	=	volume of wedge (m ³)