REVIEW

Fatty Acid Composition of Pinaceae as Taxonomic Markers

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ABSTRACT: Following our previous review on *Pinus* spp. seed fatty acid (FA) compositions, we recapitulate here the seed FA compositions of *Larix* (larch), *Picea* (spruce), and *Pseudotsuga* (Douglas fir) spp. Numerous seed FA compositions not described earlier are included. Approximately 40% of all *Picea* taxa and one-third of *Larix* taxa have been analyzed so far for their seed FA compositions. Qualitatively, the seed FA compositions in the three genera studied here are the same as in *Pinus* spp., including in particular the same Δ5-olefinic acids. However, they display a considerably lower variability in *Larix* and *Picea* spp. than in *Pinus* spp. An assessment of geographical variations in the seed FA composition of *P. abies* was made, and intraspecific dissimilarities in this species were found to be of considerably smaller amplitude than interspecific dissimilarities among other *Picea* species. This observation supports the use of seed FA compositions as chemotaxonomic markers, as they practically do not depend on edaphic or climatic conditions. This also shows that *Picea* spp. are coherently united as a group by their seed FA compositions. This also holds for *Larix* spp. Despite a close resemblance between *Picea* and *Larix* spp. seed FA compositions, principal component analysis indicates that the minor differences in seed FA compositions between the two genera are sufficient to allow a clear-cut individualization of the two genera. In both cases, the main FA is linoleic acid (slightly less than one-half of total FA), followed by pinolenic (5,9,12-18:3) and oleic acids. A maximum of 34% of total Δ5-olefinic acids is reached in *L. sibirica* seeds, which appears to be the highest value found in Pinaceae seed FA. This apparent limit is discussed in terms of regio- and stereospecific distribution of Δ5-olefinic acids in seed triacylglycerols. Regarding the single species of *Pseudotsuga* analyzed so far *(P. menziesii),* its seed FA composition is quite distinct from that of the other two genera, and in particular, it contains 1.2% of 14-methylhexadecanoic (anteiso-17:0) acid. In the three genera studied here, as well as in most *Pinus* spp., the C_{18} Δ5-olefinic acids (5,9-18:2 and 5,9,12-18:3 acids) are present in considerably higher amounts than the C_{20} Δ5-olefinic acids (5,11-20:2 and 5,11,14-20:3 acids).

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Abbreviations: Ag-TLC, argentation thin-layer chromatography; anteiso-17:0, 14-methylhexadecanoic; FA, fatty acid; FAME, fatty acid methyl ester; GLC, gas–liquid chromatography; NMR, nuclear magnetic resonance; TAG, triacylglycerol; UPIFA, unsaturated polymethylene-interrupted fatty acid.

Many attempts have been made to gain some insight into the phylogenetic interrelationships of conifers, because they are the most prominent components of the extant flora, with a very long history and particularly rich fossil record, beginning in pre-Permian time (1). The family Pinaceae already presented a significant history prior to the Late Triassic period (180 million years ago; 2,3). As we were involved in the systematic study of conifer (and more generally gymnosperm) seed fatty acid (FA) compositions, we noted that these data could be of some use as new, original, and supplementary chemometric markers for the taxonomy of this plant group (4–9).

All conifer seeds contain lipids that include part of a series of FA that were considered until recently as "unusual" (10), Δ5-unsaturated polymethylene-interrupted FA (Δ5-UPIFA). These FA have been shown in the meantime not only to be common constituents of seed oils from all Coniferophyte families but also to be characteristic of some Cycadophyte families (10–12). In gymnosperms (Coniferophytes and Cycadophytes), Δ5-UPIFA have the structures 5,9-18:2 (taxoleic); 5,11-18:2 (ephedrenic); 5,9,12-18:3 (pinolenic); 5,9,12,15-18:4 (coniferonic); 5,11-20:1; 5,11,14-20:3 (sciadonic), and 5,11,14,17-20:4 (juniperonic) acids, all ethylenic bonds being in the *cis* configuration. In addition to seeds, these FA also occur in the leaf and wood lipids of Coniferophytes and likely of some Cycadophytes (10,13–16).

The family Pinaceae (Coniferophytinae) contains a total of 11 or 12 genera: *Abies*, *Cathaya*, *Cedrus*, *Keteleeria*, *Larix*, *Nothotsuga*, *Picea*, *Pinus*, *Pseudolarix*, *Pseudotsuga*, *Tsuga*, and *Hesperopeuce*, the latter with an ill-defined taxonomic position (also considered a *Tsuga* species) (17,18). Among these genera, *Pinus* is the largest and most heteromorphic genus. The seed FA compositions available for the most common pine species, totaling approximately one-half of extant species, have been recently reviewed (8). The genera *Larix* and *Picea* are closely related to *Pinus*, although their relationships are still poorly understood. *Pinus*, *Larix*, and *Picea* are sometimes put together along with *Cathaya* and *Pseudotsuga* into a "Pinoid" group, as opposed to an "Abietoid" group that embraces *Abies*, *Cedrus*, *Tsuga*, *Nothotsuga*, *Pseudolarix*, and *Keteleeria* (19). But other subfamily arrangements have been proposed, e.g., Pinoideae (*Pinus*), Laricoideae (*Larix*, *Pseudolarix*, *Cedrus*), and Abietoideae (*Abies*, *Cathaya*, *Keteleeria*, *Picea*, *Pseudo-*

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tsuga, *Tsuga*); Pinoideae (*Pinus*), Piceoideae (*Picea*), Laricoideae (*Larix*, *Cathaya*, *Pseudotsuga*), Abietoideae (all other genera) (20); or more recently (21), Pinoideae, encompassing three tribes [Pineae (*Pinus*), Abieteae (*Cathaya*, *Picea*, *Tsuga*, *Cedrus*, *Keteleeria*, and *Abies*), and Lariceae (*Larix*, *Pseudotsuga*)], and Pseudolariceae (*Pseudolarix*). Clearly, there is a lack of general agreement as regards to the intergeneric relationships among Pinaceae.

In this study, a compilation of data available on *Picea*, *Larix*, and *Pseudotsuga* seed FA compositions is made, including numerous unpublished seed FA compositions. Species examined here represent approximately 40% of *Picea* and almost one-half of *Larix* species and varieties. Despite the fact that the three genera present rather similar seed FA compositions, principal component analysis and discriminant analysis allow distinction between them, improving our previous analysis of Pinaceae genera (5). This allows preliminary conclusions to be drawn on general features of the quantitative distribution of Δ5-UPIFA and other constituent seed FA in *Picea*, *Larix*, and *Pseudotsuga*.

EXPERIMENTAL PROCEDURES

Seeds, oil extraction, and FA methyl ester (FAME) preparation. Most seeds were purchased from Lawyer Nursery, Inc. (Plains, MT), F.W. Schuhmacher Co., Inc. (Sandwich, MA), and Sandeman Seeds (Pulborough, Great Britain). *Picea abies* seeds from 15 different French orchards and indigenous stands and one location in Poland were kindly donated by Vilmorin S.A. (La Ménitré, France). Seeds were kept at 4°C until use. Lipid extraction, always performed by starting with 10-g samples taken from 15 ± 5 g of powdered seeds, and FAME preparation were performed as described in detail elsewhere for other gymnosperm seeds (4–7). All FAME preparations were made in duplicate and each solution was analyzed once by gas–liquid chromatography (GLC). Generally, FAME were prepared within 24 h after lipid extraction and immediately analyzed.

Analytical GLC. All FAME preparations were analyzed by GLC in a Carlo Erba 4130 chromatograph (Carlo Erba, Milano, Italy) equipped with a DB-Wax column (30 m × 0.32 mm i.d., 0.5 μm film; J&W Scientific, Folsom, CA). The oven temperature was 190°C, and the inlet pressure of the carrier gas (helium) was 140 kPa. Occasionally, to confirm some identifications, a CP-Sil 88 column (50 m × 0.25 mm i.d., 0.2 μm film; Chrompack, Middelburg, The Netherlands) was operated with temperature programming in a Carlo Erba HRGC chromatograph from 150 to 185°C at 4°C/min with H_2 at 100 kPa. The injector (split mode) and flame-ionization detector were maintained at 250°C for both columns. Quantitative data were calculated by SP 4290 integrators (Spectra Physics, San Jose, CA). In some instances, particularly to detect potential late-eluting components but also to confirm identifications, a Silar 5 CP (50 m × 0.25 mm i.d., 0.2 μm film; Chrompack), fitted in a Hewlett-Packard HP 5890 gas chromatograph (Avondale, PA), was used in the temperature program mode (isothermal for 1 min at 165°C; from 165 to 205°C at a rate of 1°C/min; isothermal at 205°C for 60 min). Nitrogen was the carrier gas, and the injector and detector temperatures were maintained at 230 and 260°C, respectively (22).

Identification of FAME peaks. The seed lipids from selected conifer species (23,24) or Ranunculaceae species (25) were used as sources of Δ5-olefinic acid methyl esters with known structures to identify FA from seed lipids by GLC, either by coinjection, comparison of the equivalent chain lengths (DB-Wax column), or retention times (CP-Sil 88 and Silar 5 CP).

Data analysis. Principal component analysis was performed with the program STATBOX (Grimmer, Paris, France). The classifications of *Picea* spp. were performed with the program XLSTAT (copyright T. Fahmy, Paris, France). To compare the variability of intra- and interspecific seed FA compositions of *P. abies* and *Picea* spp., respectively, ascending hierarchical classifications were computed using the Ward method. This method consists in minimizing the loss of intraclass inertia at each step. The results are presented as dendrograms (see below) in which the aggregation level can be interpreted as a dissimilarity index between the objects (i.e., *Picea* species, or *P. abies* locations).

RESULTS AND DISCUSSION

Comments on Δ5-UPIFA and other FA. Regarding the genera studied here, most Δ5-UPIFA were initially structurally characterized in *L. kaempferi* [reported as *L. leptolepis* (26)] seed lipids by mass spectrometry coupled with GLC, further in *P. jezoensis* (27), and later supported by GLC in the same two *Larix* species (15). The presence of the 5,9-18:2 and 5,9,12-18:3 acids was recently confirmed by similar techniques in the seeds from *P. glauca engelmannii* ("interior spruce," a hybrid) and *P. glauca* (28). All Δ5-UPIFA reported in the seeds have also been characterized in the leaves of many *Picea* and *Larix* species (14), as well as in the wood of *P. abies* (13,16).

Detailed comments on the resolution of individual FA, including Δ5-UPIFA, have been presented elsewhere (8). All FA reported in the present study are baseline resolved except for *cis*-vaccenic acid, which is not completely resolved from oleic acid. Qualitatively, with respect to both the C_{18} and the C_{20} acid series, the routinely observed FA in the seed lipids from the genera *Picea*, *Larix*, and *Pseudotsuga* are exactly the same as in the genus *Pinus* (8).

The minor FA eluting from 12:0 to 15:0, as well as those eluting after 22:0 acid, are not reported individually in the present study and are included in the category "others" in the tables. On the other hand, the anteiso-17:0 (14-methylhexadecanoic) and 17:1 acids (likely the Δ9 isomer) are included. Anteiso-17:0 acid was unambiguously characterized by mass spectrometry in *Larix leptolepis* (26) as well as in *Pinus* seed lipids (29). In contrast, the 19:0 and "branched" 19:0 acids identified by mass spectrometry in the former species [each accounting for 0.2% of total FA (26)] have not been reported by other authors and are not included in the present study. It is likely that these acids are masked by other more important FA,

owing to similar GLC behavior. No unsaturated C_{22} acids have been reported in *Larix* or *Picea* seed lipids, but a 13-22:1 acid occurs in *Pseudotsuga menziesii* [0.1% (30)].

It is worthwhile to mention the presence of anteiso 19:1, anteiso 5,9-19:2, anteiso 9,12-19:2, and anteiso 5,9,12-19:3 acids, the latter three acids totaling *ca.* 1.8% of total polyunsaturated acids in *P. abies* wood extracts (13). These acids, to our knowledge, have not yet been identified in conifer seeds, although occasionally we noted small unknown peaks in the chromatographic zone where these branched acids are supposed to elute (in the neighborhood of 9,12-18:2 and 9,12,15-18:3 acids). A better insight into these rare minor FA can be obtained by "bidimensional" chromatography that associates GLC and argentation thin-layer chromatography (Ag-TLC) of FAME. The latter analytical procedure, applied to total FAME, allows their fractionation according to the number of ethylenic bonds (provided they all are in the *cis*-configuration) with, however, subtle effects linked to their position along the hydrocarbon chain and to the chain length.

When such isolated fractions are concentrated *ca*. 10 times prior to further GLC analysis, a considerable number of minor components are then observable on chromatograms (results not shown). For *L. decidua* seed lipids (Deluc, L.G., and Wolf, R.L., unpublished results), the anteiso-19:0 acid can be located on chromatograms of the saturated fraction. It accounts for approximately 0.3% of total FA. However, this branched FA, on chromatograms of unfractionated FAME, elutes under the main 9,12-18:2 acid, and cannot be quantitated. In the same way, there are indications of an anteiso-19:1 acid in the 1Δ Ag-TLC fraction (*ca*. 0.3% of total FA) that co-elutes with the 5,9,12-18:3 acid under routine analytical conditions. Such overlaps are the limitations in the accuracy of data presented here, but they should be of very minor importance as regards to our conclusions.

A word should be added concerning juniperonic acid, which apparently does not occur in any significant amounts in *Larix* and *Picea* seed FA when total (4,5, current paper), neutral, or polar (15) lipids are analyzed under routine analytical conditions. Minor amounts (<0.1%) of this FA would, however, occur in one case. On the other hand, applying the bidimensional chromatographic procedure described above to FAME prepared from *L. decidua* seeds allowed unambiguous characterization of juniperonic acid, as well as of its putative metabolic precursor, 11,14,17-20:3 acid, but in trace amounts only, even after concentration of the fraction. Under such conditions, no arachidonic or eicosapentaenoic acids, recently characterized in the seeds and leaves of species from the Araucariaceae family (31,32), could be observed in the species analyzed here. It should, however, be noted that arachidonic acid was reported to be present in the cambium zone of *L. sibirica* (cited in Ref. 33; original article in Russian), though other detailed and thorough studies of *P. abies* wood extracts did not mention such an occurrence (13,16).

Comments on Picea*,* Larix*, and* Pseudotsuga *classification and nomenclature.* Several proposals have been made regarding subdivisions of the genus *Picea*, essentially based on morphological characters, e.g., the shape and structure of needles, buds, and cone-scales (34,35). Except for Liu (34), who divided the genus *Picea* into two subgenera (*Omorika* and *Picea*), other systems use "sections," "series," or "phyla." However, according to Wright (36) or Debazac (35), any divisions of the genus *Picea* are unlikely to correspond to well-differentiated evolutive phyla, owing to the large occurrence of natural hybridization. This may be illustrated by the gradual morphological transition from one species to another in the wild, e.g., from *P. abies* to *P. obovata* (*P.* × *fennica*). *Picea abies* can also cross, naturally or experimentally (more or less successfully), with morphologically similar species, separated by wide ranges that, however, are connected by "intermediate" species (Asia: *P. montigena*, *P. likiangensis*, *P. koyamae*), or with morphologically distinct species with neighboring (Europe; *P. orientalis*) or widely separated (North America; *P. mariana*, *P. rubens*, *P. sitchensis*) ranges (36). It was recently (37) inferred from nuclear ribosomal 18S sequence analysis that *P. rubens* and *P. mariana* (North America) are more closely related to the European species *P. omorika* (limited to a small area in Bosnia-Herzegovina) than to other North American *Picea*. Thus, even geographical grouping (35) is questionable.

With respect to *Larix*, tentative divisions of the genus have also been suggested, based primarily on female cone morphology and anatomy (38), but recent chloroplast and nuclear ribosomal DNA fragment analyses were not consistent with such classifications (39,40). Rather, they gave some molecular evidences for clades linked to geographical locations (e.g., *Larix* spp. from Eurasia vs. *Larix* spp. from North America), a situation that would also hold for *Pseudotsuga* (40). However, several *Larix* species can hybridize with one another, e.g., *L. laricina* (North America), *L. decidua* (Europe), and *L. kaempferii* (Japan) (41). The hybrid between the two latter species is known as *L. eurolepis* (35).

Consequently, owing to the lack of agreement, no classifications of the genera *Picea*, *Larix*, and *Pseudotsuga* are adopted here.

Latin as well as trivial names given in Tables 1–3 are from a compilation of descriptions by Wright (36), Debazac (35), and Liu (34), and from tree-seed seller catalogs, corrected wherever possible for synonymy according to Farjon (42). Names reported in original references but not "officially" recognized by Farjon (42) have been modified, e.g., *L. leptolepis* in Takagi and Itabashi (15) and Wolff *et al*. (4) is reported here as *L. kaempferi*. Spelling of names in original references or in tree-seed seller catalogs may also differ from Farjon's recommendations (42), when they are still in usage, e.g., *P. omorika*, instead of *P. omorica*. A few varieties, e.g., *P. pungens* var. *glauca*, or *L. decidua* var. *sudetica*, recognized by foresters or horticulturists but not mentioned by Farjon (42), have also been kept unchanged. For *Pseudotsuga*, some infrageneric taxa are diversely regarded as valid species [e.g., Debazac (35)] or varieties. The nomenclature retained here is mostly that of Farjon (42), but supplementary varieties recognized by tree-seed sellers are also included in Table 3 (e.g., *P. menziesii* var. *caesia*).

TABLE 1
List of *Picea* Species for Which the Seed Fatty Acid Compositions Have (or have not yet) Been Described (including species analyzed in the present study)

Species[a]	Trivial name[b]	Reference[c]
1. *P. abies* var. *abies*	Norway spruce, common spruce	4,43, this study
2. *P. abies* var. *acuminata*	—	—
3. *P. alcoquiana* var. *acicularis*	—	—
4. *P. alcoquiana* var. *alcoquiana*	Alcock's spruce	—
5. *P. alcoquiana* var. *reflexa*	—	—
6. *P. asperata* var. *asperata*	Dragon spruce	This study
7. *P. asperata* var. *heterolepis*	—	—
8. *P. asperata* var. *ponderosa*	—	—
9. *P. aurantiaca*	—	—
10. *P. brachytyla* var. *brachytyla*	Sargent spruce	—
11. *P. brachytyla* var. *complanata*	—	—
12. *P. brachytyla* var. *rhombisquamea*	—	—
13. *P. breweriana*	Brewer spruce	This study
14. *P. chihuahuana*	Chihuahua spruce	—
15. *P. crassifolia*	Qinghai spruce	—
16. *P. engelmannii* var. *engelmannii*	Engelmann spruce	5
17. *P. engelmannii* var. *mexicana*	—	—
18. *P. farreri*	—	—
19. *P. glauca* var. *albertiana*	Alberta spruce	—
20. *P. glauca* var. *glauca*	White spruce	This study
21. *P. glehnii*	Sakhalin spruce	—
22. *P. jezoensis* spp. *hondoensis*	Hondo spruce	This study
23. *P. jezoensis* spp. *jezoensis*	Yezo spruce	15
24. *P. koraiensis* var. *koraiensis*	Korean spruce	This study
25. *P. koraiensis* var. *pungsanensis*	—	—
26. *P. koyamae*	Koyama spruce	This study
27. *P. likiangensis* var. *hirtella*	—	—
28. *P. likiangensis* var. *likiangensis*	Lijiang spruce	This study
29. *P. likiangensis* var. *linzhiensis*	—	—
30. *P. likiangensis* var. *montigena*	—	—
31. *P. likiangensis* var. *rubescens*	—	—
32. *P. mariana*	Black spruce, bog spruce	This study
33. *P. maximowiczii* var. *maximowiczii*	—	—
34. *P. maximowiczii* var. *senanensis*	—	—
35. *P. meyeri*	Meyer spruce	This study
36. *P. morrisonicola*	Taiwan spruce	—
37. *P. neoveitchii*	Veitch spruce	—
38. *P. obovata*	Siberian spruce	This study
39. *P. omorika*	Serbian spruce	5
40. *P. orientalis*	Oriental spruce	5
41. *P. pungens*	Colorado spruce, blue spruce	4, this study
42. *P. purpurea*	Purple-coned spruce	—
43. *P. retroflexa*	—	This study
44. *P. rubens*	Red spruce	This study
45. *P. schrenkiana* var. *schrenkiana*	Shrenkiana spruce	—
46. *P. schrenkiana* var. *tianschanica*	Tian-Shan spruce	This study
47. *P. sitchensis*	Sitka spruce	4
48. *P. smithiana*	Himalayan spruce	This study
49. *P. spinulosa*	East Himalayan spruce	—
50. *P. torano*	Tigertail spruce	—
51. *P. wilsonii*	Wilson's spruce	This study

[a]List mostly based on Farjon's *World Checklist and Bibliography of Conifers* (42). Hybrids are not included. See text, however, for synonymy and spelling.
[b]List mostly based on descriptions by Liu (34), Debazac (35), and Wright (36), and on tree seeds sellers' catalogs. The web site http://www.geocities.com/RainForest/Canopy was also consulted.
[c]A dash indicates that the seed fatty acid composition of the species has not yet been established.

The meaning of seed FA compositions as chemotaxonomic markers. A study of the variability of the seed FA composition of *P. abies* as a possible function of the geographical origin of the seeds was conducted. For this purpose, seeds from 15 *P. abies* stands located in different regions of France and growing at different altitudes were analyzed. Two lots from each origin were extracted, and each lipid extract was used to prepare FAME for further GLC analysis. The results are

TABLE 2
List of *Larix* Species for Which the Seed Fatty Acid Compositions Have (or have not yet) Been Described (including species analyzed in the present study)

Species[a]	Trivial name[b]	Reference[c]
1. *L. czekanowskii*	—	—
2. *L. decidua* var. *carpatica*	—	—
3. *L. decidua* var. *decidua*	European larch	5
4. *L. decidua* var. *polonica*	—	—
5. *L. gmelinii* var. *japonica*	—	—
6. *L. gmelinii* var. *gmelinii*	Dahurian larch	This study
7. *L. gmelinii* var. *olgensis*	Olga Bay larch	This study
8. *L. gmelinii* var. *principis-rupprechtii*	Prince Rupprecht larch	—
9. *L. griffithii* var. *griffithii*	—	—
10. *L. griffithii* var. *speciosa*	—	—
11. *L. kaempferi*	Japanese larch	15
12. *L. laricina*	Tamarack, Eastern larch	This study
13. *L. lyallii*	Subalpine larch	—
14. *L. mastersiana*	—	—
15. *L. occidentalis*	Tamarack, Western larch	This study
16. *L. potaninii* var. *chinensis*	—	—
17. *L. potaninii* var. *himalaica*	—	—
18. *L. potaninii* var. *macrocarpa*	—	—
19. *L. potaninii* var. *potaninii*	—	—
20. *L. sibirica*	Siberian larch	This study
21. *L. sukaczewii*	Siberian larch	This study

[a]List mostly based on Farjon's *World Checklist and Bibliography of Conifers* (42). Hybrids are not included.
[b]List mostly based on Debazac (35) descriptions, and tree seeds sellers' catalogs. The web site http://www.geocities.com/RainForest/Canopy was also consulted.
[c]A dash indicates that the seed fatty acid composition of the species has not yet been established.

graphically expressed as dendrograms in Figure 1. Intraspecific dissimilarities between *P. abies* from different French stands are visibly of minor importance as compared to interspecific dissimilarities between other *Picea* species. Tillman-Sutela *et al*. (43), who conducted a similar study on *P. abies* from 10 locations in Finland, reached a similar conclusion on the near invariability of *P. abies* seed FA compositions.

It can be inferred from these observations that the seed FA composition of *P. abies* is almost unaffected by edaphic or climatic growing conditions. The very minor differences noted for *P. abies* between France and Finland (Table 4) may as well be linked to differences in analytical procedures and equipment. A similar conclusion regarding the invariability of seed FA was drawn in a study conducted with *Pinus sylvestris* (8). Considering larger distribution areas (Eurasia instead of France), however, showed some small but significant variations for a few FA in *P. sylvestris* seeds from France eastward to Mongolia (8). However, *P. sylvestris* is very heteromorphic [150 "variants" have been described (44)], and at least three varieties are recognized (42). Moreover, the crossability of *P. sylvestris* with Asian pines of the *Sylvestres* subsection is poorly known, and seed FA variations may be linked to introgressions.

TABLE 3
List of *Pseudotsuga* Species for Which the Seed Fatty Acid Compositions Have (or have not yet) Been Described

Species[a]	Trivial name[b]	Reference[c]
1. *P. japonica*	—	—
2. *P. macrocarpa*	Big cone spruce, big cone Douglas fir	—
3. *P. menziesii* var. *caesia*	Grey Douglas fir	
4. *P. menziesii* var. *glauca*	Blue Douglas fir, Colorado Douglas fir, Rocky Mountain Douglas fir	—
5. *P. menziesii* var. *menziesii*	Douglas fir, Coast Douglas fir	5,30
6. *P. sinensis* var. *brevifolia*	—	—
7. *P. sinensis* var. *gaussenii*	—	—
8. *P. sinensis* var. *sinensis*	—	—

[a]List mostly based on Farjon's *World Checklist and Bibliography of Conifers* (42). See text, however.
[b]List mostly based on Debazac (35) and the web site http://www.geocities.com/RainForest/Canopy.
[c]A dash indicates that the seed fatty acid composition of the species has not yet been established.

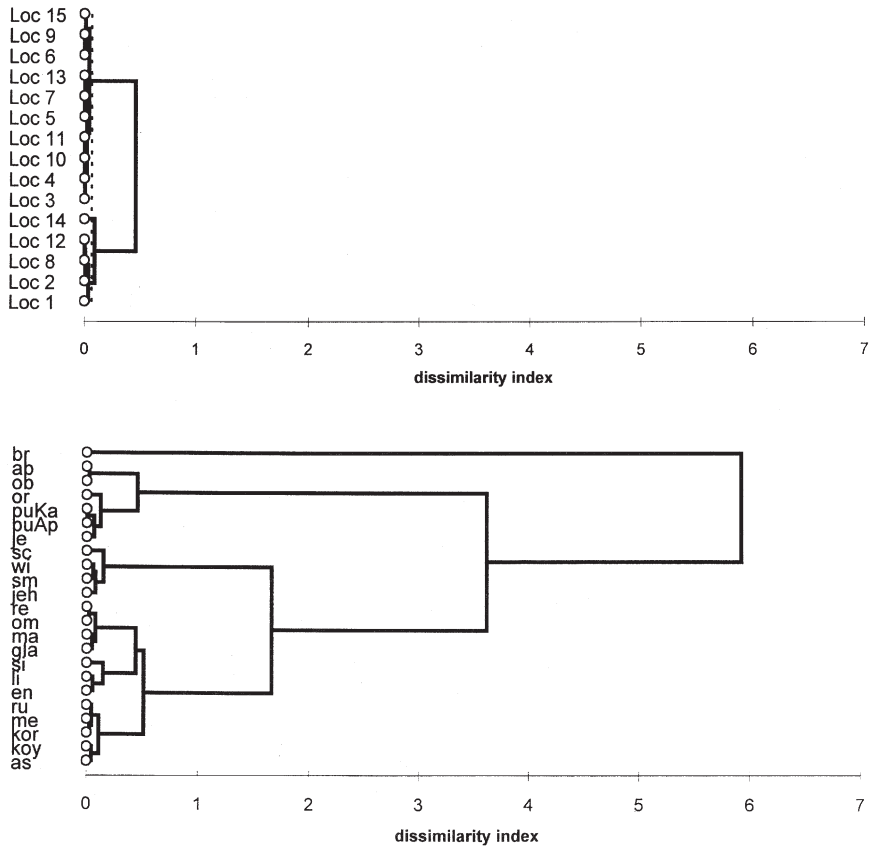

FIG. 1. Intraspecific dissimilarity for *Picea abies* from different locations (Loc) in France (upper dendrogram) and interspecific dissimilarity for *Picea* spp. (lower dendrogram). Abbreviations for species correspond to those listed in Table 4.

Seed FA compositions of Picea *spp*. Within the Pinaceae family, *Picea* is one of the largest genera (*ca*. 34 species, Table 1) being second to *Abies* and third to *Pinus*. This genus is reported to be rather heteromorphic, but subjected to natural cross-pollination (see above). *Picea* and *Pinus* are most often considered as sister groups, despite a gap of 20 to 70 million years in their fossil history (3,34). *Picea* spp. seeds are rather small, *ca*. 3–6 mm in length [weight of 1000 seeds, 2–9 g (35)]. The oil content is high, in the range 30–40% on a wet weight basis (results not shown). *Picea* spp. seed FA compositions are displayed in Table 4. It is immediately observable that the compositions of species analyzed so far show remarkable similarities. As regards to the species number and the limited variability in seed FA compositions, *Picea* spp. are in sharp contrast with *Pinus* spp. (8).

Total saturated acids in *Picea* spp. are approximately 5% of total FA (data not shown), which is less than in most *Pinus* spp. (*ca.* 10% in most instances). However, in both genera, the prevalence order of individual saturated FA is 16:0 > 18:0 > 20:0 > 22:0, as in *Pinus* spp. As mentioned above, a few branched-chain saturated acids occur. The main visible one is anteiso-17:0 acid, in the narrow range 0.10–0.26%, which is within the range found in most *Pinus* spp. This acid might be an important chemotaxonomic marker, as it does not occur in all conifer families.

The most common unsaturated FA is linoleic acid, with oleic acid being second. Linoleic acid accounts on average for 47.6%, varying in the narrow range 45.3–50.5% of total FA, whereas the corresponding values for oleic acid are 16.5% and 11.4–19.2%, respectively. α-Linolenic acid is a minor component that does not exceed 0.4%. These rankings are similar to those found in most pines (8). The level of *cis*-vaccenic acid in *Picea* seed lipids is relatively high as compared to that in *Pinus* spp. of the *Strobus* subgenus, but not clearly distinct from that occurring in several sections of the *Pinus* subgenus (8).

When considering the distribution profile of Δ5-UPIFA, similarities among the majority of pines are apparent. In particular, the C_{18} Δ5-UPIFA are present in considerably greater proportions than the C_{20} Δ5-UPIFA. Some pine species are not considered here for comparison purposes, e.g., those from the *Parrya* section, or those from the "Mediterranean coast and island" group (45), for reasons discussed elsewhere (mostly because of their exceptionally low total Δ5-UPIFA content) (8). Within the C_{18} Δ5-UPIFA series, the 5,9,12-18:3 acid is always higher than the 5,9-18:2 acid, in the ranges 20.8–26.2%, and 2.1–3.7%, respectively, in *Picea* spp. In *Pinus* spp., the corresponding ranges are somewhat larger (after exclusion of the above-mentioned species, and some others) (8). The minor C_{20} Δ5-UPIFA 5,11-20:2 and 5,11,14-

20:3 acids are always less than 0.09 and 1.24%, respectively, which resemble values found in the haploxyl pine subsection *Strobus*. With regard to sums of Δ5-UPIFA (including the metabolically related 7,11,14-20:3 acid) in *Picea* spp., they are in the range 25.0–30.4% (mean, 28.2%), which are values commonly found in many species of several subsections of the subgenus *Pinus* (e.g., practically all pine species of subsections *Sylvestres*, *Oocarpae*, and *Contortae*), but more seldom in the *Strobus* subgenus (e.g., in *P. strobus*). Bishomopinolenic (7,11,14-20:3) acid, the elongation product of pinolenic acid, is in the range 0.09-0.17%, which would correspond to an elongation rate of the latter acid of 0.6%. This FA is a usual minor component of Pinaceae seed lipids (46).

Seed FA compositions of Larix *spp*. This genus apparently has a rather short evolutionary history. No fossil records are known before the Middle or Late Eocene periods (38) or even the Oligocene period (3), and the number of admitted species, not taking into account varieties, is presently limited to 12 (Table 2). As for *Picea* spp., *Larix* spp. seeds are rather small, *ca*. 3–8 mm in length [weight of 1000 seeds, 2–12 g (35)]. Their oil content, relative to the weight of undehulled seeds, varies in the range 9–20% (results not shown).

The seed FA compositions of *Larix* species (Table 5) show remarkable similarities within the genus, and a striking resemblance with *Picea* spp. (*cf.* Table 4). The main FA is 9,12-18:2 acid in both cases, being slightly higher on average in *Larix* spp. than in *Picea* spp., 47.6 vs. 43.3%, respectively. Corresponding values for the second important common FA, 9-18:1 acid, are closer, 16.5 and 17.6%, respectively. The contents of total as well as of individual linear saturated acids in *Larix* spp. are identical to those in *Picea* spp. However, *Larix* and *Picea* spp. fundamentally differ when considering the amount of anteiso-17:0 acid, which in *Larix* is twice that in *Picea* spp. (0.36 vs. 0.18%, respectively).

As for *Picea* spp. and most *Pinus* spp., the C_{18} Δ5-UPIFA are present in *Larix* spp. in higher proportions than the C_{20} Δ5-UPIFA, with 5,9,12-18:3 acid being higher than 5,9-18:2 acid. In *Larix* spp., the range for taxoleic acid is narrower than in *Picea* spp. (2.2–2.6%), and pinolenic acid varies within limits that are definitely higher than in *Picea* spp., 25.8–30.7% vs. 20.8–26.2%. The elongation rate of the latter acid would be higher in *Larix* than in *Picea* spp. (0.9%), leading to a higher percentage of bishomopinolenic acid (mean, 0.24%).

Seed FA compositions of Pseudotsuga. Most recent authors (19–21,41,47,48) agree that *Pseudotsuga* is the closest relative to *Larix* within the Pinaceae family. The two genera also share a particular pollination mechanism not observed in other Pinaceae genera (49). This is why this genus is included in the present study. From fossil records, *Pseudotsuga* would have differentiated at the onset of the Cenozoic, slightly earlier than *Larix* (21).

Complete data for *Pseudotsuga* seed FA unfortunately are limited to two analyses of one single species, *P. menziesii*, of unknown variety (possibly the most common one, var. *menziesii*), which are not in full agreement (Table 6). No gross differences with the two preceding genera are noted for linear saturated acids. However, *P. menziesii* appears exceptional as regards to its high anteiso-17:0 acid content, *ca*. 1.2%, which seems unique among Pinaceae genera (29). Older data (50) for Douglas fir seeds indicated the presence of an unknown FA eluting between the 16:1 isomers and 18:0 acid, likely (in retrospect) the anteiso-17:0 acid, in amounts similar to those reported here. Some *Abies* and *Cedrus* species have seed FA containing as high as 0.8–0.9% of anteiso-17:0 acid (29). Whereas the contents of C_{18} Δ5-UPIFA are relatively low, in particular pinolenic acid, the C_{20} Δ5-UPIFA are relatively high, at least when compared to *Picea* and *Larix* species. Based on its seed FA composition, *P. menziesii* thus appears quite distinct from *Larix* spp., but not much more than from *Picea* spp. Obviously, complementary data are needed for *P. menziesii* varieties and for the three other species before a definitive conclusion can be drawn.

Principal component analysis. To assess whether the differences noted above between *Picea* and *Larix* spp. seed FA compositions were sufficient to distinguish the two genera on this biochemical basis, data were processed using principal component analysis. For this purpose, data for the species listed in Tables 4 and 5 were used. However, values for the very minor 17:0, 17:1, and 5,11,14,17-20:4 acids were not included as variables in calculations. Figure 2 shows the first two components which explain, respectively, 36.0 and 16.4% of the total inertia. Axis 1 clearly separates the two genera *Picea* and *Larix*. The most explanatory variables correlated with axis 1 can be divided into two groups, of which six are representative of *Larix* spp. These are the 5,9,12-18:3 and its elongation product 7,11,14-20:3; 9,12,15-18:3 and its Δ5-desaturation product 5,9,12,15-18:4; 5,11-20:2; and anteiso-17:0 acids. On the other hand, five FA are representative of *Picea* spp.: 9,12-18:2, its elongation product 11,14-20:2; the Δ5-desaturation product of the latter FA; 5,11,14-20:3; 5,9-18:2; and 20:0 acids.

As part of this study, axis 2 is not relevant to discriminate *Picea* and *Larix* spp. FA correlated with this axis lead to the separation of different species inside both genera. In particular, *P. breweriana* and *L. sukaczewii* are individualized because of a larger proportion of 18:0, 9-18:1 (*P. breweriana*), and 16:0 acids, and a small proportion of 7,11,14-20:3 acid (*L. sukaczewii*). Interestingly, *P. breweriana* is reported to have no close relatives, being locally endemic to southwest Oregon and northwest California in montane to subalpine forests of the Siskiyou Mountains (35). On the other hand, *L. sukaczewii* is reported to be relatively close to *L. sibirica* (35), but their seed FA compositions are rather different (see, e.g., the sums of Δ5-olefinic acids in Table 5). Farjon (42) even considers that *L. sukaczewii* is synonymous with *L. sibirica*, a view that is not supported by our results

Concluding remarks. *Picea* species, in contrast to *Pinus* spp., are mostly indistinguishable from one another on the basis of their seed FA compositions. Interspecific variations are even less important than in the *P. sylvestris* complex, which supports the view of Wright (36) that "taxonomically the genus (*Picea*) is more nearly comparable to a single se-

TABLE 4
Fatty Acid Composition (wt% of total fatty acids) of the Seed Lipids from *Picea* spp.

Species[a]	16:0	16:1[b]	aiso-17:0[c]	17:0	9-17:1	18:0	9-18:1	11-18:1	9,12-18:2	9,12,15-18:3	20:0	11-20:1
1. *P. abies*	2.78	0.13	0.20	0.04	—[g]	1.49	13.41	1.55	49.89	0.34	0.33	0.35
1. *P. abies* (France)	2.69	0.13	0.20	0.03	—	1.50	12.98	1.41	50.15	0.25	0.28	0.32
1. *P. abies* (Poland)	3.13	0.18	0.19	0.03	—	1.57	13.71	1.24	49.30	0.28	0.28	0.39
1. *P. abies* (Finland)	2.18	0.09	—	—	—	1.52	11.37	1.76	50.52	0.31	0.27	0.32
6. *P. asperata*	2.67	0.21	0.10	—	—	1.55	17.56	1.62	46.48	0.34	0.33	0.35
13. *P. breweriana*	3.25	0.21	0.16	0.04	0.02	1.80	25.86	1.35	39.79	0.23	0.42	0.45
16. *P. engelmanni*	2.58	0.12	0.26	0.03	—	1.28	17.28	1.51	46.39	0.41	0.34	0.42
20. *P. glauca* var. *glauca*	2.91	0.20	0.24	0.03	—	1.66	17.61	1.05	46.03	0.24	0.34	0.34
23. *P. jezoensis*[h]	2.57	0.21	(0.15)[i]	Trace[j]	(Trace)[k]	1.46	15.41	0.35	49.54	0.17	0.25	0.24
22. *P. jezoensis* var. *hondoensis*	3.16	0.15	0.17	0.02	—	1.46	19.02	1.22	47.36	0.24	0.22	0.26
24. *P. koraiensis*	2.96	0.13	0.17	0.03	Trace	1.41	16.52	1.05	47.70	0.20	0.21	0.30
26. *P. koyamae*	2.90	0.14	0.17	0.03	0.02	1.63	17.43	1.12	47.14	0.28	0.30	0.50
28. *P. likiangensis*	2.75	0.16	0.17	Trace	—	1.13	17.14	1.59	47.25	0.29	0.26	0.34
32. *P. mariana*	2.60	0.14	0.26	0.05	0.02	1.23	18.02	0.95	45.24	0.22	0.35	0.39
35. *P. meyeri*	2.51	0.16	0.16	0.03	Trace	1.35	16.78	1.35	47.45	0.27	0.28	0.34
38. *P. obovata*	3.08	0.14	0.18	0.03	Trace	1.62	12.82	1.59	49.31	0.22	0.22	0.32
39. *P. omorika*	2.44	0.17	0.17	0.03	—	1.16	16.74	1.42	45.35	0.26	0.29	0.49
40. *P. orientalis*	3.09	0.09	0.22	0.03	—	1.23	16.11	0.38	49.50	0.31	0.32	0.30
41. *P. pungens* var. *glauca* (Ap.)	2.66	0.10	0.21	0.03	—	1.22	15.12	0.95	48.47	0.37	0.27	0.36
41. *P. pungens* var. *glauca* (Ka.)	2.68	0.10	0.21	0.04	—	1.44	14.85	0.89	48.35	0.29	0.29	0.38
43. *P. retroflexa*	2.94	0.15	0.16	0.04	—	1.31	17.33	1.58	45.28	0.28	0.21	0.28
44. *P. rubens*	2.94	0.09	0.23	0.05	0.02	1.28	17.44	0.41	47.80	0.21	0.30	0.40
46. *P. schrenkiana* var. *tianshanica*	3.25	0.12	0.15	0.05	Trace	1.77	20.45	0.96	46.10	0.33	0.33	0.36
47. *P. sitchensis*	2.94	0.13	0.17	0.04	—	1.22	16.23	0.99	48.01	0.41	0.31	0.31
48. *P. smithiana*	2.67	0.14	0.15	0.05	—	1.23	19.05	1.88	45.97	0.23	0.23	0.42
51. *P. wilsonii*	3.08	0.14	0.17	0.07	—	1.73	19.16	1.23	46.06	0.30	0.32	0.36
Mean	2.70	0.14	0.19	0.04	—	1.43	16.81	1.16	47.30	0.29	0.31	0.37
SD	0.53	0.04	0.04	0.01	—	0.21	3.04	0.45	2.39	0.06	0.04	0.06
Min.	2.44	0.09	0.10	—	—	1.13	11.37	0.35	39.79	0.17	0.21	0.24
Max.	3.25	0.21	0.26	0.07	0.02	1.80	25.86	1.88	50.52	0.41	0.42	0.50

TABLE 4 (continued)

Species	11,14-20:2	22:0	5,9-18:2	5,9,12-18:3	5,9,12,15-18:4	5,11-20:2	5,11,14-20:3	7,11,14-20:3	$\Sigma\Delta5$[d]	Others[e]	Abbreviation[f]	Reference[g]
1. *P. abies*	0.58	0.19	3.25	24.67	0.03	0.05	0.94	0.16	29.10	—	—	4
1. *P. abies* (France)	0.71	0.10	3.23	24.99	0.03	0.03	0.96	0.16	29.40	—	abFr	This study
1. *P. abies* (Poland)	0.70	0.09	3.13	24.62	0.04	0.04	0.90	0.16	28.89	0.02	AbPol	This study
1. *P. abies* (Finland)	0.69	0.11	2.98	26.21	—	—	1.07	0.17	30.43	0.43	abFi	43
6. *P. asperata*	0.73	0.11	3.20	22.83	0.06	Trace	1.00	0.15	27.24	0.71	as	This study
13. *P. breweriana*	0.54	0.18	3.39	21.55	0.04	Trace	0.55	0.19	25.72	—	br	This study
16. *P. engelmanni*	0.78	0.15	2.21	24.89	0.06	0.03	0.83	0.17	28.19	0.26	en	5
20. *P. glauca* var. *glauca*	0.66	Trace	3.64	24.06	0.05	Trace	0.68	0.13	28.56	0.13	gla	This study
23. *P. jezoensis*	0.44	Trace	3.37	25.01	Trace	Trace	0.71	—	29.09	0.12	je	15
22. *P. jezoensis* var. *hondoensis*	0.48	Trace	3.50	22.02	Trace	Trace	0.60	0.06	26.18	0.06	jeh	This study
24. *P. koyamae*	0.56	0.14	4.17	22.33	0.04	0.07	0.89	0.10	27.60	0.04	koy	This study
26. *P. koraiensis*	0.46	Trace	4.57	23.40	Trace	Trace	0.77	0.12	28.86	0.00	kor	This study
28. *P. likiangensis*	0.63	0.19	2.65	23.75	0.05	0.07	1.24	0.15	27.91	0.19	li	This study
32. *P. mariana*	0.44	0.15	4.62	24.19	Trace	0.09	0.97	0.08	29.95	—	ma	This study
35. *P. meyeri*	0.62	0.09	3.71	23.53	0.03	0.03	1.02	0.13	28.45	0.16	me	This study
38. *P. obovata*	0.55	0.11	3.34	25.14	Trace	Trace	0.70	0.07	29.25	0.56	ob	This study
39. *P. omorika*	0.50	0.14	3.51	25.02	0.04	0.07	1.00	0.17	29.81	1.03	om	5
40. *P. orientalis*	0.41	0.18	2.71	23.54	0.06	0.08	1.09	0.16	27.64	0.19	or	5
41. *P. pungens* var. *glauca* (Ap.)[f]	0.76	0.16	3.23	24.66	0.03	0.03	1.10	0.13	29.18	0.14	puAp	4
41. *P. pungens* var. *glauca* (Ka.)[f]	0.75	0.14	3.50	24.59	0.06	0.06	1.10	0.10	29.41	0.18	puKa	This study
43. *P. retroflexa*	0.55	0.07	3.74	24.61	0.04	0.03	0.94	0.18	29.61	0.28	re	This study
44. *P. rubens*	0.54	0.13	3.74	23.31	0.03	0.07	0.87	0.09	28.11	0.05	ru	This study
46. *P. schrenkiana* var. *tianshanica*	0.50	0.15	4.10	20.24	0.04	0.09	0.88	0.06	25.41	0.07	sc	This study
47. *P. sitchensis*	0.47	0.19	2.10	25.75	—	0.07	0.66	0.16	28.74	—	si	4
48. *P. smithiana*	0.48	0.15	3.69	21.90	0.05	0.09	1.01	0.13	26.87	0.48	sm	This study
51. *P. wilsonii*	0.60	0.76	3.27	20.83	0.05	0.03	0.77	0.09	25.04	0.98	wi	This study
Mean	0.59	0.19	3.32	23.76	0.05	0.06	0.92	0.14	28.21	0.23		
SD	0.12	0.19	0.60	1.61	0.01	0.02	0.17	0.04	1.49	0.30		
Min.	0.41	Trace	2.10	20.83	Trace	Trace	0.55	0.06	25.04	—		
Max.	0.78	0.76	4.62	26.21	0.06	0.09	1.24	0.19	30.43	1.03		

[a]Initial nomenclature modified to fit recent recommendations. Abbreviations of origins, Ap. and Ka., Apache and Kaibab National Forests, Arizona. Data for *P. abies* from France and Finland are the means of values obtained from 15 and 10 different locations, respectively. Original data for Finland were given as mol% and have been recalculated as wt%.
[b]Two isomers, 7- and 9-16:1 acids.
[c]14-Methylhexadecanoic, or anteiso-17:0 acid.
[d]Sum of Δ5-olefinic acids, including the 7,11,14-20:3 acid.
[e]Minor and unidentified components.
[f]Abbreviations refer to Figures 1 and 2.
[g]Not detected or not reported.
[h]Reported as *Pinaceae jezoensis*.
[i]Reported as 16:2n-6.
[j]Trace amounts.
[k]Reported as 16:3n-3.

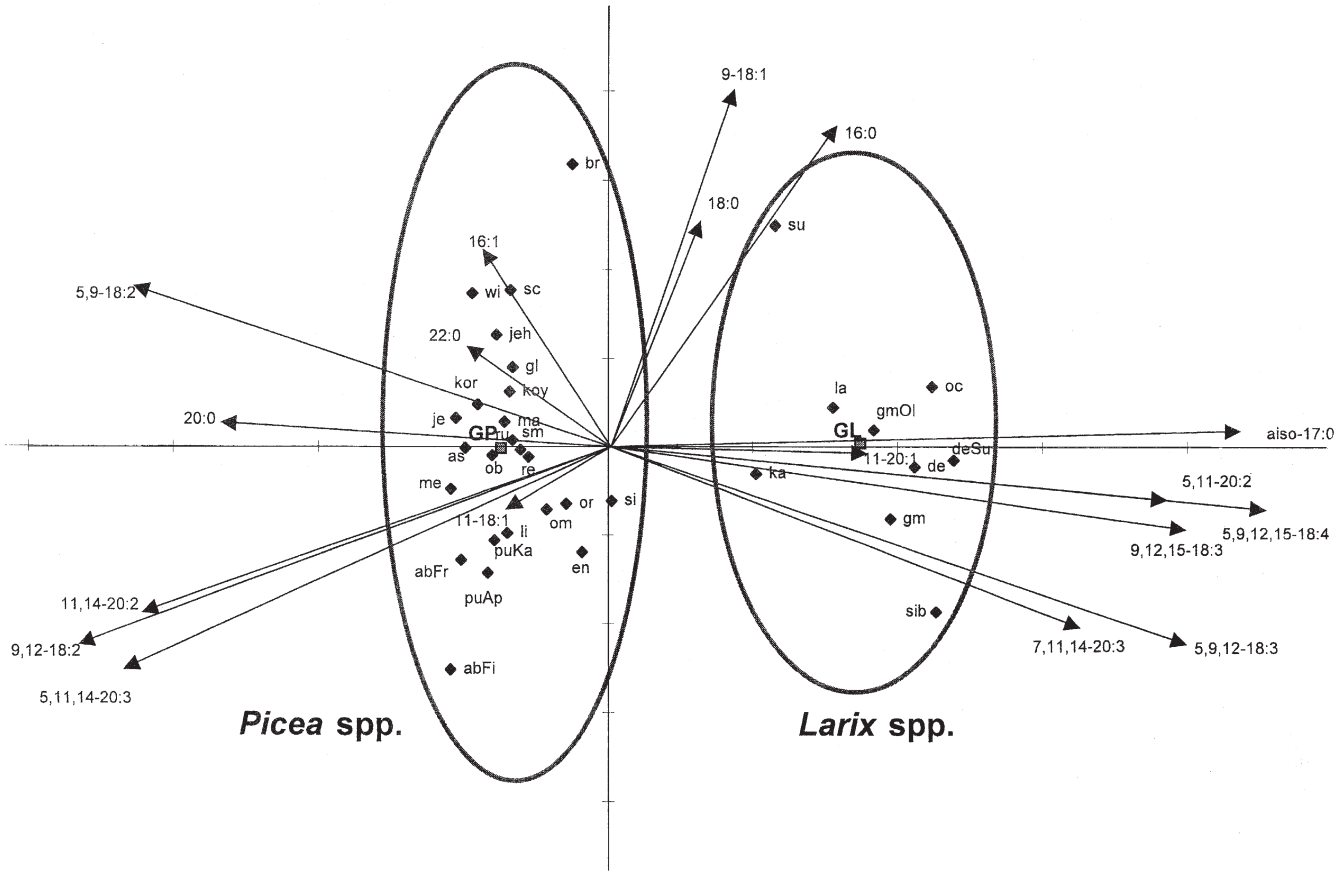

FIG. 2. Principal component analysis of *Picea* and *Larix* species and varieties. Abbreviations for species correspond to those listed in Tables 4 and 5. GP and GL, gravity centers.

ries in pine, maple, or ash than to any one of these complete genera." Apparently, the same holds for *Larix* spp. Although *Picea* and *Larix* spp. present on average rather similar seed FA compositions, multicomponent analysis quite clearly distinguishes these two genera. Moreover, our previous statistical analyses of *Picea*, *Larix*, and *Pinus*, though based on a smaller number of species in each genus, showed that *Picea* and *Larix* consistently differed from *Pinus* (5).

This study also confirms our previous observation that total Δ5-UPIFA cannot be higher than one-third of total FA in Pinaceae seeds (51,52). This indeed occurs in the genus *Larix*, for which GLC data were confirmed by ^{13}C nuclear magnetic resonance (NMR) spectroscopy (53). A probable explanation for this feature may be the stereospecificity of acylation of these acids to the glycerol backbone of triacylglycerols (TAG). It was shown for a great number of conifers, including some *Larix* and *Picea* species, that Δ5-UPIFA were enriched in the α (external) positions as compared to the β (internal) position of TAG (11). By applying a new regiospecific analysis method (54) that uses GLC of dibutyroyl derivatives of monoacylglycerols generated from TAG by partial deacylation with a Grignard reagent, levels of less than 5% of Δ5-UPIFA (a value close to the limit of detection by ^{13}C NMR spectroscopy) were shown to occur in the *sn*-2 position of TAG from *L. gmelinii* var. *olgensis* and *P. shrenkiana* seeds (Destaillats, F., Angers, P., Wolff, R.L., and Arul, J., unpublished data). Somewhat lower values were reported for *P. jezoensis* (15) and *L. decidua* (55). No data, however, are available yet for *P. menziesii*. In a smaller number of cases, including *L. decidua*, stereospecific analysis of conifer seed TAG has shown that Δ5-UPIFA are esterified mostly (*ca.* 90%) to the *sn*-3 position (56), independently of the chain length and the number of ethylenic bonds. Other studies on the seed TAG distribution profile of two *Pinus* species, *P. koraiensis* (57,58) and *P. pinaster* (57), have shown that TAG molecular species containing two or three Δ5-UPIFA are scarce or absent. It is thus probable that Δ5-UPIFA are mostly restricted to the *sn*-3 position of TAG, with the consequence that they cannot be higher than one third or so of total FA.

Incidentally, it should be noted that *Sciadopitys verticillata* (Sciadopityaceae) seed lipids contain in small amounts 2-monoacylglycerols, part of which are esterified with sciadonic acid (59). This would suggest that Δ5-olefinic acids can indeed esterify the *sn*-2 position of TAG, although it cannot be excluded that 2-sciadonoyl-glycerol is an artifact that derives from *sn*-3 monoacylglycerols through isomerization, e.g., during oil extraction.

TABLE 5
Fatty Acid Composition (wt% of total fatty acids) of the Seed Lipids from *Larix* spp.

Species[a]	16:0	16:1[b]	aiso-17:0[c]	17:0	9-17:1	18:0	9-18:1	11-18:1	9,12-18:2	9,12,15-18:3	20:0	11-20:1
1. *L. decidua*	2.80	0.12	0.43	0.04	—[h]	1.46	18.76	0.97	43.10	0.56	0.23	0.40
1. *L. decidua* var. *sudetica* (Slov.)	3.21	0.15	0.41	0.05	—	1.52	17.56	0.90	42.21	0.55	0.18	0.45
7. *L. gmelinii*	2.64	0.11	0.28	0.05	—	1.56	16.80	1.11	42.84	0.41	0.17	0.40
8. *L. gmelinii* var. *olgensis*	3.13	0.12	0.38	0.04	0.03	1.67	18.18	1.07	42.70	0.40	0.18	0.43
12. *L. kaempferi*	2.62	0.34	(0.30)[i]	0.02	Trace[j]	1.26	17.64	0.59	46.02	0.36	0.16	0.38
12. *L. kaempferi*	2.62	0.14	0.38	0.04	—	1.36	18.38	1.11	45.53	0.35	0.31	0.50
13. *L. laricina*	2.79	0.08	0.29	0.05	0.02	1.48	19.37	0.65	43.55	0.37	0.21	0.29
16. *L. occidentalis*	3.35	0.19	0.54	0.06	0.02	1.72	16.30	1.50	42.56	0.51	0.16	0.37
21. *L. sibirica*	2.80	0.10	0.36	0.05	Trace	1.30	15.03	1.21	42.35	0.40	0.24	0.44
22. *L. sukaczewii*	3.83	0.14	0.35	0.05	0.03	1.33	20.51	1.02	41.82	0.34	0.11	0.35
Mean	2.81	0.12	0.36	0.05	—	1.45	17.65	0.99	43.26	0.44	0.22	0.41
SD	0.21	0.03	0.06	0.01	—	0.10	1.57	0.20	1.21	0.09	0.05	0.07
Min.	2.62	0.08	0.28	0.02	—	1.26	15.03	0.59	41.82	0.34	0.11	0.29
Max.	3.83	0.34	0.54	0.06	0.03	1.72	20.51	1.50	46.02	0.56	0.31	0.50

Species	11,14-20:2	22:0	5,9-18:2	5,9,12-18:3	5,9,12,15-18:4	5,11-20:2	5,11,14-20:3	7,11,14-20:3	$\sum\Delta5$[d]	Others[e]	Abbreviation[f]	Reference[g]
1. *L. decidua*	0.35	0.10	2.20	27.39	0.12	0.14	0.51	0.20	30.56	0.12	de	4
1. *L. decidua* var. *sudetica* (Slov.)	0.41	0.13	2.50	28.21	0.15	0.13	0.67	0.29	31.95	0.32	deSu	This study
7. *L. gmelinii*	0.38	0.13	2.55	28.84	0.17	0.14	0.61	0.25	32.56	0.56	gm	This study
8. *L. gmelinii* var. *olgensis*	0.42	0.10	2.24	27.72	0.10	0.12	0.56	0.23	30.97	0.18	gmolg	This study
12. *L. kaempferi*	0.37	Trace	2.25	27.00	0.08	0.08	0.30	—	29.71	0.23	ka1	15
12. *L. kaempferi*	0.39	Trace	2.24	25.81	0.08	0.08	0.52	0.22	28.95	—	ka2	4
13. *L. laricina*	0.23	0.09	2.41	27.38	0.11	0.14	0.27	0.10	30.41	0.12	la	This study
16. *L. occidentalis*	0.39	Trace	2.11	28.90	0.14	0.06	0.33	0.18	31.72	0.61	oc	This study
21. *L. sibirica*	0.46	0.09	2.30	30.68	0.18	0.14	0.72	0.36	34.38	0.76	si	This study
22. *L. sukaczewii*	0.20	Trace	3.75	25.53	0.06	0.06	0.25	0.06	29.71	0.03	su	This study
Mean	0.37	0.11	2.37	28.05	0.14	0.13	0.55	0.24	31.25	0.29		
SD	0.08	0.02	0.14	1.64	0.04	0.02	0.16	0.09	1.63	0.26		
Min.	0.20	Trace	2.11	25.53	0.06	0.06	0.25	0.06	28.95	—		
Max.	0.46	0.13	3.75	30.68	0.18	0.14	0.72	0.36	34.41	0.76		

[a]Initial nomenclature modified to fit recent recommendations (e.g., *L. kaempferi* was reported as *L. leptolepis*). Abbreviations of origins: Slov., Slovakia.
[b]Two isomers, 7- and 9-16:1 acids.
[c]14-Methylhexadecanoic, or anteiso-17:0 acid.
[d]Sum of Δ5-olefinic acids, including the 7,11,14-20:3 acid.
[e]Minor and unidentified components.
[f]Abbreviations refer to Figure 2.
[g]Not detected or not reported.
[h]Reported as 16:2n-6.
[i]Trace amounts.

TABLE 6
Fatty Acid Composition (wt% of total fatty acids) of the Seed Lipids from *Pseudotsuga menziesii*

Species	16:0	16:1[a]	aiso-17:0[b]	17:0	9-17:1	18:0	9-18:1	11-18:1	9,12-18:2	9,12,15-18:3	20:0	11-20:1
P. menziesii	3.53	0.11	1.15	0.04	—[e]	1.42	17.75	0.61	49.53	0.60	0.35	0.40
P. menziesii	3.5	0.3	1.3	0.1	Trace[f]	1.8	18.1	0.8	44.0	0.6	0.6	0.9

Species	11,14-20:2	22:0	5,9-18:2	5,9,12-18:3	5,9,12,15-18:4	5,11-20:2	5,11,14-20:3	7,11,14-20:3	5,11,14,17-20:4	$\Sigma\Delta5^c$	Others[d]	Reference
P. menziesii	0.11	0.15	2.84	18.37	—	0.29	2.04	0.11	—	23.65	0.60	4
P. menziesii	0.5	0.5	2.8	20.1	0.1	0.4	1.7	—	—	25.1	1.9	30

[a]Two isomers, 7- and 9-16:1 acids.
[b]14-Methylhexadecanoic, or anteiso-17:0 acid.
[c]Sum of Δ5-olefinic acids, including the 7,11,14-20:3 acid.
[d]Minor and unidentified components.
[e]Not detected or not reported.
[f]Trace amounts.

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