



## ON THE THERMODYNAMICS OF FATTY ACID OXIDATION

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**Abstract.** The energy yield from the combustion of fatty acids and the ATP yield of their oxidation increases with the length of the acyl chain and decreases with unsaturation. Simple expressions describing these relationships are compared with data from the literature, and expressions for the yield of ATP and reducing equivalents are given. From these we derive the corresponding expressions for the oxidation of triacylglycerol. These expressions are used to estimate the energy yields from the oxidation of selected fats and oils of known composition.

**Keywords:** fatty acids, combustion, oxidation, ATP yield, reducing equivalents.

### Introduction

It is commonly stated that fat is an efficient source of metabolic energy. For example, the standard energy content of fat is usually taken to be 37 kJ g<sup>-1</sup><sup>[DARVEY 1998]</sup> or 39.5 kJ g<sup>-1</sup><sup>[GNAIGER 1983]</sup>. Irrespective of this discrepancy, it is rare to find any evidence in support of either assertion, and the relevant thermodynamic data are surprisingly difficult to find. Moreover, the relevant measure *in vivo* is how much ATP can be obtained from the oxidation of fat. Here we analyse systematically the yield of energy and of ATP from the oxidation of fatty acids (FAs) and triacylglycerols (TAGs), and provide some insight into the different values reported in the literature. We estimate the enthalpy of formation ( $\Delta_f H^0$ ) of FAs which we use to calculate the heat of combustion ( $\Delta H_c$ ) of FAs that are needed to calculate the  $\Delta H_c$  of TAGs.

### Sources of data

Measurements of the enthalpy of formation ( $\Delta_f H^0$ ) of biologically relevant FAs were obtained from the literature<sup>[AMEND & HELGESON 1997, DEAN 1999, DOMALSKI 1972, LIDE & KEHAIANN 1994, VATANI ET AL. 2007, WILHOIT 1969]</sup> and from the National Institute of Standards Institute (NIST) Chemistry Webbook<sup>[BURGESS 2011]</sup>. Measurements of the enthalpy of combustion ( $\Delta H_c$ ) were obtained from Adriaanse *et al.*<sup>[1965]</sup>, Domalski<sup>[1972]</sup>, Livesey and Elia<sup>[1988]</sup> and the NIST Chemistry Webbook<sup>[BURGESS 2011]</sup>. Data manipulation and statistical analyses were carried out using R<sup>[IHAKA & GENTLEMAN 1996]</sup>.

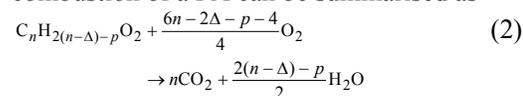
In assessing expressions for  $\Delta_f H^0$  and  $\Delta H_c$ , we calculated the average absolute deviation using

$$\langle R \rangle = \frac{1}{N} \sum |v_{\text{exp}} - v_{\text{calc}}| \quad (1)$$

where  $v_{\text{exp}}$  and  $v_{\text{calc}}$  are the measured and calculated values and the summation is taken over  $N$  values.

### Fatty acid combustion

Fatty acids have  $n$  carbon atoms, two oxygen atoms and a number of hydrogen atoms that depends on the degree of saturation of the FA ( $\Delta$ ) and the protonation of the carboxyl group ( $p$ ). So, the general form of a FA is  $C_n H_{2(n-\Delta)-p} O_2$ , since the number of hydrogen atoms in a saturated FA is  $2n$  (3 for the terminal methyl group, 1 for the carboxyl group and 2 for each of the methylene groups), every double bond ( $\Delta$ ) reduces the number of hydrogen atoms by 2 and deprotonation removes one more hydrogen atom. Consequently, the complete combustion of a FA can be summarised as



where  $\Delta$  is the number of double bonds and  $p$  is 0 for a protonated acid and 1 for a deprotonated acid. Since  $pK_a \approx 4.8$  for most FAs<sup>[MARKLEY 1947, EBERSON 1969]</sup>, they are usually unprotonated *in vivo* (so it can be assumed that  $p = 1$ ). Similarly, the molar mass of a FA is given by

$$M_{\text{FA}} = 14.016n - 2.016\Delta - p + 31.990, \quad (3)$$

where we have retained three decimal places



in the coefficients only because  $n$  can be large. The combustion of FA yields

$$\Delta H_c(\text{FA}) = n\Delta_f H^0(\text{CO}_2) + \frac{2(n-\Delta)-p}{2}\Delta_f H^0(\text{H}_2\text{O}) - \frac{6n-2\Delta-p-4}{4}\Delta_f H^0(\text{O}_2) - \Delta_f H^0(\text{FA}) \quad (4)$$

where  $\Delta_f H^0$  for  $\text{O}_{2(\text{g})}$ ,  $\text{H}_2\text{O}_{(\text{liq})}$  and  $\text{CO}_{2(\text{g})}$  are  $0 \text{ kJ mol}^{-1}$ ,  $-285.83 \text{ kJ mol}^{-1}$  and  $-393.51 \text{ kJ mol}^{-1}$ , respectively<sup>[HOARE 1985, ATKINS 1990]</sup>. The value used by nutritionists to express the calorific value of foods is  $-\Delta H_c$  expressed on a mass basis and so (3) can be used to correct values expressed in  $\text{kJ mol}^{-1}$ . Of course, after collecting terms and using the constants, (4) becomes

$$\Delta H_c(\text{FA}) = -679.34n + 285.83\Delta + 142.915p - \Delta_f H^0(\text{FA}) \quad (5)$$

and an empirical estimate of  $\Delta_f H^0(\text{FA})$  can be obtained using published data.

The values of  $-\Delta_f H^0(\text{FA})$  increase with the number of methylene groups (Figure 1) and decrease with each double bond (Figure 2). Measurements of  $\Delta_f H^0(\text{FA})$  for saturated FAs were obtained from seven different sources and it is clear that there is good agreement, whether in the liquid or condensed state (Figure 1). The values for methanoic acid (for which  $n = 1$ ) are very similar, but do not lie on the regression line through the remaining 77 values. The presence of one or more double bonds makes  $\Delta_f H^0(\text{FA})$  less negative by about  $130 \text{ kJ mol}^{-1}$  for each double bond (Figure 2). The combined equation, obtained using multiple regression, is

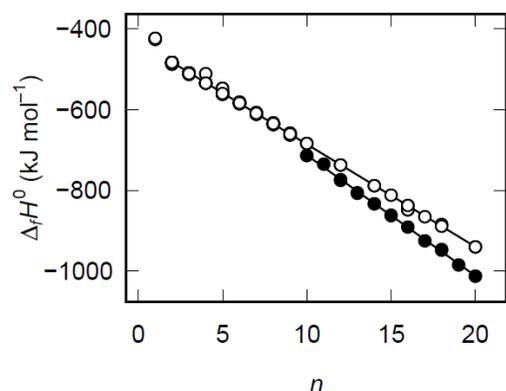


Figure 1. Relationship between  $\Delta_f H^0$  and  $n + 1$  for saturated FAs in liquid ( $\circ$ ) and condensed ( $\bullet$ ) states. The solid lines are

regression lines for the liquid ( $\Delta_f H^0 = -(25.37 \pm 0.09)n - (432.4 \pm 0.8)$ ,  $r^2 = 0.999$ ,  $p < 0.001$ ) and condensed FAs ( $\Delta_f H^0 = -(29.9 \pm 0.2)n - (415 \pm 3)$ ,  $r^2 = 0.999$ ,  $p < 0.001$ ).

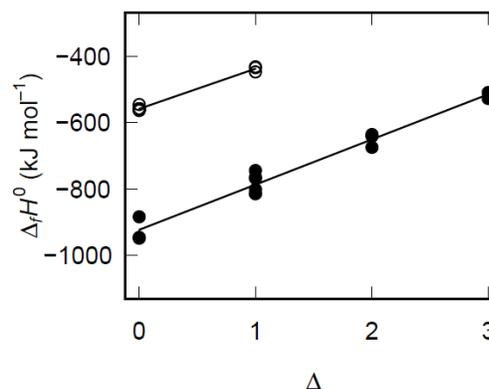


Figure 2. Relationships between  $\Delta_f H^0$  and  $\Delta$  for FAs. The solid lines are the regression lines for  $n = 18$  ( $\bullet$ :  $\Delta_f H^0 = (136 \pm 7)n - (923 \pm 12)$ ,  $r^2 = 0.967$ ,  $p < 0.001$ ) and  $n = 5$  ( $\circ$ :  $\Delta_f H^0 = (121 \pm 4)n - (558 \pm 2)$ ,  $r^2 = 0.991$ ,  $p < 0.001$ ).

$\Delta_f H^0(\text{FA}) = -(25.8 \pm 0.2)n + (123 \pm 2)\Delta - (430 \pm 2)$  ( $r^2 = 0.991$ ,  $p < 0.001$ ), indicating that  $\Delta_f H^0(\text{FA})$  changes by  $-25.8 \text{ kJ mol}^{-1}$  per methylene group, similar to the  $-25.3 \text{ kJ mol}^{-1}$  per methylene approached in the longer alkanes<sup>[ALBERTY & GEHRIG 1984]</sup>.

Deprotonation of the FA has little effect on  $\Delta_f H^0(\text{FA})$ . For example, the enthalpy of the deprotonation of ethanoic acid is only  $-0.41 \text{ kJ mol}^{-1}$ <sup>[GOLDBERG et al. 2002]</sup>, although the values surveyed by Goldberg *et al.*<sup>[2002]</sup> ranged from  $-0.90 \text{ kJ mol}^{-1}$  to  $+0.38 \text{ kJ mol}^{-1}$ . The enthalpy of deprotonation of other short chain FAs is no more than  $3 \text{ kJ mole}^{-1}$ <sup>[WILHOIT 1969, EBERSON 1969, SIMONETTA & CARRÀ 1969]</sup>.

Incorporating the value for ethanoic acid into (6) yields

$$\Delta_f H^0(\text{FA}) = -25.8n + 123\Delta - 0.4p - 430, \quad (7)$$

where we have omitted the error estimates, and substituting (7) into (5) yields an estimate of the heat of combustion

$$\Delta H_c(\text{FA}) = -653.5n + 163\Delta + 143.3p + 430. \quad (8)$$

Expressions for  $\Delta_f H^0(\text{FA})$ <sup>[AMEND & HELGESON 1997, SIMONETTA & CARRÀ 1969, DUTT et al. 1992]</sup>

or  $\Delta H_c$ <sup>[ADRIAANSE et al 1965, DUTT et al 1992, LIVESEY 1984]</sup> corresponding to (7) and (8), respectively,



have been reported previously. Of these, only two [DUTT ET AL 1992, LIVESY 1984] explicitly consider the effects of unsaturation, and one of those [DUTT ET AL 1992] is based on the connectivity of the molecules rather than just  $n$  and  $\Delta$ . Equation (7) provides a better estimate of  $\Delta_f H^0(\text{FA})$  ( $\langle R \rangle = 2.8$ ) than that of Dutt *et al.* [DUTT ET AL 1992] ( $\langle R \rangle = 12.7$ ) and it is the logical basis of (8). Equation (8) is a slightly better estimator of  $\Delta H_c$  ( $\langle R \rangle = 132.7$ ) than that of Livesey [1984] ( $\langle R \rangle = 151.2$ ), and both are better than that of Dutt *et al.* [DUTT ET AL 1992] ( $\langle R \rangle = 168.0$ ). In each case, the expressions of Dutt *et al.* [DUTT ET AL 1992] deviate systematically from the data, especially for  $n > 14$ .

According to (8), the effect of a double bond is to change  $\Delta H_c$  by  $+163 \text{ kJ mole}^{-1}$ , similar to the prediction of Livesey [1984], but quite different from Dutt *et al.* [1992] according to whom it increases by  $550 \text{ kJ mole}^{-1}$ . Comparison of the values of  $\Delta H_c$  for alkanes and the corresponding alkenes gives a value of about  $115 \text{ kJ mole}^{-1}$  per double bond [ALBERTY & GEHRIG 1984, ALBERTY & GEHRIG 1985], and the data reported by Markley [1947] for three unsaturated FAs yield an average value of  $168 \pm 8 \text{ kJ mole}^{-1}$  per double bond. These data prompt the suggestion that the unsaturation correction in (8) is more likely to be appropriate than is that inherent in the expression of Dutt *et al.* [1992].

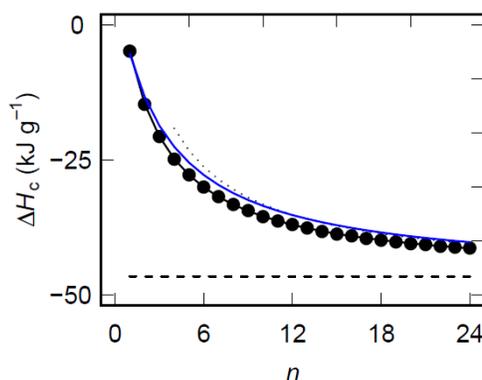


Figure 3. Relationships between  $\Delta H_c$  and  $n$  for saturated FAs ( $\bullet$ ), unsaturated ( $\Delta = 3$ ) FAs ( $\cdots$ ) and  $\text{FA}_{\text{eq}}$  (blue curve). The horizontal dashed line indicates the limiting value of  $\Delta H_c$ .

From (3) and (8), it will be apparent

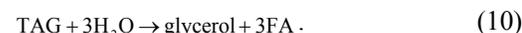
that  $\Delta H_c(\text{FA})$  approaches  $-46.6 \text{ kJ g}^{-1}$  for long chain FAs (Figure 3). However, biologically relevant FAs are heterogeneous mixtures in which  $n$  ranges up to about 24 and so combustion will yield less energy. Values of  $\Delta H_c$  can be estimated for mixtures of FAs using

$$\Delta H_c(\sum \text{FA}) = \sum_{\text{FA}} p(\text{FA}) \frac{\Delta H_c(\text{FA})}{M_{\text{FA}}}, \quad (9)$$

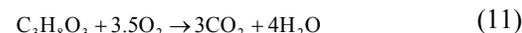
where  $p(\text{FA})$  is the proportion of the mass contributed by a particular FA. Combustion of the FAs from human fat or rattite or seed oils yields  $\Delta H_c \approx 39.5 \text{ kJ g}^{-1}$  despite quite different FA compositions (Table 1).

### Triacylglycerol combustion

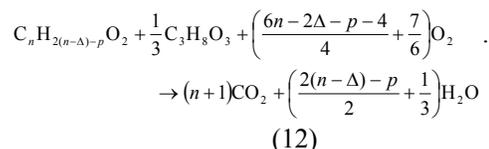
Fatty acids are stored as triacylglycerols (TAGs) in which three FAs are esterified to glycerol. Lipolysis involves a range of lipases [HIDE ET AL. 1992] catalysing hydrolytic reactions that release FAs. Of course, TAGs are highly heterogeneous molecules, so the overall reaction depends on the FA composition of the TAG, but the mobilisation of TAG can be summarised as



The combustion of glycerol ( $\text{C}_3\text{H}_8\text{O}_3$ ) can be written



and, as there are three FAs per glycerol, the combustion of one FA-equivalent of TAG ( $\text{FA}_{\text{eq}}$ ) could be written



and so the enthalpy of combustion is

$$\Delta H_c(\text{FA}_{\text{eq}}) = \Delta H_c(\text{FA}) + \frac{1}{3}\Delta H_c(\text{glyc}) - \Delta_f H^0(\text{H}_2\text{O}). \quad (13)$$

Values of  $\Delta H_c$  can be estimated for TAGs containing mixtures of FAs using

$$\Delta H_c(\text{TAG}) = \sum_{\text{FA}} p(\text{FA}) \frac{3\Delta H_c(\text{FA}) - 265.79}{3M_{\text{FA}} + 38.016}. \quad (14)$$

Combustion of the TAGs containing the same FA composition as human fat or rattite or seed oils yields,  $\Delta H_c \approx 37\text{-}38 \text{ kJ g}^{-1}$  despite the different FA compositions (Table 1).

**Fatty acid oxidation *in vivo***

The yield of ATP from FA oxidation *in vivo* can be obtained from the number of reducing equivalents (both from the cycle of  $\beta$ -oxidation and from the oxidation of acetyl CoA by the tricarboxylic acid (TCA) cycle), their oxidation by the electron transfer chain and the resulting synthesis of ATP [EATON et al. 1996, KUNAU et al. 1996, RASMUSSEN & WOLFE 1999] that is summarised in Figure 4. Specifically, the oxidation of an  $n$ -carbon FA acid requires cycles of  $\beta$ -oxidation ( $\frac{1}{2}n - 1$  or  $\frac{1}{2}(n - 3)$  for even or odd  $n$ , respectively) each of which yields NADH, ubiquinol (UQH<sub>2</sub>, a product of the reaction catalysed by the electron transfer flavoprotein:UQ oxidoreductase) and acetyl CoA, and the final cycle also yields a second acetyl CoA ( $n$  even) or propionyl CoA ( $n$  odd). For  $n$  even, the oxidation of each of the  $\frac{1}{2}n$  molecules of acetyl CoA by the TCA cycle yields a further 3 NADH, 1 UQH<sub>2</sub> (from the succinate:ubiquinone oxidoreductase reaction [BROWN, 2000]) and 1 GTP. Summing these yields  $(2n - 1)$  NADH,  $(n - 1)$  UQH<sub>2</sub> and  $0.5n$  GTP, and the activation of each FA requires the equivalent of 2ATP. Therefore the oxidation of a simple saturated FA with,  $n$  even, has an ATP yield of

$$Y_{\text{ATP}} = (n_{\text{Q}} + 2n_{\text{H}} + 0.5)n - n_{\text{Q}} - n_{\text{H}} - 2 \quad (15)$$

where  $n_{\text{Q}}$  and  $n_{\text{H}}$  are the ATP/ $2e^-$  ratios for the oxidation of FAD- and NAD<sup>+</sup>-linked substrates, respectively (these values are  $n_{\text{Q}} = 1.5$  and  $n_{\text{H}} = 2.5$ ).

For saturated FAs with an odd number of carbons, the final cycle of  $\beta$ -oxidation yields propionyl CoA that is carboxylated and then converted to succinyl CoA, which is oxidised by the TCA cycle yielding NADH, UQH<sub>2</sub> and GTP (Figure 4). The remainder of the chain is oxidised in the usual manner yielding  $\frac{1}{2}(n - 3)$  NADH,  $\frac{1}{2}(n - 3)$  UQH<sub>2</sub> and  $\frac{1}{2}(n - 3)$  acetyl CoA, so the yield of ATP following the oxidation of each of these intermediates is

$$Y_{\text{ATP}} = (n_{\text{Q}} + 2n_{\text{H}} + 0.5)n - 2n_{\text{Q}} - 5n_{\text{H}} - 3.5 \quad (16)$$

which, using the standard ATP/ $2e^-$  ratios, is 5 ATP smaller than that from the oxidation of a fatty acid with one fewer carbons. However, if the oxaloacetate produced from the metabolism of propionyl CoA is carboxylated, by phosphoenolpyruvate carboxykinase, to phosphoenolpyruvate which can be oxidised

by pyruvate kinase, pyruvate dehydrogenase and the TCA cycle, the yield of ATP increases by  $5n_{\text{H}} + 2n_{\text{Q}} + 1$  (Figure 4). Therefore (16) becomes

$$Y_{\text{ATP}} = (n_{\text{Q}} + 2n_{\text{H}} + 0.5)n - 2.5 \cdot \quad (17)$$

Finally, the oxidation of a FA containing  $\Delta$  double bonds requires  $\Delta$  NADPH to complete the process. Since NADPH is energetically equivalent to NADH, the yield of ATP is  $\Delta n_{\text{H}}$  smaller than that of the corresponding saturated FA. Combining this with (15) and (17) gives an expression for the ATP yield for the oxidation of any FA

$$Y_{\text{ATP}} = \begin{cases} (n_{\text{Q}} + 2n_{\text{H}} + 0.5)n - n_{\text{Q}} - (\Delta + 1)n_{\text{H}} - 2 & n \text{ even} \\ (n_{\text{Q}} + 2n_{\text{H}} + 0.5)n - \Delta n_{\text{H}} - 2.5 & n \text{ odd} \end{cases} \quad (18)$$

The most common FAs have an even number of carbons. For the saturated, 16-carbon FA palmitate, as is well known [STRYER 1995, ZUBAY 1998],  $Y_{\text{ATP}} = 106$ , which is equivalent to about -3604 kJ mole<sup>-1</sup> ( $= \Delta G_{\text{ATP}} Y_{\text{ATP}}$ , where  $\Delta G_{\text{ATP}} = -34$  kJ mole<sup>-1</sup> is the value of the Gibbs function for ATP hydrolysis [ALBERTY 2000]).

For very large  $n$ , (18) approaches  $7n$  and so, combined with (3), the limiting yield of ATP is about 0.5 mol g<sup>-1</sup>. The oxidation of the FAs from human fat or rattite or seed oils yields about 0.41 mol ATP g<sup>-1</sup> (9) despite quite different FA compositions (Table 1).

Naturally, the ATP yield increases with  $n$  and decreases only slightly with  $\Delta$ , consistent with (7). For  $n = 16$ , the introduction of a double bond results in a decrease in the yield of ATP from 106 mol mol<sup>-1</sup> to 103.5, which amounts to about 2.3%, comparable with the approximately 1.6% change in  $\Delta H_{\text{c}}$  associated with unsaturation.

As Darvey [1999] has pointed out, the yield of energy during  $\beta$ -oxidation is significantly smaller than that from the subsequent oxidation of the acetyl CoA by the TCA cycle. However, it is clear from Figure 4 that the fraction of the ATP yield due to  $\beta$ -oxidation is

$$\frac{(0.5n - 1)(n_{\text{Q}} + n_{\text{H}}) - \Delta n_{\text{H}}}{(n_{\text{Q}} + 2n_{\text{H}} + 0.5)n - (\Delta + 1)n_{\text{H}} - n_{\text{Q}} - 2} \quad (19)$$

for  $n$  even, which approaches 0.286 for long chain FAs, using the standard values of  $n_{\text{H}}$  and  $n_{\text{Q}}$ . For  $n$  odd, the same limit is reached, but it is approached more slowly with increasing  $n$ .



Table 1.

Calculated  $\Delta H_c$  and ATP yield of the oxidation of the FAs and the corresponding TAGs of selected fats and oils.

	$\Delta H_c$ (kJ g <sup>-1</sup> )		$Y_{ATP}$ (mol g <sup>-1</sup> )	
	FA	TAG	FA	TAG
Human fat				
neonate <sup>[Sarda et al. 1987]</sup>	-39.2	-37.7	0.413	0.401
infant <sup>[Widdowson et al. 1975]</sup>	-39.3	-37.8	0.413	0.401
adult <sup>[Jacobsen et al. 1983]</sup>	-39.0	-37.6	0.410	0.399
Rattite oil				
emu <sup>[Grompone et al. 2005]</sup>	-39.4	-38.0	0.414	0.403
ostrich <sup>[Basuny et al. 2011]</sup>	-39.3	-37.9	0.414	0.402
rhea <sup>[Grompone et al. 2005]</sup>	-39.3	-37.9	0.414	0.402
Seed oil				
cotton <sup>[Arafat et al. 2011]</sup>	-39.3	-37.9	0.413	0.401
sema <sup>[Arafat et al. 2011]</sup>	-39.4	-38.0	0.414	0.402
monsa <sup>[Arafat et al. 2011]</sup>	-39.4	-37.9	0.414	0.402

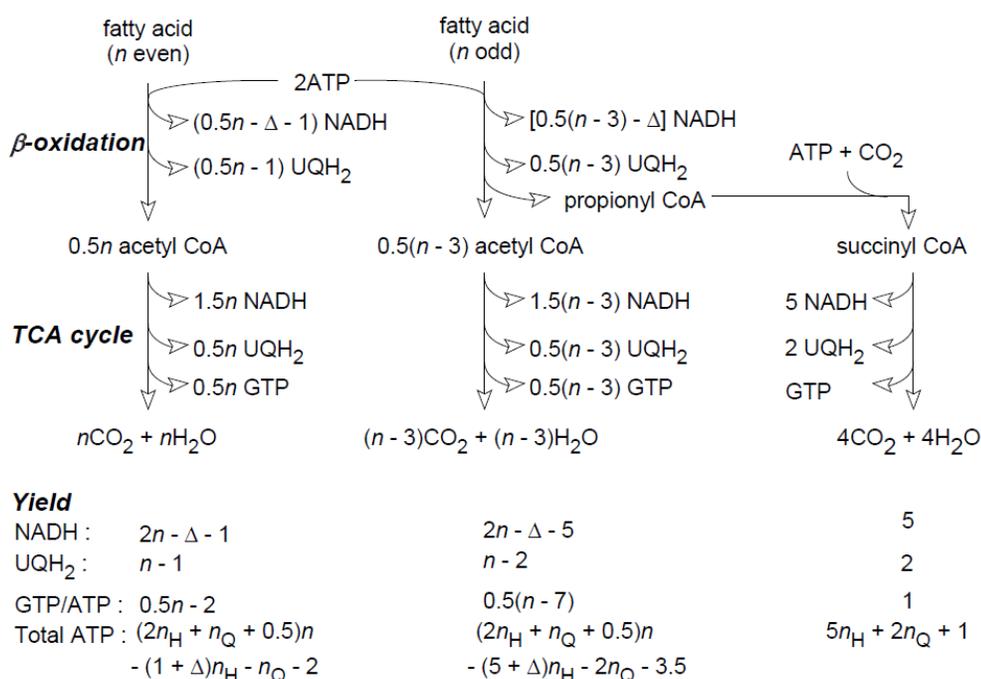


Figure 4. Energy yield from the oxidation of  $n$ -carbon FAs. The upper section represents the cycle of  $\beta$ -oxidation, the central section represents the operation of the TCA cycle and the bottom section summarises the yield of NADH, UQH<sub>2</sub> and GATP/ATP and the overall yield of ATP following the oxidation of NADH and UQH<sub>2</sub>. The values given under oxaloacetate represent the yield of its oxidation by the path described in the text.

### Triacylglycerol oxidation *in vivo*

Of course, the yield of ATP from the oxidation of  $FA_{eq}$  depends on the metabolism of the glycerol. In essence, glycerol is phosphorylated to glycerol 3-phosphate and oxidised to dihydroxyacetone phosphate which is oxidised by glycolysis, the TCA cycle and electron transfer chain. The overall

yield of ATP for this process is  $1 + 6n_H + n_Q$  or the equivalent of 17.5 ATP, so the yield of ATP from the oxidation of  $FA_{eq}$  is  $(Y_{ATP} + 35/6)$  ATP. The yield of ATP from the oxidation of TAGs with a given FA composition can be estimated using the logic underlying (14). For TAGs containing the same FA composition as human fat or rattite



or seed oils yield about 0.4 mol ATP g<sup>-1</sup> (Table 1).

### Conclusions

Simple expressions for the heat of combustion for FAs, TAGs and mixtures of FA-containing molecules have been derived based on an empirical expression for  $\Delta_f H^\circ(\text{FA})$ . These prompt us to suggest that the difference in the standard energy content of fat relates to the combustion of TAGs (37 kJ g<sup>-1</sup><sup>[DARVEY 1998]</sup>) or FAs (39.5 kJ g<sup>-1</sup><sup>[GNAIGER 1983]</sup>). Moreover, estimates of  $\Delta H_c$  for a small number of fats and oils prompt the observation that their energy density is highly consistent despite the variation in FA composition and the considerable dependence of  $\Delta H_c$  on  $n$ . Correspondingly, the oxidation of FAs and TAGs from different sources yields similar amounts of ATP.

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Received: December 3, 2011

Accepted: January 28, 2012

