The Distribution and Phylogeny of Aluminium Accumulating Plants in the Ericales

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Abstract: **The distribution of aluminium (Al) accumulation in the Ericales is surveyed, based on semi-quantitative tests of 114 species and literature data. Al accumulation mainly characterises the families Diapensiaceae, Pentaphylacaceae, Symplocaceae, Ternstroemiaceae, and Theaceae. Al accumulation is consistently present or absent in most families examined, but the character appears to be more variable in a few taxa (e.g., Lecythidaceae, Myrsinaceae). Although the interfamilial relationships within the Ericales require further research, the ability to accumulate high levels of Al appears to show considerable taxonomic significance. While the majority of Al accumulating Ericales includes woody, tropical plants, the feature is remarkably present in several herbaceous Diapensiaceae, which have a distribution in cold to temperate areas. The association of different mycorrhizae types with plant roots is suggested to play a role in the exclusion of high Al levels from the shoot.**

Key words: **Aluminium accumulation, Ericales, phylogeny, Diapensiaceae, Pentaphylacaceae, Symplocaceae, Ternstroemiaceae, Theaceae.**

Introduction

A high proportion of trivalent Al^{3+} ions generally becomes bioavailable and detrimental to plants when the soil pH falls below 5.5 in acid soils (Marschner, 1995). The majority of native plants growing in acid soils avoid the toxic effects of high Al levels by excluding this metal from their shoot tissues, although several crop plants are well known to be sensitive to high levels of soluble Al (Foy et al., 1978; Roy et al., 1988; Kochian, 1995). Indeed, Al toxicity forms the primary factor limiting production of wheat, corn, barley, and soybean in acid soils. Moreover, about 5% of angiosperms take up Al in their aboveground tissues in quantities far above the average of 200 mg kg^{-1}. These plants have developed special mechanisms for the internal detoxification of Al in their shoots (Jansen et al., 2002 a, 2004; Watanabe and Osaki, 2002). According to Chenery (1946, 1948 a, b), plants that have Al levels of at least 1000 mg kg^{-1} in their leaf dry matter can be defined as Al accumulators.

Al accumulating plants have mainly been studied from an ecological and physiological point of view because of substantial questions about the possible significance of Al accumulation. Since little attention has been paid to the systematic distribution and phylogenetic significance of Al accumulators, we have previously investigated the evolution of Al accumulation in the Rubiaceae (Gentianales) and Melastomataceae (Myrtales) (Jansen et al., 2000 a, b, 2003; Jansen et al., 2002 b). These two families show by far the highest number of Al accumulators in angiosperms. The order Ericales represents the third largest group of Al accumulating plants. It is well known, for instance, that Al accumulation is present in the tea bush (*Camellia sinensis* L.), in which Al levels range from 5000 to 30 000 mg kg^{-1} in mature leaves (Matsumoto et al., 1976). The commercial tea plant belongs to the Theaceae family, which is now included in the enlarged order Ericales (APG II, 2003; Smets and Pyck, 2003). Chenery (1955) has already paid extensive attention to Al accumulation in the tea bush and several others have investigated the distribution, concentration, and speciation of Al in tea leaves (Memon et al., 1981; Nagata et al., 1992, 1993; Echlin, 1996, 1999; Ruan and Wong, 2001). Furthermore, the occurrence of Al accumulation has been studied in families such as the Symplocaceae, Diapensiaceae, and Theaceae (Yoshii and Jimbo, 1932), but no study has surveyed this feature in the entire order Ericales.

Interest in studying Al compounds has increased over recent years due to the possible role of Al in neurodegenerative disorders such as Alzheimer's disease, although this link is still debatable (Exley, 2001, 2003). Since tea is the second most-consumed beverage in the world after water, it is probably the most important single source of dietary Al for many people. Accordingly, several studies have investigated the impact of tea on human health (Flaten and Ødegård, 1988; Flaten, 2002; Wong et al., 2003). A better understanding of the distribution of Al accumulation and its underlying physiological mechanisms may serve as a basis for the development of more resistant crop plants. It may also contribute to forest management, soil improvement, and remediation of degraded lands in tropical rain forests or savannas.

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This paper aims to illustrate the distribution and evolution of Al accumulators in the order Ericales. Since our knowledge of Al accumulators is limited to a few substantial contributions published more than 50 years ago, we have analysed 114 species from most families distinguished within the Ericales. A summary of the literature data allowed us to compare the new data with earlier results. The phylogenetic significance of Al accumulation in the order is evaluated based on the recent molecular phylogenetic studies of Anderberg et al. (2002), Bremer et al. (2002), and Geuten et al., 2004. Finally, some physiological, chemical, and ecological aspects are briefly discussed, linking a wide range of topics to the distribution of accumulators and non-accumulators in the study group. Indeed, a multidisciplinary approach is required to better understand the biology of Al accumulating plants.

Materials and Methods

Herbarium leaves of the Ericales were collected from the herbarium of the National Botanic Garden of Belgium (BR). Leaf material for the Lissocarpaceae, Pellicieraceae, Sladeniaceae, and Tertrameristaceae was not available. All specimens tested are listed in Table **1**. We have analysed only one specimen for most species because the presence of Al accumulation is generally consistent at the species level (Jansen et al., 2002 a, 2004). High Al concentrations in leaves were detected using the "aluminon" test as described by Chenery (1948 b) and followed by Jansen et al. (2000 a, 2002 b). This simple but adequate test permits assessment by intensity of colour to arrange the specimens tested according to Al accumulators (crimson to dark red or red colour) or non-accumulators (colour varying from pink to yellow or dark brown). The distribution of Al accumulating taxa was then plotted on three trees using MacClade 4.0 (Maddison and Maddison, 2000).

Several Ericales have been reported to accumulate more than 10 000 mg kg^{-1} in their leaves and can therefore be labelled as Al "hyperaccumulators". Since precise quantitative data on the Al content were not obtained using the semi-quantitative spot tests, we use the term "accumulators" throughout this paper for all accumulating plants, even if the exact Al content could be far above 10 000 mg kg^{-1}.

Results

A summary of the distribution of Al accumulation in the Ericales is presented in Table **1**, including our own tests and literature data.

Only 12 out of the 114 species tested by us appeared to show a positive result, indicating Al accumulation in the leaves. All other species were found to be negative. The majority of the families included non-accumulators, but the feature appeared to be strongly present in the Diapensiaceae, Pentaphylacaceae, Symplocaceae, Ternstroemiaceae, and most Theaceae. Al accumulators were also found in at least two genera of the Lecythidaceae (including Scytopetalaceae), namely *Brazzeia* and *Pierrina,* although most genera in this family were negative. There were no new records of Al accumulating families, but the feature was reported for the first time in the genus *Pierrina* (Lecythidaceae).

In general, there was good agreement between our data and earlier tests. However, the genera *Galax* and *Shortia* (Diapensiaceae), *Diospyros* (Ebenaceae), *Brazzeia* (Lecythidaceae), *Rapanea* (Myrsinaceae), and *Adinandra* (Ternstroemiaceae) gave negative results according to our analyses, while positive results were previously recorded by Chenery (1948 a, b) and Masunaga et al. (1998).

Discussion

The distribution of Al accumulators

The combination of our new analyses and literature data provides a good overview of the occurrence of Al accumulation in the Ericales. As illustrated by the new record of Al accumulation in *Pierrina,* further sampling will probably reveal other previously unknown Al accumulators, but the overall distribution seems to be clear. The data obtained may allow us to distinguish two different groups: (1) families in which Al accumulation is exclusively absent, and (2) families in which Al accumulation is partly to almost entirely present. Most families in the Ericales belong to the group of non-accumulators, as the character is exclusively absent in 18 out of 27 families (Table **1**). The Al accumulating group includes the families Diapensiaceae, Pentaphylacaceae, Symplocaceae, Ternstroemiaceae, and Theaceae, which are thought to include strong, possibly absolute or obligate Al accumulators. Obligate Al accumulators can be defined as species in which the Al content of the shoot is constantly above 1000 mg kg^{-1}, irrespective of the concentration of soluble Al in the soil or seasonal changes (Jansen et al., 2002 a).

While the presence or absence of Al accumulation is of constant occurrence in most families, the character appears to be more variable in the Lecythidaceae and Myrsinaceae. The low number of Al accumulators and the mixed occurrence of positive and negative results may suggest that facultative rather than absolute accumulators occur in these families. The internal Al concentration in facultative accumulators more or less reflects the external soil level and thus may depend on environmental conditions such as soil acidity and availability of soluble Al. It was not possible, however, to consider environmental aspects in this study because precise ecological data on the herbarium specimens studied were not available. Although exact analytical data may help to clarify the sporadic occurrence of Al accumulation, this feature seems to be restricted to *Rapanea* within the Myrsinaceae, and to *Brazzeia* and *Pierrina* within the Lecythidaceae (including Scytopetalaceae).

Furthermore, Al accumulation appears to be absent or very rare in the Ebenaceae and Sapotaceae, since all data based on Chenery's "aluminon" test are negative. The single records of Al accumulation in the Ebenaceae and Sapotaceae include a relatively high Al level of 15 270 mg kg^{-1} in an unidentified species of *Diospyros* (Ebenaceae), while Al concentrations in *Diospyros sumatrana* Miq., *Ganua mottleyana* Pierre ex Dubard (Sapotaceae), and *Palaquium obovatum* Engl. (Sapotaceae) were only slightly above the 1000 mg kg^{-1} criterion (Masunaga et al., 1998). Moreover, Masunaga et al. (1998) proposed a threshold of 3000 mg kg^{-1} to differentiate Al accumulators from non-accumulators.

Table 1 Distribution of Al accumulation in the Ericales; classification is according to Anderberg et al. (2002) and Bremer et al. (2002); data are compiled from Yoshii and Jimbo (1932)[1], Hutchinson (1943)[2], Chenery (1948 a, b)[3], Webb (1954)[4], Masunaga et al. (1998)[5], and own tests; taxa with at least one Al accumulating specimen are printed in bold; if known, the nominator gives the number of Al accumulating specimens, the denominator is the total number of specimens tested; W = Al accumulation in wood, according to Kukachka and Miller (1980)

Family	Genera and specimens tested for Al accumulation
Actinidiaceae	*Actinidia* (0/2)[3]; *Clematoclethra scandens* (Franch.) Maxim. subsp. *tomentella* (Franch.) Y. C. Tang et Q. Y. Xiang, China, Si Chuan, Guan Xian, Menkasnshan, W. Zhang-tao et al. 8700290; *Saurauia oblancilimba* Quisumb., Philippines, Mt. Nañgaoto, Luzon, M. S. Sulit 7686
Balsaminaceae	(0/2)[1]; *Impatiens pallida* Nutt., USA, J. H. Wibbe, BR-S. P. 844 226; *Hydrocera triflora* (L.) Wight and Arn., Sri Lanka, Welisara, Ragama, A. G. Robyns 7260
Clethraceae	(0)[3]; *Clethra lancifolia* Turcz., Philippines, Mt. Bulusan, Sorsogon Province, Luzon, G. E. Edaño and H. Gutierrea 37839; *Purdiaea nutans* Planch., Colombia, Prov. of Ocana, L. Schlim 344
Cyrillaceae	(0/1)[3]; *Cliftonia monophylla* (Lam.) Sarg., USA, Florida, Bay County, Pine Log State, *ca.* 10 miles N of Laguna Beach along FL 79, F. H. Utech 92-014; *Cyrilla racemiflora* L., USA, Texas, Hardin County, P. Fryxell 2997
Diapensiaceae	***Berneuxia*** (1/1)[3]; ***Diapensia*** (1/1)[1]; (1/1)[2]; (2/2)[3]; ***D. lapponica*** L., Canada, University of Sherbrooke, A. Legault and S. Brisson 7786; ***Galax*** (1/1)[2]; (1/1)[3]; *G. aphylla* L., USA, Virginia, Isle of Wight County, R. D. Bray 84 – 27; ***Pyxidanthera*** (1/1)[3]; (1/1)[2]; ***P. barbulata*** Michx., origin unknown, R. K. Godfrey and R. N. White 7099; ***Shortia*** (1/1)[1]; (2/2)[2]; (3/3)[3]; *S. uniflora* Maxim., Japan, Mt. Daihiyama, Yamashiro, H. Kubo, M. Togasi and T. Matsuoka 1336
Ebenaceae	(0/1)[1]; (0/2)[3]; **Diospyros** (2/2)[5]; (0/8)[4]; *D. cargillia* F. Muell., Australia, Camberwarra, A. Meebold 2898; *D. suluensis* Merr., Borneo, Tawao, Elphinstone Prov., A. D. E. Elmer 21204; *D. oubatchensis* Kosterm., New Caledonia, Pouebo, Mandjelia, MacKee 37782; *D. ovalifolia* Wight, Sri Lanka, Madhu Road Sanctary, L. Bernardi 15347; *Euclea crispa* (Thunb.) Gürke, Malawi, Mlanje Mt. Forest, Nyasaland, J. D. Chapman 457; *E. polyandra* (L. f.) E. Mey ex Hiern, South Africa, Bo Kouga, Eastern Cape, R. D. A. Bay 1372; *E. racemosa* Murr, South Africa, Hagelkraal poort, SW Cape, L. Huigo 1593
Ericaceae	*Leucothoe* (0/1)[1]; *Gaultheria* (0/4)[3]; (0/9)[4]; (0/44)[3]; *Rhododendron japonicum* C. K. Schneid., Japan, Honshu, H. Kanai and H. Ohashi 731209; *R. japonicum* Suringar, Japan, Kadzo ranch, Nishinomaki-mura Kanra-gun, Kodsoke, Honshu, S. Kobayashi 16428; *R. vidalli* Rolfe, Philippines, Mt. Data, Luzon, G.L. Alcasid 1838; *R. vidalli* Rolfe, Philippines, Bontoc, Luzon, M. Vanoverbergh 70; *Vaccinium bracteatum* Thunb., Japan, Hondo, Yamamoto in Settsu, M. Togasi 640; *V. bracteatum* Thunb., Japan, Kyushu, Mt. Shira-tahe, Sumo, Shimoagatagun, Tsushima Island, H. Ohashi, H. Ohba and Y. Tateishi 29; *V. dunalianum* Wight, Sikkim, India, J. D. H., BR-S.P. 834 466
Fouquieriaceae	(0)[3]; *Fouquieria shrevei* I. M. Johnst., Mexico, Coahuila, P. Fryxell 3027
Lecythidaceae (including **Scytopetalaceae**)	(0)[3]; *Asteranthos brasiliensis* Desf., Colombia, Rio Guainia, Puerto Colombia, Schultes, Baker and Cabrera 18214; ***Brazzeia*** (3/3)[3]; *B. congoensis* Baill., Democratic Republic of Congo-Kinshasa, P. N. Odzala, Mbandza, D. Champluvier 5275, BR-S.P. 129 736; *B. soyauxii* (Oliv.) Tiegh., Cameroon, N'Kolandom, J. J. F. E. de Wilde 8156; *Eschweilera pachysepala* (Spruce) Mart. ex Berg, Brazil, basin of Rio Madeira, Amazonas, Mun. Humayata, B. A. Krukoff 7116; *Gustavia hexapetala* (Aubl.) A. C. Sm., Surinam, Zanderij I, P. J. Eyma 4370; *Lecythis lanceolata* Poir., Brazil, A. Glaziou 658; ***Pierrina zenkeri*** Engl., Cameroon, Kribi, J. J. Bos 5422; ***P. zenkeri*** Engl., Cameroon, Kribi, J. J. Bos 3856; *Rhaptopetalum coriaceum* Oliv., Nigeria, Ekinta, P. P. C. van Neer, 1110a; *R. evrardii* Germ., Democratic Republic of Congo-Kinshasa, Botsima, D. Matchu-Mandje 1058; *Scytopetalum pierreanum* (De Wild.) Tiegh., origin unknown, Kalina, E. Jans 559; *S. tieghemii* Hutch. and Dalziel, Ivory Coast, Chevalier 33057
Lissocarpaceae	*Lissocarpa* (0)[3]
Maesaceae	*Maesa edulis* C. T. White, New Caledonia, Boësa Island, R. Iserentant 9776; *M. formosana* Mez, Taiwan, Pref. Hualie, Tienhsiang, T. Shimizu and M. T. Kao 10536; *M. japonica* Moritzi and Zoll., Japan, Hondo, Minomo in Settsu, M. Togasi 1261
Marcgraviaceae	*Marcgravia* (0/3)[3]; *Norantea* (0/2)[3]; *N. delpiniana* Wittm., Brazil, Chapéu, Braço Norte, Espirito Santo, G. and M. Hatschbach 597282, BR-S.P. 834 498; *Ruyschia* (0/2)[3]; *Souroubea* (0/1)[3]; *S. corallina* (Mart.) de Roon, Brazil, Amazonas, Mun. São Paulo de Olivença, B. A. Krukoff 8699 a; *S. guianensis* Aubl. subsp. *amazonica* (Mart.) de Roon, Brazil, Amazonas, Mun. Humayta, near Livramento, B. A. Krukoff 6725
Myrsinaceae	(0/4)[1]; (0/8)[4]; (0/15)[3]; *Ardisia pulchella* Mez, Philippines, Mt. Nañgaoto, Luzon, M. D. Sulit 7713; *Discocalyx* sp., Netherlands New Guinea, Kebar valley, *ca.* 100 km N of Manokwari, P. van Royen 3920; *Glaux maritma* L., Iran, Route de Kerman à Bam, J. Léonard 6025; *G. maritima* L., France, Cayeux sur mer Somme, R. Dechamps 3014; *Myrsine capitellata* Wall., Sri Lanka, Handepan Ella Plains, A. Kostermans 28116; *M. guianensis* (Aubl.) Kuntze, USA, Florida, Nixon-Lewis Hammock, J. K. Small and C. A. Mosier 6391; ***Rapanea*** (4/7)[3]; *R. acrosticta* Mez, New Guinea, Morobe District, Yimziang, Clemens 2372; *R. diminuta* Mez, New Caledonia, Paita, R. Schlechter 14915; *R. macrophylla* Mez, New Caledonia, Mt. Humboldt, R. Schlechter 15293; *R. neriifolia* Mez, Japan, Hondo, Irozaki, Idzu, M. Togasi 447; *Tapeinosperma vieillardii* Hook. f., New Caledonia, ou-Hinna, R. Schlechter 15700
Pellicieraceae	*Pelliciera* (0/1)[3]
Pentaphylacaceae	***Pentaphylax*** (3/3)[3]; ***P. euryoides*** Gardner and Champ., Hong Kong, Sha Lo Shan, Wa Mei Tong Village, Sin-Jung District, Y. W. Taam 251; ***P. euryoides*** Gardner and Champ., Hong Kong, Hauce, BR-S.P. 834 465
Polemoniaceae	(0/3)[3]; *Ipomopsis aggregatata* (Pursh) V. E. Grant, USA, Kaibab National Forest, Arizona, Coconino County, G. Thomas Robbins 2190; *Phlox pilosa* L., USA, Piatt County, along Sangamon River, G. N. Jones 13684; *Polemonium occidentale* Greene, USA, Idaho, Lemhi Forest, R. B. Johnson 137
Primulaceae	(0/6)[1]; *Dionysia oreodoxa* Bornm., Iran, Kerman Prov., J. Bornmüller 3873; *Dodocatheon alpinum* (A. Gray) Greene, USA, California, South Lake, J. Bouharmont 8711; *Primula calliantha* Franch., China, Yunnan, District of Chung-tien, J. F. Rock 24643; *P. szechuanica* Pax, China, Djesi-La, Djesi-Longba, J. F. Rock 17713

continued →

Table 1 continued

Family	Genera and specimens tested for Al accumulation
Roridulaceae	(0)[3]; *Roridula dentata* L., South Africa, Cape Province, A. L. Grant 3476; *R. gorgonias* Planch., South Africa, Vogelgat, R. Schlechter 9546
Sapotaceae	(0/2)[1]; (0/12)[4]; *Argania spinosa* (L.) Skeels, Morocco, Cap Rhiz, Tamri, J. Lewalle 6909; *Beccariella baueri* (Montrouz.) Aubrév., New Caledonia, Lukuma, Ngoye, R. Schlechter 15260; *Englerophytum kennedyi* Aubrév., Cameroon, Buea-Douala, D. Thomas 2248; ***Ganua*** (1/1)[5]; *Isonandra* sp., Sri Lanka, near base of Adamspeak rock, Maskeliya, trail from Moray Estate, A. Kostermans 27571; *Labourdonnaisia madagascariensis* Pierre ex Baill., Madagascar, Antalaha, between Amelabe, and Ambohitralanan, R. Capuron 27747-SF; *Lecomtedoxa klaineana* (Pierre ex Engl.) Dubard, Gabon, Ogooue-Maritime, Setté Cama, G. McPherson 16835; *Madhuca* sp., Borneo, Tawao, Elphinstone Prov., A. D. E. Elmer 21571; *M. fulva* (Thwaites) J. F. Macbride, Sri Lanka, Kanneliya forest near Hiniduma, Galle District, Kostermans 27630; *M. sericea* (Miq.) H. J. Lam, Sumatra, Masihi Forest Reserve, Asahan, East Coast, B. A. Krukoff 4144; *Manilkara decrescens* T. D. Penn., Brazil, Rod. BA-365, Mun. Buritizeiro, Minas Gerais, G. and M. Hatschbach and J. M. Silva 62052; *Mimusops subsericea* Mart., Brazil, Herbarium Martii, Galeottii, BR-S.P. 834 484; *Omphalocarpum bomanehense* De Wild., Democratic Republic of Congo-Kinshasa, Gimbi Vallée de la Fuka, L. Toussaint 437; ***Palaquium*** (1/1)[5], *P.* sp., Sri Lanka, Botanic Garden of Peradeniya, Kostermans 27515; *P. canaliculatum* (Thwaites) Engl., Sri Lanka, Red Cliff on seacoast near Weligama, A. Kostermans 28565; *Pouteria reticulata* (Engl.) Eyma subsp. *surinamensis* T. D. Penn., Surinam, BR-S.P. 834 483; *Pradosia lactescens* (Vell.) Radlk., Brazil, Rio Pequeno, Mun. Antonina, Paraná, G. Hatschbach 41775; *Sideroxylon buxifolium* Hutch., Sultanate of Oman, Wadi Mistal, Habish, S. A. Ghazanfar 1944; *S. lanuginosum* Michx. subsp. *rugidum* (A.Gray) T. D. Penn., Mexico, Monterey, C. G. Pringle 4506; *Synsepalum dulcificum* (Schum. and Thonn.) Daniell, Sri Lanka, Bot. Garden Peradeniya, A. Kostermans 27359; *Tridesmostemon claessensi* De Wild., Democratic Republic of Congo-Kinshasa, Yangambi, C. Donis 3388; *Vitellariopsis kirkii* (Baker) Dubard, Tanzania, Tanga Prov., Mkaramo, Mkwaja, R. E. S. Tanner 3176
Sarraceniaceae	(0/1)[3]; *Darlingtonia californica* Torr., USA, California, Mt. Eddy, Siskiyou County, E. B. Copeland 3812; *Sarracenia psittacina* Michx., USA, Georgia, St. Mary's, Rugel 14
Sladeniaceae	*Sladenia* (0/1)[3]; *Ficalhoa laurifolia* Hiern, Zambia, Isoka district, A. Angus 802
Styracaceae (including Halesiaceae)	(0/7)[3]; *Alniphyllum fortunei* Makino, China, Jiangkou Xian, Mt. Fanjing Shan, Sino-American Guizhou Botanical Expedition 945; *Bruinsmia styracoides* Boerl. and Koord., New Guinea, Geelvinckbaai, N.E. Coast Japan Isl., Woda, Ch. Koster BW 11240; *Halesia carolina* L., USA, Creek bank, Gap Creek Road, River Falls, South Carolina, Greenville County, N. E. Mullens and C. L. Rogers 67036; *H. diptera* L., USA, Possum and Teal Islands, Savannah River, South Carolina, Jasper County, S. W. Leonard 2655; *Sinojackia rehderiana* Hu, China, Yizhang, Hunan, S. H. Chen 1947; *Styrax glabratum* (Spruce) Schott, Brazil, Paraná, Pontal do Sul, Mun. Paranaguá, Hatschbach and A. R. Campos 59759; *S. pulverulenta* Michx., USA, Florida, near Jacksonville, A. H. Curtis 1768; *S. warscewiczii* Perkins, Costa Rica, J. J. Cooper 10321
Symplocaceae	***Symplocos***[2]; (6/6)[1]; (141/142)[3]; (8/8)[4]; W; ***S. guianensis*** (Aubl.) Gürke, Guyana, J. C. Lindeman 6564; ***S. itatiaiae*** Wawra, Brazil, Santa Catarina, Serra da Boa Vista, São José, Reitz and Klein 9858
Ternstroemiaceae	***Adinandra*** (21/24)[3]; *A. dumosa* Jack, Sumatra, Masihi Forest Reserve, Asahan, East Coast, B. A. Krukoff 4255; *Anneslea* (0/2)[3]; *Archboldiodendron* (0/1)[3]; ***Cleyera*** (5/6)[3]; ***Eurya*** (2/2)[1]; (1/1)[2]; (21/21)[3]; (1/1)[5]; ***E. acuminata*** DC., Sumatra, Hoeta Padang, Asahan, East Coast, B. E. Krukoff 4404; ***E. chinensis*** R. Br., Sri Lanka, Thwaites 784, BR-S.P. 834 450; ***Freziera*** (12/16)[3]; ***F. undulata*** (Sw.) Willd., Grenada, W. E. Broadway 4474z; ***Symplococarpon*** (2/2)[3]; ***Ternstroemia*** (0/1)[1]; (1/2)[4]; (7/89)[3]; ***T. japonica*** Thunb., Japan, Honshu, Mt. Kiyosumi in Awa, N. Naruyama and K. Okamoto 1619; *Visnea* (0/1)[3], *V. mocanera* L. f., Teneriff, Crux de Taganana, Cumbre, J. Bornmüller 927
Tetrameristaceae	*Tetramerista* (0/1)[3]
Theaceae	***Camellia*** (3/3)[1]; (3/3)[2]; (27/27)[3]; W; *Franklinia* (0/1)[3]; ***Gordonia*** (25/32)[3]; (1/1)[4]; (2/2)[5]; W; ***Pyrenaria*** (12/12)[3], W; ***Schima*** (4/10)[3], (1/1)[5], *S. wallichii* (DC.) Choisy, Malaysia, Sarawak, Kuching, Mt. Serapi, J. L. Panero et al. 6267; ***Stewartia*** (1/1)[1], (1/1)[2], (5/5)[3]
Theophrastaceae (including Samolaceae)	(0)[3]; *Clavija longifolia* Ruiz and Pav., origin unknown, Curarina Sacha, J. Schunke-Vigo 12180; *Deherainia smaragdina* (Linden) Decne., British Honduras, Eldorado, Punta Gada, W. A. Schipp 1023; *Jacquinia arborea* Vahl, origin unknown, BR-S.P. 834 503; *J. armillaris* Jacq., Venezuela, Prov. de Caraboba, J. Linden 1553; *Samolus ebracteatus* Kunth, USA, Florida, A. H. Curtis 1811; *S. praviflorus* Raf., Japan, Honshu, Oundari, Torami in Kazusa, K. Hisauchi 1053

The phylogeny of Al accumulation

Although a limited number of species were tested in this study, the consistent presence or absence of Al accumulation in most families of the Ericales is remarkable. The distribution of Al accumulating families was plotted on three trees that are based on recent molecular phylogenetic studies (Anderberg et al., 2002; Bremer et al., 2002; Geuten et al., 2004; Figs. **1–3**). These molecular analyses provide strong support for the following clades: a balsaminoid, primuloid, ternstroemioid (Penthaphylacaceae sensu APG II, 2003), and ericoid group. Non-accumulators seem to characterise the families that constitute the primitive clade of Balsaminaceae, Marcgraviaceae, Pellicieraceae, and Tetrameristaceae. The feature is also absent in the Polemoniaceae–Fouquieriaceae clade, as well as in the well-supported ericoid clade (including Ericaceae, Cyrillaceae, Clethraceae, Roridulaceae, Sarraceniaceae, Actinidiaceae). On the other hand, the Al accumulating families appear to be more or less closely related, but there is no evidence for a single origin of Al accumulation in the order. It should be emphasized that exact interfamilial relationships in Ericales remain unclear and this obviously hinders any discussion on the evolution of the character in this group.

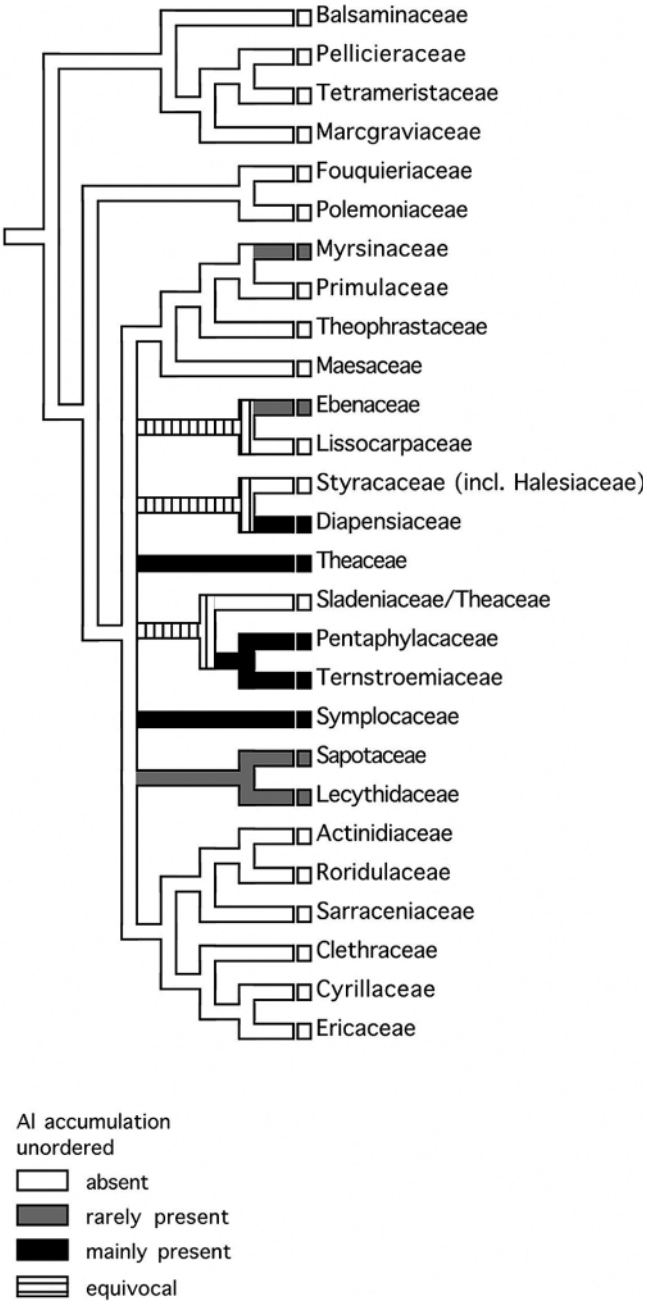

Fig. 1 Distribution of Al accumulation in the Ericales, plotted on the parsimony jackknife tree based on analysis of molecular data from five genes (Anderberg et al., 2002).

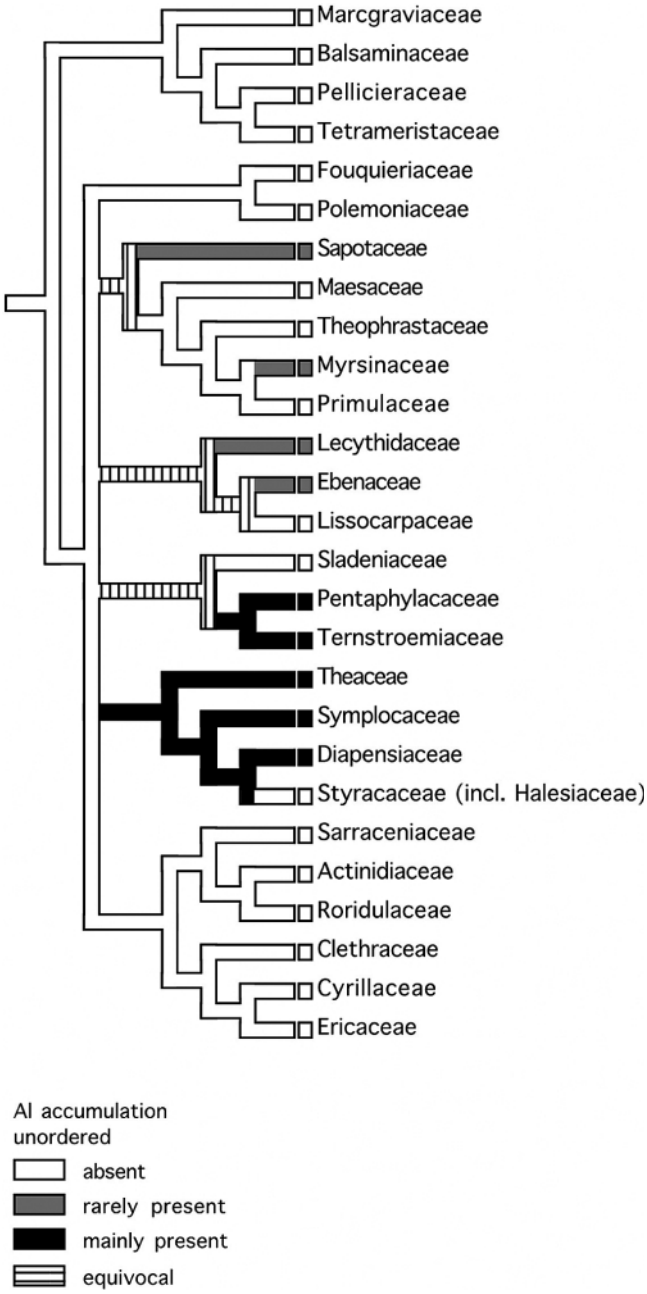

Fig. 2 Distribution of Al accumulation in the Ericales, plotted on the strict consensus tree based on analysis of molecular phylogenetic data from six markers (Bremer et al., 2002)

A possible relation between the Ternstroemiaceae and Pentaphylaceae is supported by the common occurrence of Al accumulation. The Ternstroemiaceae and Sladeniaceae are included in an enlarged Pentaphylacaceae s.l. according to APG II (2003). Al accumulation is absent in *Sladenia* (Sladeniaceae) according to Chenery (1948 b). A lack of high Al levels is also found in *Ficalhoa,* which came out as a sister group of *Sladenia* in the molecular analyses of Anderberg et al. (2002). Therefore, absence of Al accumulation may support the basal position of *Sladenia* and *Ficalhoa* within the Pentaphylacaceae s.l., but non-accumulators are also found within several Ternstroemiaceae.

As far as we know, the highest content of Al recorded in any plant is 72 240 ppm in *Symplocos spicata* Roxb. (Symplocaceae) (von Faber, 1925). The bark and leaf tissues of *Symplocos* species have been used for centuries in traditional dyeing technologies as the high Al levels were used as a mordant instead of alum (Hutchinson, 1943). The taxonomic position of *Symplocos* has recently been discussed in Caris et al. (2002). Geuten et al. (2004) concluded that the Theaceae sensu APG II (2003) are the closest relatives of the Symplocaceae. The occurrence of strong Al accumulation in *Symplocos* may confirm its affinity with the Theaceae. It is clear that Al accumulation in the Theaceae is not restricted to the genus *Camellia,* but also commonly

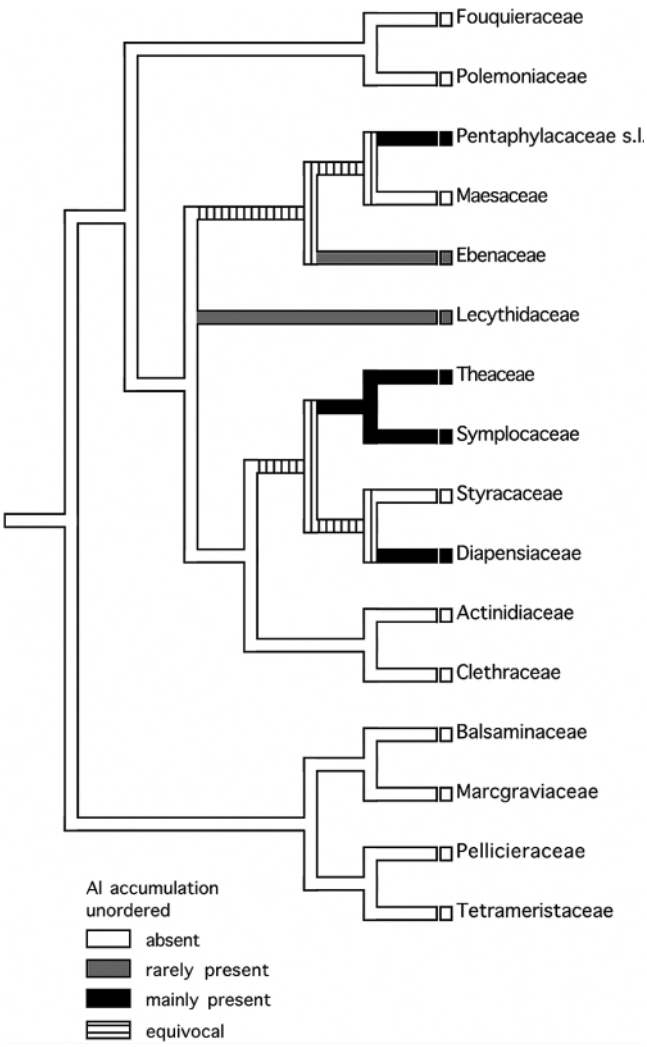

Fig. 3 Distribution of Al accumulation in the Ericales, plotted on the consensus topology of a hierarchical model Bayesian analysis (Geuten et al., 2004); Pentaphylacaceae s.l. include Ternstroemiaceae and Sladeniaceae.

present in *Gordonia, Pyrenaria, Stewartia,* and to a lesser extent in *Schima.*

The majority of Al accumulating plants are woody shrubs or trees from tropical areas (Chenery and Sporne, 1976; Jansen et al., 2002 a, 2004). The Diapensiaceae are remarkable Al accumulators, which include perennial herbs and small shrubs from cold to temperate areas in chiefly alpine regions of North America and Eurasia. Although Al accumulation is seemingly present in all species of this family, the single species of *Shortia* and *Galax* tested were negative. The unusual presence of Al accumulation in this mainly herbaceous family may reflect a possible relationship with other Al accumulating families. Most molecular analyses suggest a strong relationship of the Diapensiaceae with the non-accumulating Styracaceae (Soltis et al., 2000; Anderberg et al., 2002; Bremer et al., 2002; Geuten et al., 2004). While a possible – though weakly supported – sister group relationship of the Diapensiaceae–Styracaceae clade with the Symplocaceae was proposed by Soltis et al. (2000) and Bremer et al. (2002). Geuten et al. (2004) found strong support for a relationship of the Styracaceae–Diapensiaceae with the Theaceae-Symplocaceae (Fig. **3**). Together with the morphological evidence for a relationship between the Symplocaceae and Theaceae, this could lead to the assumption that the strong Al accumulating families Diapensiaceae, Symplocaceae, and Theaceae share a common ancestry. Nevertheless, more studies, both morphological and molecular, are needed to increase support for these relationships.

Contrary to the systematic significance of Al accumulation in the strong accumulating Ericales, there is so far no evidence illustrating that the very rare occurrence of Al accumulation shows any taxonomic significance within the Lecythidaceae (including Scytopetalaceae), Sapotaceae, Ebenaceae, and Myrsinaceae. Although records in the Sapotaceae are restricted to the genera *Ganua* and *Palaquium,* which both belong to the tribe Isonandreae (Pennington, 1991), the Sapotaceae tested here suggest that Al accumulation is absent in this family. Moreover, the Al accumulating genera *Brazzeia* and *Pierrina* belong to the same subfamily, Rhaptopetaloideae (Scytopetalaceae), but absence of Al accumulation in *Rhaptopetalum* suggests that this feature does not characterise the Rhaptopetaloideae entirely (Appel, 2004).

Some ecophysiological aspects of Al accumulation

It has been illustrated that the uptake of high Al concentrations has a beneficial effect on the growth of the tea bush (Chenery, 1955; Konishi et al., 1985; Konishi, 1992; Tsuji et al., 1994). Growth and phosphorus (P) uptake in tea plants are enhanced by Al application in hydroponic culture. Konishi et al. (1985) demonstrated that Al stimulates P uptake under low P conditions and alleviates P toxicity under high P conditions. This suggests that Al plays a regulatory role in the effective uptake and utilization of P. Matsumoto et al. (1976) assumed that the increased growth of tea shoots depends on the positive effect of Al on the roots. Moreover, Chenery (1955) reported that tea plants grown in alkaline soils are very stunted and their leaves are chlorotic. Brushing the leaves with an Al solution, however, results in complete recovery. Therefore, it is clear that Al has some beneficial effect on the shoots of tea plants, but the exact physiological mechanisms remain unclear. It would be interesting to investigate whether this stimulating effect also occurs in other Al accumulating Ericales. At present, similar results have been reported for *Melastoma* (Melastomataceae), *Miconia* (Melastomataceae), *Hydrangea* (Hydrangeaceae), and *Vochysia* (Vochysiaceae), which are all Al accumulating genera (Machado, 1985; Haridasan, 1988; Osaki et al., 1997; Watanabe et al., 1997).

There is usually a clear coincidence between the ability to accumulate and detoxify high internal Al levels in aerial parts of the plant and distribution of substances that have a strong affinity to bind Al. Therefore, tannins, flavonols (e.g., quercetin, myricetin, kaempferol), flavonol-3-ols (e.g., catechin), and anthocyanidins (e.g., delphinidin) may be implicated in vacuolar storage of Al (Barceló and Poschenrieder, 2002). It has been demonstrated that Al is transported through the stem of tea plants as an Al-Fe complex, but is accumulated as an Al-catechin complex in the leaves (Nagata et al., 1992; Liang et al., 1996). Higher levels of Al in the cell walls of tea leaves are also associated with increased levels of Si and Mg (Echlin, 1999).

However, the chemical speciation in other Al accumulating Ericales is entirely unknown.

Also, there could be interactions between Al response mechanisms and mycorrhizal associations in plant roots, of which different types have been found in some families in the Ericales (Shaw, 1987). Ericoid mycorrhizae, for instance, characterise the Ericaceae s.l. (including Empetraceae and Epacridaceae), and arbuscular mycorrhizae have been found in the Clethraceae (Cullings, 1996; Kubota et al., 2001). Mycorrhizae clearly play an important role in calcifuges like the Ericaceae s.l., because they allow them to establish in, and often dominate, acidic environments such as heathlands, ecosystems of low mineral availability, high humic accumulation, and limited nitrogen availability (Read, 1991). Most Ericaceae are exposed to high concentrations of available Al, Fe, and Mn. The regulation of Fe, Cu, and Zn by ericoid mycorrhizal plants has been studied by Shaw et al. (1990) and Bradley et al. (1981, 1982), but very little seems to be known about their effect on Al. Martin et al. (1994) showed that Al was rapidly taken up and accumulated into polyphosphate complexes in the vacuoles of the mycorrhizal basidiomycete *Laccaria bicolor* Marie (Orton). Although there are also reports of enhancement of micronutrient uptake in the shoot by mycorrhizal plants, we suggest that mycorrhizae form an effective external resistance mechanism in several Ericales, especially in Al-excluding representatives of the ericoid clade.

Finally, we understand very little about the functional significance of Al accumulation in plants. Al accumulation does not appear to be an essential strategy, but one of several options that plants may use to deal with Al toxicity in acid soils (Haridasan and Araújo, 1987). It has also been suggested that Al accumulation in leaves may lower the nutritional value for herbivores and thus acts as a chemical defence against animals (Nascimento, 1989, Nascimento et al., 1990).

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