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THE $C_{16:3}/C_{18:3}$ FATTY ACID BALANCE IN PHOTOSYNTHETIC TISSUES FROM 468 PLANT SPECIES

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Abstract—Two kinds of plants may be distinguished according to their (n–3) trienoic fatty acid composition in photosynthetic tissues. The *cis*-7,10,13-hexadecatrienoic acid/*cis*-9,12,15-octadecatrienoic acid balance directly reflects the biosynthesis pathways (a plastidial one and an extra-plastidial one) of chloroplastic lipids. We analysed the correlation between the existence of these pathways and the evolutionary classification of Cormophytes (particularly Angiosperms). By using *cis*-7,10,13-hexadecatrienoic acid as a marker for the existence of the plastidial pathway, we studied the overall fatty acid composition of 468 plant species (280 already described in the literature and 188 new ones) distributed among 141 botanical families. The data strongly suggest that the plastidial pathway was lost during evolution and that, in the case of dicotyledonous plants, this loss probably occurred independently and at different rates. The data are also discussed from an environmental and chemotaxonomic point of view.

INTRODUCTION

Plants can be classified according to the presence or absence of *cis*-7,10,13-hexadecatrienoic acid ($C_{16:3}$) esterified to galactolipids, namely monogalactosyldiacylglycerols (MGDG) and digalactosyldiacylglycerols (DGDG), the main lipids in leaves [1, 2]. This directly reflects the glycerolipid metabolism of the plant.

Glycerolipid synthesis in higher plant leaves involves two discrete pathways (see [3–5] for review). Fatty acids synthesised in the chloroplasts may either enter the 'prokaryotic' chloroplastidial pathway or be exported to the endoplasmic reticulum (ER), where they are incorporated into lipids through the 'eukaryotic' pathway (Fig. 1). The former pathway is situated in the chloroplast envelope and involves the sequential action of acyl-ACP glycerol 3-phosphate acyltransferase and acyl-ACP:lysophosphatidic acid acyltransferase. These enzymes produce phosphatidic acid, with almost exclusively C_{16} fatty acids at the *sn*-2 position of glycerol [6]. This lipid is either used for the synthesis of phosphatidylglycerols (PG) or is hydrolysed by the phosphatidate phosphatase to form diacylglycerols. Diacylglycerol moieties containing C_{16} fatty acids at the *sn*-2 position are the precursors for the synthesis of prokaryotic galactolipids (review, [7]). Sequential desaturations occurring in the chloroplasts lead to the formation of *sn*-1-$C_{18:3}$, *sn*-2-$C_{16:3}$ prokaryotic galactolipids [8]. This positional distribution of $C_{16:3}$ in prokaryotic galactolipids is highly specific; the fatty acid is present only at the *sn*-2 position of glycerol and is almost completely excluded from the *sn*-1 position.

On the other hand, the microsomal acyltransferases, which are responsible for phosphatidic acid synthesis by the 'eukaryotic pathway' in the ER, give rise to lipids that contain C_{18} fatty acids exclusively at the *sn*-2 position and either C_{18} or $C_{16:0}$ fatty acids at the *sn*-1 position [6]. The eukaryotic phosphatidic acid enters the Kennedy pathway and is used to synthesize extrachloroplastic phospholipids. Phosphatidylcholine or at least a part of it, is then transferred to plastids and used as a substrate for the synthesis of eukaryotic MGDG and DGDG (see, for example, [9, 10, 11], for hypotheses concerning the mechanism of this transfer). Hence, C_{16} fatty acids, when present, are saturated and esterified only to the *sn*-1 position of the glycerol of these eukaryotic galactolipids. The other (and major) fatty acids have 18 carbon atoms (especially $C_{18:3}$).

In some plants, called '16:3 plants', both pathways

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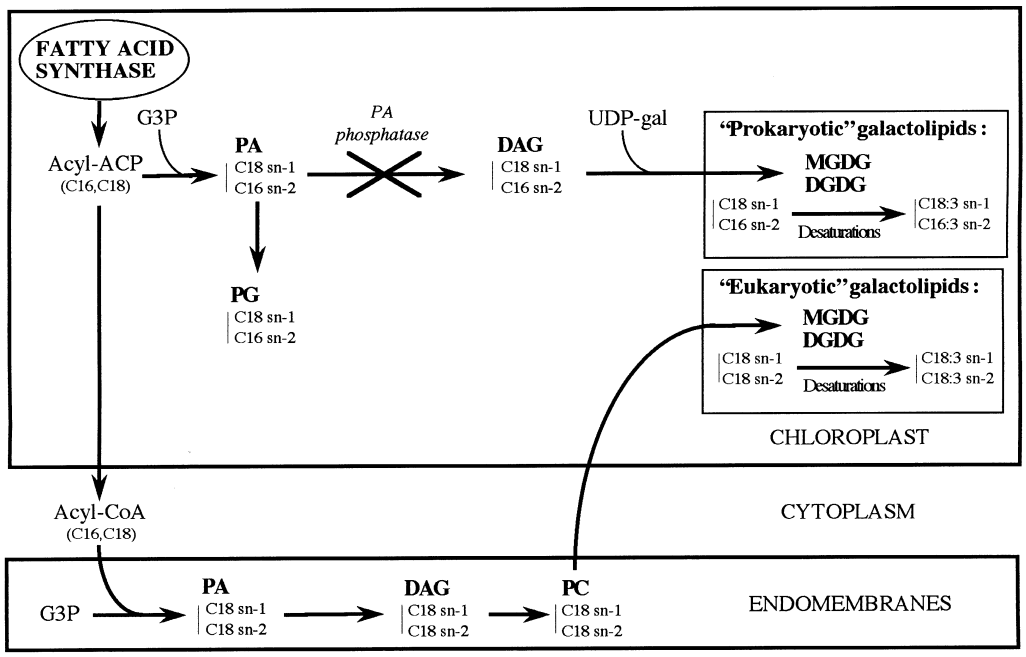

Fig. 1. Scheme of the lipid metabolism pathways in photosynthetic tissues.

are involved in lipid metabolism, so that their leaf tissues contain large amounts of $C_{16:3}$ and $C_{18:3}$ fatty acids. Other plants use the prokaryotic pathway for the sole synthesis of PG (which does not contain triunsaturated C_{16} fatty acid). MGDG, DGDG and sulfolipids in these plants are synthesised exclusively by the eukaryotic pathway. Hence, these plants contain no $C_{16:3}$ but $C_{18:3}$ fatty acids and, thus, are called '18:3 plants'.

The only difference between plants having either both or only one metabolic pathway(s) is assumed to be the presence or the absence of plastidial phosphatidate phosphatase activity (Fig. 1). In good agreement with this assumption, this activity was not detected *in vitro* when using isolated chloroplasts from 18:3 plants [12]. Nevertheless, it must be noted that some plants—not yet described in the literature—could contain a chloroplastic acyltransferase which provides only 1-C_{18}, 2-C_{18} lipids and an active phosphatidate phosphatase. While containing a prokaryotic pathway, such putative plants would be regarded as 18:3 plants (without $C_{16:3}$). Moreover, a putative ER acyltransferase using $C_{16:3}$ fatty acid as substrate could produce lipids containing $C_{16:3}$ fatty acids in a plant with an inactive prokaryotic pathway.

It is assumed that 18:3 plants, at some point in their evolution, have lost the ability to synthesize prokaryotic chloroplast lipids. Therefore, the question arises as to whether the loss of phosphatidate phosphatase activity is beneficial for the plant. Why do these two types of plant still co-exist on earth? Could the 16:3 or 18:3 phenotype depend on environmental conditions (climate, aquatic environment, etc.), on the general anatomy of the plant (ligneous, herbaceous, etc.), Is there a relation between these biochemical criteria and the botanical classification (taxonomy)?

To our knowledge, no analysis of leaf lipids *vs* taxonomic classification has previously been carried out. Because we did not find in the literature the leaf fatty acid composition of plants from important families for such a study (tropical families, archaic families, etc.), we sampled material from 188 additional species and analysed their leaf fatty acid composition.

RESULTS AND DISCUSSION

We first analysed the overall leaf fatty acid composition of several plant families that have been poorly investigated previously. In the present study, wild plants rather than horticultural species (mostly the results of breeding) were sampled and, whenever possible, three species per family were analysed. The fatty acid composition of total leaf lipids was determined by gas chromatography and the proportion of $C_{16:3}$ fatty acid was expressed as a percentage of the sum of $C_{14:0}$, $C_{16:0}$, $C_{16:1}$*cis*, $C_{16:1}$*trans*, $C_{16:2}$, $C_{16:3}$, $C_{18:0}$, $C_{18:1}$, $C_{18:2}$, $C_{18:3}$ and very long-chain fatty acids peak areas. Plants containing $C_{16:3}$ were assumed to contain a prokaryotic pathway.

Table 1 shows both the results of our analyses, as well as data reported in the literature [11–85]. Information dealing with the fatty acid composition of seeds, roots or non-photosynthetic tissues (e.g. parasitic plants) were not taken into account. The scientific name of plant species and, when possible, the vernacular French and English names are also indicated in Table 1. Depending on the authors, the percentage of $C_{16:3}$ in photosynthetic tissues was calculated from

Table 1. Content (%) of *cis*-7,10,13-hexadecatrienoic acid in Cormophyte photosynthetic tissues. Plant families of Angiosperms are listed in alphabetic order

	Vernacular French and English name of plant species		References
BRYOPHYTES			
Hepaticae	4 species	23.1–39% in MGDG	[13, 14, 15]
Sphaganales	4 species	17.1–21.4% in MGDG	[13, 14, 15]
Polytrichales	3 species	18.7–27.4% in MGDG	[13, 14, 15]
Dicranales	8 species	3.9–27.1% in MGDG	[13, 14, 15]
Bryales (Mosses)	18 species	3.9 to 27% in MGDG	[13, 14, 15]
Catharinea undulata		12.6; 1.9 (b)	[16]
PTERIDOPHYTES (Ferns)			
Ophioglossum vulgatum L.	Ophioglosse vulgaire/Adder's tongue	5.2 (a)	This study
Equisetum arvense L.	Prêle des champs/	9.4 (a) 23.4; 1.7 (b)	[14, 15, 16, 17, 18]
Pteridium aquilinum (L.) Kuhn	Fougère aigle/Bracken	26.6; 0.5 (b)	[14, 15, 16, 18]
Onoclea sensibilis L.	/	5.3 (a)	[17]
Matteuccia struthiopteris (L.) Tod.	/	4.1 (a)	[17]
GYMNOSPERMS (Conifers)			
Cedrus libani A. Rich.	Cèdre du Liban/Cedar of Lebanon	1.6 (a)	This study
Juniperus communis L.	Genévrier commun/Common juniper	1.5 (a)	This study
Pinus sylvestris L.	Pin sylvestre/Scots pine	13.0; 1.0 (b)	[14, 19]
Picea excelsa Link.	Epicéa/Norway spruce	5.5 (c)	[15, 18, 19]
Taxus baccata L.	If/Yew	16.0; 2 (b)	[19]
Larix decidua Mill.	Mélèze d'Europe/European larch	13.0; 3 (b)	[19]
Taxodium distichum (L.) L.C.M. Rich	Cyprès chauve/Bald cypress	1.26 (a)	This study
PRESPERMATOPHYTES			
Ginkgo biloba L.	Arbre aux cent écus/Maidenhair tree	4.9 (a); 11.0; 0 (b)	[14, 16, 17, 18]
Dioon spinulosum Dyer	/	14.6 (c)	[15, 18]
Cycas revoluta Thunb.	Cycas/Cycad	6.6 (c)	[15, 18]
CHLAMYDOSPERMS			
GNETACEAE			
Gnetum gnemon L.	/	22.0 (c)	[15, 18]
EPHEDRACEAE			
Ephedra fragilis Desf.	Ephédra/	0.2 (a)	This study
Ephedra distachya L.	Raisin de mer/Sand cherry	0.6 (a)	This study
ANGIOSPERMS			
ACANTHACEAE			
Acanthus mollis L.	Acanthe à feuilles molles/Artist's acanthus	0.8 (a)	This study
ACERACEAE			
Acer saccharum Marsh.	Erable à sucre/Sugar maple tree	0 (a)	[20]
Acer pseudoplatanus L.	Erable faux platane, Sycomore/Sycamore maple	0.5 (a)	[21]
Acer campestre L.	Erable champêtre/Hedge maple	tr. (a)	[21]
ACTINIDIACEAE			
Actinidia chinensis Planch.	Kiwi/Kiwi, Chinese gooseberry	0.6 (a)	This study
AGAVACEAE			
Agave stricta Salm–Dyck.	Agave/Agave	0 (a)	This study
Agave sp.	/	0.2 (a)	This study
ALISMATACEAE (Alismaceae)			
Sagittaria sagittifolia L.	Sagittaire flèche d'eau/Hawaii arrowhead	0 (a)	This study
Alisma plantago-acquatica L.	Plantain d'eau/European water-plantain	0 (a)	[22]
ALOACEAE			
Aloe milotii Reyn.	/	0.3 (a)	This study
AMARANTHACEAE			
Amaranthus lividus L.	Amarante livide/Purple amaranth	tr. (a)	[12]
Alternanthera sessilis (L.) Br. *ex* DC.	/Sessile joyweed	0 (a)	[23]
Amaranthus gangeticus L.	/Joseph's-coat	0 (a)	[24]
ANACARDIACEAE			
Rhus vernix L.	Arbre à perruque/Poison sumac	0.6 (a)	This study
Pistacia terebinthus L.	Pistachier térébinthe/Petelin	0.9 (a)	This study
ANNONACEAE			
Asimina triloba (L.) Dun.	Asiminier trilobé/Common pawpaw	1.1 (a)	This study
APIACEAE (Umbelliferae)			
Heracleum sphondylium L.	Berce spondyle/Hogweed	16.6 (a) 55.3; 7.5 (b)	[19, 21]
Petroselinum crispum (Mill.) A. W. Hill	Persil/Parsley	11.8 (a) 76; ? (b)	[25, 26]
Anthriscus cerefolium (L.) Hoffm.	Cerfeuil/Chervil	26.6; 3.0 (b)	[27, 28]
Chaerophyllum temulentum L.	Cerfeuil penché/Rough chervil	16.2 (a)	[21]
Daucus carota L.	Carotte/Wild carrot	16.7 (a)	[21, 29]
Apium graveolens L.	Céleri/Celery	(d, 16:3 plant)	[30]
Myrrhis odorata (L.) Scop.	Cerfeuil musqué/Sweet cicely	16.7 (a)	This study
Angelica sylvestris L.	Angélique sauvage/Woodland angelica	16.2 (a)	This study
Eryngium campestre L.	Panicaut champêtre/Field eryngo	8.2 (a)	This study
Hydrocotyle vulgaris L.	Ecuelle d'eau/Pennywort, White-rot	11.1 (a)	This study
APOCYNACEAE			
Nerium oleander L.	Laurier rose/Oleander	0.6 (a)	This study
Vinca major L.	Grande pervenche/Greater periwinkle	0.9 (a)	This study

continued

Table 1—*continued.*

	Vernacular French and English name of plant species		References
AQUIFOLIACEAE (Ilicaceae)			
Ilex aquifolium L.	Houx/Holly	0 (a)	[19]
ARACEAE			
Zantedeschia aethiopica (L.) Spreng.	Arum des jardins/Calla lily	0 (a)	[31]
ARALIACEAE			
Hedera helix L.	Lierre grimpant/English ivy	6.2 (a) 36.0; 2.0 (b)	[14, 17, 21]
Oreopanax nymphaeifolium Dcne. & Planch	Lierre du Guatemala/	3.4 (a)	This study
ARISTOLOCHIACEAE			
Aristolochia rotunda L.	Aristoloche/	1.0 (a)	This study
ASCLEPIADACEAE			
Hoya carnosa (L.f.) R. Br.	Fleur de porcelaine, quadrille/Porcelain-flower	0.4 (a)	This study
Ceropegia woodii Schlrcht.	Chaîne des coeurs/	0.4 (a)	This study
Periploca graeca L.	Bourreau des arbres/Silk vine	1.4 (a)	This study
ASTERACEAE (Compositae)			
Lactuca sativa L.	Laitue/Garden lettuce	tr. (a)	[26]
Centaurea nigra L.	Centaurée noire/Lesser knapweed	0 (a)	[21]
Taraxacum officinale Weber.	Pissenlit/Common dandelion	0 (a)	[21]
Artemisia princeps Pamp.	Armoise/Sagebrush	0 (a)	[32, 33]
Carthamus tinctorius L.	Carthame, Safran bâtard/Safflower	1.0; ? (b)	[34]
Helianthus annuus L.	Tournesol/Common sunflower	0 (a)	[25, 35]
Senecio jacobaea L.	Séneçon Jacobée/Ragwort, Stinking-willie	0 (a)	[21]
Achillea millefolium L.	Achillée millefeuille/Common yarrow	0 (a)	[21]
Onopordum acanthium L.	Chardon aux ânes/Scottish thistle	0 (a)	[21]
BALSAMINACEAE			
Impatiens parviflora DC.	Balsamine à petites fleurs/Small balsam	1.2 (a)	This study
BEGONIACEAE			
Begonia parva	/	1.0 (a)	This study
Begonia caroliniaefolia Regel.	/	0.9 (a)	This study
Begonia goegoensis N.E. Br.	/Fire-king Begonia	1.1 (a)	This study
BERBERIDACEAE			
Berberis pruinosa Franch.	/	2.9 (a)	This study
Nandina domestica Thunb.	Bambou sacré/	0.8 (a)	This study
Berberis vulgaris L.	Epine vinette commune/Barberry	4.1 (a)	[21]
BETULACEAE (Corylaceae)			
Corylus avellana L.	Noisetier, Coudrier/Common filbert, Cob-nut	2.0 (a)	This study
Carpinus betulus L.	Charme commun/European hornbeam	2.5 (a)	This study
Alnus glutinosa (L.) Gaertn.	Aulne glutineux/European alder	1.4 (a)	This study
Betula pendula Roth.	Bouleau blanc d'Europe/European weeping birch	tr. (a)	[21]
BIGNONIACEAE			
Catalpa bignonioides Walt.	Catalpa commun/Southern catalpa	0.4 (a)	This study
BIXACEAE			
Bixa orellana L.	Rocouyer/Lipstick-tree	0.8 (a)	This study
BORAGINACEAE			
Borago officinalis L.	Bourrache officinale/Common borage	(d, 18:3 plant)	[36]
Symphytum officinale L.	Consoude officinale/Common comfrey	0 (a)	[15, 18, 21, 37]
Echium vulgare L.	Vipérine/Common viper's bugloss	0 (a)	[21]
Echium plantagineum L.	Vipérine faux plantain/Salvation jane	0 (a)	[38]
Myosotis scorpioides L.	Myosotis des marais/True water forget-me-not	0 (a)	[14, 17, 19, 21, 37]
Myosotis arvensis (L.) Hill	Myosotis des près/Common forget-me-not	0 (a)	[21, 37]
Myosotis alpestris F.W. Schmidt	Myosotis des Alpes/Alpine forget-me-not	0 (a)	[21, 37]
Pulmonaria officinalis L.	Pulmonaire officinale/Lung wort	0 (a)	[21, 37]
Mertensia maritima (L.) S.F. Gray	Mertensie maritime/Northern shorewort, Oysterleaf	0 (a)	[21]
Anchusa sp.	Buglosse/Bugloss	0 (a)	[17, 32]
BRASSICACEAE (Cruciferae)			
Arabidopsis thaliana (L.) Heynh.	Arabette des dames/Thalecress	13.8 (a)	[39, 40]
Armoracia rusticana Gaertn., Ney et Scherb	Raifort/Horse radish	24.0; 1.8 (b)	[15, 18]
Brassica oleracea L.	Chou/Cauliflower, Cabbage	15.9 (a)	[16, 19, 21, 41]
Brassica napus L.	Colza, Rutabaga, Navet/Turnip, Rape	29.0; 3.0 (b)	[15, 42]
Brassica rapa L.	Rave/Turnip	(d, 16:3 plant)	[43]
Brassica juncea (L.) Czern. et Coss.	Moutarde de chine/Chinese mustard	0 (f)	[44]
Sinapis alba L.	Moutarde blanche/Mustard	20.7; 2.5 (b)	[16, 18, 19, 45, 46, 47]
Alyssum saxatile L.	Corbeille d'or/Basket-of-gold	28.0;2.1 (b)	[15, 18]
Alyssum citrinum	/	18.0; 1.2 (b)	[15, 18]
Matthiola incana R. Br.	Violier/Ten-Weeks Stock	28.0; 1.3 (b)	[15, 18]
Sisymbrium austriacum Jacq.	Sisymbre d'Autriche/Erysimum	32.0; 2.9 (b)	[15, 18]
Cheiranthus cheiri L.	Giroflée des murailles/Wallflower	11.1 (a)	[21]
Cardamine pratensis L.	Cardamine des près/Lady's smock	11.3 (a)	[21]
Nasturtium officinale R. Br.	Cresson de fontaine/Watercress	16.9 (a)	[21]
BROMELIACEAE			
Tillandsia usneoides L.	Barbe grise/Spanish moss	0.6 (a)	This study
Tillandsia cyanea Linden.	/	0.5 (a)	This study
Aechmea sp.	/	1.1 (a)	This study
Ananas comosus (L.) Merr.	Ananas/Pineapple	0.4 (a)	This study

Table 1—*continued*.

	Vernacular French and English name of plant species		References
BUTOMAEAE			
Butomus umbellatus L.	Butome en ombelle, Jonc fleuri/Flowering rush	0 (a)	[22]
BUXAXEAE			
Buxus sempervirens L.	Buis commun/Common box	0.3 (a)	This study
Buxus longifolia Boiss.	/	0 (a)	This study
CACTACEAE			
Aporocactus flagelliformis (L.) Lem.	Queue de rat/Rat's tail cactus	0.3 (a)	This study
Opuntia ficus-indica (L.) Mill.	Figuier de Barbarie/Prickly pears	0.3 (a)	This study
CAESALPINIACEAE			
Tamarindus indica L.	Tamarinier/Tamarind	0 (a)	[23]
Trigonella foenumgraecum L.	Fenugrec/Fenugreek	0 (a)	[23]
Cercis siliquastrum L.	Arbre de Judée/Love tree	0.5 (a)	This study
Caesalpinia gilliesi (Wall. et Hook.) Benth.	Mimosa du Japon/Bird of paradise	0.6 (a)	This study
Baouhinia aculeata L.	/	0.7 (a)	This study
CALLITRICACEAE			
Callitriche stagnalis Scop.	Callitriche des eaux/Pond Water-Starwort	tr. (a)	[21]
CALYCANTHACEAE			
Calycanthus floridus L.	Calycanthe, Arbre pompadour/Pineapple shrub	1.2 (a)	This study
CAMPANULACEAE			
Jasione montana L.	Jasione des montagnes/Sheep's bit scabious	12.2 (a)	[21]
Campanula rotundifolia L.	Campanule à feuilles rondes/Harebell	8.4 (a)	[21]
Campanula trachelium L.	Campanule gantelée/ Throatwort	13.6 (a)	This study
Campanula patula L.	Campanule étalée/	6.1 (a)	This study
Lobelia inflata L.	Lobèlie enflée/Indian tabacco	3.4 (a)	This study
CANNABACEAE			
Humulus lupulus L.	Houblon/Common hop	0.9 (a)	This study
Cannabis sativa L.	Chanvre indien/Indian hemp, Marijuana, Hashish	1.0 (a)	This study
CAPPARACEAE (Capparidaceae)			
Capparis spinosa L.	Câprier/Caper bush	0.9 (a)	This study
CAPRIFOLIACEAE			
Viburnum lantana L.	Viorne laineuse/Common wayfaring tree	1.6 (a)	This study
Sambacus nigra L.	Sureau noir/European black elder	3.8 (a) 5.1; 2.5 (b)	[19]
Abelia floribunda Dcne.	Abélia/Abelia	1.6 (a)	This study
Viburnum rhytidophyllum Hemsl.	Viorne à feuilles ridées/	1.6 (a)	This study
CARICACEAE			
Carica papaya L.	Papayer/Papaw apple	1.5 (a)	This study
CARYOPHYLLACEAE			
Stellaria media (L.) Villl.	Mouron des oiseaux/Common chick weed	tr. (a)	[19, 21]
Stellaria graminea L.	Stellaire graminée/Lesser stitchwort	0.5 (a)	[21]
Stellaria holostea L.	Stellaire holostée/Greater stitchwort	0.2 (a)	[21]
Stellaria alsine Grimm	Stellaire aquatique/Bog stitchwort	tr. (a)	[21]
Silene dioica (L.) Clairville	Compagnon rouge/Red campion, Red Catchfly	0.3 (a)	[21]
Silene alba (Mill.) E. H. L. Krause	Compagnon blanc/White campion	tr. (a)	[21]
Silene vulgaris (Moench) Garcke	Silène enflée/Bladder campion	tr. (a)	[21]
Lychnis coronaria (L.) Desr.	Coqueburde des jardins/Rose campion	0.4 (a)	[21]
Lychnis flos-cuculi L.	Lychnis fleur de coucou/Ragged robin	0.2 (a)	[21]
Cerastium glomeratum Thuill	Céraiste aggloméré/Mouse-eared chickweed	tr. (a)	[21]
CELASTRACEAE			
Euonymus nanus Bieb.	Fusain nain/	0.6 (a)	This study
Euonymus alatus (Thunb.) Sieb.	Fusain ailé/	0 (a)	This study
CERATOPHYLLACEAE			
Ceratophyllum demersum L.	Cornifle nageant/Coon's tail, Common hornard	0 (a)	[22]
CERCIDIPHYLLACEAE			
Cercidiphyllum japonicum Sieb. & Zucc.	Cerdidiphylle du Japon/Katsura tree	0.4 (a)	This study
CHENOPODIACEAE			
Chenopodium album L.	Ansérine/Fat hen, Pale goosefoot	(d, 16:3 plant)	[12]
Chenopodium quinoa Willd.	Ansérine du Pérou/Quinoa	8.0; ? (b)	[34]
Spinacia oleracea L.	Epinard/Spinach	11.8 (a) 21.9; 6.9 (b)	[14, 16, 19, 21, 25, 28, 32, 34, 45, 46, 47]
Beta vulgaris L.	Betterave/Sugar beet	5.0;1.5 (b)	[15, 17, 18]
Atriplex lentiformis (Torr.) S. Wats.	/Quailbrush	13.8; 2.1/0; 0 (e)	[48]
CISTACEAE			
Cistus incanus L.	Ciste gris de Corse/Hairy rock-rose	1.0 (a)	This study
Helianthemum pilosum	/	0.9 (a)	This study
CLUSIACEAE (Hypericaceae)			
Hypericum tetrapterum Fr.	Millepertuis/Square stalked St. John's wort	0 (a)	[21]
Hypericum androsaemum L.	Androsème officinale/Tutsan	0 (a)	[21]
COMMELINACEAE			
Tradescantia navicularis Ortg.	/Spiderwort	0.4 (a)	This study
CONVOLVULACEAE			
Convolvulus arvensis L.	Liseron des champs/Field bindweed	0.9 (a)	This study
Convolvulus sepium L.	Liseron des haies/Hedge false Bindweed	0 (a)	[15, 18, 21]
Ipomoea acquatica Forsk	Ipomée aquatique/	0 (f)	[44]
Ipomoea lobata (Cerv.) Thell.	/	1.1 (a)	This study

continued

Table 1—*continued.*

	Vernacular French and English name of plant species		References
CORNACEAE			
Cornus sanguinea L.	Cornouiller sanguin/Blood-twig dogwood	1.1 (a)	This study
Aucuba japonica Thunb.	Aucuba du Japon/	4.6 (a)	This study
CRASSULACEAE			
Sedum rosea (L.) Scop.	Rhodiole/King's crown, Roseroot	tr. (a)	[21]
Sedum acre L.	Sédum âcre/Mossy stonecrop, Wall pepper	tr. (a)	[21]
Sedum telephium subsp *fabaria* W.D.J. Koch	/Witch's-moneybags	tr. (a)	[21]
CUCURBITACEAE			
Cucurbita pepo L.	Courge/Field pumpkin, Squash	0 (a)	[15, 18, 19, 25, 49, 50]
Cucumis sativus L.	Comcombre/Garden cucumber	0 (a)	[50, 51]
Cucurbita maxima Duch.	Potiron/Winter squash	0 (f)	[44]
Sechium edule (Jacq.) Swartz.	Chayotte/Chayote	0 (f)	[44]
Echinocystis lobata (Michx.)Torr. & Gray	/Wild cucumber	1.4 (a)	This study
CYMODOCEACEAE			
Cymodocea serrulata Aschers. et Magnus	/	0 (a)	[52]
Halodule universis Boiss.	/Shoalweed	0 (a)	[52]
CYPERACEAE			
Carex pendula Huds.	Laîche pendante/	1.0 (a)	This study
Carex sp.	/	0.8 (a)	This study
Carex demissa Hornem.	Carex grêle. Laîche vert-jaunâtre/Little green sedge	1.0 (a)	This study
Cyperus alternifolius L.	Souchet de Madagascar/Alternate-leaf flat sedge	0.6 (a)	This study
DIOSCOREACEAE			
Tamus communis L.	Tamier, Herbe aux femmes battues/Ladie's seal	1.3 (a)	This study
Dioscorea sp.	Igname/Yam	0.9 (a)	This study
DIPSACACEAE			
Knautia dipsacifolia (Schrank) Kreuzer	Knautia/	5.4 (a)	This study
Cephalaria uralensis (Murray) Roener	Céphalaire/	10.8 (a)	This study
Dipsacus fullonum L.	Cabaret des oiseaux, Cardère commune/ Fuller's teasel	8.2 (a)	This study
DROSERACEAE			
Drosera rotundifolia L.	Rosée du soleil/Round-leaf sundew	0 (a)	This study
Drosera intermedia Hayne	Rossolis, Drosera/Spoon-leaf sundew	0 (a)	This study
ERICACEAE			
Rhododendron ponticum L.	Rhododendron pontique/Wild rhododendron	0 (a)	[21]
Vaccinum myrtillus L.	Myrtille/Rilberry, Whortle berry	0 (a)	[21]
Erica cinerea L.	Bruyère cendrée/Scotch heath	0 (a)	[21]
ERYTHROXYLACEAE			
Erythroxylon coca Lam.	Cocaïer/	0.7 (a)	This study
EUPHORBIACEAE			
Euphorbia milii Desmoul.	Epine du christ/Crown-of-thorns	tr. (a)	This study
Euphorbia balsamifera Ait.	/	0.9 (a)	This study
Synadenium cupulare (Boiss.) Wheeler	/	0.2 (a)	This study
Euphorbia lathyris L.	Epurge/Caper-spurge	1.0 (a)	This study
Ricinus communis L.	Ricin/Castor bean, Castor-oil plant	0 (a)	[14, 19]
FABACEAE (Papilionaceae)			
Robinia pseudacacia L.	Robinier faux-acacia/Black locust, false acacia	0.5 (a)	This study
Pisum sativum L.	Pois/Garden pea	0 (a)	[12, 34, 46, 47, 51]
Vigna unguiculata (L.) Walp.	/Cow pea, Black-eyed-pea	0 (a)	[53]
Trifolium repens L.	Trèfle rampant, Trèfle blanc/White clover	0 (a)	[54]
Trifolium pratense L.	Trèfle des prés/Red clover	0 (a)	[14, 19]
Vicia faba L.	Fève/Broad bean	0 (a)	[17, 18, 25, 28, 42, 54]
Medicago sativa L.	Luzerne/Lucerne, Alfalfa	0 (a)	[14, 19]
Phaseolus multiflorus Willd.	Haricot ornemental/Runner bean	0 (a)	[14, 17, 19]
Sarothamnus scoparius	Genêt à balais/Common broom	0 (a)	[21]
Ulex europaeus L.	Ajonc d'Europe/Common gorse	0 (a)	[21]
Glycine max (L.) Merr.	Soja/Soybean	0 (a)	[55]
Anthyllis vulneraria L.	Vulnéraire/Kidney vetch, Woundwort	0 (a)	[56]
Coronilla emerus L.	Faux baguenaudier, Séné bâtard/Scorpio senna	0 (a)	[56]
Coronilla minima L.	Coronille minime/Crownvetch coronilla	0 (a)	[56]
Coronilla varia L.	Coronille bigarée, Coronille variée/Purple crownvetch	0 (a)	[56]
Cytisus sessilifolius L.	Cytise à feuilles sessiles/Sessile-leaves broom	0 (a)	[56]
Dorycnium suffruticosum Lagr.	Badasse sous-ligneuse/Canary clover	0 (a)	[56]
Lotus delortii Timb. Lagr. ex F.W. Schultz	Lotier/Deervetch, Bird's foot trefoil	0 (a)	[56]
Onobrychis saxatilis (L.) Lam.	Sainfoin des rochers/Holyclover	0 (a)	[56]
Ononis minutissima L.	Bugrane, Arrête-boeuf/Restharrow	0 (a)	[56]
Psoralea bituminosa L.	Psoralée bitumineuse/Scurf pea	0 (a)	[56]
FAGACEAE			
Quercus robur L.	Chêne pédonculé/Oak	tr. (a)	[21]
Fagus sylvatica L.	Hêtre, Fayard/Beech	tr. (a)	[21]
FLACOURTIACEAE			
Hydnocarpus wightiana Blume	/	0 (a)	[57]

Table 1—*continued.*

	Vernacular French and English name of plant species		References
FUMARIACEAE			
Fumaria officinalis L.	Fumeterre officinale/Fumitory	0 (a)	[21]
GENTIANACEAE			
Limnanthemrum peltatum Gmel.	Faux nénuphar/	0.6 (a)	This study
GERANIACEAE			
Geranium sanguineum L.	Géranium sanguin/Bloody crane's-bill	7.6 (a)	This study
Geranium molle L.	Géranium mou/Dove-foot crane's-bill	10.4 (a)	This study
Geranium robertianum L.	Herbe à Robert/Herb Robert	8.3 (a)	[21]
Erodium dunense	Bec de grue/Dune storksbill	8.7 (a)	[21]
Pelargonium X hortorum Bailey	Pélargonium des jardins/	2.4 (a)	This study
GESNERIACEAE			
Columnea gloriosa Sprague	/	1.8 (a)	This study
Columnea linearis Oerst.	/	0.7 (a)	This study
Ramonda myconi (L.) Schultz	Ramondie des Pyrènées/	1.2 (a)	This study
GROSSULARIACEAE			
Ribes sanguineum Pursh	Groseillier sanguin/Blood currant	12.6 (a)	23.2; 6.8 (b)[19, 21]
Ribes uva-crispa L.	Groseillier à maquereau/European Gooseberry	7.7 to 7.9 (a)	This study, [21]
Ribes nigrum L.	Cassissier/Black currant	4.5 (a)	This study
HAMAMELIDACEAE			
Liquidambar styraciflua L.	Liquidambar, Copalme d'amérique/Sweetgum	1.2 (a)	This study
HIPPOCASTANACEAE			
Aesculus hippocastanum L.	Maronnier d'Inde/Horse-chestnut	2.1 (a)	[21]
HYDRANGEACEAE			
Philadelphus coronarius L.	Seringat/Sweet mock orange	1.1 (a)	This study
Philadelphus sp.	/	tr. (a)	[21]
Hydrangea macrophylla (Thunb.) Ser.	Hortensia à grandes feuilles/French hortensia	1.8 (a)	This study
HYDROCHARITACEAE			
Halophila ovalis den Hartog	/Hawain sea grass	4.64 (a)	[52]
Halophila ovata Gaudich.	/	5.04 (a)	[52]
Halophila spinulosa Aschers.	/	0.39 (a)	[52]
Thalassia hemprichii Aschers	/Turtle-grass	0.33 to 0.35 (a)	[52]
Limnobium spongia L.C. Rich.	Grenouillette d'Amérique/Common frogbit	0 (a)	[52]
Elodea canadensis Michx.	Elodée du Canada/Canadian waterweed	0 (a)	[52]
IRIDACEAE			
Iris pseudacorus L.	Iris des marais/Yellow flag	1.8 to 5.6 (a) 10; 0.7 (b)	This study, [21]
Freesia sp.	Freesia/Freesia	2.5	This study
Gladiolus sp.	Glaieul/Gladiolus	2.2	This study
JUGLANDACEAE			
Pterocarya fraxinifolia (Lam.) Spach.	/Causasian wingnut	0.6 (a)	This study
JUNCACEAE (Juncaginaceae)			
Juncus conglomeratus L.	Jonc en glomérules/Common rush	0.2 (a)	[21]
LAMIACEAE (Labiatea)			
Lamium confertum Fries	/Garden Henbit, Intermediate dead nettle	0 (a)	[21]
Lavandula sp.	Lavande/Lavandins	0 (a)	[58]
Ajuga reptans L.	Bugle rampante/Common Bugle	0.2 (a)	[21]
Mentha X verticillata L.	/	0 (a)	[59]
Mentha arvensis L.	Menthe des champs/Field mint, Corn mint	0 (a)	[59]
Mentha aquatica L.	Menthe aquatique/Water mint	0.5 (a)	This study
Rosmarinus officinalis L.	Romarin officinal/Rosemary	0 (a)	[60]
LAURACEAE			
Cinnamomum camphora (L.) J. Presl.	Camphrier/Camphor tree, Pepperwood	0 (a)	This study
Umbellularia california (Hook et Arn) Nutt.	/California laurel	0.7 (a)	This study
Laurus nobilis L.	Laurier sauce/Laurel bush	1.1 (a)	This study
Persea americana Mill.	Avocatier/Avocado tree	0.9; ? (b)	[41]
LEMNACEAE			
Lemna trisulca L.	Lentille prolifère/Ivy-leaf waterweed	0 (a)	[22]
Lemna minor L.	Petite lentille d'eau/Water lentil, duckweed	0 (a)	This study, [22, 61]
LENTIBULARIACEAE			
Utricularia vulgaris L.	Utriculaire vulgaire/Greater zigzag bladderwort	1.1 (a)	This study
LILIACEAE			
Ruscus aculeatus L.	Fragon, Petit houx/Butcher's broom	1.1 (a)	This study
Ornithogalum umbellatum L.	Ornithogale, Dame d'onze heures/Sleepydick	1.1 (a)	This study
Muscari comosum Mill.	Muscari à toupet/Tassel grape-hyacinth	1.1 (a)	This study
Yucca sp.	Yucca/Yucca	0.3 (a)	This study
Allium porrum L.	Poireau/Garden leek	0 (a)	[11]
Convallaria majalis L.	Muguet/European lily of the valley	0.6 (a)	[21]
Polygonatum multiflorum (L.) All.	Sceau de Salomon/European solomon's seal	2.0 (a)	[21]
Galanthus nivalis L.	Perce-neige/Snowdrop	0 (a)	[21]
Ophiopogon jaburan (Siebold) Lodd.	Ophiopogon jaburan/Jaburan lilyturf	1.23 (a)	This study
LINACEAE			
Linum usitatissimum L.	Lin/Flax	1.0 (a)	This study
LORANTHACEAE			
Tapinanthus dodoneifolius DC.	/	0 (a)	[62]
LYTHRACEAE			
Cuphea ignea DC	Fleur cigarette/Cigar flower	1.1 (a)	This study

continued

Table 1—*continued.*

	Vernacular French and English name of plant species		References
MAGNOLIACEAE			
Magnolia denudata Desrouss.	Magnolia lys blanc/	1.2 (a)	This study
Magnolia grandiflora L.	Magnolia, Laurier-tulipier/Southern magnolia	0.5 (a)	This study
Liriodendron tulipifera L.	Tulipier de Virginie/Tuliptree	1.3 (a)	This study
MALVACEAE			
Althaea officinalis L.	Mauve/White mallow	0.8 (a)	This study
Ceiba pentandra L.	/Silk-cotton tree	0 (a)	[57]
Hibiscus manihot (L.) Medik.	/Sunset-musk-mallow	0.6 (f)	[44]
Althaea rosea L.	Rose trémière/Hollylock	0 (a)	[63]
Hibiscus esculentum L.	Gombo/Okra	0 (a)	[64]
MARANTHACEAE			
Thalia dealbata Fraser.	/Powdery alligator-flag	0.5 (a)	This study
MELASTOMATACEAE			
Medinilla magnifica Lindl.	/	1.2 (a)	This study
MENYANTHACEAE			
Menyanthes trifoliata L.	Trèfle d'eau/Buck-bean	0 (a)	[21]
MIMOSACEAE			
Albizia sp.	Albizia/	0.6 (a)	This study
MORACEAE			
Morus alba L.	Mûrier blanc/White mulberry	0.8 (a)	This study
Ficus carica L.	Figuier commun/Common fig	1.6 (a)	This study
Ficus benjamina L.	Ficus ornemental/Weeping fig, Benjamin tree	1.1 (a)	This study
MUSACEAE			
Musa basjoo Sieb. et Zucc.	Bananier ornemental/Decorative banana tree	0.8 (a)	This study
MYRICACEAE			
Myrica gale L.	Piment royal/Sweetgale	0.7 (a)	This study
MYRTACEAE			
Eucalyptus rotondifolia	Eucalyptus à feuilles rondes/Eucalyptus	0.8 (a)	This study
NELUMBONACEAE			
Nelumbo nucifera Gaertn.	Lotus rustique blanc/Sacred lotus	0.3 (a)	This study, [65]
NEPENTHACEAE			
Nepenthes sp.	/	0.8 (a)	This study
NOLANACEAE			
Nolana prostata L.	Nolane couchée/	7.8 to 10.1 (a)	This study
Nolana napiformis Phil.	/	2.3 to 4.6 (a)	This study
NYCTAGINACEAE			
Mirabilis jalapa L.	Belle de nuit/Marvel-of-Peru, four o'clock	0 (a)	This study
NYMPHEACEAE			
Nuphar lutea (L.) Smith	Nénuphar jaune/Yellow pond'lily	0 (a)	[21, 22]
OLEACEAE			
Ligustrum vulgare L.	Troène commun/European privet	0.9 (a)	This study
Jasminum nudiflorum Lindl.	Jasmin d'hiver/Winter jasmine	0.8 (a)	This study
Olea europaea L.	Olivier/Olive tree	0 (a)	[66]
Syringa vulgaris L.	Lilas commun/Common lilac	0 (a)	[21]
ONAGRACEAE (Oenotheraceae)			
Oenothera purpurea Curt.	/Tufted evening primrose	1.0 (a)	This study
Chamaenerion angustifolium (L.) Scop.	Epilobe en épi/Fireweed	0.4 (a)	[21]
Epilobium montanum Hausskn.	Herbe de la St Hean/Broad leafed willow herb	0.6 (a)	[21]
Circaea lutetiana L.	Herbe aux sorcières, Circée de Paris/ Enchanter's nightshade	0.6 (a)	[21]
ORCHIDACEAE			
Dendrobium aggregatum Roxb.	/	0.5 (a)	This study
Listera ovata (L.) R.Br.	Listère à feuilles ovales/Egg-leaf thwayblade	1.2 (a)	This study
Oncidium sp.	/	0.2 (a)	This study
Orchis latifolia	Orchis à larges feuilles/	0.3 (a)	[21]
Vanillia sp.	Vanillier/Vanilla plant	0.3 (a)	This study
OXALIDACEAE			
Oxalis acetosella L.	Parelle/Wood-sorrel	0 (a)	[21]
Oxalis corniculata L.	Oxalis cornu/Yellow wood-sorrel	0 (a)	[23]
PAPAVERACEAE			
Chelidonium majus L.	Chelidoine, Herbe aux verrues/Greater celandine	0.7 (a)	This study
Papaver rhoeas L.	Coquelicot/Poppy, Field poppy	0 (a)	[21]
Meconopsis cambrica (L.) Vig.	Méconopsis du pays de Galles/Welsh Poppy	0 (a)	[21]
PASSIFLORACEAE			
Passiflora caerulea L.	Passiflore bleue/Common-blue passion flower	0.7 (a)	This study
PIPERACEAE			
Peperomia griseargentea Yuncker	/	0.8 (a)	This study
Peperomia magnoliaefolia (Jacq.)Dietr.	/Spoon-leaf peperomia	0.4 (a)	This study
PLANTAGINACEAE			
Plantago major L.	Plantain à larges feuilles/Great plantain	tr. (a)	[21]
Plantago lanceolata L.	Plantain lancéolé/English plantain	tr. (a)	[21]
Plantago coronopus L.	Plantain corne de cerf/Buck's-horn plantain	1.0 (a)	This study
PLATANACEAE			
Platanus orientalis L.	Platane d'orient/American sycamore	0.4 (a)	This study
PLUMBAGINACEAE			
Limonium latifolium (Sm.) Kuntze	/	0.8 (a)	This study
Armeria maritima (Mill.) Willd.	Gazon d'olympe/Sea thrift	0.5 (a)	[21]
Ceratostigma plumbaginoides Bunge	Dentelaire de Lady Larpent/Blue-leadwood	0.8 (a)	This study

Table 1—*continued.*

	Vernacular French and English name of plant species		References
POACEAE (Gramineae)			
Avena sativa L.	Avoine/Oat	0 (a)	[45, 67, 68, 69, 70]
Zea mays L.	Maïs/Maize, Corn	0 (a)	[15, 45, 46, 69, 70, 71]
Triticum aestivum L.	Blé/Bread wheat	0 (a)	[17, 69, 70]
Lolium perenne L.	Gazon anglais/Ivraie, Perennial rye grass	0 (a)	[69, 70]
Hordeum vulgare L.	Orge/Common barley	0 (a)	[18, 69, 72]
Oryza sativa L.	Riz/Cultivated rice	0 (a)	[73]
Porteresia coarctata (Rosch.) Tateoka	/	0 (a)	[74]
POLYGALACEAE			
Polygala calcarea F.W. Schultz	Polygala du calcaire/Milkwort	1.5 (a)	This study
POLYGONACEAE			
Rumex obtusifolius L.	Patience sauvage/Broad leafed dock, Bitter dock	0 (a)	[21]
Rumex vesicarius L.	/Bladder dock	0 (a)	[23]
Polygonum amphibium L.	Renouée amphibie/Water smartweed	0 (a)	[21]
PONTEDERIACEAE			
Eichornia crassipes (Mart.) Solms	Jacinthe d'eau/Common water-hyacinth	1.1 (a)	This study
PORTULACACEAE			
Portulaca oleracea L.	Pourpier/Common purslane, Little-hogweed	0 (a)	This study, [75]
Montia perfoliata (Donn *ex* Willd) Howell	Claytonie perfoliée/Miner's-lettuce	11.5 (a) 19.6; 4.5 (b)	[28]
Talinum triangulare Willd.	Pourpier grand bois/Ceylon spinach	0 (a)	[23]
POSIDONIACEAE			
Posidonia australis Hook.	/	0 (a)	[76]
POTAMOGETONACEAE			
Potamogeton natans L.	Potamot nageant/Floating pondweed	2.1 (a)	This study
Potamogeton perfoliatus L.	Potamot à feuilles perfoliées/Clasping leaf pondweed	0(a)	[22]
PRIMULACEAE			
Primula veris L.	Coucou, Primevère officinale/Cowslip primrose	1.2 (a)	This study
Lysimachia vulgaris L.	Lysimaque commune/Yellow loosestrife	tr. (a)	[21]
RANUNCULACEAE			
Aquilegia vulgaris L.	Ancolie vulgaire/Columbine	9.8 (a)	[21]
Caltha palutris L.	Populage des marais/Marsh marigold	10.8 (a)	[21]
Anemone nemorosa L.	Anémone sylvie/Wood anemone	15.6 (a)	[21]
Delphinium ambiguum L.	Dauphinelle d'ajax/Larkspur	17.4 (a)	[21]
Ranunculas acris L.	Bouton d'or, Renoncule âcre/Meadow buttercup	17.5 (a) 36.8; 3.5 (b)	[19, 21]
Ranunculus ficaria L.	Ficaire/Lesser celandine, Fig buttercup	13.9 (a)	[21]
Ranunculus flammula L.	Renoncule d'eau/Greater creeping spearwort	6.2 (a)	This study
RESEDACEAE			
Reseda lutea L.	Réséda jaune/Yellow upright mignonette	0.9 (a)	This study
ROSACEAE			
Sorbus torminalis (L.) Crantz	Alisier, Sorbier commun/Mountain ash, Service tree	1.6 (a)	This study
Prunus spinosa L.	Prunellier/Blackthorn	0.6 (a)	This study
Crataegus monogyna Jacq.	Aubépine/One-seed hawthorn	3.2 (a)	This study
Pyracantha sp.	Buisson ardent, Pyracantha/Firebush, Pyracantha	1.5 (a)	This study
Sorbus aucuparia L.	Sorbier des oiseleurs/American mountain ash, Rowan	3.5 (a)	[21]
Alchemilla vulgaris Buser	Alchemille/Thin-stem lady's mantle	0.9 (a)	[21]
Geum rivale L.	Benoîte des ruisseaux/Water avens	1.2 (a)	[21]
Rubus idaeus L.	Framboisier/Common red raspberry	tr. (a)	[21]
Potentilla palutriss (L.) Scop.	Potentille, Comaret/Marsh cinquefolium	1.0 (a)	[21]
RUBIACEAE			
Rubia tinctorum L.	Garance/Madder	7.8 (a)	This study
Asperula odorata L.	Aspérule odorante/Sweet woodruff	9.1 (a) 34.7; 8.6 (b)	[19, 21]
Galium aparine L.	Gaillet gratteron/Goose grass	11.0 (a)	[21]
Galium palustre L.	Gaillet des marais/Common marsh bedstraw	3.9 (a)	This study
Coprosma baueri Endl.	Coprosme de Bauer/	2.3 (a)	This study
Coffea arabica L.	Caféier d'Arabie/Common coffee	0.4 to 0.7 (a)	This study
RUTACEAE			
Poncirus trifoliata Raf..	/Hardy-orange	0.8 (a)	This study
Aegle marmelos	/	0 (a)	[77]
Choisya ternata H.B.K.	Oranger du Mexique/	1.1 (a)	This study
SALICACEAE			
Populus nigra L.	Peuplier noir/Black poplar	0.5 (a)	This study
Populus tremula L.	Peuplier tremble/European aspen	0.3 (a)	This study
Salix cinerea L.	Saule cendré/Large gray willow	0.6 (a)	This study
Salix caprea L.	Saule marsault/Goat willow	0 (a)	[78]
Salix X dasyclados Wimm.	Saule à rameaux velus/	0 (a)	[78]
Salix myrsininofolia Salisb.	Saule noircissant/European willow	0 (a)	[78]
Salix viminalis L.	Saule des vanniers, Osier blanc/Basket willow	0 (a)	[78]
SARRACENIACEAE			
Sarracenia flava L.	Sarracenia jaune/Yellow pitcherplant	0.6 (a)	This study

continued

Table 1—*continued.*

	Vernacular French and English name of plant species		References
SAURURACEAE			
Saururus cernuus L.	Queue de lézard/Lizard's tail	0.6 (a)	This study
SAXIFRAGACEAE			
Saxifraga umbrosa L.	Saxifrage des ombrages/London pride	tr. (a)	[21]
Bergenia crassifolia (L.) Fritsch.	Bergenia/	tr. (a)	[21]
Saxifraga sarmentosa L.	Saxifrage sarmenteuse/Creeping saxifrage	0.9 (a)	This study
SCROPHULARIACEAE			
Linaria vulgaris Mill.	Linaire commune/Common Toadflax	0 (a)	[21]
Veronica chaemaedrys L.	Véronique petit chêne/Germander speedwell	0 (a)	[21]
Antirrhinum majus L.	Gueule de loup, Muflier/Garden snapdragon	0 (a)	[15, 17, 18, 21]
SIMMONDSIACEAE			
Simmondsia chinensis (Link) Schneid	Jujube/Jojoba	0 (a)	[79]
SOLANACEAE			
Solanum tuberosum L.	Pomme de terre/Irish potato	11.6 (a)	[21]
Solanum nodiflorum Jacq.	/American black nightshade	(d, 16:3 plant)	[12, 34]
Solanum dulcamara L.	Morelle douce amère, Vigne de Judée/ Woody climbing nightshade	9.6 (a) 18.6; 2.1 (b)	[18, 50]
Solanum carolinense L.	/Horse nettle, Carolina	13.5; 2.0 (b)	[50]
Solanum muricatum Ait.	Poire melon/Pepino	(d, 16:3 plant)	[30]
Physalis subglabrata	Amour en cage/Ground cherry	8.5; 1.0 (b)	[50]
Nicotiana sylvestris Spegazz et Comes	Tabac des bois/Tobacco	14.1; 1.4 (b)	[45]
Lycopersicon esculentum Mill.	Tomate/Garden tomato	13.8 (a) 32.4; 3.3 (b)	[19, 25, 35, 50]
Capsicum annuum L.	Piment/Bell pepper	11.4; 1.4 (b)	[50, 80]
Salpichroa origanifolia (Lam.) Thell.	Muguet des pampas, Plante aux oeufs de coq/	8.7 (a)	This study
STERCULIACEAE			
Sterculia foetida L.	/	0 (a)	[57]
STRELITZACEAE			
Strelitzia reginae Ait.	Oiseau du paradis/Bird of paradise	0.9 (a)	This study
TAMARICACEAE			
Tamarix pentandra Stev.	Tamaris à cinq étamines/Five-stamen tamarisk	0.7 (a)	This study
Tamarix gallica L.	Tamaris de France/French tamarisk, Manna plant	0.7 (a)	This study
THEACEAE			
Camellia sinensis Kuntze	Théier/Tea bush	0 (a)	[81]
Camellia japonica L.	Camélia/Camelia	0 (a)	[81]
Camellia sasanqua Thunb.	/Sasanqua	0 (a)	[81]
TILIACEAE			
Tilia platyphyllos Scop.	Tilleul à larges feuilles/Large-leaf linden	0.7 (a)	This study
Grewia occidentalis L.	Greuvier/Cross-berry	1.2 (a)	This study
TROPAEOLACEAE			
Tropaeolum majus L.	Grande capucine/Garden nasturtium	23.3; 2.8 (b)	[15, 18, 45]
TYPHACEAE			
Typha latifolia L.	Massette à larges feuilles/Broad-leaf cat-tail	0.8 (a)	This study
ULMACEAE			
Celtis australis L.	Micocoulier de Provence/Lotus tree	0.9 (a)	This study
Ulmus procera Salisb.	Orme champêtre/English elm	tr (a)	[21]
URTICACEAE			
Debregeasia edulis Wedd.	/	0.5 (a)	This study
Urtica dioica L.	Grande ortie/Stinging nettle	0 (a)	[17, 21]
VALERIANACEAE			
Centranthus ruber (L.) DC.	Valériane rouge,/Red valerian	7.7 to 7.9 (a)	This study
Valeriana officinalis L.	Valériane officinale, Herbe aux chats/Valerian	9.7 (a)	[21]
VERBENACEAE			
Verbena bonariensis L.	Verveine de Buenos-Aires/Purple-top vervain	0 (a)	This study
Vitex agnus-castus L.	Poivre sauvage/Lilac chastetree	0.7 (a)	This study
Clerodendron bungei Steud.	Péragut fétide/	1.9 (a)	This study
Lantana X hybrida Hort.	Lantana hybride/	1.4 (a)	This study
Lippia citriodora Kunth.	Verveine citronnelle/Lemon verbena	0.7 (a)	This study
VIOLACEAE			
Viola riviniana Reichenb.	Violette de rivin/Common violet	0 (a)	[21]
Viola X wittrockiana Gams	Pensée des jardins/Garden pansy	0 (a)	[21]
VISCACEAE			
Viscum album L.	Gui/European mistletoe	0 (a)	[62]
VITACEAE (Ampelidaceae)			
Vitis vinifera L.	Vigne/European vine	0 (a)	[82]
ZINGIBERACEAE			
Zingiber officinale Rosc.	Gingembre/Garden ginger	0.7 (a)	This study
ZOSTERACEAE			
Zostera marina L.	Zostère marine/Seawrack	7.1 to 8.6 (a)	[83, 84]
Zostera asiatica Miki	/	5.9 (a)	[84]
Phyllosphadixx iwatensis Makino	/Surf grass	6.6 to 8.4 (a)	[83, 84]
Heterozostera tasmanica den Hartog	/	3.5 (a)	[76]
Zostera muelliri	/	(d, 16:3 plant)	[85]

tr.: trace less than 0.1%.(a) % of $C_{16:3}$ in total leaf lipids (% of total).(b) The first and the second number represent % of $C_{16:3}$ esterified to MGDG and DGDG, respectively.(c) % of C_{16} fatty acids esterified to the sn-2 position of DGDG.(d) No composition is shown in the reference, authors mention only that the species under study is a 16:3 or a 18:3 plant.(e) First and second numbers represent % of $C_{16:3}$ esterified to MGDG and DGDG, respectively, when plants were grown at 18/23°. Third and fourth numbers represent % of $C_{16:3}$ esterified to MGDG and DGDG, respectively, when plants were grown at 30/43°.(f) % of $C_{16:3}$ esterified to glycolipid.

either the overall leaf fatty acid composition or the fatty acid composition of individual galactolipids (MGDG and DGDG) or glycolipids. In some references, no fatty acid composition is reported and the authors only indicated whether the species under study were either 16:3 or 18:3 plants.

Families reported in Table 1 are listed in Table 2 according to the classification of Cronquist [86], which takes into account various evolutionary characters (anatomical, morphological, paleobotanical (fossil), physiological, etc.). Plant families are listed from the least to the most evolved and subclasses, orders and families are indicated. Although the paleobotanic data showed that the monocotyledon line (Liliopsida) was established when the dicotyledon flora (Magnoliopsida) was still at a very early stage in its diversification (pre-Cretaceous) [87, 88], monocotyledonous plants are classified after dicotyledonous plants because the former are generally regarded as being slightly more 'evolved' than the latter. Globally, the more recently the families appeared in the history of evolution, the more evolved they are.

The results recorded in Table 1 show that, generally, a given family will contain exclusively 16:3 or 18:3 plants, depending on the threshold of $C_{16:3}$ fatty acids in their total lipids or acylated to MGDG and DGDG. This threshold appears to be 2% or more of $C_{16:3}$ fatty acids in total lipids (or more than 3% and 1.2% of $C_{16:3}$ esterified to MGDG and DGDG, respectively) for a 16:3 plant family. Galactolipids of 18:3 plants contained neither $C_{16:3}$ (from 0 to 2%) nor any other C_{16} fatty acids in the *sn*-2 position.

Generally, in a given family, all species are either 16:3 or 18:3 plants (Table 1). However, in some rare families, both 16:3 plant species and 18:3 species were found (e.g. Portulacaceae and Hydrocharitaceae). Interestingly, the only 16:3 Hydrocharitaceae species, namely, *Halophila ovalis* and *H. ovata*, are found in a marine biotope. Similarly, Zosteraceae is the sole family of monocotyledonous plants that could be regarded as 16:3 plants (except the Iridaceae, which have an intermediate phenotype); it is also an angiosperm family which contains marine species. Monocotyledonous plants living in fresh water would appear to be exclusively 18:3 plants (e.g. *Limnobium spongia*, *Elodea canadensis*, Hydrocharitaceae; *Potamogeton natans*, Potamogetonaceae; etc.)

Atriplex lentiformis is an interesting case [48]. This species, a member of the Chenopodiaceae (16:3 plants), grows in Death Valley (CA, USA) (approximately 43/30° day/night temperature regime) and along the Californian coast. Analysis of *A. lentiformis* fatty acid composition in its habitat shows the absence of $C_{16:3}$ fatty acid, suggesting that the prokaryotic pathway is not operative. When *A. lentiformis* is acclimated at a 23/18° temperature regime, the level of $C_{16:3}$ fatty acid is in the same order as that in other Chenopodiaceae from temperate climates (23/18° temperature regime), i.e. 13.8% and 2.1% of $C_{16:3}$ esterified MGDG and DGDG, respectively.

Nevertheless, and in contrast with what the few examples given above seem to indicate, the data given in Table 2 shows that the ecosystem does not generally govern the phenotype 16:3/18:3. In other words, a given family of species growing in various environments contains exclusively 16:3 plants (see Apiaceae, Brassicaceae, etc.) or 18:3 plants (see Euphorbiaceae, etc.). For example, *Porteresia coarctata*, a mangrove member of the Graminase sampled in 'two islands characterised by different environmental conditions' [74], is a 18:3 plant, as are all the Poaceae found in temperate climates (e.g. *Triticum aestivum*, *Avena sativa*, etc.). Moreover, *Ranunculus flammula*, from the Ranunculaceae, growing in an aquatic environment, is a 16:3 plant, like the other Ranunculaceae (e.g. *Anemone nemerosa*, *Ranunculus acris*, etc.). Nor do the 16:3/18:3 criteria seem to be dependent on the general anatomy and plant life history traits. In the same 18:3 family, plants may be herbaceous (e.g. *Pisum sativum*, Fabaceae), ligneous (e.g. *Robinia pseudacacia*, Fabaceae), monoecious, dioecious, annual, biennial, perennial, etc. From the 141 Angiosperm families analysed in Table 2, the percentage of 16:3 plant species in the Angiosperm flora was calculated as described in Experimental. We extrapolated these results and found that *ca* 12% of Angiosperm species in the world are 16:3 plants.

Interestingly, the presence or the absence of $C_{16:3}$ fatty acid can be used for chemotaxonomy studies. For example, depending on the authors, the Grossulariaceae is regarded either as distinct from [86, 89] or classified as a sub-group of [99] of the Saxifragaceae. It would appear that the Grossulariaceae species (defined according to Cronquist [86], are 16:3 plants whereas Saxifragaceae species are 18:3 plants (Table 1). These results are therefore in agreement with the existence of two distinct families (Grossulariaceae and Saxifragaceae) rather than only one. Moreover, several authors (for example, [90]) proposed bringing the Apiaceae and Araliaceae together. Since these two families have a 16:3 phenotype (Table 1), our results are not in disagreement with this proposal.

The endosymbiotic theory assumes that chloroplasts originated from oxygenic-photosynthetic prokaryotes [91], these proto-organelles being independent for their lipid synthesis. Therefore, the loss of the plastidial glycerolipid synthesis pathway can be regarded as a loss of plastidial autonomy concerning lipid synthesis. A similar loss of endosymbiotic organelle autonomy has also been observed for chloroplastic and mitochondrial genes [91–93].

In terms of lipid metabolism, an ancestral stock of primitive 16:3 plants seems to have evolved by losing phosphatidate phosphatase activity, consequently giving rise to 18:3 plants. Analysis of an *Arabidopsis thaliana* (16:3 plant) lipid mutant (*act* 1) provides some interesting data [94]. This mutation, which con-

verted a 16:3 plant into a 18:3 plant, does not seem to affect the fluidity of chloroplastic membranes and/or the characteristics of the photosynthetic apparatus. Furthermore, there were 'no apparent physiological disadvantages associated with the loss of the prokaryotic pathway' (except perhaps a slight thermal adaptative mechanism). These observations could indicate that the pressure of natural selection exerted

Table 2. Evolutionary analyses of 18:3 *vs* 16:3 plant families. Numbers in brackets represent species analysed (Table 1). Classification of angiosperms is according to Cronquist [86]. Families highlighted in grey are classified as 16:3 plant families, others are 18:3 plant families

CORMOPHYTES
BRYOPHYTES (Moss) (38)
PTERIDOPHYTES (Ferns) (5)
GYMNOSPERMS (Conifers) (7)
PRESPERMATOPHYTES (3)
CHLAMYDOSPERMS (3)
ANGIOSPERMS (412)
DICOTYLEDONS
MAGNOLIIDAE
Magnoliales
Magnoliaceae The magnolia family (3)
Annonaceae The custard-apple family (1)
Laurales
Calycanthaceae The sweetshurb family (1)
Lauraceae The laurel family (4)
Piperales
Saururaceae The lizard's tail family (1)
Piperaceae The pepper family (2)
Aristolochiales
Aristolochiaceae The bithwort family (1)
Nymphaeales (Ranales)
Nelumbonaceae The lotus family (1)
Nymphaeaceae The Water-lily family (1)
Ceratophyllaceae The hornwort family (1)
Ranunculales
Ranunculaceae The buttercup family (7)
Berberidaceae The barberry family (3)
Papaverales (Rhoeadales)
Papaveraceae The poppy family (3)
Fumariaceae The fumitory family (1)
HAMAMELIDAE
Hamamelidales
Cercidiphyllaceae The katsura-tree family (1)
Platanaceae The planetree family (1)
Hamamelidaceae The witch-hazel family (1)
Urticales
Ulmaceae The elm family (2)
Cannabaceae The hemp family (2)
Moraceae The mulberry family (3)
Urticaceae The nettle family (2)
Juglandales
Juglandaceae The walnut family (1)
Myricales
Myricaceae The bayberry family (1)
Fagales
Fagaceae The beech family (2)
Betulaceae The birch family (4)
CARYOPHYLLIDAE
Caryophyllales
Nyctaginaceae The four-O'clock family (1)
Cactaceae The cactus family (2)
Chenopodiaceae The goose foot family (5)
Amaranthaceae The amaranth family (3)
Portulacaceae The purslane family (3)
Caryophyllaceae The pink family (10)
Polygonales
Polygonaceae The buckwheat family (3)
Plumbaginales
Plumbaginaceae The leadwort family (3)
DILLENIIDAE
Theales
Theaceae The tea family (3)
Actinidiaceae The kiwi family (1)
Clusiaceae The St. John's wort family (2)
Malvales
Tiliaceae The linden family (2)
Sterculiaceae The cacao family (1)
Malvaceae The mallow family (5)
Nepenthales
Sarraceniaceae The pitcherplant family (1)
Nepenthaceae (1)
Droseraceae The sundew family (2)
Violales
Flacourtiaceae The logwood family (1)
Bixaceae The lipsticktree family (1)
Cistaceae The rock-rose family (2)
Tamaricaceae The tamarisk family (2)
Violaceae The violet family (2)
Passifloraceae The passion-flower family (1)
Caricaceae The papaw family (1)
Cucurbitaceae The cucumber family (5)
Begoniaceae The begonia family (3)
Salicales
Salicaceae The willow family (7)
Capparales (Cruciales)
Capparaceae The capper family (1)
Brassicaceae The mustard family (14)
Resedaceae The mignonette family (1)
Ericales
Ericaceae The heath family (3)
Primulales
Primulaceae The primrose family (2)
ROSIDAE
Rosales
Grossulariaceae The currant family (3)
Crassulaceae The stonecrop family (3)
Hydrangeaceae The hydrangea family (3)
Saxifragaceae The saxifrage family (3)
Rosaceae The rose family (9)
Fabales
Mimosaceae (1)
Caesalpiniaceae (5)
Fabaceae (Leguminosae) The pea family (21)
Myrtales
Lythraceae The loosestrife family (1)
Myrtaceae The myrtle family (1)
Onagraceae The evening-primrose family (4)
Melastomataceae The melastome family (1)
Cornales
Cornaceae The dogwood family (2)
Santalales
Loranthaceae The showy mistletoe family (1)
Viscaceae The christmas mistletoe family (1)
Celastrales
Celastraceae The bittersweet family (2)
Aquifoliaceae The holly family (1)
Euphorbiales
Buxaceae The box family (2)
Simmondsiaceae The jojoba family (1)

Table 2—*continued.*

Euphorbiaceae The spurge family (5)
Rhamnales
Vitaceae (Ampelidaceae) The grape family (1)
Linales
Erythroxylaceae The coca family (1)
Linaceae The flax family (1)
Polygalales
Polygalaceae The milkwort family (1)
Sapindales
Hippocastanaceae The horse-chestnut family (1)
Aceraceae The maple family (3)
Anacardiaceae The sumac family (2)
Rutaceae The orange family (3)
Geraniales
Oxalidaceae The wood-sorrel family (2)
Geraniaceae The geranium family (5)
Tropaeolaceae The nasturtium family (1)
Balsaminaceae The touch-me-not family (1)
Apiales (Umbellales)
Araliaceae The ginseng family (2)
Apiaceae (Umbelliferae) The carrot family (10)

ASTERIDAE
Gentianales (Loganiales, Apocynales)
Gentianaceae The gentian family (1)
Apocynaceae The dogbane family (2)
Asclepiadaceae The milkweed family (3)
Solanales
Nolanaceae (2)
Solanaceae The potato family (10)
Convolvulaceae The morning-glory family (4)
Menyanthaceae The dog-bean family (1)
Lamiales
Boraginaceae The borage family (10)
Verbenaceae The verbena family (5)
Lamiaceae (Labiatae) The mint family (7)
Callitricales
Callitrichaceae The water-starwort family (1)
Plantaginales
Plantaginaceae The plantain family (8)
Scrophulariales (Personales)
Oleaceae The olive family (4)
Scrophulariaceae The figwort family (3)
Gesneriaceae The gesneriad family (3)
Acanthaceae The acanthus family (1)
Bignoniaceae The trumpet-creeper family (1)
Lentibulariaceae The bladderwort family (1)
Campanulales (Campanales)
Campanulaceae The bellflower family (5)
Rubiales
Rubiaceae The madder family (6)
Dipsacales
Caprifoliaceae The honeysuckle family (5)
Valerianaceae The valerian family (2)
Dipsacaceae The teasel family (3)
Asterales
Asteraceae (Compositae) The aster family (9)

MONOCOTYLEDONS

ALISMATIDAE
Alismatales
Butomaceae The flowering rush family (1)
Alismataceae The arrowhead family (2)
Hydrocharitales
Hydrocharitaceae The tape-grass family (6)
Najadales
Potamogetonaceae The pondweed family (2)
Posidoniaceae The estuary-grass family (1)
Cymodoceaceae The manatee-grass family (2)
Zosteraceae The eel-grass family (5)
ARECIDAE
Arales
Araceae The calla lily family (1)
Lemnaceae The duckweed family (2)
COMMELINIDAE
Commelinidales
Commelinaceae The spidewort family (1)
Juncales
Juncaceae The rush family (1)
Cyperales (poales)
Cyperaceae The sedge family (4)
Poaceae (Gramineae) The grass family (7)
Typhales
Typhaceae The cat-tail family (1)
ZINGIBERIDAE
Bromeliales
Bromeliaceae The ananas family (4)
Zingiberales
Strelitziaceae (1)
Musaceae The banana family (1)
Zingiberaceae The ginger family (1)
Maranthaceae The arrowroot family (1)
LILIIDAE
Liliales
Pontederiaceae The pickerel-weed family (1)
Liliaceae The lily family (9)
Iridaceae The iris family (3)
Aloaceae The aloe family (1)
Agavaceae The century-plant family (2)
Dioscoreaceae The yam family (2)
Orchidales
Orchidaceae The orchid family (5)

on the 16:3/18:3 phenotype has not been really stringent during evolution.

It appears from the data in Table 2, that species belonging to the most primitive taxonomic groups, namely Bryophytes, Pteridophytes and Gymnosperms, are 16:3 plants. Among the Angiosperms, both 16:3 and 18:3 plants are found in the dicotyledon flora, while all monocotyledons (with the exception of marine flowering plants which are the most archaic monocotyledonous plants; see above) are 18:3 plants. However, in the case of dicotyledonous plants, the loss of the primitive 16:3 character probably occurred independently and at different rates during evolution. For example, 16:3 plants were found in families which recently appeared as Apiales (evolutive dialypetal) or Dipsacales (evolutive tetracyclic gamopetal). In addition, 16:3 plant families are distributed uniformly in each of the different dicotyledon orders and the percentage of 16:3 species in these orders is not correlated with the 'degree of evolution': 41%, 0%, 23%, 18%, 13%, 35% of the species of Magnoliidae (phylogenetically basal in the dicotyledon line), Hama-

melidae, Caryophyllidae, Dilleniidae, Rosidae and Asteridae (the most evolved order) are 16:3 plants, respectively. When using other classifications (for example [89, 95, 96, 99] the same observations were obtained (data not shown): 16:3 families seem to be uniformly distributed in the dicotyledon line. Surprisingly, among apetal flowering plants (Hamamelidae and some of the Caryophyllidae, an archaic line), no 16:3 plants have been found.

Assuming that the ancestral families are composed of 16:3 plants, the question of the origin of the Geraniaceae, Brassicaceae and Solanaceae (16:3 plant families) remains unanswered. An interesting phylogenic relationship between the Rubiales and Dipsacales has been proposed by Cronquist [86]. Since the Dipsacales are 16:3 plants, it is not surprising that the Rubiales contain 16:3 fatty acids. Similarly, Melchior [97] proposed a relationship between the Apiales/Dipsacales that we found to be two 16:3 orders. Nevertheless, this raises the problem of the origin of Apiales, since no 16:3 plants have been found in the Sapindales (Rutales), which were proposed as the phylogenetic ancestor of the Apiales [98]. Additional analyses of intermediate families and of subgroups from families already studied in this paper will, perhaps, throw light on the questions raised by systematic studies.

EXPERIMENTAL

Fatty acid analysis

Photosynthetic tissues were sampled during spring and summer from adult plants near Bordeaux (France), growing in a tropical greenhouse or in the botanical garden. Samples were heated at 80° in 1 ml of MeOH, 2.5% H_2SO_4 (v/v), as described in ref [11]. After addition of 1.5 ml of H_2O and 500 μl of hexane, fatty acid Me esters were extracted into the organic phase by shaking and a two-phase system was established by centrifugation (1500 *g*, 10 min). An aliquot of the hexane phase (1 μl) was analysed by GC on a 15 m × 0.53 mm Carbowax column (Altech). The column was programmed for an initial temp. of 160° for 1 min, followed by a 20° min^{-1} ramp to 190° and a secondary ramp of 5° min^{-1} to 210°. This final temp. was maintained for a further 3 min. Fatty acid peaks were quantified and identified by comparison of their R_ts with those of standards (Sigma). Several analyses of the same sample led to the similar results. Data are expressed in mol %.

Calculation of proportion of 16:3 *plant species*

For each family, 16:3 or 18:3 criteria were assessed from results reported in Table 1 and, then, the total number of existing species documented in 'Flowering Plants of the World' [99] was used to calculate the percentage of 16:3 plant species.

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