Fatty Acid Profiles from Forty-nine Plant Species That Are Potential New Sources of γ-Linolenic Acid

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ABSTRACT: Forty-nine plant species from Spain, belonging to the Boraginaceae, Scrophulariaceae, Onagraceae, and Ranunculaceae families, were surveyed in a search of new sources of γ-linolenic acid (18:3ω6, GLA). Fatty acid profiles from seeds, stems, roots, flowers and leaves were determined. GLA was detected mainly in seed and root tissues. High GLA amounts were found in seeds of Boraginaceae species, with a maximum of 20.25% of total fatty acids in *Myosotis nemorosa*. Within the Scrophulariaceae the highest GLA content (10.17%) was found in *Scrophularia sciophila*. Variable amounts of stearidonic acid, (18:4ω3, SDA) were present in Boraginaceae species, ranging from 0.08% of total seed fatty acids in *Anchusa azurea* to 21.06% in *Echium asperrimum*. SDA was also very abundant in all organs of *Asperugo procumbens*. A multivariate analysis was performed using our results and those reported for other plant species belonging to the same families in order to investigate a possible correlation between the fatty acid profile and the genera within these families.

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KEY WORDS: Boraginaceae, fatty acids, γ-linolenic acid, multivariate data analysis, Onagraceae, Ranunculaceae, Scrophulariaceae, seed oil, stearidonic acid.

New sources of γ-linolenic acid (18:3ω6, GLA) are being sought because of claims that GLA prevents or alleviates a wide variety of human diseases, and because it is important as a dietary and cosmetic component (1–5). GLA is synthesized from linoleic acid (18:2ω6, LA) and is the first intermediate in the conversion of LA to arachidonic acid (20:4ω6, AA) (1). The main commercial sources of GLA are seed oils from three plants: *Oenothera biennis* (evening primrose) (6,7), *Borago officinalis* (borage) (8,9) and *Ribes nigrum* (black currant) (10,11). GLA is also present in a wide variety of other plants, fungi, and microorganisms (1,2). Variable amounts of GLA have been found in some species belonging to the Onagraceae, Saxifragaceae, and Scrophulariaceae families, but the most important source is the Boraginaceae (1). In spite of a vast search, only a small number of plants have been shown to have GLA percentages in their oil comparable to those found in the traditional sources, *B. officinalis* (20–25%) and *Oenothera* spp. (9–12%). Wolf *et al*. (12) screened 45 species from the Boraginaceae, Onagraceae, Scrophulariaceae, and Saxifragaceae but found only two species with a maximal GLA content of 15%. In a study of nine species of Mongolian Boraginaceae, Tsevgsüren and Aitzetmüller (13) obtained GLA percentages ranging from 6.6 to 13%. Hansen *et al*. (14) reported 26% GLA in mature seeds of *Symphytum officinale*. High GLA levels (16%) were also found by Johansson *et al*. (15) in *R. spicatum*. Athough the occurrence of GLA within the Compositae has not been reported, a relatively high amount (10%) was found in the seed oil of *Saussurea* spp. (16). Recently, several *Echium* species from Macaronesia (a group of islands located in the mid-northeast Atlantic Ocean: Canary, Madeira, Azores, and Cabo Verde) have been described as the best sources of GLA so far found in nature (17).

Although the oil content is usually higher in the seeds, other tissues have been investigated as potential sources of GLA. GLA has been reported to be present in considerable amounts in several organs of *B. officinalis*, mainly in the leaf (2.5%) and the petiole (16%) (18).

Another fatty acid of commercial interest is stearidonic acid (18:4ω3, SDA), which is used in creams that are applied topically to reduce inflammation induced by irradiation (19). SDA has been detected together with GLA in seed oils of Boraginaceae, Primulaceae, and plants from the genus *Ribes* (Saxifragaceae) (1). Furthermore, fish oil and microalgae are good sources of SDA (20).

In this work we report the fatty acid profiles for the main organs of several plant species of the Boraginaceae, Onagraceae, Ranunculaceae, and Scrophulariaceae, looking for new sources of GLA. Using our results and other data obtained from the literature, we have applied a multivariate data analysis to investigate a possible correlation between fatty acid composition of seed oils and taxonomic relationships.

MATERIAL AND METHODS

Materials. Plants were collected at maturity from their natural habitats. Samples of *Echium asperrimum, Cymbalaria muralis, Myosotis nemorosa,* and *Myosotis secunda* were collected at Orense (Spain) in September of 1998. *Scrophularia nodosa*, *Chaenorrhinum pulverulentum*, *Linaria aeruginea,* and *Echium boissieri* were collected at Cazorla (Spain) in August 1998. *Parentucela viscosa* was collected in June 1999 from Madrid (Spain). *Myosotis alpina* was gathered at Sierra Nevada (Granada, Spain) in June 1999. *Antirrhinum majus* was obtained from gardens in Almería (Spain) in June 1999.

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The other plants were collected between March and June of 1998 from Almería (Spain). Samples were separated into organs and lyophilized, then were ground into powder using a mortar. The analyzed flowers were newly formed and included all of their organs. The dried samples were packed into new plastic bags and stored at 4°C for a maximum of 2–3 d until they were analyzed.

Oil extraction and transesterification. Rapid simultaneous oil extraction and transesterification were made according to the method of Rodríguez-Ruíz *et al.* (21). About 10 mg of seed or 40 mg for other plant organs were placed in test tubes containing 1 mL of the methylation mixture (methanol/acetyl chloride, 20:1 vol/vol) and 0.5 mL hexane, and heated at 100°C for 10 min. After cooling to room temperature, 1 mL of distilled water was added, and the upper hexane layer was taken for gas chromatography (GC) analysis. Duplicates were used for each sample, and mean values are reported in the tables (variation among the duplicate samples was routinely less than 5%).

Gas–liquid chromatography. Mixed fatty acid methyl esters (FAME) were analyzed in a Hewlett-Packard HP5890 series II gas chromatograph provided with flame-ionization detection and a HP3394 integrator (Palo Alto, CA). A capillary column of fused silica of high polarity (Supelco SP2330, Bellefonte, PA; length, 30 m; internal diameter, 0.25 mm; thickness of the film, 0.2 μm) was used. The flow rate of the carrier gas (N_2) was 0.75 L/min. Split ratio in the injector was 100:1. Injector temperature was 240°C, and the detector temperature was adjusted to 260°C. The oven starting temperature was 205°C, and it was increased at a rate of 6°C/min until 240°C. Injection volume was 5 μL, and a blank was run every 10 analyses. Peaks were identified by comparison with known methyl ester standards ("Rapeseed oil mix" and "PUFAS-1," from Sigma, St. Louis, MO). Oil contents in samples were determined using methyl heptadecanoate (17:0) as internal standard. Unidentified peaks were taken into account for further calculations.

The identity of the fatty acid peaks obtained by GC was confirmed using a gas chromatograph coupled to a mass spectrometer (MS). The GC–MS system was formed by a Hewlett-Packard HP5890A gas chromatograph connected to a Hewlett-Packard 5988A MS. The sample was compared to the patterns obtained using pure fatty acid standards analyzed in the same apparatus. A capillary column of methyl silicone (HP-1; length, 25 m; internal diameter, 0.2 mm; thickness of the film, 0.33 μm) was used. The flow rate of the carrier gas (He) was 1 mL/min. The injector temperature was 260°C, and the pressure at the head of the column was 15 psi. The oven starting temperature was 100°C and was increased at a rate of 10°C until 280°C, and then kept at 280°C for 10 min. The temperature at the interface was 280°C, and the temperature of the source in the detector was 180°C.

Statistical analyses. Statistical analyses were performed using the software package Statgraphics for Windows v. 3.0 (Manugistics, Inc., Rockville, MD). The statistics used for single variable analyses were the mean, range, and standard deviation (SD), and for multiple variable analyses were correlation, variance, and principal components analyses (PCA). The significance level was $P < 0.01$.

RESULTS AND DISCUSSION

Oil contents and fatty acids composition of seeds in the species considered in our work are listed in Table 1. In addition to seed, other organs—leaf, flower, root and stem—were analyzed, and the main fatty acids are reported for each family in Table 2.

The saponifiable oil (s.o.) content, determined as FAME, in the seeds ranged from values as low as 6.63% in *Echium humile* (Boraginaceae) to as high as 37.65% in *Odontites longiflora* (Scrophulariaceae). The mean value for all families was 22.42 ± 8.16% s.o. The Boraginaceae (20 species analyzed) had a mean value of 18.10 ± 6.10% s.o., reaching a maximum of 30.97% s.o. in *B. officinalis*. In the Ranunculaceae (three species) s.o. content was very similar, with a mean value of 17.60 ± 2.05%. For the Onagraceae only two species were analyzed belonging to genus *Epilobium*. Both showed a great similarity in s.o. (mean 29.32 ± 2.80%) and fatty acid composition (Table 1). Within the Scrophulariaceae (24 species) s.o. ranged from 13.23% in *Linaria aeruginea* to 42.8% in *Antirrhinum barrelieri*, with a mean of 26.05 ± 8.38%. After an analysis of variance (*F*-ratio = 5.483; $P < 0.01$), it was concluded that the s.o. was higher in the Onagraceae and Scrophulariaceae than in the Ranunculaceae and Boraginaceae.

Seed fatty acid profiles obtained in the plant families reported here are in agreement with previous reports (11–15) that showed the presence of high amounts of LA (18:2ω6) in the Onagraceae (73.7 ± 5.04% for 22 species), Scrophulariaceae (63.6 ± 6.77% for 6 species) and Boraginaceae (22.8 ± 8.80% for 24 species). In this work we found 74.1 ± 3.68% LA in Onagraceae (two species), 56.5 ± 19.5% in Scrophulariaceae (24 species), and 20.6 ± 8.89% in Boraginaceae (20 species).

LA and α-linolenic acid (18:3ω3, ALA) were found in similar amounts in Ranunculaceae species. Boraginaceae exhibited high percentages of ALA, LA, and oleic acid (18:1ω9, OA).

GLA occurs in three of the four families surveyed, with the exception of only the Ranunculaceae (Table 1). GLA content (4.00 ± 5.37% for all families) ranged in the four families from undetectable levels in several species to 20.25% in *Myosotis nemorosa*. GLA was present in all Boraginaceae species, sometimes at a very high percentage, with an average content of 8.29 ± 5.33%. Within the Boraginaceae the lowest value was found in *Cynoglossum creticum* (0.66%), while *M. nemorosa* represented the top of the range (20.25%). GLA content in *Epilobium* species (Onagraceae) was very small. Among Scrophulariaceae species, percentages ranged from 0.00% in several species to 10.17% for *Scrophularia sciophila*, with an average value of 0.74 ± 2.13%. Thus, GLA mainly occurs in Boraginaceae species, in agreement with previous reports (22).

GLA content (19.2%), as determined in this study in seed oil of wild *B. officinalis,* was lower than the reported value

TABLE 1
Composition of Seed Oils[a] from Four Plant Families

Species	Oil%[b]	14:0	16:0	16:1ω7	18:0	18:1ω9	18:1ω7	18:2ω6	18:3ω6	18:3ω3	18:4ω3	20:0	20:1ω9	20:2ω6	22:0	22:1ω9	24:0	24:1ω9
Boraginaceae																		
Anchusa azurea	22.52	0.09	8.63	0.35	2.19	24.1	0.43	41.78	11.11	0.43	0.08	0.23	3.57	0.18	0.37	0	0	0
Anchusa undulata	29.36	0.16	8.76	0.54	2.15	24.4	0	25.37	8.35	17.99	3.55	0.24	4.21	0.15	0.32	0	0	0
Asperugo procumbens	19.16	0.12	8.07	0.16	1.85	15.48	0.62	15.2	5.35	36.46	11.75	0.19	2.03	0.12	0.24	0	0	0
Borago officinalis	30.97	0.10	9.57	0.18	6.18	20.92	0.46	33.21	19.2	1.00	0.49	0.43	3.95	0.15	0.27	0.05	00	
Buglosoides arvensis	10.72	0.23	9.41	0.15	2.81	6.83	0.61	14.8	6.44	39.68	14.08	1.63	0.98	0	0.28	0	0	0
Cynoglossum cheirifolium	9.19	1.56	17.34	0	3.41	7.93	0	13.81	1.52	39.35	3.24	2.03	0.54	0.02	1.27	0.08	0.05	0
Cynoglossum creticum	12.21	1.55	16.25	0.35	2.92	8.57	0.35	18.27	0.66	44.75	1.16	1.88	0.42	0	1.93	0	0	0
Cynoglossum nebrodense	19.04	0.19	6.01	0.11	1.61	46.42	0	6.79	1.42	16.53	2.83	0.68	5.31	0	0.68	0	0	0
Cynoglossum officinale	17.4	0.21	7.01	0.15	1.4	42.6	0	9.02	1.68	16.14	2.48	0.68	5.14	0	0.73	0	0	0
Echium asperrimum	18.75	0.08	7.7	0.13	2.77	14.68	0	16.33	9.62	35.3	21.06	0.09	0.98	0.05	0.08	0.34	0	0.07
Echium boissieri	19.77	0	5.48	0.09	2.28	14.7	0	8.64	5.52	47.14	14.31	0.1	0.74	0.04	0.06	0	0	0
Echium creticum	14.55	0.05	5.58	0.06	2.98	8.18	0.35	14.31	9.70	42.68	14.73	0.11	0.58	0.06	0.06	0	0	0
Echium flavum	20.6	0	6.29	0.07	2.12	21.05	0.52	24.16	8.38	32.23	3.14	0.09	1.01	0.06	0.07	0	0	0
Echium humile	6.63	6.69	7.28	0.43	3.95	17.18	0.45	24.43	7.95	31.21	5.88	0.44	0.52	0.22	0	0	0	0
Echium sabulicola	20.43	0.06	5.51	0.08	2.42	8.03	0.36	16.31	10.94	40.39	14.72	0.08	0.65	0.10	0.06	0	0	0
Echium vulgare	15.26	0.14	7.38	0.06	2.52	11.14	0.44	21.18	11.74	34.14	9.68	0.1	0.74	0.07	0.08	0	0	0.04
Myosotis alpina	12.98	0.04	8.12	0.02	2.3	24.92	0.45	27.02	4.38	18.03	8.38	0.45	3.65	0.14	0.33	1.03	0	0.05
Myosotis nemorosa	19.90	0.16	13.15	0.35	3.89	20.79	0	30.76	20.25	4.69	1.56	0.27	2.57	0.10	0.16	1.23	0	0.02
Myosotis secunda	23.22	0.08	8.22	0.16	4.08	25.22	0	23.07	12.17	15.62	4.29	0.36	3.44	0.13	0.29	2.89	0	0
Nonea vesicaria	19.34	0.21	9.49	0.17	2.57	26.23	0.4	26.52	9.39	13.88	4.90	0.29	3.40	0.13	0.23	0.05	0	0
Ranunculaceae																		
Delphinium gracile	19.48	0.40	22.43	0.14	2.25	11.18	0.91	38.44	0	19.87	0	0.67	0.01	0	0.01	0	0	0
Ranunculus repens	17.92	0.37	10.46	0.20	2.07	7.36	0.73	36.55	0	39.71	0	0.27	0.13	0	0.31	0	0	0
Ranunculus peltatus	15.41	0.37	13.35	1.69	1.50	8.49	0.94	28.44	0	37.89	0	0.41	0.01	0	0.38	0	0	0
Onagraceae																		
Epilobium hirsutum	31.30	0.04	10.93	0.12	3.84	9.25	0.49	71.55	0.02	1.84	0	0.66	0.10	0.08	0.17	0	0	0
Epilobium lanceolatum	27.34	0.05	10.56	0.14	2.60	6.47	0.21	76.75	0.08	1.71	0	0.56	0.13	0.11	0.18	0	0	0
Scrophulariaceae																		
Antirrhinum barrelieri	42.80	0.04	5.13	0.17	2.58	18.04	0.81	71.77	0	0.34	0	0.13	0.11	0.04	0.02	0	0	0
Antirrhinum charidemi	27.02	0.04	6.40	0.21	1.54	15.67	0.87	73.20	0	0.53	0	0.12	0.12	0	0.08	0	0	0
Antirrhinum hispanicum	35.2	0.04	5.48	0.15	1.8	16.15	1.79	72.73	0.07	0.42	0	0.15	0.13	0.06	0.14	0	0	0
Antirrhinum majus	29.24	2.15	16.14	0.78	7.61	3.90	1.04	31.41	0	25.89	0	3.09	2.63	0.3	1.48	0	0	0
Antirrhinum molle	34.62	0.12	6.23	0.29	1.89	16.76	1.94	70.43	0.06	0.59	0	0.21	0.13	0.11	0.18	0.02	0	0
Bellardia trixago	33.61	0.05	8.71	0.17	1.76	18.37	1.06	43.56	0	24.8	0	0.36	0.16	0	0.16	0	0	0
Chaenorhinum macropodum	13.86	0.15	7.55	0	1.83	10.84	0.98	75.73	0	2.22	0	0.01	0.01	0	0.01	0	0	0
Chaenorhinum origanifolium	30.65	0.10	6.00	0.22	2.07	12.75	1.12	73.34	0	3.42	0	0.17	0.09	0.11	0.10	0	0.02	0
Chanaenorhinum villosum	35.33	0.23	5.71	0	3.87	2.03	0	73.14	0.53	2.02	0	0.21	0.12	0	0.23	0.19	0.18	0.2
Cymbalaria muralis	20.69	0.14	5.12	0	2.56	22.66	0	63.08	1.33	3.05	0	0.14	0.38	0.42	0.09	0.15	0.02	0
Digitalis obscura	19.07	0.15	8.04	0.15	2.69	18.97	2.11	60.57	0.06	4.44	0	0.42	0.07	0.04	0.21	0	0	0
Lafuentea rotundifolia	18.63	1.16	14.85	0.46	2.94	7.32	0.39	24.04	0	19.89	0	1.51	0.01	0	0.64	0-07	0.03	0
Linaria aeruginea	13.23	0.12	26.4	0	9.35	6.66	0	26.38	0	11.23	0	0.69	0.32	0	0.12	0.21	0.11	0.29
Linaria amoi	18.79	0.08	6.29	0.12	1.96	19.49	0.12	67.43	0.46	2.04	0	0.18	0.14	0	0.01	0	0	0

(*Continued*)

TABLE 1 (*Continued*)

Species	Oil%[b]	14:0	16:0	16:1ω7	18:0	18:1ω9	18:1ω7	18:2ω6	18:3ω6	18:3ω3	18:4ω3	20:0	20:1ω9	20:2ω6	22:0	22:1ω9	24:0	24:1ω9
Misopates orontium	36.71	0.04	6.90	0.11	2.34	16.38	0.54	71.45	0	0.38	0	0.37	0.12	0	0.19	0.02	0	0
Odontites longiflora	37.65	0.09	8.12	0.84	2.07	32.38	2.97	11.86	0	40.49	0	0.16	0.09	0	0.05	0.04	0	0
Parentucela viscosa	26.23	0.21	8.93	0.33	2.63	21.65	0.12	37.28	0.21	28.56	0	0.28	0.16	0.12	0.15	0.18	0	0.12
Scrophularia auriculata	27.92	0.06	12.01	0.15	2.48	14.89	2.63	63.45	2.66	0.36	0	0.39	0.13	0.03	0.13	0	0	0
Scrophularia nodosa	16.55	0.12	26.4	0	3.6	13.92	0	60.33	2.26	4.39	0	0.12	0.89	0	0.11	0	0.12	0.23
Scrophularia sciophila	22.33	0.06	11.05	0.10	2.12	10.82	0.71	63.57	10.17	0.38	0	0.34	0.10	0.05	0.17	0	0	0
Verbascum phlomoides	22.93	0.19	6.39	0.17	3.11	17.03	0.59	69.58	0	1.26	0	0.53	0.09	0.05	0.01	0	0	0
Verbascum thapsus	23.58	0.04	6.4	0.17	2.61	16.75	0.59	70.84	0	1.03	0	0.47	0.15	0.05	0.01	0.08	0	0
Veronica anagalloides	23.90	0.35	10.81	0.25	2.21	19.12	0.42	52.12	0	12.24	0	0.36	0.16	0	0.43	0	0	0
Veronica persica	14.75	1.24	15.82	0.68	2.43	28.87	0.54	28.39	0	19.24	0	0.59	0.41	0	0.4	0	0	0[a]

[a]Percentages on figures on a dry wt basis. Other fatty acids of undetermined structure bring the total to 100%.
[b]g/100 g of seeds.

for cultivated varieties, which can reach 25% (1). The wild and cultivated varieties might be different genetically, but most likely these differences are due to the environments in which they were grown. It has been suggested that the blue-flowered northern European genotypes have higher GLA levels than white-flowered cultivated genotypes from Spain (1).

In *B. officinalis*, the GLA percentage in the s.o. represents 5.95% of the GLA on a seed weight basis. A similarly high value (4.03%) is also found in seeds of *M. nemorosa*. Nevertheless, the use of *M. nemorosa* could be an interesting alternative to *Borago* cultivation due to its larger seed size, a feature that can improve the ease of harvesting. Another interesting plant is *Anchusa azurea* (Boraginaceae) with 11.11% GLA in the seed oil. Although the GLA content is only moderately high, its fatty acid profile is particularly suitable for GLA purification by the urea method (23) due to the very low levels of ALA and SDA. These polyunsaturated fatty acids co-purify with GLA thus hindering the fractionation process. Among the Scrophulariaceae species, *Scrophularia sciophila* also shows a suitable profile. Besides lacking ALA and SDA, monounsaturated C_{20} fatty acids are present in trace amounts in seeds of this plant, another feature that may facilitate the purification process.

Another fatty acid of commercial interest is SDA. We found SDA only in seed of the Boraginaceae species, which is in agreement with previous reports (12–14,16,17). SDA is also found in Grossulariaceae species (15), a family we did not consider in this work. SDA content ranged from 0.08% in seeds of *Anchusa azurea* to a 21.06% for *Echium asperrimum*, with an average of 7.12 ± 6.06% in the oil of Boraginaceae species. The high SDA amount exhibited by *E. asperrimum* is comparable to the value (21.4%) reported for *Hackelia deflexa* (13), which is the richest source found in nature to date. The contents of other polyunsaturated fatty acids found in seeds were in agreement with previous reports (12,13,17).

Although it is generally accepted that seed represents the best source of GLA, high amounts of this acid have been reported in other plant organs (18). Table 2 summarizes the GLA contents in the main organs of the plant, except for the seed. The s.o. was particularly abundant in roots (6.72% for *Veronica anagalloides*) and leaves (6.31% as a maximum for *Asperugo procumbens*). Similar amounts of palmitic acid (16:0, PA) and OA were found in all organs analyzed in plants from the four families. The maximum OA content (23.7% s.o.) was present in flowers of *Echium boissieri*. LA percentage was particularly high in roots from all plant families, reaching a maximum in *Antirrhinum charidemi* (43.4% s.o.). GLA was present in all organs, but mainly from Boraginaceae species. GLA content in the leaf showed a maximum of 6.89% s.o. for *M. nemorosa,* which represents 0.03% of GLA on a dry weight basis. The root of *Echium creticum* showed a 12.6% GLA s.o. (0.08% of dry wt). Stems of *E. creticum* also showed high GLA percentages (8.83% GLA s.o.; 0.1% of dry wt). Flowers of *B. officinalis* contain 8.13% GLA s.o. (0.25% of dry wt). Another value in this range was 7.90% GLA s.o.

TABLE 2
Average ± SD and Range for the Main Fatty Acids[a] from Organs of the Species from Four Plant Families

Organs/families	Oil %[b]	16:0	18:1ω9	18:2ω6
Leaf				
Boraginaceae	2.78 ± 0.84 (1.33–4.45) (*A. undulata–A. procumbens*)	12.7 ± 6.04 (9.51–21.4) (*A. procumbens–A. undalata*)	2.99 ± 1.84 (1.15–10.1) (*N. vesicaria–E. boissieri*)	7.38 ± 2.94 (5.28–15.7) (*E. vulgare–C. cheirifolium*)
Scrophulariaceae	3.13 ± 1.24 (0.71–6.31) (*V. thapsus–A. barrelieri*)	10.8 ± 4.24 (7.52–15.5) (*A. barrelieri–A. majus*)	3.30 ± 3.00 (0.92–12.6) (*V. anagalloides–V. phlomoides*)	9.05 ± 4.03 (2.79–18.9) (*A. barrelieri–D. obscura*)
Ranunculaceae	3.27 ± 1.37 (2.25–4.83) (*R. peltatus–D. gracile*)	33.5 ± 34.4 (12.9–73.1) (*R. repens–D. gracile*)	1.43 ± 0.36 (1.31–1.83) (*D. gracile–R. repens*)	4.95 ± 1.74 (2.96–6.16) (*D. gracile–R. peltatus*)
Onagraceae	2.92 ± 0.51 (2.56–3.28) (*E. lanceolatum–E. hirsutum*)	15.3 ± 2.22 (13.7–16.8) (*E. hirsutum–E. lanceolatum*)	3.46 ± 2.44 (1.24–5.18) (*E. lanceolatum–E. hirsutum*)	12.3 ± 0.98 (11.6–13.0) (*E. lanceolatum–E. hirsutum*)
Root				
Boraginaceae	0.636 ± 0.308 (0.30–1.40) (*E. vulgare–B. officinalis*)	13.6 ± 8.86 (11.4–23.7) (*C. creticum–E. creticum*)	4.55 ± 3.21 (2.27–7.28) (*B. officinalis–E. boissieri*)	26.1 ± 6.91 (16.6–38.9) (*C. creticum–A. azurea*)
Scrophulariaceae	0.77 ± 0.35 (0.21–1.42) (*A. charidemi–V. anagalloides*)	10.7 ± 6.62 (6.46–18.9) (*D. obscura–B. trixago*)	4.46 ± 2.34 (1.43–10.5) (*A. hispanicum–B. trixago*)	23.7 ± 10.6 (7.70–43.4) (*D. obscura–A. charidemi*)
Ranunculaceae	2.69 ± 3.51 (0.33–6.72) (*D. gracile–R. peltatus*)	23.6 ± 7.98 (18.6–32.8) (*R. peltatus–D. gracile*)	11.1 ± 10.6 (1.96–22.7) (*R. repens–R. peltatus*)	20.4 ± 6.17 (15.7–27.4) (*R. peltatus–D. gracile*)
Onagraceae	0.77 ± 0.28 (0.57–0.97) (*E. lanceolatum–E. hirsutum*)	16.3 ± 6.95 (11.4–21.2) (*E. hirsutum–E. lanceolatum*)	4.99 ± 1.87 (3.67–6.32) (*E. lanceolatum–E. hirsutum*)	28.0 ± 1.84 (26.7–29.3) (*E. hirsutum–E. lanceolatum*)
Stem				
Boraginaceae	0.85 ± 0.33 (0.31–1.44) (*C. officinale–N. vesicaria*)	15.5 ± 7.20 (9.21–22.4) (*B. officinalis–E. creticum*)	5.96 ± 2.95 (0.77–9.84) (*B. officinalis–C. officinale*)	18.4 ± 4.94 (10.7–25.5) (*B. officinalis–E. creticum*)
Scrophulariaceae	0.97 ± 0.42 (0.44–1.67) (*A. majus–A. barrelieri*)	17.0 ± 3.29 (9.71–22.4) (*A. barrelieri–V. thapsus*)	4.75 ± 2.95 (1.99–10.0) (*V. anagalloides–B. trixago*)	21.9 ± 6.61 (11.6–36.3) (*B. trixago–A. majus*)
Ranunculaceae	0.88 ± 0.088 (0.80–0.97) (*R. peltatus–R. repens*)	28.4 ± 16.2 (16.0–46.7) (*R. repens–D. gracile*)	4.10 ± 1.86 (2.37–6.07) (*R. repens–R. peltatus*)	16.1 ± 1.94 (14.6–18.3) (*D. gracile–R. peltatus*)
Onagraceae	0.95 ± 0.028 (0.93–0.97) (*E. lanceolatum–E. hirsutum*)	18.6 ± 0.82 (18.0–19.2) (*E. hirsutum–E. lanceolatum*)	5.76 ± 0.32 (5.83–5.98) (*E. hirsutum–E. lanceolatum*)	17.2 ± 0.81 (16.6–17.8) (*E. lanceolatum–E. hirsutum*)
Flowers				
Boraginaceae	2.76 ± 1.05 (1.48–4.96) (*E. boissieri–A. azurea*)	12.7 ± 6.60 (10.7–18.7) (*C. cheirifolium–E. boissieri*)	3.47 ± 2.87 (1.73–7.28) (*A. procumbens–E. boissieri*)	16.7 ± 7.00 (9.11–20.5) (*C. cheirifolium–E. sabulicola*)
Scrophulariaceae	2.88 ± 0.49 (1.53–5.13) (*A. majus–S. sciophila*)	14.9 ± 2.46 (12.1–20.5) (*L. rotundifolia–S. auriculata*)	4.72 ± 5.19 (1.70–23.7) (*M. orontium–C. origanifolium*)	20.6 ± 7.01 (8.94–30.0) (*V. thapsus–A. molle*)
Ranunculaceae	3.75 ± 1.47 (2.11–4.93) (*D. gracile–R. peltatus*)	31.1 ± 10.9 (24.4–43.7) (*R. peltatus–D. gracile*)	2.27 ± 0.71 (1.76–3.08) (*D. gracile–R. repens*)	26.6 ± 3.56 (22.6–27.8) (*D. gracile–R. peltatus*)
Onagraceae	2.88 ± 0.48 (2.53–3.22) (*E. hirsutum–E. lanceolatum*)	16.7 ± 0.28 (16.5–16.9) (*E. lanceolatum–E. hirsutum*)	4.22 ± 0.71 (4.16–4.28) (*E. lanceolatum–E. hirsutum*)	19.1 ± 0.33 (18.8–19.3) (*E. lanceolatum–E. hirsutum*)

Organs/families	18:3ω6	18:3ω3	18:4ω3
Leaf			
Boraginaceae	1.45 ± 1.20 (0–6.89) (ssp.–*M. nemorosa*)	38.6 ± 0.54 (9.18–57.8) (*C. officinale–A. azurea*)	7.37 ± 5.88 (0–17.7) (*C. creticum–A. procumbens*)
Scrophulariaceae	0.30 ± 0.68 (0–2.62) (ssp.–*S. sciophila*)	38.1 ± 11.6 (11.6–61.6) (*A. barrelieri–V. anagalloides*)	1.36 ± 3.91 (0–15.5) (ssp.–*S. sciophila*)
Ranunculaceae	0.033 ± 0.058 (0–0.10) (ssp.–*D. gracile*)	32.2 ± 20.8 (21.7–53.7) (*D. gracile–R. repens*)	0–0
Onagraceae	0.81 ± 0.83 (0.22–1.40) (*E. lanceolatum–E. hirsutum*)	41.1 ± 0.95 (40.4–41.8) (*E. lanceolatum–E. hirsutum*)	0–0
Root			
Boraginaceae	7.16 ± 2.66 (2.90–12.6) (*C. creticum–E. creticum*)	12.0 ± 4.29 (5.19–19.7) (*B. officinalis–A. procumbens*)	2.76 ± 2.33 (1.58–8.80) (*C. creticum–A. procumbens*)
Scrophulariaceae	0.27 ± 0.68 (0–2.19) (ssp.–*S. sciophila*)	10.2 ± 5.69 (1.85–23.6) (*D. obscura–V. persica*)	0.29 ± 1.29 (0–4.96) (ssp.–*S. sciophila*)
Ranunculaceae	0–0	20.3 ± 17.9 (1.94–37.8) (*D. gracile–R. repens*)	0–0
Onagraceae	0–0	22.5 ± 11.2 (14.5–30.4) (*E. lanceolatum–E. hirsutum*)	0–0
Stem			
Boraginaceae	4.04 ± 2.36 (1.29–8.83) (*C. creticum–E. creticum*)	24.5 ± 9.70 (5.37–39.6) (*B. officinalis–A. azurea*)	4.12 ± 2.21 (1.38–8.64) (*C. creticum–A. procumbens*)
Scrophulariaceae	0.70 ± 2.00 (0–7.90) (ssp.–*S. sciophila*)	27.1 ± 7.42 (11.8–40.2) (*A. barrelieri–V. phlomoides*)	0.59 ± 1.62 (0–6.32) (ssp.–*S. sciophila*)
Ranunculaceae	0–0	31.7 ± 10.5 (20.9–41.9) (*D. gracile–R. repens*)	0–0
Onagraceae	0–0	32.0 ± 1.73 (30.8–33.2) (*E. hirsutum–E. lanceolatum*)	0–0
Flowers			
Boraginaceae	3.56 ± 2.39 (0.79–8.13) (*A. azurea–B. officinalis*)	30.0 ± 9.56 (12.6–45.4) (*B. officinalis–C. cheirifolium*)	5.46 ± 3.04 (0.86–10.0) (*C. creticum–A. procumbens*)
Scrophulariaceae	0.28 ± 0.54 (0–1.66) (ssp.–*S. sciophila*)	28.6 ± 12.4 (14.5–52.2) (*A. barrelieri–V. phlomoides*)	0–0
Ranunculaceae	0–0	18.3 ± 8.44 (10.9–27.5) (*D. gracile–R. repens*)	0–0
Onagraceae	0–0	25.5 ± 5.81 (21.4–29.6) (*E. lanceolatum–E. hirsutum*)	0–0

[a]Figures on a dry wt. basis. Other fatty acids of undetermined structure bring the total to 100%.
[b]g/100 g of seeds.

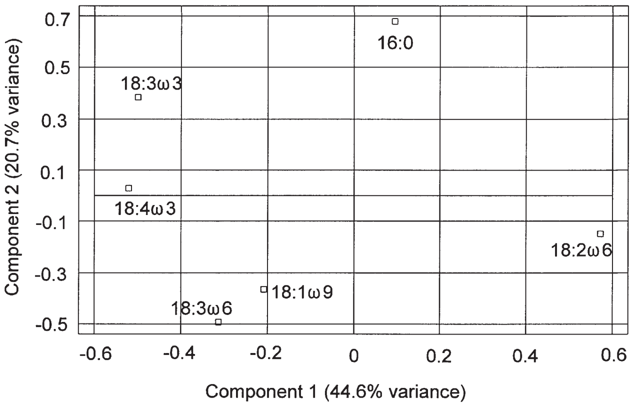

FIG. 1. Plot of the first two seed oil component weights.

in the stem of *Scrophularia sciophila* (0.12% of dry wt). Unfortunately, although GLA levels referred to s.o. were relatively high, the low s.o. contents make these organs an inappropriate GLA source. ALA content was high in all organs from most of the tested species, particularly in the leaves. Values ranged from 1.85% s.o. in the roots of *Digitalis obscura* to 61.6% s.o. in *V. anagalloides*.

SDA was found to be abundant in leaves, roots, stems and flowers of *Asperugo procumbens* (17.7, 8.80, 8.64, and 10.0% s.o., respectively). High leaf s.o. in this species (4.89% of dry wt) leads to a value 0.86% of SDA in this organ.

SDA was only found in Boraginaceae and Scrophulariaceae. Although it is not present in seeds of Scrophulariaceae species, it occurs in leaves, roots, and stems of several plants belonging to this family. This can be due to the fact that SDA is synthesized only from ALA and not from GLA. The presence of low levels of ALA in seeds of these plants would lead to a reduced synthesis of SDA. This is similar to the situation described in *B. officinalis* where the desaturase enzymatic systems responsible for the synthesis of GLA and SDA have been studied in some detail (24) .

To investigate a possible correlation between fatty acid profiles and phylogenetic relationships among these species/families, we performed correlation and multivariate analyses using seed fatty acid compositions obtained by us, and reported by others in the literature (12–16,19,27). A similar analysis was performed for *Echium* species from Macaronesia (17), and a good correlation was found between the taxonomic sections defined by morphological data and polyunsaturated fatty acid profiles. PCA was initially applied to the main seed fatty acids, PA, OA, LA, ALA, GLA and SDA, for all species computed. In these analyses, the first two principal components (PC) explained 44.6 and 20.7%, respectively, of the total variance. A plot of the first two component weights (Fig. 1) showed that the ω3 fatty acids (ALA and SDA) were positively correlated ($r = 0.676$, $P < 0.01$). In these analyses, all fatty acids had a major influence on the model. The resulting scatterplot (Fig. 2) provides a conceptual overview of the samples and explains 65.3% of the total variance, thus indicating that species can be grouped according to their fatty acid contents. The component plot and scatterplot can be interpreted together because objects with high scores for a specific PC also have high values for the variables with high loading plots and low values for those with low loadings (25,26). The scatterplot showed that similarities between species were coincident in most cases within families.

Influence on group formation can be assigned to a particular fatty acid, for instance LA has a great influence in the Onagraceae; PA on the Ranunculaceae; ALA, SDA, GLA, and OA on Boraginaceae; and GLA and OA on Saxifragaceae. For the Scrophulariaceae, results were the most diffuse, but PA, LA and OA seem to be the most descriptive in the distribution of these species. Although for several genera the plants appear grouped and well resolved in the scatterplot, as with *Anchusa* (B5), *Epilobium* (O1) or *Lappula* (B14), distribution in other genera remained somewhat diffuse.

The possibility of using the plot for taxonomical purposes remains an open question that should be addressed by botanists. In any case, a simultaneous inspection of the plot and scatterplot may be useful in order to give an approximate prediction of the fatty acid profile for an unknown species belonging to the taxonomic groups considered in this study.

The above correlation among fatty acids can be analyzed in the light of their metabolic relationships. There are two possible pathways for the biosynthesis of SDA using either ALA or GLA as the precursor. The positive correlation between ALA and SDA is therefore particularly interesting because it indicates that it is ALA, and not GLA, that is the main precursor of SDA *via* a reaction catalyzed by a Δ-6 desaturase. The fact that SDA is only present in those plants containing GLA suggests that the Δ-6 desaturase responsible for the synthesis of GLA from LA is the same as that which is responsible for ALA producing SDA.

The fatty acid profiles of the organs of plants having significant amounts of GLA or SDA in seeds are shown in Table 3. Note that although *B. officinalis* has high GLA content in seeds, the remaining organs have low amounts of GLA. The high SDA level in seeds of *Echium asperrimum* was not found in the other organs, and the high GLA seed percentage of *M. nemorosa* was not correlated with the rest of the plant tissues. In *Scrophularia sciophila*, only the root shows a GLA amount comparable to percentages found in the seeds.

GLA content in the species tested in this work indicates that GLA appears unexpectedly in moderate amounts in some plant genera. This is the case for *M. nemorosa*, which can be considered as a potential new source of GLA. This shows that the search for new sources of GLA in nature is an important task. In addition, data from our screening reinforces the notion that the Boraginaceae family should still be considered as the main target when looking for new species rich in GLA.

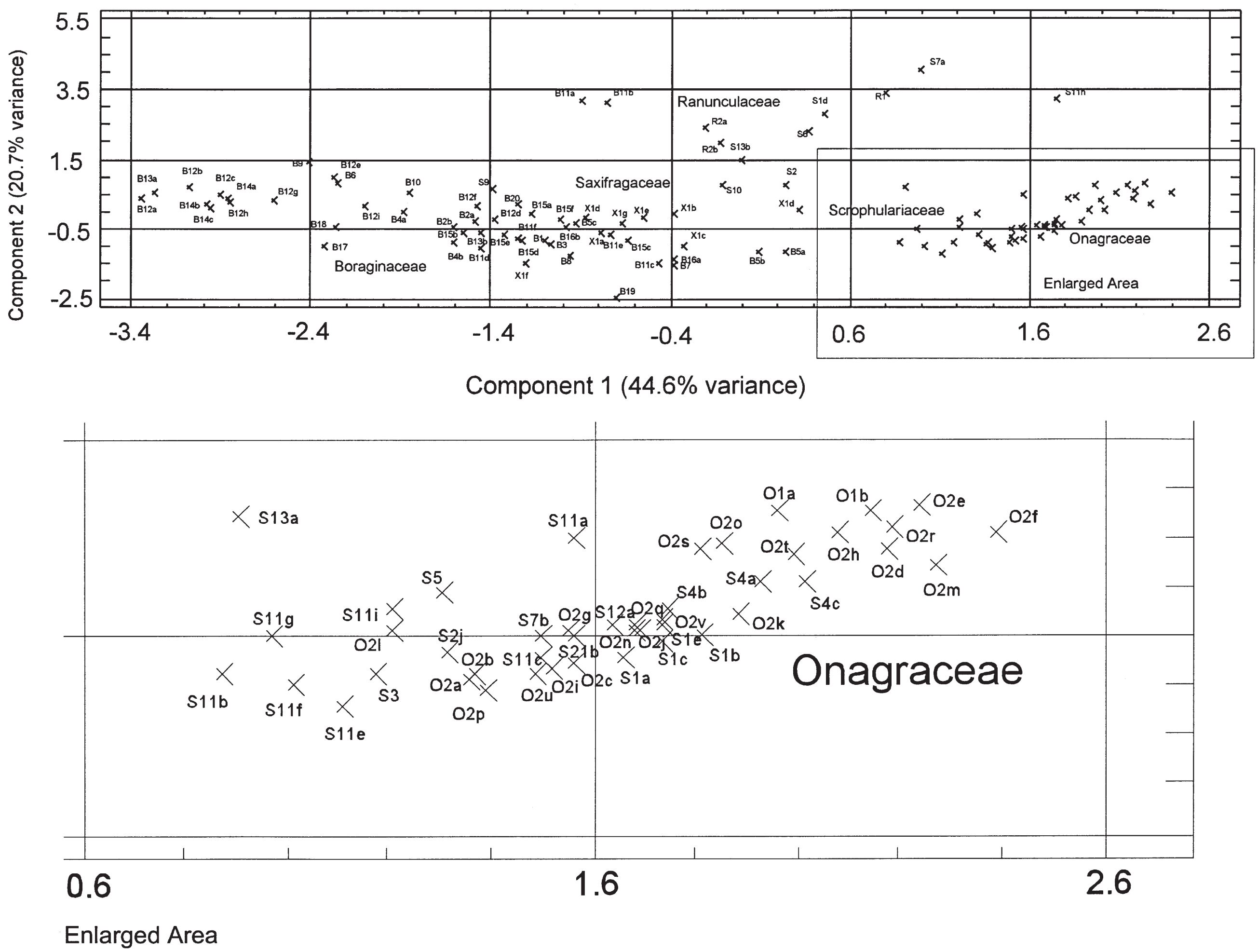

FIG. 2. Scatterplot for the first two seed oil component weights. B1 *Adelocaryum coelestinum*; B2a *Alkanna froedinii*; B2b *Alkanna orientalis*; B3 *Amblynotus rupestris*; B4a *Amsinckia intermedia*; B4b *Amsinckia lunaris*; B5a *Anchusa azurea*; B5b *Anchusa strigosa*; B5c *Anchusa undulata*; B6 *Asperugo procumbens*; B7 *Borago officinalis*; B8 *Brunnera orientalis*; B9 *Buglossoides arvensis*; B10 *Cryptantha grayi*; B11a *Cynoglossum cheirifolium*; B11b *Cynoglossum creticum*; B11c *Cynoglossum divaricatum*; B11d *Cynoglossum nebrodense*; B11e *Cynoglossum nervosum*; B11f *Cynoglossum officinale*; B12a *Echium asperrimum*; B12b *Echium boissieri*; B12c *Echium creticum*; B12d *Echium flavum*; B12e *Echium glomeratum*; B12f *Echium humile*; B12g *Echium plantagineum;* B12h *Echium sabulicola*; B12i *Echium vulgare*; B13a *Hackelia deflexa*; B13b *Hackelia floribunda*; B14a *Lappula myosotis*; B14b *Lappula intermedia*; B14c *Lappula granulata*; B15a *Myosotis alpina*; B15b *Myosotis caespitosa*; B15c *Myosotis nemorosa*; B15d *Myosotis secunda*; B15e *Myosotis suaveolens*; B15f *Myosotis sylvatica*; B16a *Nonea macrosperma*; B16b *Nonea vesicaria*; B17 *Onosmodium hispidissimum*; B18 *Pectocarya platycarpa*; B19 *Symphytum officinale*; B20 *Trichodesma zeylanicum*; R1a *Delphinium gracile*; R2a *Ranunculus peltatus*; R2b *Ranunculus repens*; O1a *Epilobium hirsutum*; O1b *Epilobium lanceolatum*; O2a *Oenothera agrillicola*; O2b *Oenothera biennis*; O2c *Oenothera bookeri*; O2d *Oenothera brevipes*; O2e *Oenothera cardiophylla*; O2f *Oenothera clavaeformis*; O2g *Oenothera depressa*; O2h *Oenothera drummondii*; O2i *Oenothera elata*; O2j *Oenothera grandiflora*; O2k *Oenothera laciniata*; O2l *Oenothera lamarckiana*; O2m *Oenothera leptocarpa*; O2n *Oenothera missouriensis*; O2o *Oenothera odorata*; O2p *Oenothera parviflora*; O2q *Oenothera rhombipetala*; O2r *Oenothera rosea*; O2s *Oenothera serrulata*; O2t *Oenothera stricta*; O2u *Oenothera strigosa*; O2v *Oenothera tetragona*; S1a *Antirrhinum barrelieri*; S1b *Antirrhinum charidemi*; S1c *Antirrhinum molle*; S1d *Antirrhinum majus*; S1f *Antirrhinum hispanicum*; S2 *Bellardia trixago*; S3 *Cymbalaria muralis*; S4a *Chaenorhinum macropodum*; S4b *Chaenorhinum origanifolium*; S4c *Chanaenorhinum villosum*; S5 *Digitalis obscura*; S6 *Lafuentea rotundifolia*; S7a *Linaria aeruginea*; S7b *Linaria amoi*; S8 *Misopates orontium*; S9 *Odontites longiflora*; S10 *Parentucela viscosa*; S11a *Scrophularia auriculata*; S11b *Scrophularia canina*; S11c *Scrophularia grayana*; S11d *Scrophularia koraiensis*; S11e *Scrophularia lanceolata*; S11f *Scrophularia marilandica*; S11g *Scrophularia michoniana*; S11h *Scrophularia nodosa*; S11i *Scrophularia sciophila*; S12a *Verbascum thapsus*; S12b *Verbascum phlomoides*; S13a *Veronica anagalloides*; S13b *Veronica persica*; X1a *Ribes alpinum*; X1b *Ribes inebrians*; X1b *Ribes montigenum*; X1c *Ribes nigrum*; X1d *Ribes orientale*; X1e *Ribes rubrum*; X1f *Ribes spicatum*; X1g *Ribes uva-crispa*.

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TABLE 3
Fatty Acid Profile for Organs of Significant Plants from This Study[a]

	Oil %[b]	14:0	16:0	16:1ω7	18:0	18:1ω9	18:1ω7	18:2ω6	18:3ω6	18:3ω3	18:4ω3	20:0	20:1ω9	20:2ω6	22:0	22:1ω9	24:0	24:1ω9
Borago officinalis																		
Leaf	3.31	0.61	12.34	0	3.09	1.92	0	7.58	4.73	35.22	17.38	1.36	0	0.31	1.13	0.23	0.23	0.12
Root	1.40	0.91	12.27	0.53	1.58	2.27	0.49	18.14	6.98	5.19	3.30	0	0	0	0.12	0.98	0.08	0.29
Stem	1.20	0	9.21	0	1.38	0.77	0	10.66	5.95	5.37	2.35	2.78	0	0	2.34	0.09	0.28	0.45
Flowers	3.07	0.38	13.59	0.25	3.78	2.84	0	18.75	8.13	12.64	7.13	1.71	0.50	0.50	1.13	1.54	0.09	0.34
Echium asperrimum																		
Leaf	3.25	2.23	18.05	0.40	2.33	4.09	0.23	6.55	1.04	41.34	7.24	1.35	0.38	0	1.23	0	0	0.23
Root	0.53	0	21.33	0	2.99	5.78	0.46	30.05	8.22	9.98	3.40	1.49	0	0	2.40	0	0.32	0.12
Stem	0.78	1.10	20.45	0.29	3.00	4.49	0.89	18.98	7.93	23.87	6.01	0.65	0	0	0.40	0.07	0	0
Flowers	2.19	0.62	17.32	0.45	4.03	4.54	0	18.39	6.09	22.19	5.32	0.34	0	0	0.34	0.12	0	0
Myosotis nemorosa																		
Leaf	2.45	1.20	14.49	0	2.12	3.28	0	13.31	0.90	40.05	3.90	1.30	0.19	0	0.29	0.49	0	0.08
Root	0.68	0.83	20.60	0	2.98	5.88	0	29.01	6.87	15.90	3.87	2.31	0.20	0	0.11	1.10	0.23	0.21
Stem	1.05	1.09	17.09	0.76	3.23	5.00	0.12	24.93	3.19	28.09	4.50	0.96	0	0	0.54	0.98	1.10	0
Flowers	3.09	2.21	13.98	0.12	0.12	3.39	0.11	14.43	1.14	38.03	4.69	1.49	0.35	0	0	1.33	0.22	0.34
Scrophularia sciophila																		
Leaf	4.65	0.58	11.87	0.26	1.61	3.94	0.25	8.09	2.62	33.56	15.53	0.37	0.14	0.11	0.32	0	0	0
Root	1.12	0	11.27	0.33	2.70	4.07	0.93	13.38	2.19	11.87	4.96	5.22	0	0	5.18	0	0	0
Stem	1.50	0.75	19.48	0.41	3.37	5.87	0.53	19.07	7.90	26.70	6.32	1.24	0	0	0.76	0	0	0
Flowers	5.13	0.37	19.75	0.18	3.43	3.63	0.31	63.57	1.66	0.38	5.43	1.22	0.23	0.14	0.76	0	0	0

[a]Percentage on a dry weight basis. Other fatty acids of undetermined structure bring the total to 100%.
[b]g/100 g of organ.

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