

ABIES

**Abies, especially Abies growing in the
Southeastern United States**

Part five

including the pages 298-305 (of 247-305)
of the review with the title:

**THE GENERA OF PINACEAE IN THE
SOUTHEASTERN UNITED STATES**

by Robert A. Price

Published April, 1989, in

Journal of the Arnold Arboretum
Volume 70, Number 2, pp 247-305

Republished with the kind permission of

Copyright © President and Fellows of Harvard College

4. **Abies** Miller, Gard. Dict. abr. ed. 4. Vol. 1 (alph. ord.). 1754.

Pyramidal evergreen trees (rarely shrubs at high elevation or latitude) with well-separated "whorls" of branches. Bark with frequent resin blisters, smooth on younger trunks, becoming fissured with age. Wood pale, without normal resin canals (occasionally with traumatic ones); ray tracheids only occasionally present; axial parenchyma present. Leaves spirally arranged (often appearing 2-ranked due to twisting of the leaf bases), linear to linear-lanceolate, flattened and bearing 2 whitened abaxial stomatal bands [less often triangular or quadrangular in cross section and with stomata frequent above, as well as below], obtuse and often notched at apex or acute [to sharply pointed in *Abies bracteata*]; fibrovascular bundle double; resin canals 2 [rarely to 12], in the medial parenchyma [or near the leaf margin]; leaf scars circular, nearly flush with twig [to somewhat raised]. Pollen cones (microsporangiate strobili) short stalked, pendent, borne singly in axils of leaves of previous year; apex of microsporophyll prolonged into a short knob; microsporangia opening transversely; pollen bisaccate. Ovulate cones borne on upper side of topmost branches, maturing the first year; mature cones erect, ovoid [to cylindrical], short stalked or sessile; bracts fimbriate, with apiculate to long-attenuate tips, exerted [or more commonly included]; ovuliferous scales fan shaped, with margin deeply indented near base; bracts and scales abscising from the persistent cone axis. Seeds compressed; body triangular with acute base, the thin terminal wing broadest and often oblique at apex, partially folded over open surface of seed; seed coat thin, with large resin vesicles. Cotyledons [2-]4 or 5[-8 or rarely 14]. Chromosome number $2n = 24$. LECTOTYPE SPECIES: *Abies alba* Miller (*Pinus Picea* L., not *A. Picea* Miller); see Britton, N. Am. Trees, 74. 1908. (Classical Latin name for fir or related conifers.)—FIR, SILVER FIR.

A genus of approximately 40 species, *Abies* is widely distributed in temperate and boreal portions of the Northern Hemisphere, with the largest number of species in mountainous areas. The centers of distribution are in eastern and central Asia (ca. 17 species), southern Europe and North Africa (ca. eight), the western United States and Canada (eight), and Mexico and Guatemala (ca. six). *Abies sibirica* Ledeb. ranges north of the Arctic Circle in the U.S.S.R.,

while *A. lasiocarpa* (Hooker) Nutt. and *A. balsamea* (L.) Miller extend well into the subarctic of North America. *Abies balsamea* and *A. Fraseri* (Pursh) Poiret occur in eastern North America, but only the latter is native to our region.

Infrageneric groups in *Abies* are based on a limited number of morphological characters, which are probably subject to considerable homoplasy, and thus a number of conflicting classifications have been proposed (see comparisons in Critchfield, 1988; Liu). Liu's recent monographic treatment, which is followed here, recognizes two subgenera, PSEUDOTORREYA (Hickel) Franco (including only the unusual California endemic *A. bracteata* D. Don) and ABIES, continuing the precedent of Franco (1942, 1950). Within subg. ABIES, Liu recognized 14 sections based on ovulate-cone, leaf, and branchlet characters. Each of these sections is quite restricted in geographic range, usually to part of a continent. Franco (1950) divided subg. ABIES into seven sections and seven series, with the 11 terminal taxa very similar in composition to those of Liu. The North and Central American species of subg. ABIES fall into three sections (one including two series) in Franco's classification and five in Liu's. The less-formal classification of Gaussen, in which the genus is divided into five sections (one for *A. bracteata* only) and 14 species groups, differs in having sections that include both American and Eurasian species. A significantly different classification by Matzenko (1964, 1968) split the genus into four sections and 18 series based largely on relative size and form of the bracts and scales in the ovulate cone. This treatment often agrees poorly with the preponderance of morphological data and utilizes names without regard to nomenclatural priority. The terminal groups recognized by Liu, Franco, and Gaussen for the North American taxa have proved useful in predicting additional character states such as crossability and distribution of wood crystals. The sectional classifications of the entire genus seem to be fairly arbitrary, however, and should be evaluated using further data on crossability and biochemistry.

Subgenus ABIES is characterized by emarginate to acute (vs. acuminate and callose-tipped) leaf apices, ovate to globose (vs. fusiform) winter buds, and included or exserted bracts without a long-aristate middle lobe. Section BALSAMEAE Engelm. *emend.* Liu (leaves with median resin canals; fibrovascular bundles distinct; ovulate cones oblong to ovoid) comprises three species of the United States and Canada: *A. balsamea*, *A. lasiocarpa*, and the sole species in our region, *A. Fraseri* (*A. balsamea* var. *Fraseri* (Pursh) Spach), Fraser fir, southern balsam fir, she-balsam. Fraser fir is restricted to higher elevations (ca. 1200–2040 m) in the Appalachian Mountains of southwestern Virginia, eastern Tennessee, and western North Carolina. It occurs in pure stands on cool, moist slopes above 1500 m altitude on Mount Rogers, Roan Mountain, Grandfather Mountain, Mount Mitchell, and Clingman's Dome, and in mixed stands with red spruce (*Picea rubens*) and various hardwoods at lower elevations (Coker & Totten; Liu). In recent years several populations of *A. Fraseri* (e.g., on Mount Mitchell) have declined significantly in size, possibly as a result of the effects of acid rain.

Abies Fraseri is closely related to *A. balsamea*, differing most prominently in having the bracts of the ovulate cone strongly exserted and reflexed (vs.

included or somewhat exserted but not strongly reflexed). *Abies Fraseri* tends to have more lines of stomata per band on the leaves (Fulling, 1934; Rehder, 1940), and its young branchlets pubescent with generally reddish (vs. grayish) hairs. Plants of *A. balsamea* from New England and eastern Canada with somewhat exserted bracts were treated by Fernald as var. *phanerolepis*. Although bract/scale ratio is apparently positively correlated with elevation, it exhibits considerable variation within the northeastern populations (Jacobs *et al.*; Lester, 1968; Myers & Bormann), making this variety not very distinct. Similar plants with a tendency toward exserted bracts are also found scattered in the mountains of West Virginia and northern Virginia in the area between the allopatric ranges of *A. balsamea* and *A. Fraseri*. Several studies (Jacobs *et al.*; Robinson & Thor; Thor & Barnett) have compared these populations to *A. Fraseri* and eastern *A. balsamea* and have found intermediacy but no significant increase in variability in regard to morphological features, terpenoid profiles, or electrophoretic alleles. This is consistent with the hypothesis that these populations are remnants of a previous continuum from which *A. Fraseri* has diverged, rather than products of hybridization. *Abies Fraseri* shows significant differences from *A. balsamea* in the percentage composition of several monoterpenes in the wood and balsam oleoresins (Thor & Barnett; Zavarin & Snajberk, 1972), but only minimal divergence in electrophoretic alleles (Jacobs *et al.*). The two taxa are highly crossable (Hawley & DeHayes, 1985a, b) but are kept distinct by geographic isolation. Given the number of other species in the genus that are subject to partial intergradation, *A. Fraseri* is treated here as a separate species, albeit presumably a recent derivative of *A. balsamea*.

Abies is a distinct genus characterized by a unique combination of characters that separate it from the other abietoid genera of Pinaceae. *Cedrus* and *Pseudolarix* differ from *Abies* in their pronounced shoot dimorphism; *Keteleeria* and *Tsuga* differ in their ovulate cones with persistent scales; and *Tsuga* differs in its cones that are terminal and usually pendulous at maturity. *Abies*, *Keteleeria*, and *Pseudolarix* all have cone scales that are strongly indented at the base, with the seed apex extending beyond the cone scale and the seed wing consequently partially folded over the abaxial surface of the seed, a condition most pronounced in *Abies*. *Abies* and *Keteleeria* are also similar in having circular, only slightly raised leaf scars, but *Keteleeria* differs in its clustered pollen cones, along with its persistent cone scales. Immunological comparison of seed proteins indicates that *Abies* is most similar to *Cedrus* and *Keteleeria* (Price *et al.*).

While the genus is a distinct one, species delimitation within *Abies* is often problematic. Intergradation in morphology and chemistry occurs in a number of areas where related species are geographically adjacent. This could be due to incomplete evolutionary differentiation of taxa or to hybridization between distinct ones, and both of these situations probably occur in *Abies* (Critchfield, 1988). In addition to the *A. balsamea*-*A. Fraseri* complex discussed above, intermediate populations have been documented in other North American species pairs: *A. concolor*-*A. grandis* in sect. GRANDES Engelm. (Hamrick & Libby; Von Rudloff, 1976; Zavarin *et al.*, 1977a), *A. balsamea*-*A. lasiocarpa* in sect. BALSAMEAE Engelm. (Hunt & Von Rudloff; Parker *et al.*; Von Rudloff, 1975a), and *A. magnifica*-*A. procera* in sect. NOBILES Engelm. (Liu). Inter-

mediate populations between related species are also known in Europe—for example, involving *A. alba* and *A. cephalonica* (Mitsopoulos & Panetsos)—and Asia (Jain; Liu). Disagreements persist as to the distinctness of several Chinese taxa (cf. Cheng & Fu; Gaussen, 1964; Liu; Rushforth, 1983, 1984). Studies of morphological and chemical variation in the Chinese firs are badly needed.

Several artificial interspecific hybrids have been reported in *Abies* (Critchfield, 1988; Hawley & DeHayes, 1985a, b; Klaehn & Winieski; Mergen *et al.*), but many of the early reports were not verified using F_1 morphology or chemistry. Critchfield's (1988) recent review indicates that at least for the North American taxa, interspecific hybrids can frequently be produced within the sections of Liu, but seldom between them. None of the crosses of American and exotic species attempted by Critchfield succeeded, except for that of *A. concolor* with Mexican *A. religiosa*, although earlier reports of unverified crosses of American and Eurasian species need further investigation. In some cases failure of crosses due to embryo abortion or pollen-tube inhibition have been documented (Kormutak; Kormutak & Dubovsky).

Chromosome counts (all $2n = 24$) have been obtained for 22 of the 39 species recognized by Liu and for one putative interspecific hybrid (see especially Khoshoo; Mergen & Burley); *Abies Fraseri* apparently has never been counted. Natural polyploidy within species seems to be very rare. Karyotypes have been investigated by several authors (e.g., Mehra & Khoshoo; Mergen & Burley; Sax & Sax). According to Mergen & Burley, who compared six species of diverse taxonomic affinities and analyzed the effects of different chemical treatments, the three chromosomes with the smallest short arm are clearly heterobrachial and the two with the next longest ones are sometimes heterobrachial. This compares to earlier reports of five heterobrachial chromosomes by Mehra & Khoshoo and Sax & Sax. Secondary constrictions were found by Mergen & Burley to be variable in position and number, even within individual trees.

The pollination mechanism of *Abies* entails adherence of the pollen to microdroplets on the funnel-shaped integument tip, followed by slight infolding of the tip (Doyle & Kane; Owens & Molder; Singh & Owens, 1981, 1982). The pollen is then dormant for up to two months before germinating and growing into the nucellus (megasporangium). Syngamy occurs within a week of pollen germination in the North American species studied by Owens and coworkers. Inefficiencies in the pollination mechanism may be a factor in the high frequency of unfilled seeds seen in several species of firs (Franklin; Owens & Molder). Seed crops also tend to vary substantially in size over two- to several-year cycles (Franklin).

Variation in the form of the bracts and their length relative to the scales in the mature ovulate cones is particularly marked among—and sometimes within—species of *Abies* (Liu). The color of young cones at the time of pollination also varies strikingly, ranging from green or yellowish to various shades of purplish, bluish, or reddish among and sometimes within species (Liu; Sturgeon & Mitton).

Features of leaf anatomy, including number and position of resin canals, presence and distribution of hypodermal cells, degree of separation of the fibrovascular bundles, and distribution of stomata, are often useful in separating species of *Abies* (Fulling, 1934; Liu), although care must be taken to assure

sufficient and comparable samples, since there can be considerable intraspecific variability.

Distribution of calcium-oxalate crystals in the ray parenchyma of the wood has been compared among the nine species of *Abies* native to the United States (Kennedy *et al.*). Rhomboid and elongate crystals are both regularly present in wood samples from five of the western species but are sparse or absent in the western *A. amabilis* (Douglas) Forbes and in the three species of sect. BALSAMEAE (except for elongate crystals in some samples of *A. lasiocarpa*). Rhomboid or elongate crystals have also been reported from the wood of several Asian species (Greguss, 1955, 1972).

Terpenoid profiles from leaf, wood, or bark oleoresins have been used in a number of systematic comparisons among or within species of *Abies* (e.g., Von Rudloff, 1976; Von Rudloff & Hunt; Zavarin & Snajberk, 1965, 1972; Zavarin *et al.*, 1973, 1977a, b, 1978), with emphasis on the North American taxa (see reviews by Critchfield, 1984; Giannasi & Crawford; Von Rudloff, 1975a). These studies have been particularly useful in assessing intergradation among species and in highlighting geographic races within such widespread species as *A. concolor*, *A. balsamea*, and *A. lasiocarpa*. A survey of cortical terpenoids in the Japanese and Taiwanese firs (Zavarin *et al.*, 1978) yielded a diversity of monoterpenoid and sesquiterpenoid compounds and showed partial agreement with previous morphological classifications.

A particularly interesting sesquiterpenoid derivative isolated from the wood of *Abies balsamea* is juvabione, the "paper factor," which exhibits juvenile hormone activity in certain hemipteran insects (Williams). Juvabione and related todomatuic-acid derivatives with juvenile hormone activity have been found in several other *Abies* species and appear to be produced in response to woolly-aphid attack in some (Puritch & Nijholt). This group of compounds has also recently been found in the wood of *Cedrus Deodara* (see Hegnauer, 1986), which is of interest in light of the morphological similarities between these genera. Himachalene sesquiterpenoids characteristic of *Cedrus* have also been found in *Abies* (Zavarin *et al.*, 1978).

Several species of *Abies* are important as ornamental trees, particularly in cool-temperate areas. *Abies balsamea* and others, including *A. Fraseri*, are highly sought after as Christmas trees. Several species of *Abies* are important sources of pulpwood, and fir wood is used for a variety of purposes not requiring great durability. "Canada balsam," employed as a mounting medium in microscopy and as an optical cement, is an oleoresin obtained from the bark blisters of *A. balsamea*, while "Strasbourg turpentine," used in varnishes and artists' paints, is a refined oleoresin from *Abies alba*. Bark and leaf oleoresins from *Abies* have also been utilized medicinally by native peoples in North America to treat colds and to aid wound healing, among other purposes (Arnason *et al.*; Krochmal & Krochmal).

REFERENCES:

Under family references see ARNASON *et al.*; L. H. BAILEY; BEAN; BOUREAU; BUCHHOLZ, 1920, 1931, 1942; BUTTS & BUCHHOLZ; CAMPO & SIVAK; CAMPO-DUPLAN; CHANG; CHENG & FU; C. R. CHOWDHURY, 1962; K. A. CHOWDHURY; COKER & TOTTEN; CRITCHFIELD,

- 1984; DALLIMORE & JACKSON; DOYLE, 1945, 1963; DOYLE & KANE; G. ERDTMAN, 1957, 1965; FERRÉ; FLORIN, 1931, 1963; FLOUS; GAUSSEN, 1964; GIANNASI & CRAWFORD; GREGUSS, 1955, 1972; HEGNAUER, 1962, 1986; HICKEL; HUNTLEY & BIRKS; KHOSHOO, 1961; KONAR & NAGMANI; KROCHMAL & KROCHMAL; KRÜSSMANN; LITTLE, 1971, 1980; MAHESHWARI & SINGH; MEHRA & KHOSHOO; MILLER, 1976, 1977, 1985; NORIN; OWENS & SIMPSON; PHILLIPS; PILGER; PILGER & MELCHIOR; PRICE *et al.*, 1987; REHDER, 1940, 1949; SARGENT; SAX & SAX; SIVAK; TIEGHEM; UENO; VON RUDLOFF, 1975a; and WATTS.
- BOIVIN, B. *Abies balsamea* (Linné) Miller et ses variations. *Nat. Canad.* **86**: 219–223. 1959. [Suggests that *A. lasiocarpa* be included as a subspecies.]
- CLARKSON, R. B., & D. E. FAIRBROTHERS. A serological and electrophoretic investigation of eastern North American *Abies* (Pinaceae). *Taxon* **19**: 720–727. 1970. [Comparison of seed proteins of *A. Fraseri* and *A. balsamea* by immunology and disc electrophoresis.]
- CRITCHFIELD, W. B. Hybridization of the California firs. *Forest Sci.* **34**: 139–151. 1988. [Reviews crossability among *Abies* species and compares classifications of the genus.]
- DANIELS, J. D. Variation and intergradation in the grand fir–white fir complex. 235 pp. Unpubl. Ph.D. dissertation, Univ. Idaho, Moscow. 1969.* [*A. grandis*, *A. concolor*.]
- DEVORE, J. E. Fraser fir in the Unicoi Mountains. *Castanea* **37**: 148, 149. 1972. [Range extension to Haw Knob on the North Carolina/Tennessee border.]
- ENGELMANN, G. A synopsis of the American firs (*Abies* Link). *Trans. Acad. Sci. St. Louis* **3**: 593–602. 1878.
- FERNALD, M. L. A new variety of *Abies balsamea*. *Rhodora* **11**: 201–203. 1909. [*Abies balsamea* var. *phanerolepis*.]
- FRANCO, J. DO A. Sub-gêneros e secções do género *Abies* Mill. *Bol. Soc. Port. Ci. Nat.* **13**(Suppl. 2): 163–170. *figs. 1–5*. 1942.
- . Abetos. (In Portuguese.) *Anais Inst. Sup. Agron. Lisboa* **17**: 1–260. *figs. 1–109*. 1950. [Monographic treatment of *Abies*; keys, illustrations for the 20 species cultivated in Portugal.]
- FRANKLIN, J. F. *Abies*. Pp. 168–183 in *Seeds of woody plants in the United States*. U. S. Dep. Agr. Agr. Handb. **450**. 1974.
- FULLING, E. H. Identification, by leaf structure, of the species of *Abies* cultivated in the United States. *Bull. Torrey Bot. Club* **61**: 497–524. *pls. 26–32*. 1934. [Keys and extensive illustrations.]
- . *Abies intermedia*, the Blue Ridge fir, a new species. *Castanea* **1**: 91–94. 1936. [For plants from Virginia and West Virginia that are intermediate between *A. balsamea* and *A. Fraseri*.]
- HAMRICK, J. L., & W. J. LIBBY. Variation and selection in western U. S. montane species I. White fir. *Silvae Genet.* **21**: 29–36. 1972. [*A. concolor*.]
- HAWLEY, G. J., & D. H. DEHAYES. Hybridization among several North American firs. I. Crossability. *Canad. Jour. Forest Res.* **15**: 42–49. 1985a. [*A. balsamea*, *A. Fraseri*, *A. lasiocarpa*.] II. Hybrid verification. *Ibid.* 50–55. 1985b.
- HUNT, R. S., & E. VON RUDLOFF. Chemosystematic studies in the genus *Abies*. I. Leaf and twig oil analysis of alpine and balsam firs. *Canad. Jour. Bot.* **52**: 477–487. 1974. [Significant differences between the terpenoid profiles of *A. lasiocarpa* and of *A. balsamea*, and between eastern and western populations of the latter.]
- HUTCHINSON, A. H. The male gametophyte of *Abies*. *Bot. Gaz.* **57**: 148–153. 1914.
- . Fertilization in *Abies balsamea*. *Ibid.* **60**: 457–472. 1915.
- . Embryogeny of *Abies*. *Ibid.* **77**: 280–288. 1924.
- JACOBS, B. F., C. R. WERTH, & S. I. GUTTMAN. Genetic relationships in *Abies* (fir) of eastern United States: an electrophoretic study. *Canad. Jour. Bot.* **62**: 609–616. 1984. [Compares *A. Fraseri* to eastern *A. balsamea*.]
- JAIN, K. K. Introgressive hybridization in the West Himalayan silver firs. *Silvae Genet.* **25**: 107–109. 1976. [*A. spectabilis*, *A. Pindrow*.]
- KENNEDY, R. W., C. S. R. SASTRY, G. M. BARTON, & E. L. ELLIS. Crystals in the wood

- of the genus *Abies* indigenous to Canada and the United States. *Canad. Jour. Bot.* **46**: 1221–1228. *pl. 1*. 1968.
- KIM, Y. D. Karyological relationships of the genus *Abies* in Korea. (In Korean.) *Jour. Korean Forestry Soc.* **62**: 60–67. 1983.*
- & S. S. KIM. Studies on the morphological and anatomical characteristics of the genus *Abies* in Korea. *Jour. Korean Forestry Soc.* **62**: 68–75.*
- KLAEHN, F. U., & J. A. WINIESKI. Interspecific hybridization in the genus *Abies*. *Silvae Genet.* **11**: 130–142. 1962. [Results of artificial crosses.]
- KORMUTAK, A. Cytological study on crossability of some *Abies* species. *Biol. Bratislava* **36**: 245–251. 1981.*
- & J. DUBOVSKY. Embryo inviability in *Abies concolor* var. *Lowiana* × *Abies alba* crossing. *Biol. Bratislava* **39**: 3–14. 1984.*
- LAING, E. V. The genus *Abies* and recognition of species. *Scot. Forestry* **10**: 20–25. 1956. [Keys to vegetative and reproductive material.]
- LAMB, W. H. A conspectus of North American firs (exclusive of Mexico). *Proc. Soc. Am. Foresters* **9**: 528–538. 1914.
- LESTER, D. T. Variation in cone morphology of balsam fir, *Abies balsamea*. *Rhodora* **70**: 83–94. 1968.
- . Geographic variation in leaf and twig monoterpenes of balsam fir. *Canad. Jour. Forest Res.* **4**: 55–60. 1974.
- LIU, T.-S. A monograph of the genus *Abies*. 608 pp. Taipei. 1971. [Includes detailed illustrations and distribution maps.]
- MARTÍNEZ, M. Tres especies nuevas mexicanas del género *Abies*. *Anal. Inst. Biol. Méx.* **13**: 621–634. 1942. [*A. durangensis*, *A. mexicana*, *A. Vejari*, *figs. 1–10*.]
- . Los *Abies* mexicanos. *Ibid.* **19**: 11–104. 1948.
- MATZENKO, A. E. The firs of the Eastern Hemisphere. (In Russian; English summary.) *Acad. Sci. USSR, Inst. Bot. V. L. Komarov. Flora et Syst. Pl. Vasc.* **13**: 1–103. 1964. [New generic classification emphasizing bract and scale characters; extensive bibliography.]
- . Series novae generis *Abies* Mill. *Acad. Sci. USSR, Inst. Bot. V. L. Komarov. Novitates Syst. Pl. Vasc.* **1968**: 9–12. 1968. [Diagnoses and species for the sections and series in the classification of MATZENKO (1964).]
- MEHRA, P. N. Conifers of the Himalayas with particular reference to the *Abies* and *Juniperus* complexes. *Nucleus* **19**: 123–139. 1976. [*A. Forestii*, *A. Pindrow*, *n = 12*.]
- MERGEN, R., & J. BURLEY. *Abies* karyotype analysis. *Silvae Genet.* **13**: 63–68. 1964. [*A. alba*, *A. cephalonica*, *A. × Borisii-regis*, *A. lasiocarpa*, *A. firma*, *A. procera*, *A. guatemalensis*, all *n = 12*.]
- , ———, & B. A. SIMPSON. Artificial hybridization in *Abies*. *Züchter* **34**: 242–251. 1964.*
- & D. T. LESTER. Microsporogenesis in *Abies*. *Silvae Genet.* **10**: 146–156. 1961.
- MITSOPOULOS, D. J., & C. P. PANETSOS. Origin of variation in fir forests of Greece. *Silvae Genet.* **36**: 1–15. 1987. [Chemical and morphological comparisons of *A. alba*, *A. cephalonica*, and putative hybrid derivatives.]
- MYERS, O., JR., & F. H. BORMANN. Phenotypic variation in *Abies balsamea* in response to altitudinal and geographic gradients. *Ecology* **44**: 429–436. 1963.
- OWENS, J. N., & M. MOLDER. Sexual reproduction of *Abies amabilis*. *Canad. Jour. Bot.* **55**: 2653–2667. 1977.
- PARKER, W. H., J. MAZE, & G. E. BRADFIELD. Implications of morphological and anatomical variation in *Abies balsamea* and *A. lasiocarpa* from western Canada. *Am. Jour. Bot.* **68**: 843–854. 1981. [Multivariate and univariate comparisons indicate significant intergradation.]
- PURITCH, G. S., & W. W. NIJHOLT. Occurrence of juvabione-related compounds in grand fir and Pacific silver fir infested by balsam woolly aphid. *Canad. Jour. Bot.* **52**: 585–

587. 1974. [Compounds related to juvabione appear to be produced in response to aphid attack on *A. grandis* and *A. amabilis*.]
- RAMSEUR, G. S. A hybrid index for the mid-Appalachian *Abies* (fir or balsam). (Abstract.) ASB Bull. 8: 31. 1961.
- REHDER, A. The firs of Mexico and Guatemala. Jour. Arnold Arb. 20: 281–287. 1939.
- ROBINSON, J. F., & E. THOR. Natural variation in *Abies* of the southern Appalachians. Forest Sci. 15: 238–244. 1969.
- ROLLER, K. J. Resin canal position in the needles of balsam, alpine and Fraser firs. Forest Sci. 12: 348–355. 1966.
- RUSHFORTH, K. D. Notes on Chinese silver firs 3. Notes Roy. Bot. Gard. Edinburgh 43: 269–275. 1986. [See also *Ibid.* 41: 333–338. 1983; *Ibid.* 535–540. 1984.]
- SINGH, H., & J. N. OWENS. Sexual reproduction in subalpine fir (*Abies lasiocarpa*). Canad. Jour. Bot. 59: 2650–2666. 1981.
- & ———. Sexual reproduction in grand fir (*Abies grandis*). *Ibid.* 60: 2197–2214. 1982.
- STURGEON, K. B., & J. B. MITTON. Cone color polymorphism associated with elevation in white fir, *Abies concolor*, in southern Colorado. Am. Jour. Bot. 67: 1040–1045. 1980.
- THOR, E., & P. E. BARNETT. Taxonomy of *Abies* in the southern Appalachians: variation in balsam monoterpenes and wood properties. Forest Sci. 20: 32–40. 1974.
- VIGUIÉ, M.-T., & H. GAUSSEN. Révision du genre *Abies*. Bull. Soc. Hist. Nat. Toulouse 57: 369–434. 1928; 58: 245–564. 1929. [Reprinted in Trav. Lab. Forest. Toulouse, Tome II, Art. I: 1–386. 1929.]
- VON RUDLOFF, E. Chemosystematic studies in the genus *Abies*. II. Leaf oil analysis of grand fir. Canad. Jour. Bot. 54: 1926–1931. 1976. [Terpenoid variation in south-central Oregon consistent with introgression involving *A. concolor*.]
- & R. S. HUNT. Chemosystematic studies in the genus *Abies*. III. Leaf and twig oil analysis of amabilis fir. Canad. Jour. Bot. 55: 3087–3092. 1977.
- WARD, D. S. The first record of the Fraser fir. Castanea 27: 78, 79. 1962.
- WILLIAMS, C. M. Hormonal interactions between plants and insects. Pp. 103–132 in E. SONDHEIMER & J. B. SIMEONE, eds., Chemical ecology. New York and London. 1970. [Juvenile hormone activity of “paper factor” from *Abies balsamea*.]
- ZAVARIN, E., & K. SNAJBERK. Chemotaxonomy of the genus *Abies*. I. Survey of the terpenes present in *Abies* balsams. Phytochemistry 4: 141–148. 1965. [Preliminary comparison of 17 species, including *A. balsamea* and *A. Fraseri*.]
- & ———. Geographical variability of monoterpenes from *Abies balsamea* and *A. Fraseri*. *Ibid.* 11: 1407–1421. 1972.
- , ———, & W. B. CRITCHFIELD. Monoterpene variability of *Abies amabilis* cortical oleoresin. Biochem. Syst. Ecol. 1: 87–93. 1973.
- , ———, & ———. Terpenoid chemotaxonomic studies of *Abies grandis*. *Ibid.* 5: 89–93. 1977a.
- , ———, & ———. Relation of cortical monoterpene composition of *Abies* to tree age and size. Phytochemistry 16: 770–772. 1977b.
- , ———, & C.-J. LEE. Chemical relationships between firs of Japan and Taiwan. Biochem. Syst. Ecol. 6: 177–184. 1978. [Cortical terpenoids of six species.]

END OF ABIES