Internal Lower Oxygen Limits of Apple Fruit

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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^is) as well as external atmospheres (LOL^es) as it is the internal O_2 partial pressure ($p^i_{O_2}$, Pa), close to equilibrium with the cytosol, that mediates important physiological processes. The study tested whether LOL^is of 'Cox's Orange Pippin' and 'Braeburn' apples were affected by temperature, elevated CO_2, 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 CO_2 ($p^i_{CO_2}$) versus internal ($p^i_{O_2}$) and external ($p^e_{O_2}$) O_2, and *FT* in terms of plots of both a measure of the respiratory quotient (RQ_{ia}) and ethanol (EtOH) concentration versus $p^i_{O_2}$ and $p^e_{O_2}$. 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^is of postclimacteric fruit of both cultivars tended to increase slightly between 0° and 28°C and sharply at 32°C. LOL^is ranged between 0.5 kPa and 2.2 kPa $p^i_{O_2}$; values for FT^i_{RQ} and FT^i_{EtOH} tended to be higher than for ACP^i. Elevated $p^e_{CO_2}$ (0 to 8 kPa at 0° and 20°C) did not significantly affect LOL^is at 20°C, but increases in FT^i_{RQ} and FT^i_{EtOH} occurred for fruit at 0°C. A small decrease in O_2 uptake and RQ_{ia} was measured for fruit in 2 to 8 kPa $p^e_{CO_2}$ at 20°C. No consistent changes in LOL^is were observed for either cultivar in relation to physiological age (preclimacteric, climacteric, or postclimatceric 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^is, 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	=	1-aminocyclopropane-1-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
$c^i_{O_2,H_2O}$	=	concentration of O_2 in water (mol m^{-3})
c^T_{j,H_2O}	=	concentration of gas j in water at temperature T (mol m^{-3})
$c^T_{O_2,H_2O}$	=	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})
$\Delta p^{\Delta t}_{C_2H_4}$	=	difference in partial pressure of C_2H_4 between initial and final measurements over time Δt (Pa)
$\Delta p^{\Delta t}_{CO_2}$	=	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)
$\Delta p^{\Delta t}_{O_2}$	=	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 (m^3 m^{-3})
EC	=	energy charge
EFE	=	ethylene forming enzyme
EP	=	extinction point
$error^{sat,T}_{wvp}$	=	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 (mm^3 s^{-1})
FF	=	fruit firmness (N)
Fig(s).	=	figure(s)
f_{N_2}	=	flow rate of N_2 (mm^3 s^{-1})

f_{O_2} = flow rate of O_2 ($mm^3\ s^{-1}$)

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^e_{EtOH} = external fermentation threshold based on ethanol accumulation

FT^i_{EtOH} = internal fermentation threshold based on ethanol accumulation

FT_{RQ} = fermentation threshold based on respiratory quotient

FT^e_{RQ} = external fermentation threshold based on respiratory quotient

FT^i_{RQ} = 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_l = $p^i_{O_2}$ at which $r^T_{O_2}$ is half maximal (Pa)

k_f = a fruit constant (mol $kg^{-1}\ s^{-1}\ Pa^{-1}$)

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
liq	=	liquid phase
LOLs	=	lower oxygen limits
$LOL^e s$	=	external lower oxygen limits
LOL^is	=	internal lower oxygen limits
M	=	fruit mass (kg)
m	=	metre
M_a	=	mass of non-infiltrated wedge in air (kg)
MA	=	modified-atmosphere
MAP	=	modified-atmosphere packaging
Mg	=	magnesium
M_i	=	apparent mass of infiltrated wedge submerged in water (kg)
μl	=	microliter
μmol	=	micromole
mm	=	millimetre
mmol	=	millimole
M_n	=	apparent mass of non-infiltrated wedge submerged in water (kg)
mol	=	mole
M_R	=	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 dinucleotde (oxidised form)
NADH	=	adenine dinucleotide (reduced form)
NADPH	=	nicotinamide adenine dinucleotide phosphate
nmol	=	nanomole
N_j	=	mole fraction of gas species *j* (%, mol mol^{-1} , μl l^{-1})
N_{CO_2}	=	mole fraction of CO_2 (mol mol^{-1})

$N_{CO_2,core}$	=	mole fraction of CO_2 in the core cavity (mol mol^{-1})
$N_{CO_2,room}$	=	mole fraction of CO_2 in the room (mol mol^{-1})
N_{O_2}	=	mole fraction of O_2 required (mol mol^{-1})
$N_{O_2,core}$	=	mole fraction of O_2 in the core cavity (mol mol^{-1})
$N_{O_2,room}$	=	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 (μl l^{-1})
N_{stock}	=	mole fraction of stock standard (μl l^{-1})
O_2	=	oxygen
O_2^-	=	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
$p_{H_2O}^{sat,T}$	=	saturated water vapour partial pressure at temperature T (Pa)
p_j^e	=	partial pressure of gas j in the external atmosphere (Pa)
$P'_{C_2H_6}$	=	fruit permeance to ethane (mol s^{-1} m^{-2} Pa^{-1})
P'_{CO_2}	=	fruit permeance to CO_2 (mol s^{-1} m^{-2} Pa^{-1})
p_{CO_2}	=	partial pressure of CO_2 (Pa)
$p_{CO_2}^e$	=	external (or package) partial pressure of CO_2 (Pa)
$p_{CO_2}^i$	=	internal partial pressure of CO_2 (Pa)

P_j	=	skin or fruit permeability to gas j (mol s^{-1} m m^{-2} Pa^{-1})
P_j'	=	skin or fruit permeance to gas j (mol s^{-1} m^{-2} Pa^{-1})
p_{O_2}	=	partial pressure of O_2 in the intercellular air space (Pa)
$p_{O_2}^e$	=	external (or package) partial pressure of O_2 (Pa)
$p_{O_2}^i$	=	internal partial pressure of O_2 (Pa)
p_{tot}	=	total system partial pressure (Pa)
P_{O_2}'	=	fruit permeance to O_2 (mol s^{-1} m^{-2} Pa^{-1})
PPi-PFK	=	pyrophosphate phosphofructokinase
Q_{10}	=	temperature coefficient (= [rate of O_2 uptake at (T+10°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 m^3 Pa mol^{-1} K^{-1})
r_{CO_2}	=	specific rate of transfer of CO_2 between internal and external atmospheres (mol kg^{-1} s^{-1})
$r_{C_2H_4}$	=	specific rate of transfer of C_2H_4 between internal and external atmospheres (mol kg^{-1} 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})
$\rho_{H_2O}^{20}$	=	density of water at 20°C (kg m^{-3})
r_j	=	specific rate of transfer of gas j between internal and external atmospheres (mol kg^{-1} s^{-1})
r_{O_2}	=	specific rate of transfer of O_2 between internal and external atmospheres (mol kg^{-1} s^{-1})
$r_{O_2}^{',ACP^i}$	=	rate of transfer of O_2 for the system at the ACP^i (mol s^{-1})
$r_{O_2}^{air,T}$	=	specific rate of transfer of O_2 in air at temperature T (mol kg^{-1} s^{-1})
$r_{O_2}^{air,0}$	=	specific rate of transfer of O_2 in fruit in air at 0°C (mol kg^{-1} s^{-1})

$r'^{air}_{O_2}$ = rate of transfer of O_2 for the system in air (mol s^{-1})

$r'^{T}_{O_2}$ = rate of transfer of O_2 for the system at temperature T (mol s^{-1})

$r^{T}_{O_2}$ = specific rate of transfer of O_2 at temperature T (mol kg^{-1} s^{-1})

$r^{max,T}_{O_2}$ = specific maximum rate of O_2 uptake when $p^{i}_{O_2}$ is non-limiting, at temperature T (mol kg^{-1} s^{-1})

$r'^{max,T}_{O_2}$ = rate of transfer of O_2 for the system when $p^{i}_{O_2}$ 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

$s^{T}_{O_2,H_2O}$ = solubility of O_2 in H_2O 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)