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Bioenergetic Considerations in the Improvement of Oil Content and Quality in Oil-Seed Crops

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Summary. Production values (PVs), defined as the weight of the end product/weight of the substrate required for carbon skeletons and energy production, were calculated for plant fatty acids. The PVs varied from 0.361 to 0.300 with linolenic acid having the lowest value. In general, the PVs of unsaturated fatty acids were lower than those of saturated fatty acids of similar chain lengths. Using this basic information, PVs of (A) oils from different oilseed crops, based on their standard fatty acid composition and (B) seed biomass with specified oil content and fatty acid composition were calculated. $\frac{1}{PV}$ gives the glucose required for the biosynthesis of 1 g end product and thus an estimate of the photosynthate requirement for the desired breeding goal can be estimated. Such calculations show that increasing oil percentage in seeds has a maximum energy cost when the increase in oil is associated with a decrease in the amount of carbohydrates where there is no change in protein concentration. Reduction of erucic acid content in the rapeseed oil did not alter its PV. It is inferred that there are no serious bioenergetic constraints in altering the fatty acid composition.

Key words: Production values – Fatty acids – Oil – seed Crops

Introduction

There is considerable interest in increasing the oil content and in altering the fatty acid composition of the oilseed crops by plant breeding. Large heritable variations in the oil content and in the fatty acid composition have been found in varietal collections (Downey and McGregor 1975; Cherry 1977).

It has recently been shown that increasing grain protein concentration in cereals or altering their amino acid composition to increase the amount of nutritionally limiting amino acids like lysine causes an additional demand of photosynthate for seed biomass (Bhatia and Rabson 1976). Lipids have an average energy content of 9500 calories per gram which is much higher than that of proteins (5700) and carbohydrates (4000), the other major constituents of the stored products in plant seeds. Conversely, after extensive examination of biochemical pathways and the energy requirement of the component reactions, Penning de Vries et al. (1974) concluded that in plants under aerobic conditions, 1 g glucose (photosynthate) can be used to produce 0.83 g carbohydrates or, alternatively, 0.40 g protein (assuming nitrate as the nitrogen source) or 0.33 g of lipids. Thus, any increase in the amount of lipids in seed would increase its energy content and this additional energy can come only from the photosynthesis of the plant producing the seed. It is, therefore, of considerable interest to examine the bioenergetics of the lipid metabolism in plant seeds and to consider its implications for plant breeding objectives.

In the present study, using the approaches of Penning de Vries et al. (1974), we have calculated the PVs for the synthesis of: (a) plant fatty acids, (b) oils of different oil seed crops based on their standard fatty acid composition and (c) seed biomass with specified oil content and fatty acid composition. Energetic costs associated with breeding for increased oil content and with low erucic acid in rape are also examined.

Methods

Production value (PV) is defined as the weight of the end product/weight of the substrate required for carbon skeletons and the energy production. 1/PV gives the amount of glucose required for the biosynthesis. Our calculations are based, with some modifications, on the methods of Penning de Vries et al. (1974). These changes are considered necessary in view of the more recent information available on the biochemical pathways for the synthesis of

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Table 1. Calculations of PV, ORF, CPF, ERF and HRF for sesame oil

Fatty acid	g/ 100g oil	Mole/ 100g oil	PV	ORF	CPF	ERF	HRF	Glucose requirement	Oxygen requirement	Carbon dioxide production	Moles ATP requirement	Moles $NADH_2$ requirement
								g	g	g		
1	2	3	4	5	6	7	8	9	10	11	12	13
16:0	9.1	0.0355	0.3399	0.08943	0.5320	0.05078	−0.007813	26.77	2.394	14.24	0.4621	−0.091000
18:0	4.3	0.0151	0.3331	0.09082	0.5375	0.05282	−0.007042	12.90	1.172	6.939	0.2271	−0.030280
20:0	0.8	0.0025	0.3277	0.09195	0.5423	0.05449	−0.006410	2.44	0.2245	1.324	0.04359	−0.005128
18:1	45.4	0.16099	0.3225	0.13574	0.5641	0.06028	−0.003546	140.78	19.11	79.41	2.737	−0.161000
18:2	40.4	0.14429	0.3112	0.17775	0.5867	0.06786	0.000000	129.83	23.08	76.17	2.741	0.000000
Total	100	0.3583	–	–	–	–	–	312.72	45.98	178.81	6.211	−0.2874

Column (3) = (2)/M.W. of fatty acid; (9) = (2)/(4); (10) = (2) × (5)/(4); (11) = (2) × (6)/(4); (12) = (2) × (7); (13) = (2) × (8)

Other costs:

[A] Esterification of fatty acids to glycerol phosphate : 1 mole glycerol–P/3 moles fatty acyl Co A

[B] Production of fatty acyl Co A : 1 mole ATP/mole fatty acid (the cost of SHCoA is not considered)

[C] Cost of production of glycerol–P : 0.6051 mole glucose + 0.131 mole O_2 → 1 mole of glycerol–P + 0.631 mole CO_2 + 1.131 mole H_2O (assuming that 0.5 glucose + 1 $NADH_2^+$ 1 ATP → 1 glycerol–P + H_2O)

Or Production of 1 mole of glycerol–P requires : 108.92 grams glucose; 4.192 grams O_2; 1 mole ATP; 1 mole $NADH_2$ and 27.76 grams CO_2 will be evolved.

[D] Active transport of glucose : 1 mole ATP/mole glucose

Computations for:

A. 0.3583/3 = 0.119 mole glycerol-P

B. 1 × 0.3583 = 0.3583 mole ATP = 1.70 g glucose + 1.81 g O_2 − 2.49 g CO_2 (assuming that oxidation of 1 mole glucose will yield 1 mole glucose + 6 moles O_2 → 6 moles CO_2 + 6 moles H_2O + 38 moles ATP)

C. 0.119 mole glycerol-P = 13.00 g glucose + 0.500 g O_2 − 3.30 g CO_2

Glucose requirement excluding uptake cost:

312.72	Column (9)
1.70	− B
13.00	− C
327.42	

D. 327.42/180 (M.W. of glucose) = 1.82 moles ATP = 8.61 glucose + 9.19 g O_2 − 12.64 g CO_2

Final calculations for 100 g oil

(1) Total glucose requirement : 327.42 + 8.61 = 336.03 g

(2) Total O_2 : 45.98 + 1.81 + 0.500 + 9.19 = 57.48 g

(3) Total CO_2 production : 178.81 + 2.49 + 3.30 + 12.64 = 197.24 g

(4) Total ATP requirement : 6.211 + 0.3583 + 1.82 + 0.119 = 8.51 moles
(Production of 0.119 mole glycerol-P needs 0.119 mole ATP)

(5) Total $NADH_2$ requirement : −0.2874 + 0.119 = −0.1684 (Production of 0.119 moles glycerol-P needs 0.119 mole $NADH_2$)

$$PV = \frac{100}{336.03} = 0.2976 \qquad CPF = \frac{197.24}{336.03} = 0.5870 \qquad HRF = \frac{-0.1684}{100} = -0.001684$$

$$ORF = \frac{55.48}{336.03} = 0.1711 \qquad ERF = \frac{8.51}{100} = 0.0851$$

PV (Production Value) = Weight of the end product/weight of substrate required for C – skeletons and energy production

ORF (Oxygen requirement factor) = Weight of oxygen consumed/weight of substrate required for C – skeletons and energy production

CPF (Carbon dioxide production factor) = Weight of carbon dioxide produced/weight of substrate required for C – skeletons and energy production

HRF (Hydrogen requirement factor) = g moles of $NADH_2$ required/weight of end product

ERF (Energy requirement factor) = $\frac{\text{g moles of ATP required}}{\text{weight of end product}}$

plant fatty acids (Sedgwick 1973; Stumpf 1976). The following assumptions have been made:

1. The biosynthesis of fatty acids in plants is aerobic.
2. The fatty acid synthesis is 'microsomal' and requires malonyl Co A and NADPH for elongation.
3. Fatty acid synthesis needs acyl-carrier protein (ACP). However, the energetic cost for its production is not considered in the calculations since it is recycled in the system.
4. The biosynthesis of unsaturated fatty acids requires the enzyme desaturase, O_2 and NADPH. Fatty acids 16:1, 18:1, 18:2 and 18:3 are synthesised respectively from 16:0, 18:0, 18:1 and 18:2. Fatty acids 20:1 and 22:1 are also derived from 18:1 by chain elongation (Stumpf 1976).
5. The hydroxylation of oleic acid (18:1) to ricinoleic acid (18:1) is mediated through oleyl Co A hydroxylase, O_2 and NADH.
6. Malonyl Co A production is mediated by acetyl Co A carboxylase, ATP and CO_2.
7. Cost for the transport (ATP/mole fatty acid) of fatty acid from mitochondria to hyaloplasm is not considered.
8. The conversion pathway of glycerophosphate considered is 0.5 glucose + $NADH_2$ + ATP $\longrightarrow$ glycerophosphate + H_2O.
9. The esterification cost of fatty acids to glycerophosphate for the production of 1 mole of fat is:

1 glycerophosphate + 3 fatty acids + 3 HS Co A + 3ATP $\longrightarrow$ 1 fat + $3H_2O$

Calculation of PV is illustrated in Table 1 taking sesame oil as an example.

Results and Discussion

Production Values of Individual Fatty Acids

The values characterizing the conversion of glucose into commonly occurring plant fatty acids are given in Table 2. Since palmitic acid (16:0) is a common constituent of most vegetable oils, the glucose requirements of each fatty acid relative to it are given for easy comparison. The PV decreases with the increase in chain length of fatty acids and consequently their production costs are higher. In general, the unsaturated fatty acids have low PVs in comparison to saturated fatty acids of similar chain lengths. Linolenic acid (18:3) shows the lowest PV and the highest ORF, CPF and ERF. Its $NADH_2$ requirement expressed as HRA, is positive while for all other fatty acids considered here HRFs are negative. A negative HRF indicates a contribution of ATP to the system following the oxidation of excess $NADH_2$ formed during the fatty acid synthesis. Two different pathways for the synthesis of linolenic acid have been reported recently in plants (Stumpf 1976): it can be synthesized either from 16:0 $\longrightarrow$ 16:1 $\longrightarrow$ 16:2 $\longrightarrow$ 16:3 followed by chain elongation to 18:3 or from 18:1 $\longrightarrow$ 18:2 $\longrightarrow$ 18:3 pathway. The PVs considering the two pathways are same.

Table 2. Values characterizing the conversion process of glucose into individual fatty acids excluding the cost of glucose uptake

Name	No. of carbon atoms: double bond	PV	ORF	CPF	ERF	HRF	Percent glucose requirement relative to palmitic acid to synthesise 1 g product
Saturated							
Lauric acid	12:0	0.361	0.08507	0.514	0.04500	−0.01000	94
Myristic acid	14:0	0.349	0.08758	0.524	0.04825	−0.00877	97
Palmitic acid	16:0	0.340	0.08943	0.532	0.05078	−0.00781	100
Stearic acid	18:0	0.333	0.09082	0.538	0.05282	−0.00704	102
Eicosanoic acid	20:0	0.328	0.09195	0.542	0.05449	−0.00641	104
Behenic acid	22:0	0.323	0.09286	0.546	0.05588	−0.00588	105
Lignoceric acid	24:0	0.320	0.09361	0.549	0.05707	−0.00544	106
Unsaturated							
Palmitoleic acid	16:1	0.327	0.13979	0.560	0.05906	−0.00394	104
Ricinoleic acid	18:1	0.333	0.17300	0.572	0.06795	−0.00105	102
Oleic acid	18:1	0.323	0.13574	0.564	0.06029	−0.00355	105
Linoleic acid	18:2	0.311	0.17775	0.587	0.06786	0.00000	109
Linolenic acid	18:3	0.300	0.21783	0.609	0.07554	+0.00360	113
Eicosenoic acid	20:1	0.318	0.13199	0.565	0.06129	−0.00323	107
Erucic acid	22:1	0.313	0.13333	0.570	0.06509	−0.00296	109
Nervonic acid	24:1	0.309	0.13435	0.575	0.06831	−0.00298	110

Note: The cost of moles ATP computed in column (12) is not considered since it is included in the PVs of fatty acids. Likewise the glucose equivalent of excess production of $NADH_2$ in column (13) or $NADH_2$ requirement for glycerol-P synthesis (as in A). has been excluded because the adjustments are included in the PVs of the fatty acids. Excess production of $NADH_2$ is adjusted as NADH + 0.5 O_2 → H_2O + 3 ATP. $NADPH_2$ is taken as $NADH_2$ + ATP according to Penning de Vries et al. (1974)

Malonyl Co A, necessary for fatty acid synthesis, is normally obtained in plants by the carboxylation of acetyl Co A. This reaction is catalysed by the enzyme acetyl Co A carboxylase. However, this enzyme is apparently absent in some plants and in its absence malonyl Co A is synthesised from malonate by the malonate thiokinase reaction which is as follows: malonate + ATP + HS Co A → malonyl Co A + ADP + Pi. Malonate is derived from the oxidative decarboxylation of oxaloacetate (See Sedgwick 1973). The PVs of fatty acids if synthesized via this pathway are about 15 per cent less than the values obtained with the acetyl Co A carboxylase pathway.

Production Value of Oils

Based on the values for individual fatty acids (Table 2) and the standard fatty acid composition (Table 3), PV and other parameters for the synthesis of oil from different crop plants were calculated (Table 4). The calculation method is illustrated in Table 1. Considering the genetic variability for fatty acid composition of oil within a species, the standard composition can only be taken as indicators. PVs for oils will change with the alterations in their fatty acid composition.

Table 4 shows that the castor bean oil has the highest

Table 3. Fatty acid composition of oil from different oilseed crops

Crop	Constituent fatty acids g/100 g fatty acids Carbon atom: double band													Per cent unsaturated fatty acid	Per cent oil
	12:0	14:0	16:0	16:1	18:0	18:1 (OH)	18:1	18:2	18:3	20:0	22:0	22:1	24:0		
Maize	–	1.4	10.2	1.5	3.0	–	49.6	34.3	–	–	–	–	–	85.4	5
Cotton	–	1.4	23.4	2.0	1.1	–	22.9	47.8	–	1.3	–	–	–	72.7	25
Mustard	–	1.3	–	–	–	–	27.2	16.6	1.8	–	1.1	51.0	1.0	96.6	48
Safflower[a]	12:0 – C 22:0 = 6.9					–	18.8	70.9	3.4	–	–	–	–	93.1	33
Castor bean	C 12:0 – C 18:0 = 2.4					87.0	7.4	3.1	–	–	–	–	–	97.5	45
Sesame			9.1		4.3	–	45.4	40.4	–	0.8	–	–	–	85.8	54
Soybean	0.2	0.1	9.8	0.4	2.4	–	28.9	50.7	6.5	0.9	–		–	86.5	20
Linseed	–	–	6.3	–	2.5	–	19.0	24.1	47.4	0.5	0.2	–	–	90.5	38
Sunflower	–	–	5.6		2.2	–	25.1	66.2	–	0.9	–	–	–	91.3	29
Peanut	–	–	8.3	–	3.1	–	56.0	26.0	–	2.4	3.1	–	1.1	82.0	45

[a] adjusted to 100% from the original data

Source: Handbook of Biochemistry, pp E20-21. Cleveland, Ohio: The Chemical Rubber Company 1968

Table 4. Values characterizing the conversion process of glucose into oils of different corps with standard fatty acid compositions

Crop	PV	ORF	CPF	ERF	HRF	Percent glucose requirement relative to castor oil to synthesise 1 g product
Castor bean	0.309	0.1906	0.593	0.08232	–0.0006658	100
Groundnut	0.299	0.1638	0.581	0.08373	–0.002072	103
Cotton	0.299	0.1689	0.581	0.08425	–0.001784	103
Corn	0.298	0.1681	0.582	0.08449	–0.001741	104
Sesame	0.298	0.1711	0.587	0.08510	–0.00168	104
Soybean	0.296	0.1802	0.588	0.08668	–0.000936	104
Mustard	0.295	0.1660	0.588	0.08669	–0.002615	105
Sunflower	0.294	0.1834	0.592	0.08771	–0.000349	105
Safflower	0.293	0.1886	0.595	0.08906	–0.000204	105
Linseed	0.289	0.2036	0.603	0.09201	+0.001517	107

Standard fatty acid composition of various oils used for these calculations are given in Table 3

Table 5. Seed biomass productivity of oilseed crops

Crop	Composition (percent of dry weight)				(1/PV) X 100 = glucose requirement for the production of 100 g seed biomass	Biomass productivity seed/g photosynthate	Energy content Kcal/100g dry matter
	Carbohydrate	Protein	Lipid	Ash			
Maize	84	10	5	1	142.98	0.699	440
Cotton	47	25	25	3	202.71	0.493	568
Sunflower	48	20	29	3	206.47	0.484	581
Safflower	50	14	33	3	207.87	0.481	593
Soybean	38	38	20	4	208.35	0.478	558
Linseed	32	26	38	4	235.04	0.426	649
Groundnut	25	27	45	3	248.12	0.403	681
Rape	25	23	48	4	250.33	0.399	687
Sesame	19	20	54	7	254.10	0.393	703

Composition of seed: Handbook Biological Data (ed. Spector W.S.), p. 87. Philadelphia: Saunders 1956

PVs for carbohydrate and protein are considered as 0.83 and 0.4, respectively. PV for lipid of each crop is taken from Table 4

Table 6. Energetic cost of increasing seed oil concentration in groundnut at the cost of either carbohydrate or protein or both

	Component	Amount g/100 g seed	PV		Equivalent glucose required (g)	% increase in photosynthate demand relative to standard cultivar
I	**Standard cultivar**					
	Carbohydrate (CHO)	25	0.83		30.12	
	Protein	27	0.40		67.50	
	Oil	45	0.299		150.50	0
	Minerals	3	–			
				Total	248.12	
II	**Cultivar with 5% more oil and 5% less CHO**					
	CHO	20	0.83		24.10	
	Protein	27	0.40		67.50	
	Oil	50	0.299		167.22	4.3
	Minerals	3	–			
				Total	258.82	
III	**Cultivar with 5% more oil and 5% less protein**					
	CHO	25	0.83		30.12	
	Protein	22	0.40		55.00	
	Oil	50	0.299		167.22	1.7
	Minerals	3	–			
				Total	252.34	
IV	**Cultivar with 5% more oil and 2.5% less CHO and 2.5% less protein**					
	CHO	22.5	0.83		27.11	
	Protein	24.5	0.40		61.25	
	Oil	50	0.299		167.22	3.0
	Mineral	3	–			
				Total	255.58	

PV while the linseed oil has the lowest. The former contains 87 per cent ricinoleic acid (18:1) which has a PV of 0.333. Linolenic acid (18:3) with a PV of 0.300 is the most abundant fatty acid in linseed oil. The bioenergetic cost of linseed oil is 7% higher in comparison to the castor bean oil.

Seed Biomass Productivity

Like the PV for a chemical end product, the PV for seed biomass can be calculated based on its chemical composition. Sinclair and de Wit (1975) called it seed biomass productivity and defined it as gram of seed biomass production per gram of photosynthate. In their calculations they used the gross PVs for lipids (0.33), proteins (0.40) and carbohydrates (0.83). More precise estimates of seed biomass productivity which would be useful in plant breeding research can be made for the genotypes specifying their fatty and amino acid composition. PVs for the seeds of different oil-yielding plants considering their standard fatty acid composition are given in Table 5. Sesame shows the lowest PV and it is pertinent to point out that the sesame seeds have the highest energy content and the lowest average yield among the oilseed crops considered here.

Bioenergetic Cost of Increasing Oil Percentage

The bioenergetic cost of increasing the oil percentage is illustrated in Table 6, taking groundnut as an example. Any increase in the oil percentage has to be associated with an equivalent decrease in the amount of other constituents of seed biomass. As proteins and carbohydrates are the other two major components, the three alternatives are:

1. Proteins are not altered and carbohydrates are reduced.
2. Carbohydrates remain the same while the protein concentration is reduced.
3. Both proteins and carbohydrates are reduced equally. It is evident that there is an increase in the bioenergetic cost in all the three alternatives, being least when the increase in oil percentage is accompanied by an equivalent reduction in the amount of proteins. Of course, from the breeding point of view this is not desirable as the meal after extraction is an important source of food and feed proteins in most oil seeds. A negative correlation between oil and protein concentration is reported in soybean (Hymowitz et al. 1972) and maize (Dudley et al. 1977). Significant negative correlations ($r = -0.72$) were obtained between the oil and protein values reported by Cherry (1977) for 21 groundnut cultivars. The most desired objective in a breeding programme would be to increase the oil percentage at the cost of carbohydrates. From the bioenergetic considerations this, of course, is the most expensive. These conclusions are equally valid for other oil seeds.

Bioenergetic Cost of Altering the Fatty Acid composition

Plant breeding research is attempting to modify the fatty acid composition of oilseeds. Rapeseed and safflower varieties with modified fatty acid composition are already under commercial cultivation (Downey and McGregor 1975). From nutritional considerations it is desirable to reduce the amount of erucic (22:1) and eicosenoic (20:1) acids in rape and mustard oils. In some of the low erucic acid cultivars, a decrease in erucic and eicosenoic acids is associated with an increase in oleic (18:1) and linolenic (18:3) acids (Downey et al. 1975). The PV of oleic acid (0.323) is 3.2 and 1.6% higher while that of linolenic acid (0.300) is 4.1 and 5.6% lower than those of erucic (0.313) and eicosenoic (0.318) acids, respectively. Thus the overall change in the PV of oil is expected to be marginal.

PVs for the oil of two low erucic acid cultivars of rape were calculated and compared to PVs of normal cultivars (Table 7). Only a marginal (less than 1%) change in the PVs of low erucic acid oils can be seen in comparison to normal erucic acid oils. Yield of these low erucic acid cultivars is also similar to cultivars with oil containing normal erucic acid. Reduction in linolenic acid content to improve the keeping quality of oil is another important breeding objective in many oilseed crops. Below normal linolenic acid stocks in low erucic acid strains of rape have been reported (Rakow and McGregor 1975). Such stocks would be even more advantageous from the bioenergetic point of view.

Table 7. PV of oil seed composition and yield of low and normal erucic rape cultivars[a]

Character/ Cultivar	Rape Target	Turnip rape Midas	Echo	Torch
PV of oil	0.2929	0.2953	0.2941	0.2960
$\frac{1}{PV} \times 100$ (g. glucose)	341	339	340	338
% oil	42.7	42.7	39.4	38.5
% protein	42.7	39.3	41.4	40.4
% eruric acid	43.2	0.4	27.7	0.1
% eicosenoic acid	13.8	2.9	12.9	0.9
% oleic acid	15.6	55.1	25.4	56.2
% linolenic acid	7.5	10.5	9.6	12.3
Yield (Kg/ha)	1610	1740	1420	1410
Days to maturity	104	103	88	87

[a] Fatty acid composition and yield data are from Downey, Stringham and McGregor (1975) and Downey (1975), respectively

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