Effect of Alleles Governing 16:0 Concentration on Glycerolipid Composition in Developing Soybeans

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ABSTRACT: Soybean [*Glycine max* (L.) Merr.] oil typically contains 11% palmitic acid, but germplasm with recessive alleles at *Fap* gene loci exhibit from less than 4% to about 35% 16:0. Although these alleles are used to develop new cultivars, little is known about how they influence palmitic acid concentration. One theory suggests that *fap* alleles may mediate differences in triacylglycerol composition through genetic effects on the activity or substrate specificity of acyltransferases, such as diacylglycerol acyltransferase (EC 2.3.1.20). Based on logistic function analysis of developing seed, differences in *fap* allele expression are evident in the rate of palmitic acid accumulation in triacylglycerol, with peak deposition near mid-seed fill. Acetate saturation kinetics also reveal a strong positive relation between the relative amount of *de novo* palmitic acid synthesis and the indigenous palmitic acid concentration in triacylglycerol among *fap* genotypes. However, no differences appear in the kinetics of palmitoyl-CoA metabolism in developing seed of these genotypes. Therefore, the *fap* alleles apparently do not encode or regulate the activities of glycerolipid acyltransferase enzymes. Rather, major genetic effects on triacylglycerol composition accrue through regulation of palmitic acid production in the plastids of developing soybean cotyledons.

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KEY WORDS: Developing-seed, *fap*-alleles, genetics, glycerolipid composition, *Glycine max*, logistic function, metabolism, oil, palmitic acid, saturated fat.

Inheritance studies have shown that palmitic acid (16:0) concentration in soybean oil is influenced by certain gene mutations that have been induced by chemical mutagenesis at one or more loci designated as *Fap*. Germplasm carrying homozygous recessive fap_2 alleles [C1727, (1)], fap_{2b} alleles [A21, (2)], fap_4 alleles [A24, (2)], fap_5 alleles [A27, (3)], or combinations of these alleles (3) produce soybean oil with a greater than normal concentration of 16:0. Germplasm carrying homozygous recessive fap_1 alleles [C1726, (1)], homozygous recessive fap_3 alleles [A22, (2)], or a combination of these alleles exhibits lower than normal 16:0 concentration (4). Simultaneous with the latter disclosure, Wilcox *et al.* (5) demonstrated that the first known low-16:0 soybean germplasm [N79-2077-12, (6,7)] carried a serendipitous natural mutation that segregated independently of the fap_1 allele and that mating N79-2077-12 × C1726 produced inbred lines with northern (C1943) and southern maturity (N94-2575) that also exhibited very low 16:0 concentration (8). Although the recessive allele responsible for the low-16:0 phenotype in N79-2077-12 has been described as fap_3 (9,10), it now is designated fap_{nc} until it can be shown to be independent or allelic to the chemically induced mutation resident in A22 germplasm. In addition, another chemically induced mutation in ELLP2 germplasm, with the temporary descriptor *fap**, has been shown to segregate independently of fap_1 (11).

Phenotypic variation for 16:0 concentration ranges from 9 to 18% among accessions of the U.S. Department of Agriculture Soybean Germplasm Collection (12). As reported above, combinations of the recessive *fap* alleles expand phenotypic variation for 16:0 from less than 4% to about 35% of crude oil in mature seed. However, the manner by which *fap* alleles affect altered 16:0 levels in soybean oil is virtually unknown. It also is unclear how certain "modifier genes," which exert minor effects on 16:0 concentration, might interact with *fap* loci (13). One of the few studies to investigate the potential metabolic targets for *fap* and related modifier gene action (6) suggests that altered triacylglycerol (TG) composition attributed to fap_{nc} primarily is a function of 16:0-intermediate availability and utilization in TG synthesis by diacylglycerol acyltransferase (DGAT). This investigation reopens that early inquiry with a more detailed evaluation of 16:0 metabolism in soybean germplasm exhibiting fap_1, fap_2, and fap_{nc} alleles.

MATERIALS AND METHODS

Plant material. Five highly inbred soybean [*Glycine max* (L.) Merr.] germplasm lines homozygous at *Fap* loci were grown at the Central Crops Research Station in Clayton, NC. These lines included: C1726 (fap_1fap_1 Fap_2Fap_2 $Fap_{nc}Fap_{nc}$), C1727 (Fap_1Fap_1 fap_2fap_2 $Fap_{nc}Fap_{nc}$), N79-2077-12 (Fap_1Fap_1 Fap_2Fap_2 $fap_{nc}fap_{nc}$), N94-2575 (fap_1fap_1 Fap_2Fap_2 $fap_{nc}fap_{nc}$), and the cv. Dare (Fap_1Fap_1 Fap_2Fap_2 $Fap_{nc}Fap_{nc}$). The stage of seed development was reported in days after flowering (DAF) for each genotype.

Tissue analyses. Representative dry mass and oil content were determined in seed (20 to 30 g fresh weight) harvested at intervals between 30 and 70 (mature) DAF. Oil concentration

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was measured with Maran pulsed nuclear magnetic resonance (pNMR) (Resonance Instruments Ltd., Whitney, Oxfordshire, United Kingdom). Glycerolipid extraction and isolation of glycerolipid classes followed the methods described by Wilson and Kwanyuen (14). Fatty acid methyl esters (FAME) were prepared from glycerolipids by heating with 1 mL 5% (vol/vol) sulfuric acid in methanol at 80°C for 90 min. After cooling to ambient temperature, the reaction mixture was vortexed with 1.5 mL 1.5% NaCl plus 1 mL hexane and held at –20°C to allow phase separation. The hexane phase (top) was removed, dried under nitrogen at 55°C, and resuspended in 100 μL 2:1 (vol/vol) chloroform/methanol prior to analysis by gas chromatography (GC). Individual FAME (16:0, 18:0, 18:1, 18:2, and 18:3) derived from total phospholipids (TPL), diacylglycerol (DG), and TG were separated by reversed-phase thin-layer chromatography (TLC) developed using 10% $AgNO_3$ in acetonitrile/1,4-dioxane/acetic acid (80:20:1, vol/vol/vol) (15). Fatty acid composition was determined with a Hewlett-Packard model 5890-II gas chromatograph (Palo Alto, CA) equipped with a model 7673 auto sampler, dual flame-ionization detectors (FID), and dual 0.53 mm × 30 m AT-Silar capillary columns (Alltech Associates Inc., Deerfield, IL). Operating conditions were: carrier, He (3 mL/min); 25:1 (vol/vol) split injection; injection temperature, 250°C; detector temperature, 275°C; and column temperature, 190°C.

Logistic function. The deposition of 16:0 in TG during reproductive development was modeled as a function of time (16). Based on the observation that product deposition followed a sigmoidal pattern (17), cumulative deposition of 16:0 in TG (mg/seed) was predicted on given days of seed development from known data points by application of the logistic function (Eq. 1). The first derivative of the logistic function (Eq. 2) yielded the incremental rate of product accumulation (mg/seed/d), where W is the amount of seed product at T (DAF), a is the amount of constituent at seed maturity, dW/dT is the rate of constituent deposition at T, and k and b are empirical constants.

$$W = a/[1 + be^{(-kT)}] \quad [1]$$

$$dW/dT = kabe^{-kT} / (1 + be^{-kT})^2 \quad [2]$$

In vivo *16:0-CoA or acetate saturation kinetics.* Whole cotyledons (0.5 g fresh weight) harvested at 35 DAF were incubated at 25°C in 3 mL 0.2 N 2-[N-morpholino]ethane-sulfonic acid (MES) buffer, pH 5.5, with either 0.5 μCi [1-^{14}C]16:0-CoA (55 mCi mmol^{-1}; American Radiolabeled Chemicals, Inc., St. Louis, MO) plus one of four levels (0.0, 0.01, 0.1, or 1.0 (mol) of 16:0-CoA (Sigma Chemical Co., St. Louis, MO); or 5 μCi [2-^{14}C]acetate (57 mCi mmol^{-1}; American Radiolabeled Chemicals, Inc.) plus one of three levels (0.0, 1.0, or 10.0 (mol) of potassium acetate (Fisher Scientific Co., Fair Lawn, NJ). Reactions were terminated at 2 h. Glycerolipid extraction and analysis followed the methods described above. Radioactivity in lipid fractions was measured with a Packard Tri-CARB 2100TR liquid scintillation spectrometer (Meriden, CT) and expressed relative to the specific activity of total 16:0-CoA or acetate added to each reaction. The resultant data emulated sigmoidal curves from which kinetics of the synthetic reactions at saturating substrate levels were interpreted with Hofstee plots (18). All data were reported as means of three replications.

RESULTS AND DISCUSSION

Combinations of homozygous recessive or dominant fap_1, fap_2, and fap_{nc} alleles produced significant effects on 16:0 concentration of crude seed oil. At seed maturity, these genotypes ranged from 4.4 to 16.2% 16:0, with the cultivar Dare representing the normal 16:0 concentration typically found in commercial soybean varieties (Table 1). A strong positive relation (R^2, 0.99) between the observed 16:0 concentration of respective genotypes and the difference in 16:0 concentration relative to Dare indicated these alleles may be additive in gene action. Previously, evidence for additive gene action has been demonstrated in separate cases for fap_1 and fap_2 (1), and fap_1 and fap_{nc} (5). Expression of these various *fap* alleles had no apparent effect on stearic acid (18:0) concentration (Table 1). This observation was consistent with the findings of Rebetzke *et al.* (19) that showed the genetic systems controlling 16:0 and 18:0 concentration in soybean oil were independent of each other. Based on other populations segregating for fap_{nc}, Rebetzke *et al.* (20) also postulated a significant negative relation between 16:0 and 18:1 concentration. A similar correlation may be found among these data, which is not due to associated genetic effects on oil concentration or seed mass.

Actual 16:0 content (mg 16:0 seed^{-1} in TG) at various stages during seed development was determined for each geno-

TABLE 1
Lipid Composition of Soybean Germplasm Exhibiting Genetic Variation at *Fap* Gene Loci

Germplasm	Alleles	16:00 (% dry weight at seed maturity)	18:00 (% dry weight at seed maturity)	Other[a] (% dry weight at seed maturity)	Oil (% dry weight)	Dry weight (mg/seed)
C1727	Fap_1 fap_2 $Fapnc$	16.2	3.6	80.2	19.2	156.8
N79-2077-12	Fap_1 Fap_2 $fapnc$	5.9	3.6	90.5	20.8	195.1
C1726	fap_1 Fap_2 Fap_{nc}	7.9	3.8	88.3	20.4	156.1
N94-2575	fap_1 Fap_2 fap_{nc}	4.4	3.4	92.2	18.0	184.1
DARE	Fap_1 Fap_2 Fap_{nc}	11.5	3.6	84.9	21.2	126.3
$LSD_{0.05}$		2.4	0.3	2.6	2.1	27.1

[a]Other: 18:1 + 18:2 + 18:3. LSD, least significant difference.

type. Because 16:0 deposition in soybean follows a sigmoidal pattern (21), Equation 1 may be used to estimate cumulative daily 16:0 content of TG (Fig. 1). Over all genotypes, TG accounted for 89.7 ± 2.9% of the total amount of 16:0 in total lipids (TL). Thus, these trend lines represented an approximation of the impact of *fap* alleles on cumulative production of total 16:0. Given that assumption, we would expect the following relations between *fap* alleles and capacity to produce 16:0: C1727 (Fap_1Fap_1 fap_2fap_2 $Fap_{nc}Fap_{nc}$) > Dare (Fap_1Fap_1 Fap_2Fap_2 $Fap_{nc}Fap_{nc}$) > C1726 (fap_1fap_1 Fap_2Fap_2 $Fap_{nc}Fap_{nc}$) = N79-2077-12 (Fap_1Fap_1 Fap_2Fap_2 $fap_{nc}fap_{nc}$) > N94-2575 (fap_1fap_1 Fap_2Fap_2 $fap_{nc}fap_{nc}$).

Furthermore, the derivative of the fitted equation was used to estimate incremental rates of 16:0 accumulation in TG over the reproductive growth period (Fig. 2). These curves presented a normal distribution where the peak accumulation rate (mg 16:0 seed^{-1}d^{-1} in TG) occurred at the midpoint of the linear phase of concurrent 16:0 deposition. Peak rates of 16:0 deposition ranged from 0.075 (fap_1fap_1 Fap_2Fap_2 fap_{nc} fap_{nc}) to 0.230 (Fap_1Fap_1 fap_2fap_2 $Fap_{nc}Fap_{nc}$) mg 16:0 seed^{-1}d^{-1} in TG. The approximate date of this occurrence was estimated by solving the derivative for $T_{1/2}$, the period in DAF when 50% of total 16:0 in TG of mature seed was achieved (17). The average $T_{1/2}$ value for peak 16:0 deposition in TG among genotypes was 35.4 ± 0.3 DAF. Although these rate curves varied in amplitude and width, expression of the various *fap* alleles failed to engender any significant temporal distortion in the developmental pattern of 16:0 synthesis. In all cases, 90.1 ± 1.3% of the final amount of 16:0 in TG accumulated during the period from 26 to 43 DAF. Also, a strong positive relation (R^2 = 0.88) was found between the maximum rates of 16:0 accumulation in TG and the 16:0 content of mature seed. Hence, the opportune stage of seed development for investigation of genotypic differences of 16:0 metabolism appeared to be about 35 DAF.

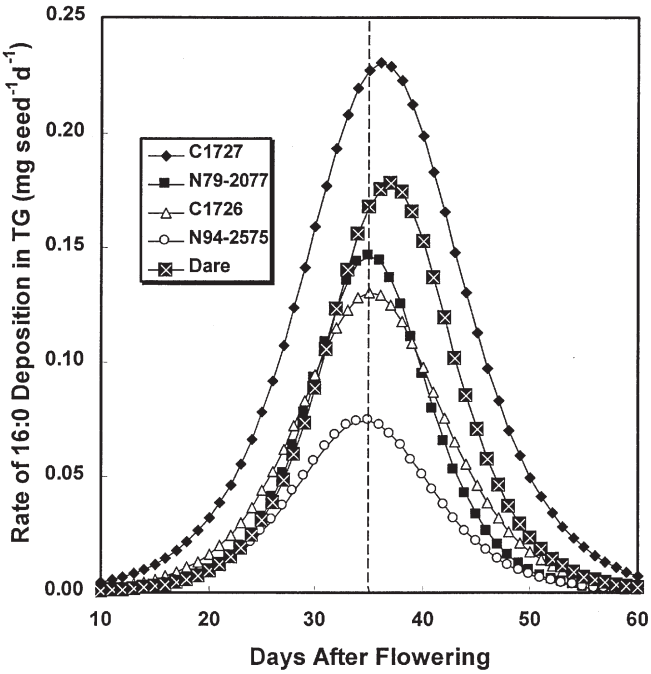

FIG. 2. Genotypic differences in rate of 16:0 accumulation in TG during soybean seed development. Incremental 16:0 accumulation rates were estimated from data in Figure 1 using the first derivative of the logistic function (Eq. 2, Materials and Methods section). For abbreviations see Figure 1.

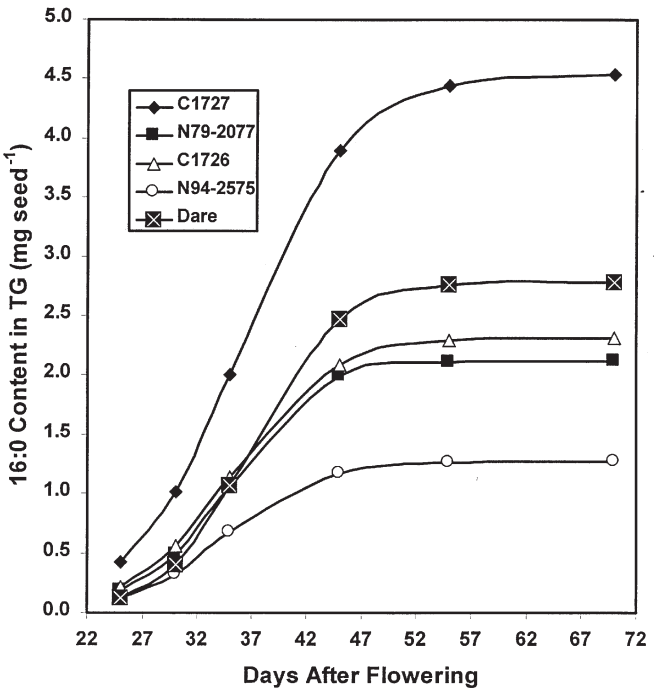

FIG. 1. Genotypic differences in 16:0 accumulation in triacylglycerol (TG) during soybean seed development. Concurrent 16:0 accumulation was estimated from measured data using the logistic function (Eq. 1, Materials and Methods section). Germplasm lines exhibiting allelic variation at *Fap* loci where: C1726 (fap_1fap_1 Fap_2Fap_2 $Fap_{nc}Fap_{nc}$), C1727 (Fap_1Fap_1 fap_2fap_2 $Fap_{nc}Fap_{nc}$), N79-2077-12 (Fap_1Fap_1 Fap_2Fap_2 $fap_{nc}fap_{nc}$), N94-2575 (fap_1fap_1 Fap_2Fap_2 $fap_{nc}fap_{nc}$), and the cv. Dare (Fap_1Fap_1 Fap_2Fap_2 $Fap_{nc}Fap_{nc}$). The stage of seed development was reported in days after flowering as determined by comparison with pods of known age in each genotype.

In various plant species, it is generally believed that TG composition is determined in part by differences in acyl-CoA specificities among acyltransferase enzymes in the glycerolipid synthetic pathway, such as glycerol-3-phosphate acyltransferase (G3PAT), lysophosphatidic acid acyltransferase (LPAAT), and diacylglycerol acyltransferase (DGAT) (22,23). It therefore is conceivable that *fap* alleles or associated modifier genes may affect genotypic variation in the affinity for 16:0-CoA and thus influence the activity of one or more of these glycerolipid acyltransferase enzymes. *In vivo* saturation kinetics of exogenous 16:0-CoA metabolism in developing seed at 35 DAF was used to test this hypothesis (Table 2). Although this analysis would not be expected to reveal minor changes in 16:0-CoA substrate specificity for glycerolipid acyltransferase enzymes attributed to modifier genes, major genetic effects of *fap* alleles should be detectable in estimates of maximal synthetic velocity for TPL, DG, and/or TG. However, exogenous 16:0-CoA metabolism showed no evidence that glycerolipid acyltransferase activi-

TABLE 2
***In vivo* 16:0-CoA Saturation Kinetics in Developing Soybean Cotyledons[a]**

Genotype	TPL	DG	TG	TL kinetics[b]		
	%V_{max} TL			V_{max} (nmol 16:0-CoA h^{-1} g dwt^{-1})	[16:0-CoA]$_{90}$ (mM)	V_{max}/K_m^{app} (h^{-1})
Fap$_1$ *fap*$_2$ *Fap*$_{nc}$	76.6	7.8	15.6	132.2	0.39	1.02
Fap$_1$ *Fap*$_2$ *fap*$_{nc}$	79.5	5.7	14.8	102.3	0.29	1.06
fap$_1$ *Fap*$_2$ *Fap*$_{nc}$	77.2	5.2	17.6	107.6	0.31	1.04
fap$_1$ *Fap*$_2$ *fap*$_{nc}$	77.9	6.4	15.7	108.6	0.33	0.99
Fap$_1$ *Fap*$_2$ *Fap*$_{nc}$	78.9	7.8	13.3	114.8	0.34	1.01
LSD$_{0.05}$	1.6	1.6	2.1	15.6	0.05	0.02

[a]TPL, total phospholipid; DG, diacylglycerol; TG, triacylglycerol; TL, total lipid. See Table 1 for other abbreviation.
[b]TL kinetics at 35 d after flowering; V_{max}, maximal velocity 16:0-CoA incorporation into TL from Hofstee plot analysis; [16:0-CoA]$_{90}$, (–9K_m^{app}) substrate concentration for V_{max} 16:0-CoA incorporation into TL; V_{max}/K_m^{app}, estimated first-order rate 16:0-CoA incorporation into TL.

ties were impaired or enhanced. No gross genotypic differences were found in the relative V_{max} for TPL, DG, or TG synthesis among the subject germplasm. In addition, there was no significant statistical difference among genotypes in the estimated first-order rate constant for 16:0-CoA incorporation into TL (Table 2). Thus, it appeared that these *fap* alleles had little effect on the ability of glycerolipid acyltransferase activities, or any event downstream of acyl-CoA formation, to metabolize 16:0-CoA.

Bao and Ohlrogge (24) recently demonstrated that the amount of TG synthesized in oilseeds was in part determined by the total amount of fatty acid produced in plastids. Presumably, this premise also might apply to the production of a particular fatty acid and the amount deposited in TG. *In vivo* saturation kinetics of exogenous acetate metabolism in developing seed at 35 DAF was used to test this hypothesis (Table 3). This experiment revealed strong positive relations among genotypes [R^2, 0.80 (TPL); 0.95 (DG); 0.94 (TG); 0.90 (TL)] between the estimated V_{max} for 16:0 synthesis and 16:0 concentration at 35 DAF in each glycerolipid class. In addition, a strong positive relation (R^2, 0.85) indicated a genotypic relation between V_{max} for 16:0 synthesis from acetate in TG and the peak rate of 16:0 deposition in TG at about 35 DAF, whereas no correlation was found when 16:0 in TG was derived from 16:0-CoA (Fig. 3).

Significant genotypic differences also were found in the estimated first-order rate constant for 16:0 synthesis from acetate saturation kinetics in TL. These rate constants were used to calculate the approximate half-life ($t_{0.5}$) or time required to convert 50% of the 16:0 synthesized from exogenous acetate into total glycerolipid. Similar calculations were made from saturation kinetics with 16:0-CoA. When plotted against 16:0 concentration in TL at maturity, $t_{0.5}$ for 16:0 produced from acetate gave a strong negative genotypic response (R^2, 0.95), but no relation was evident for the $t_{0.5}$ for 16:0 produced from 16:0-CoA (Fig. 4). Based on these interpretations of acetate and 16:0-CoA saturation kinetics, it may be concluded that 16:0 composition of TG in N94-2575 (*fap*$_1$*fap*$_1$ *Fap*$_2$*Fap*$_2$ *fap*$_{nc}$*fap*$_{nc}$) was determined by the lowest capacity for *de novo* 16:0 synthesis, which mediated the slowest rate of 16:0 metabolism in glycerolipid synthesis. In contrast, C1727 (*Fap*$_1$*Fap*$_1$ *fap*$_2$*fap*$_2$ *Fap*$_{nc}$*Fap*$_{nc}$) exhibited the largest capacity for *de novo* 16:0 synthesis and the fastest rate of 16:0 metabolism in glycerolipid synthesis. However, these *fap* alleles exhibited no discernible genetic effects on oil composition when the respective genotypes were given equal amounts of exogenous 16:0-CoA. This would imply that genes identical to mutations at *Fap* loci did not encode glycerolipid acyltransferase enzymes, and that TG composition of soybeans

TABLE 3
***In vivo* Acetate Saturation Kinetics of 16:0 Synthesis in Developing Soybean Cotyledons**

Genotype	TPL[b]	DG	TG	Kinetics of 16:0 synthesis (TL)[a]		
	%V_{max} 16:0 in TL			V_{max} (nmol acetate h^{-1} g dwt^{-1})	[acetate]$_{90}$ (mM)	V_{max}/K_m^{app} (h^{-1})
Fap$_1$ *fap*$_2$ *Fap*$_{nc}$	73.2	9.4	17.4	915.5	11.5	0.24
Fap$_1$ *Fap*$_2$ *fap*$_{nc}$	73.4	9.9	16.8	583.2	13.1	0.13
fap$_1$ *Fap*$_2$ *Fap*$_{nc}$	71.1	10.4	18.5	640.5	14.0	1.14
fap$_1$ *Fap*$_2$ *fap*$_{nc}$	70.7	10.6	18.7	457.3	12.2	0.11
Fap$_1$ *Fap*$_2$ *Fap*$_{nc}$	75.3	8.6	16.1	809.3	12.8	0.19
LSD$_{0.05}$	1.2	0.5	0.7	117.1	1.1	0.03

[a]16:0 synthesis in TL at 35 d after flowering; V_{max}, maximal velocity 16:0 synthesis from acetate in TL, from Hofstee plot analysis; [acetate, (–9K_m^{app}) substrate concentration for V_{max} 16:0 synthesis from acetate into TL; V_{max}/K_m^{app}, estimated first-order rate constant for 16:0 synthesis from acetate into TL.
[b]See Tables 1 and 2 for abbreviations.

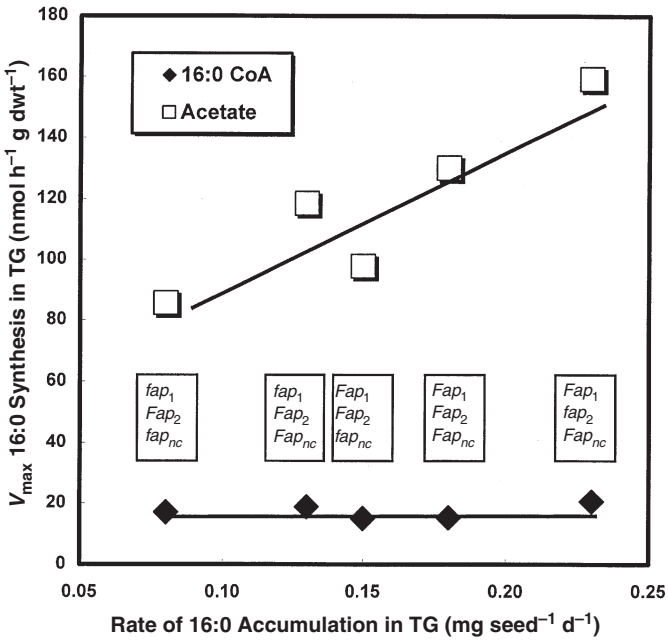

FIG. 3. Relation of 16:0 synthesis and deposition in TG. Maximal rates (V_{max}) of 16:0 incorporation in TG were estimated from *in vivo* acetate or 16:0-CoA saturation kinetics at 35 d after flowering. Peak rates of 16:0 accumulation in TG were calculated from data presented in Figure 2. For abbreviations see Figure 1.

having various *fap* alleles primarily was attributed to the total amount of 16:0 produced in plastids.

Supply of endogenous acyl-CoA from plastids for glycerolipid synthesis also may influence TG molecular species composition. As an example, earlier work (6) showed that mature seed of N79-2077-12 exhibited distinct differences in the relative distribution of 16:0 among TG molecular species compared to the cv. Dare. In particular, palmitoyl-diolein concentration was about twofold greater in N79-2077-12; and oleoyl-dipalmitin concentration was nearly twofold greater in Dare. The former observation seemed consistent with DGAT kinetics with exogenous 16:0-CoA and diolein, where V_{max} for 16:0-CoA was about twofold greater with the enzyme from N79-2077-12 than Dare. However, inherent differences in substrate utilization for TG synthesis by DGAT appeared to be secondary to the genetic effects on 16:0 synthesis, because enzyme systems rarely experience saturating substrate levels *in vivo*. Based on acetate saturation kinetics with a wider range of genetic mutations at *Fap* loci, we now can put this argument in a better perspective. A strong positive relation (R^2, 0.97) was found between the relative maximal rate of 16:0 incorporation into TG and 16:0 concentration in TG at 35 DAF (Fig. 5). In contrast, a strong negative relation (R^2, 0.94) was apparent when the relative maximal rate of 18:1 incorporation into TG was regressed against TG 16:0 concentration, and no relation (R^2, 0.005) was found for 18:0 incorporation into TG. Thus, reduced supply of 16:0 for TG synthesis was compensated by an increased supply of 18:1 in N79-2077-12. In the cv. Dare, increased supply of 16:0 was associated with lower supply of 18:1. In view of inherent genotypic differences in substrate specificity by DGAT, these data provide a causal relation for the previously observed levels of palmitoyl-diolein and oleoyl-dipalmitin in these two germplasm lines.

In attempts to identify specific genes and gene products that are synonymous with fap_1, fap_2, and fap_{nc} alleles at *Fap*

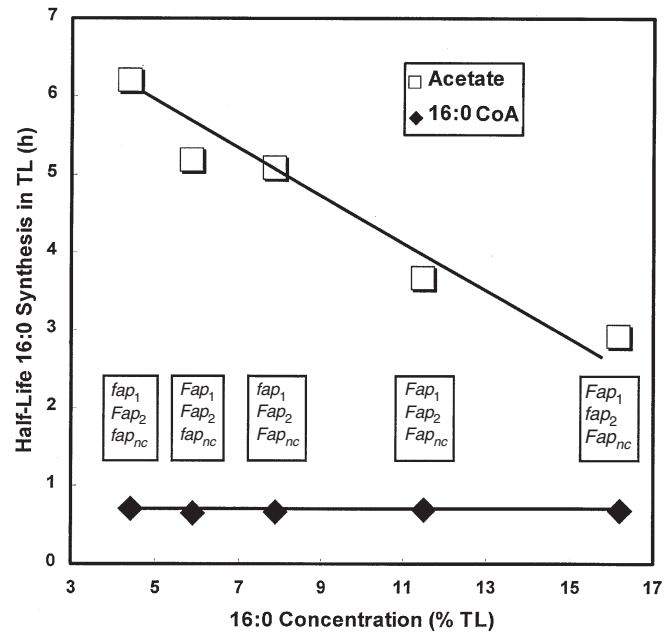

FIG. 4. Relation of metabolic turnover of 16:0 with 16:0 concentration of total lipids (TL) in mature soybean seed. Approximate half-life ($t_{0.5}$) or time required to convert 50% of the 16:0 synthesized from acetate or 16:0-CoA into total glycerolipid was calculated as a function of the first-order rate constant from the respective saturation kinetics at 35 d after flowering, [$t_{0.5} = 0.693/(V_{max}/K_m^{app})$].

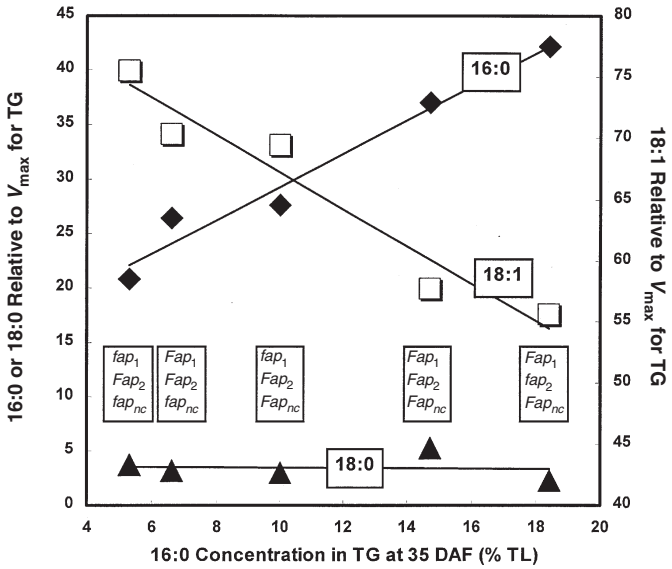

FIG. 5. Effect of *fap* alleles on incorporation of *de novo* synthesized fatty acids in TG of developing soybean cotyledons. V_{max} for 16:0, 18:0, and 18:1 relative to total fatty acid incorporation in TG were estimated from acetate saturation kinetics at 35 d after flowering. For abbreviations see Figures 1 and 4.

loci in soybeans show that these alleles do not alter the activities of glycerolipid acyltransferase enzymes or regulate other events after the formation of acyl-CoA. In that regard, genetic effects of these mutations appear to be focused on the mechanism of 16:0 synthesis in plastids of developing soybean cotyledons.

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