Lipids in the Germ, Endosperm and Pericarp of the Developing Maize Kernel

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ABSTRACT

Acyl lipids were quantified in the germ, endosperm and pericarp of LG-11 maize kernels at eight stages of development from 9 to 87 days after pollination (DAP). Changes in the lipids are discussed in relation to morphological events in the developing kernel. Storage lipids (triglyceride, steryl ester) and membrane lipids (diacylphospholipids) accumulated in germ until 52-76 DAP, then decreased slightly without formation of lipid degradation products, presumably due to respiration. Triglyceride accumulated in endosperm until 36-42 DAP and then decreased. Maximum values for galactosyldiglycerides and diacylphospholipids (nonstarch lipids) were reached at 16-23 DAP, and all decreased to very low values at maturity. Loss of these functional (membrane) lipids during the period of endosperm cell filling is unexpected. Starch contained 82% of the lysophospholipids and 64% of the free fatty acids in endosperm at 76 DAP. Endosperm lysophospholipids increased until 76 DAP and then decreased slightly, while free fatty acids increased continuously to maturity. It is thought that free fatty acids were mostly inside starch granules at all stages of development, and any possible decrease after 76 DAP was masked by acids formed by hydrolysis of aleurone and endosperm nonstarch lipids from 52 DAP. In pericarp, glycolipids were prominent only at 9 DAP, and phospholipids decreased after 42 DAP. Loss of these lipids is associated with senescence of most pericarp tissue. Triglycerides and steryl esters accumulated steadily to maturity, while the main accumulation of unsaponifiables occurred after 52 DAP about the time of suberin formation.

INTRODUCTION

In a recent paper (1) we described the quantitative distribution of various acyl lipids in the germ, endosperm, pericarp and tip cap of amylomaize, normal maize (LG-11) and waxy maize. Substantial quantities of free fatty acids and partial glycerides in the pericarp and endosperm nonstarch lipids suggested that there had been extensive degradation of lipids in these tissues during development when there would still have been net synthesis of lipids in the whole kernel.

Several authors have described the accumulation in developing maize of oil (2-7), and changes in fatty acids (2,6-11), nonpolar lipids (7,12), glycolipids and phospholipids (9,12,13), diol lipids (14-16), sterols (17), tocopherols (11), carotenoids (18) and the stereo-specific distribution of fatty acids in the triglycerides (10,19). However, there has been no comprehensive study of all the acyl lipids in the principal parts of developing maize kernels, and hence there is no direct evidence to support our suggestion (1) that there is substantial degradation of lipids in the developing pericarp and nonstarch fraction of the endosperm.

In this paper we describe a study of the lipids in developing LG-11 maize which complements our previous work (1) and shows patterns of lipid synthesis and degradation in various parts of the kernel.

EXPERIMENTAL PROCEDURES

LG-11 (a triple-cross hybrid forage maize) seed was provided by Mr. D.S. Kimber, National Institute for Agricultural Botany, Cambridge, and was grown under glass at the Botany Department Research Laboratories of the University of Glasgow by courtesy of Dr. J. Hillman. Natural pollination occurred on July 5th, 1977 (± 2 days), and development is expressed as days after pollination (DAP) from this date.

Samples consisting of equal number of kernels taken from three zones (3 cm from the base, 3 cm from the apex, and from the centre) of each cob were used for immediate determination of moisture and dry weight, and for total hydrolysate lipid as fatty acid methyl esters, FAME (1). Kernel dry weights varied by ± 60% at 6 DAP, and by less than ± 15% at all other harvesting dates. Analyses were always made on fresh samples. Stored, refrigerated or frozen samples were never used.

Similar samples were treated to inactivate enzymes before dissection and analysis of lipid classes. Germ and whole kernels at 6 and 9 DAP were boiled in methanol, while all other samples were heated in water-saturated *n*-butanol at 100 C for 10 min. The methanol treatment failed to prevent some formation of phosphatidyl-methanol artifact, probably due to incomplete inactivation of phospholipase-D. Methods for extraction and analysis of lipids have been described in a recent paper (1). Nonpolar lipids and glycolipids were separated by thin layer chromatography (TLC) and quantified as FAME by gas chromatography, while phospholipids separated by TLC were quantified from their phosphorus content. Each result is a single mean value of all analyses (minimum three per sample) of two or three cob samples taken at each harvesting date.

The fatty acid compositions of all nonpolar and glycolipid classes and of the total phospholipids were determined in the course of this work. Significant changes are mentioned in the text, but the full data have not been presented. The complete results can be obtained directly from the authors.

RESULTS AND DISCUSSIONS

Gross Changes

Changes in the lipids of developing kernels are discussed (below) in relation to recorded morphological events (20-26) which have been summarized in Figure 1. Although the time scale of development will obviously differ between studies and even between individual kernels from the same cob, the sequence of events will always be the same. In the present study, samples for each stage of development probably represent a spread of several days in kernel maturity and also in cell maturity throughout the developing endosperm and germ of individual kernels.

A cool period of weather from 42 DAP also prolonged the period of cell filling in endosperm and germ (and hence the time to reach full maturity), and the DAP time scale was thus somewhat extended latterly.

The water content of the whole kernel and endosperm

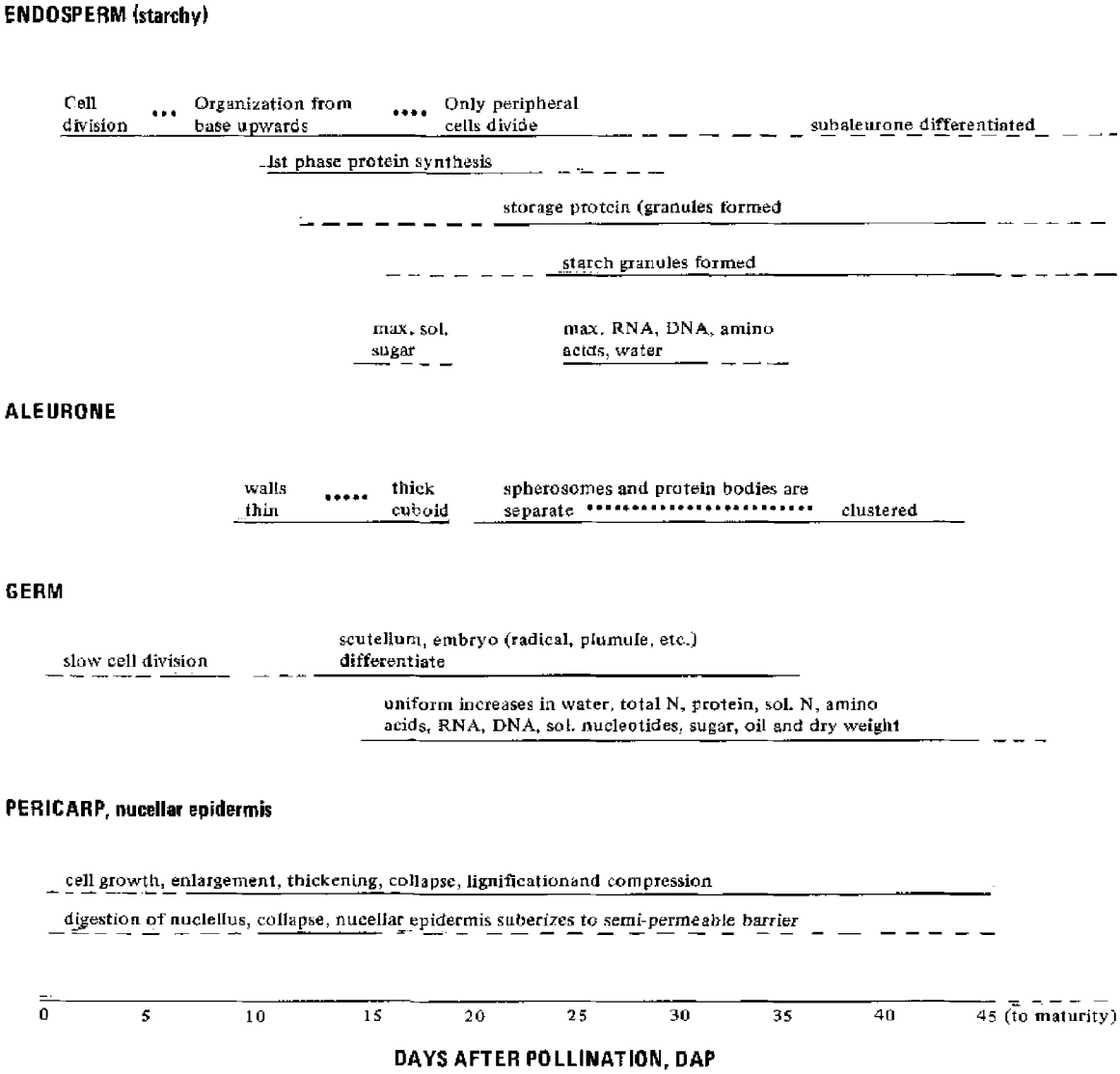

FIG. 1. Events in the developing maize kernel (adapted from refs. 20-26).

reached a maximum ca. 23 DAP and then declined (Table I), while in germ it reached a later maximum ca. 52 DAP and decreased to an exceptionally low level (12.8%) at 87 DAP. The pericarp lost water steadily throughout development, while the water content of the tip cap varied irregularly. Similar patterns have been reported previously for water in the whole kernel, endosperm and germ (3).

Maximum values for dry weight, nitrogen and lipid (as FAME) were reached at 52 DAP, or occasionally at 76 DAP, in all tissues except pericarp where maximum nitrogen was at 6 DAP (Table I). These results are consistent with known morphological changes (Fig. 1) if it is assumed that in the whole kernel and endosperm most of the dry matter is starch from 16 DAP.

It appears that physiological maturity measured by the above criteria was reached in endosperm at 35% moisture and in germ at 50% moisture. These figures are well above accepted moisture levels for harvesting. Similar early maxima in oil content have been observed in some maize varieties (2,6-8,10) but not in others (2,3,5-8,11,12).

Germ Lipids

Changes found in germ lipids are consistent with known developmental events (Fig. 1). Germ develops slowly until 12-15 DAP, then develops rapidly until ca. 45 DAP (3,21,24,25). Since germ remains viable but dormant at maturity, it is reasonable to expect that cellular organization will be mostly intact and components such as lipids undegraded.

In LG-11 germ, the diacyl phospholipids, which would be in various membranes, increased rapidly between 16 and 52-76 DAP (Table II) and then decreased slightly without accumulation of lysophospholipids. Phosphatidylcholine, phosphatidylethanolamine and phosphatidylinositol are characteristic phospholipids in cereal germ (27) and in the spherosome unit membrane (28,29). In the total phospholipids (the fatty acids of individual classes were not analyzed), linoleate decreased from 58% to 50%, while oleate increased from 8% to 18% and other acids maintained fairly constant proportions throughout development.

Since most of the kernel phospholipids are in the germ (Tables II and III), limited comparisons can be made with previous studies of whole kernel phospholipids. There is general agreement that phospholipid levels reach a maximum before maturity (7,12) and that during development there is a decrease in linoleate and an increase in oleate in

total phospholipids (9), and in phosphatidylcholine, phosphatidylglycerol, phosphatidylinositol and phosphatidylethanolamine (7). However, the differences between sweetcorn varieties (9,12) are sufficient to caution against drawing further conclusions at this stage.

Triglycerides, stored in germ spherosomes, accumulated rapidly until 52-76 DAP, then declined sightly (Table II). Linoleate content increased uniformly throughout development from 52% to 62%, while oleate decreased from 27% to 23% and palmitate from 20% to 13%. Previous studies (6-10,12,13) have shown both similar and opposite trends in the fatty acid composition of germ oil and whole kernel triglycerides, these being largely germ triglyceride at all later stages of development.

Steryl ester in germ also increased until 76 DAP and then decreased sharply. The percentage composition of the principal fatty acids showed a maximum (72% linoleate) and minimum (13% palmitate, 9% oleate) at 52 DAP. Unsaponifiable matter, which is mostly sterol, increased continuously to maturity and may have included deacylated steryl ester at 87 DAP.

Changes in the quantities of diglycerides, monoglycerides, free fatty acids and glycolipids were irregular, but all reached low levels at 87 DAP (Table II) comparable to previous analyses of mature LG-11 maize (1). Some changes in fatty acid composition occurred at 23 DAP. At this point diglyceride had maximum linoleate (42%)and minimum palmitate (16%), while monoglyceride had minimum linoleate (27%) and maximum palmitate (45%), and acylstearylglycoside had minimum linoleate (20%) and maximum palmitate (50%). There were no significant changes in the other fatty acids of these lipids. The only consistent changes in the galactosylglycerides were decreases in linolenate from 20-34% at 9 DAP to 1-2% at 87 DAP.

Changes in germ lipids up to 52-76 DAP appear to be normal. The late disappearance of storage lipids (Triglyceride, steryl ester) and structural lipids (diacylphospholipids) without formation of degradation products such as diglycerides, monoglycerides, lysophospholipids and free fatty acids, suggests that these lipids were required for respiration when energy from photosynthesis was no longer available. Since loss of germ lipids does not always occur (2,3,5-8,11,12), the presumed respiration may be a varietal characteristic or it may be caused by less favorable growing conditions during the later stages of kernel development.

Endosperm Lipids

Lipids in the endosperm of maize (1) and wheat (30,31) have been separated into aleurone, nonstarch and starch fraction lipids, each with a characteristic composition. Aleurone lipids resemble germ lipids, and are mostly triglyceride with some phospholipids (spherosome lipids), Nonstarch lipids consist of triglycerides and free fatty acids (spherosome lipids?), glycolipids and phospholipids (membrane lipids), while starch lipids are free fatty acids and lysophospholipids which are firmly retained within the starch granules (27).

Composition of the nonstarch (plus aleurone) and starch lipids from kernels at 76 DAP (Table IV) agreed well with previous analyses of mature LG-11 (1). Unfortunately, it was not practicable to obtain similar data for immature kernels, and the results for total endosperm lipids (Table III) have therefore been interpreted by extrapolating from data for mature samples, assuming that the starch lipids were stable once formed.

Triglyceride is stored in spherosomes in aleurone and germ tissue (spherosomes have not been identified in mature starchy endosperm although triglyceride is present). The quantity of triglyceride reached a maximum at 36-42 DAP, when the aleurone cells should have been fully dif-

TABLE I

Proximate Analyses of Developing LG-11 Maize Kernels (All Data as mg/Kernel)

DAP[b]	Whole kernel[a]				Endosperm				Germ				Pericarp				Tip cap			
	Dry wt.	H_2O	N	FAME[c]	Dry wt.	H_2O	N	FAME[c]	Dry wt.	H_2O	N	FAME[c]	Dry wt.	H_2O	N	FAME[c]	Dry wt.	H_2O	N	FAME[c]
6	10	69	0.34	0.31																
9	37	153	0.99	1.14	28	102	0.80	0.94	1.1	3.5	0.60	0.35	10.1	51.8	0.20	0.09	3.6	7.4	0.07	0.04
16	80	180	1.82	2.80	66	104	1.28	1.62	3.7	8.3	0.13	1.41	12.4	39.8	0.17	0.11	2.9	4.5	0.09	0.06
23	110	209	2.21	4.50	95	146	2.08	1.69	7.3	12.1	0.20	2.51	14.2	36.5	0.17	0.12	2.5	3.4	0.10	0.05
36	241	197	4.89	11.41	184	113	3.84	2.42	26.8	30.0	0.95	9.40	20.1	23.2	0.17	0.13	3.4	3.5	0.11	0.09
42	275	191	5.53	13.10	211	108	4.78	2.66	32.0	34.7	0.97	11.14	19.3	19.1	0.15	0.11	4.2	4.8	0.13	0.10
52	321	209	6.40	16.48	244	131	5.06	2.74	38.0	37.4	1.31	12.30	22.4	18.5	0.14	0.15	5.3	6.3	0.14	0.10
76	317	107	6.07	16.33	263	72	4.83	2.69	46.0	25.0	1.44	12.46	19.6	4.7	0.12	0.13	4.0	1.3	0.10	0.11
87	293	59	5.43	13.34	184	50	3.57	2.48	36.2	5.4	1.31	10.78	17.5	2.5	0.08	0.10	3.0	0.6	0.06	0.10

[a]Whole kernel data are experimental results, therefore not same as sum of data for kernel parts.
[b]DAP = days after pollination.
[c]FAME = fatty acid methyl esters.

TABLE II

Lipid Classes in the Germ of Developing LG-11 Maize Kernels (μg Lipid/Germ)

Lipid class	Days after pollination, DAP							
	9	16	23	36	42	52	76	87
Steryl ester	13	16	18	152	225	325	357	117
Triglyceride	229	1365	2196	7453	9833	11346	10786	10016
Diglyceride	28	189	110	335	454	370	355	99
Free fatty acid		7	9	56	72	98	96	50
Monoglyceride[a]		4	5	52	60	56	114	26
Acylsterylglycoside	20	36	32	87	142	111	198	78
Monogalactosyldiglyceride	17	23	22	30	36	44	107	22
Monogalactosylmonoglyceride		22	12	9	41	48	34	16
Digalactosyldiglyceride		73	63	85	114	76	89	31
Digalactosylmonoglyceride			66	62	86	61	71	
Phosphatidylethanolamine[b]	10	25	39	90	122	125	100	110
Phosphatidylcholine	14	55	91	214	335	368	403	369
Phosphatidylinositol	5	14	21	100	109	95	142	140
Lysophosphatidylethanolamine[c]	1	1	2	11	10	11	6	4
Lysophosphatidylcholine	trace	1	2	11	11	17	11	9
Phosphatidic acid	trace	2	2	11	12	27	13	15
Nonpolar acyl lipids	270	1581	2338	8048	10644	12195	11708	10308
Glycolipids	37	154	175	273	419	340	499	147
Phospholipids	30	98	157	437	599	643	675	647
Unsaponifiable		26	310	425	530	1178	1200	1470
Total lipids[d]	337	1834	2966	9075	12089	14162	13831	12483

[a]Includes some 6-O-acylmonogalactosyldiglyceride.

[b]Includes some phosphatidylglycerol.

[c]Includes some lysophosphatidylglycerol.

[d]Corrected for sterol shown twice in steryl ester, acylsterylglyceroside and in unsaponifiables.

TABLE III

Lipid Classes in the Endosperm of Developing LG-11 Maize Kernels (μg Lipid/Endosperm)

Lipid class	Days after pollination, DAP							
	9	16	23	36	42	52	76	87
Steryl ester	33	48	85	135	79	119	151	105
Triglyceride	445	781	839	909	906	814	663	637
Diglyceride	63	112	124	159	96	121	67	80
Free fatty acid	23	26	49	499	522	895	1310	1352
Monoglyceride[a]	9	24	22	58	68	50	64	24
Acylsterylglycoside	17	50	48	78	44	46	51	28
Monogalactosyldiglyceride	15	72	76	53	60	53	26	8
Monogalactosylmonoglyceride		10	14	46	47	32	29	12
Digalactosyldiglyceride	135	246	235	202	178	170	52	15
Digalactosylmonoglyceride		59	95	107	83	83	55	24
Phosphatidylethanolamine[b]	102[c]	120	91	77	70	53	19	18
Phosphatidylcholine	167	286	314	193	128	102	67	42
Phosphatidylinositol	59	83	107	79	68	38		27
Lysophosphatidylethanolamine[d]	11	24	41	72	62	67	101	73
Lysophosphatidylcholine	5	62	130	410	451	498	497	402
Phosphatidic acid	10	24	23	20	62	38	20	22
Nonpolar acyl lipids	573	991	1119	1760	1671	1999	2255	2198
Glycolipids	163	437	468	486	412	384	213	87
Phospholipids	354	599	706	851	841	796	704	584
Unsaponifiable		189	277	414	490	673	667	620
Total lipid[e]	736	2171	2510	3415	3359	3778	3749	3431

[a]Includes some 6-O-acylmonogalactosyldiglyceride.

[b]Includes some phosphatidylglycerol.

[c]Includes 5 μg diphosphatidylglycerol.

[d]Includes some lysophosphatidylglycerol.

[e]Corrected for sterol shown twice in steryl, acylsterylglycoside and in unsaponifiables.

ferentiated and filled with protein bodies and spherosomes (Fig. 1 and refs. 20-23). The subsequent decrease suggests lipolysis and possibly also respiration during the final stages of endosperm development. Lipolysis would also account for the large amounts of diglyceride and free fatty acids previously found in amylomaize aleurone lipids (1). Triglyceride fatty acid composition was remarkably constant throughout development.

Steryl esters, diglycerides and monoglycerides reached maximum values between 36 and 76 DAP with intermediate lower values at 42 or 52 DAP, but generally paralleled the levels of triglycerides. No particular significance can be given to these results on the limited evidence available.

Glycolipids and diacylphospholipids are typical membrane lipids, and most are found in the nonstarch lipid fraction (1,27,30-32). Acylsterylglycoside may function also as a transport intermediate (33). Monogalactosyldiglyceride and digalactosyldiglyceride reached early maxima at 16-23 DAP (Table III) during the period of active endosperm cell division (Fig. 1 and refs. 21,22,25) and then decreased to very low levels at maturity. Maximum values for the corresponding galactosylmonoglycerides and acylsterylglycoside occurred at 36 DAP. The significance of

TABLE IV

Lipid Classes in the Aleurone plus Nonstarch and Starch Fraction Lipids of LG-11 Endosperm at 76 DAP (μg Lipid/Endosperm)

Lipid class	Aleurone plus nonstarch fraction	Starch fraction
Steryl ester	113	38[a]
Triglyceride	605	61[a]
Diglyceride	53	9[a]
Free fatty acid	475	835
Monoglyceride[b]	38	25
Acylsterylglycoside	40	10[a]
Monogalactosyldiglyceride	14	19[a]
Monogalactosylmonoglyceride	17	12[a]
Digalactosyldiglyceride	38	15[a]
Digalactosylmonoglyceride	31	25[a]
Phosphatidylethanolamine[c]	19	—
Phosphatidylcholine	51	16[a]
Phosphatidylinositol	20	—
Lysophosphatidylethanolamine	38	63
Lysophosphatidylcholine	68	429
Phosphatidic acid	4	17[a]
Nonpolar acyl lipids	1284	968
Glycolipids	140	81
Phospholipids	200	525
Unsaponifiable	632	30[a]
Total lipid	2256	1604

[a]Typical nonstarch lipids attributed to contamination of the starch fraction.

[b]Includes some 6-0-acylmonogalactosyldiglyceride.

[c]Includes some phosphatidylglycerol.

TABLE V

Lipid Classes in the Pericarp of Developing LG-11 Maize (μg Lipid/Pericarp)

Lipid class	Days after pollination, DAP						
	9	16	23	36	42	52	87
Steryl ester	9	10	19	21	20	21	11
Triglyceride	24	42	36	53	49	75	69
Diglyceride	9	6	9	9	7	7	4
Free fatty acid	10	5	9	7	9	10	9
Monoglyceride	4	2	3	3	3	3	2
Acylsterylglycoside	42	8	10	7	7	4	4
Phosphatidylethanolamine[a]		14	10	7	13	2	1
Phosphatidylcholine		43	26	32	33	4	2
Phosphatidylinositol		10	8	12	10	3	2
Lysophosphatidylethanolamine[b]		3	5	6	5	1	trace
Lysophosphatidylcholine		7	3	3	3	2	1
Phosphatidic acid		7	9	3	17	5	3
Nonpolar acyl lipids	56	65	76	93	88	116	95
Glycolipids	42	8	10	7	7	4	4
Phospholipids		84	61	63	81	17	9
Unsaponifiable		14	28	48	28	43	133
Total lipids[c]	98	163	172	198	191	169	234

[a]Includes some phosphatidylglycerol.

[b]Includes some lysophosphatidylglycerol.

[c]Corrected for sterol shown twice in steryl ester, acylsterylglycoside and in unsaponifiables.

these results is not known, but it is noteworthy that diol lipids, and acylethyleneglycolgalactoside (which was not distinguished from monogalactosyldiglyceride in the present study) are present in large amounts only at the earliest stages of kernel development (14-16).

In monogalactosyldiglyceride the linoleate decreased from 70% at 9-16 DAP to 46% at 52-87 DAP, while palmitate increased from 12% to 28% and oleate from 7% to 14%. These changes in fatty acids were not fully coincident with changes in the quantity of lipid. On the other hand, digalactosyldiglyceride exhibited a clear maximum of 67% linoleate and minimum of 11% palmitate and 6% oleate at 23 DAP which did coincide with the maximum level of lipid. There were no significant changes in the fatty acids of acylsterylglycoside or monogalactosylmonoglyceride, but there was a steady decrease in linoleate (54% to 28%) and increases in palmitate (29% to 40%), stearate (5% to 16%) and oleate (8% to 18%) in digalactosylmonoglyceride.

In previous studies (12,13) no distinction was made between glycolipids in germ and endosperm. In the present study the majority were in endosperm until 52 DAP, and then in germ (Tables II and III), the combined maximum being at 42 DAP (831 μg glycolipids/kernel). This agrees with data for inbred H51 (13), but maximum levels were attained earlier in some sweetcorn mutants (12).

The principal diacylphospholipids also reached early maximum – phosphatidylethanolamine at 16 DAP and phosphatidylcholine and phosphatidylinositol at 23 DAP. Parallel behavior between triglycerides (maximum at 36-42 DAP) and diacylphospholipids in aleurone might be expected (cf. germ lipid results, Table II), but, if this existed, it was masked by changes in the nonstarch phospholipids. In any case, it is clear that there was substantial degradation of diacylphospholipids from about the end of cell division

in starchy endosperm and aleurone. Previous results (1) indicate that phospholipid degradation is almost complete in the nonstarch lipids. This is remarkable because these lipids are usually regarded as essential for membrane integrity, which in turn is necessary for synthesis of storage protein and starch. Since accumulation of protein and starch (endosperm cell filling) continued up to 76 DAP (Table I), there is clearly a problem to be resolved here.

Starch lipids in mature LG-11 maize are mostly free fatty acids and lysophospholipids (1). In kernels at 76 DAP at least 64% of the free fatty acids (835 μg/kernel) and 82% of the lysophospholipids (429 μg/kernel) were in the starch lipids. Unfortunately, it was not possible to obtain data at earlier stages of development, and it has therefore been assumed that at least 80% of the lysophospholipids were in starch lipids at all stages of development.

There was rapid accumulation of lysophospholipids between 16 and 52 DAP during the period of dry weight gain (Table I), cell filling and starch synthesis (Fig. 1). The terminal decrease in lysophospholipids coincided with decreases in dry weight and nitrogen (Table I). This probably indicates consumption of some starch and protein reserves in the maturing endosperm, when some protein and lipid reserves were being consumed in germ (see above).

If the proportions of free fatty acids and lysophospholipids are constant in starch throughout development (there is no evidence for or against this view), then the levels of free fatty acids would have reached a maximum at 52-76 DAP. However, it has already been deduced that there was some hydrolysis of aleurone and nonstarch lipids, and this could account for the increase in total endosperm free fatty acids from 52 to 87 DAP when there might otherwise have been a small decrease paralleling that in the lysophospholipids.

Pericarp Lipids

Development of pericarp from ovary wall tissue is complete ca. 18 DAP (21) and is followed by cell degeneration, cell collapse, lignification and suberization (Fig. 1).

Triglycerides and steryl esters accumulated throughout development (Table V) and may be reserve substances. Glycolipids, which seem to be associated with developing tissue (see endosperm results and discussion), were prominent at 9 DAP and were then reduced to very low levels.

Diacylphospholipids (associated with membranes) maintained fairly constant levels until 42 DAP and then decreased sharply about the time of cell degeneration and collapse (Fig. 1). Since lysophospholipids and free fatty acids did not accumulate, these hydrolysis products must have been consumed in subsequent metabolic processes.

The large increase in unsaponifiable matter, especially between 52 and 87 DAP, is probably a measure of suberin formation since the unsaponifiables include large quantities of aliphatic alcohols (1).

General Discussion

Changes in the lipids of germ, endosperm and pericarp are mostly consistent with known morphological events in the developing maize kernel (Fig. 1).

Membrane and storage lipids in germ comprised the bulk of the kernel lipids. Small losses due to respiration seem to have occurred between 76 and 87 DAP, during the final drying-out stage. These losses may be a varietal characteristic, or they may have been caused by a period of less favorable growing conditions.

Endosperm contained a substantial part of the whole kernel lipids up to 23 DAP, and this may well apply also in sweetcorn varieties which are harvested at similar stages of development (9,12).

The extensive degeneration of aleurone and nonstarch lipids from 36 DAP is remarkable. This seems to be a feature of maize, since previous analyses of mature kernels also showed high levels of free fatty acids and very little glycolipids and diacylphospholipids (1). There have been no comparable studies of other cereals, but analyses of mature wheat endosperm (30) and white flour (27,30-32) show high levels of glycolipids and diacylphospholipids and low levels of free fatty acids, and there is thus no *prima facie* evidence of significant degradation of nonstarch lipids in developing wheat.

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