AMBORELLA TRICHOPODA – CULTIVATION OF THE MOST ANCESTRAL ANGIOSPERM IN BOTANIC GARDENS

Bernadette Große-Veldmann[1], *Nadja Korotkova*[2], *Bernhard Reinken*[3], *Wolfram Lobin*[4] & *Wilhelm Barthlott*[5]

ABSTRACT

Amborella trichopoda Baill., the most ancestral angiosperm, has been successfully cultivated in the Botanic Gardens of the University of Bonn in Germany (BG Bonn) for more than a decade. The distribution of this plant – limited to the South Pacific island of New Caledonia – and its cultivation has so far only been achieved in a few botanic gardens. This paper provides details about the cultivation and propagation of *Amborella*, and information on its cultivation in botanic gardens around the world. The authors propose that the collections of this plant in botanic gardens could be used to establish *ex situ* conservation collections.

INTRODUCTION

The Botanic Gardens of the University of Bonn (BG Bonn) have ten years' experience in the cultivation of *Amborella*. The largest plant is 3m tall, flowers consistently and has even produced fruits. It flowered for the first time in 2003 and last flowered in October 2010. Many horticultural observations have been made during this time. The main purpose of this paper is to share our knowledge and experience with the botanic garden community in the hope that it encourages other botanic gardens to cultivate this plant.

TAXONOMY

Amborella trichopoda Baill. was described in 1869 by H.E. Baillon (1869). Because of its similarity to the flowers of *Hedycarya*, he placed it in the Monimiaceae (Laurales). Baillon knew only the male flowers and it was not until some 80 years later that Bailey & Swamy (1948) described the female flowers. In the same year, the genus was placed into its own monogeneric family, Amborellaceae, still in the Laurales (Pichon, 1948). Cronquist (1981) noted that it had several archaic characteristics, such as vessel-less wood, alternate leaves and essentially hypogynous flowers (with stamens, petals and

1. Bernadette Große-Veldmann is a student at the Nees Institute for Biodiversity of Plants, University of Bonn. Address: Nees-Institut für Biodiversität der Pflanzen, Meckenheimer Allee 170, D-53115 Bonn. E-mail: botgart@uni-bonn.de
2. Nadja Korotkova finished her PhD at the Nees Institute for Biodiversity of Plants, and is now a member of the scientific staff at the Botanical Museum, Berlin Dahlem and the Institut für Botanik. Address: Botanischer Garten und Botanisches Museum, Königin-Luise-Str. 6–8, D-14191 Berlin.
3. Bernhard Reinken is a Horticulturist at the Botanic Gardens of the University of Bonn and is responsible for *Amborella.* Address: Botanische Gärten der Universität Bonn, Meckenheimer Allee 171, D-53115 Bonn.
4. Wolfram Lobin is Curator of the Botanic Gardens of the University of Bonn. Address: as above.
5. Wilhelm Barthlott is Director of the Botanic Gardens of the University of Bonn and of the Nees Institute for Biodiversity of Plants. Address: as above.

sepals attached above the ovary). Takhtajan (1997) also regarded Amborellaceae as being the most archaic family within the Laurales and wrote, "*Amborella* is one of the most remarkable living fossils."

This changed following molecular studies in which *Amborella* was found to be sister to all other angiosperms (Qiu *et al*., 1999; Soltis *et al*., 1999). This placement as the most basal angiosperm was confirmed by subsequent molecular phylogenetic studies (Borsch *et al*., 2003; Mathews & Donoghue, 1999; Soltis *et al*., 2008).

In 2003 the APG classification recognised *Amborella* as a monotypic family, Amborellaceae, within its own order, Amborellales (APGII, 2003; APGIII, 2009). Its new placement caused the species to become very well-known within the botanical establishment.

The basal position of *Amborella* and the assumed plesiomorphic, or ancestral, state of many of its characters resulted in a further study of various aspects of its biology, such as flower morphology and anatomy (Buzgo *et al*., 2004; Endress & Igersheim, 2000; Posluszny & Tomlinson, 2003; Thien *et al*., 2003; Williams, 2009; Yamada *et al*., 2001).

Amborella was not known in cultivation before 1980 and is still rare in cultivation today. To the authors' knowledge, a small number of botanic gardens currently grow *Amborella* and only three plants have flowered in cultivation (Appendix 1). The cultivation and *ex situ* conservation of this plant species is considered to be important at BG Bonn.

DISTRIBUTION

Amborella is endemic to New Caledonia, a French dependent territory forming an archipelago in the South Pacific, off the north-east coast of Australia. It is one of the smallest – although still very important – centres of biodiversity, in which very high levels of vascular plant endemism are found (Kier *et al*., 2009) with 76 per cent of the 3,063 native plant species being endemic (Jaffré *et al*., 1998). Furthermore, New Caledonia has 108 endemic plant genera and 5 endemic plant families: Amborellaceae, Paracryphiaceae, Phellinaceae, Oncothecaceae and Strasburgeriaceae.

Amborella only occurs on the main New Caledonian island of Grande Terre. It grows in the understory of wet evergreen forests from about 100m to 1,000m above sea level, but most plants have been found at altitudes of between 500m and 800m. The main locations are Sarraméa (Plateau de Dogy, Col d'Amieu), Tchamba (Haute Tchamba) and Touho. A distribution map is shown in Fig. 1.

New Caledonia is situated between 20° and 23° latitude south and has a tropical climate which is modified by south-easterly trade winds. The temperature at about 300m ranges from 16°C to 24°C during the year. The highest precipitation occurs from January to March, whereas September, October and November are the driest months (Golte, 1993). A climograph of a representative habitat of *Amborella* is illustrated in Fig. 2.

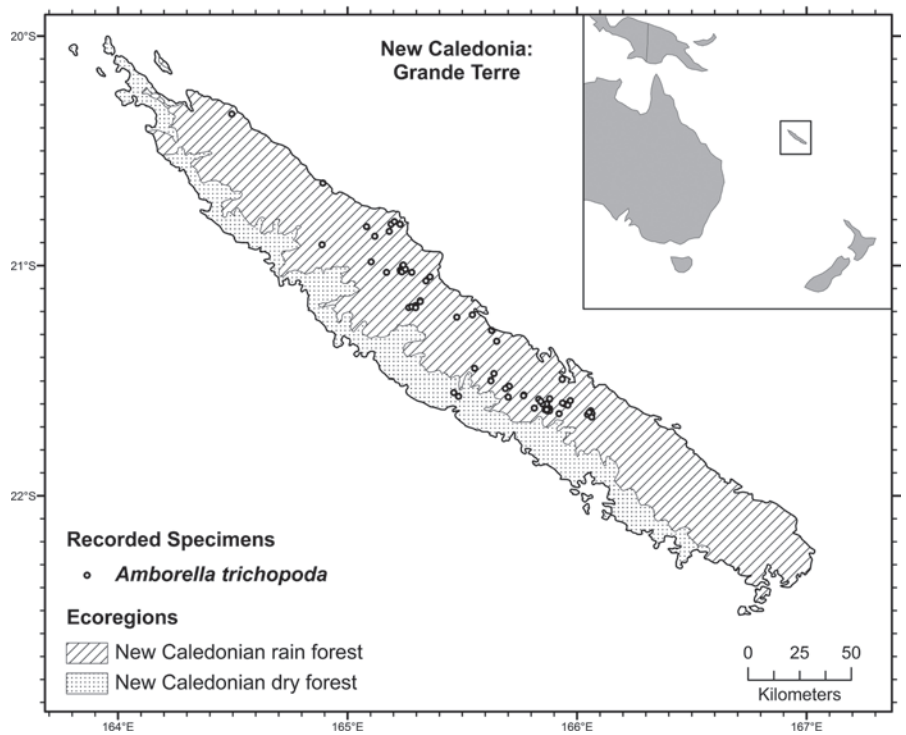

Fig. 1 Distribution map of *Amborella trichopoda.* Data sets taken from: Herbier de Nouvelle-Calédonie, Tropicos and Muséum nationale d'Histoire naturelle, Paris. Map drawn by: Laurens Geffert and Jens Mutke.

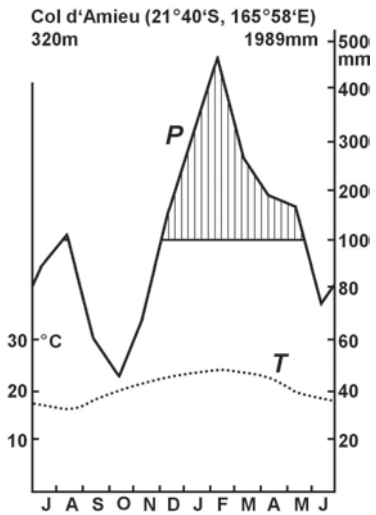

Fig. 2 Climograph with precipitation (P) and temperature (T) for Col d'Amieu, Grande Terre, New Caledonia. After Golte (1993) (used with permission).

Threats to Amborella *in the wild*

The already limited habitat of *Amborella* is threatened. Among the main threats are natural hazards such as bush fires, and anthropogenic impacts such as road building, logging and mining. Because of an abundance of rare metals, mining is the country's main source of revenue (Jaffré *et al*., 1998). Furthermore, the introduction of exotic species has become a serious problem for New Caledonia where about 800 neophytes currently compete with native species (Gargominy *et al*., 1996).

Conservation of Amborella

Ex situ conservation of this species is required. Since it has awakened great interest in the flora of New Caledonia, conservation efforts on New Caledonian plants are increasing (Husby *et al*., 2010). In New Caledonia, *Amborella* is currently propagated and cultivated in at least one nursery as well as in the Institut Agronomique Néo-Calédonien (Chad Husby, pers. comm.). However, cultivation in botanic gardens is still rare. Further cultivation in managed collections would act as a contribution to its conservation.

DESCRIPTION

Habit and vegetative morphology

In its natural habitat the species grows up to 8m tall (Jérémie, 1982), whereas at BG Bonn the plant has reached a height of 3m and a width of about 2.5m (noted in 2011), making it almost certainly the largest specimen in cultivation (see Fig. 3).

The plant flowers consistently more or less every year; however, the actual month is not predictable and varies from one flowering event to the other. These have been noted in November 2003, August 2008, December 2009 and October 2010. Most recently the plant flowered for three months and produced fruits.

Plant form: Medium-sized shrub; semi-self-supporting; maintaining its upright habit by leaning against the surrounding vegetation (Thomas Speck, pers. comm.); *stems* divided in two branches at ground level, one 9.5cm, the other 10cm in diameter; numerous lateral scandent branches; new shoots mainly emerge at the terminal part of the branches. *Leaves*: evergreen; alternate; coriaceous; oblong-lanceolate; tip slightly acuminate, base obtuse; petiole up to 1cm; venation reticulate lamina 10(–16)cm × 4(–6) cm; stipules absent; leaf margin slightly incurved, undulate and serrate; leaf tip slightly recurved; marginal teeth allow the plant to hook into other branches or other plants (see Figs 4 & 5). *Inflorescence*: Cymose; up to 2.5cm long; numerous inflorescences arise from one leaf axil which gives the plant a bushy appearance; the bud is about 2mm in diameter before opening; 2 usually 5 flowers per inflorescence; inflorescences of the basal branches of the plant open first (see Figs 5 & 6).

Flowers: Small; dioceous; spiral; greenish to whitish; nocturnal scent absent; open at day and night. Female flowers: 3–5mm in diameter; tepals whitish to slightly greenish

Fig. 3 *Amborella trichopoda* specimen growing at BG Bonn. Photo: Wilhelm Barthlott.

Fig. 4 *Amborella trichopoda* branch showing the alternate leaves and flowering axillary inflorescence. Photo: Wilhelm Barthlott.

Fig. 5 *Amborella trichopoda* stem showing the undulate leaf margin and cymose inflorescence. Photo: Wilhelm Barthlott.

Fig. 6 Cymose inflorescence of *Amborella trichopoda* with male flowers. Photo: Wilhelm Barthlott.

with a white margin; staminodes whitish; ovaries greenish; stigma whitish to yellow; 7–8 tepals; 4–6, mostly 5 carpels; ovary pitcher-shaped; 0–3, mostly 2 staminodes, large, with two thecae, thecae with two pollen sacs (see Fig. 7). Male flowers: tepals greenish; stamens: filament greenish, anther whitish; 10–14 stamens; outer stamens larger than the inner ones; filament broad flat; anther pointed with four pollen sacs in two thecae (see Fig. 8).

Fruits: Oval, 8–10 × 6–8mm, green when immature, ripening to red (Endress & Igersheim, 2000).

The plant at BG Bonn developed fruits for the first time after the recent flowering period in December 2010. These were green at the end of March 2011. The authors believe these to be the first fruits ever to develop in cultivation (see Fig. 9).

Dioecy and sex change

Male flowers were observed when our plant flowered for the first time. During the subsequent flowering events, the flowers were either functionally male or functionally female with rudimentary male organs. The functionally female flowers had up to three staminodes that were empty, that is, no pollen was found. Our observations are confirmed by previous studies of Buzgo *et al.* (2004), Endress (2001), Endress & Igersheim (2000) and Thien *et al*. (2003).

Fig. 7 Female flower of *Amborella trichopoda*; one staminodium can be seen. Photo: Katja Rembold and Eberhard Fischer.

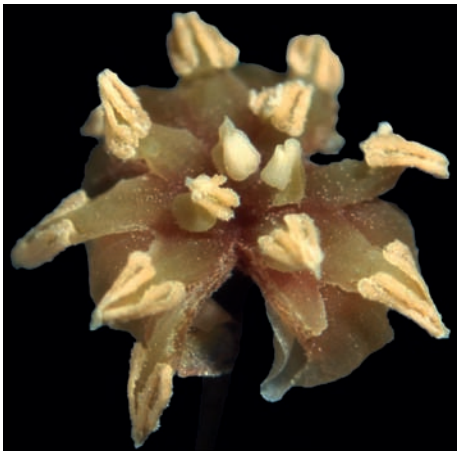

Fig. 8 Male flower of *Amborella trichopoda*. Photo: Wilhelm Barthlott.

Fig. 9 Young fruit of *Amborella trichopoda* at BG Bonn. Photo: Annie Schulz.

CULTIVATION

The cultivation of *Amborella* is fairly straightforward in a cool glasshouse. Temperature appears to be the most important factor for successful cultivation. High temperatures (above 25°C) should be avoided because they increase the occurrence of fungal infections. Changes in air humidity have a negligible effect.

At BG Bonn the plant has been grown in three environments to find out where it grows best; these are a temperate glasshouse with a minimum temperature of 13°C, a conservatory with a minimum temperature of 10°C and outside during the summer months. *Amborella* grows well under all of these conditions but the best results were achieved by growing it in the Fern House between large tree ferns such as *Cyathea* sp. and *Dicksonia* sp. The average temperature in this glasshouse is 16–18°C.

In summer the plants grow well outdoors. The city of Bonn is situated in the winter hardiness zone 8 with an average annual temperature of 9.5°C (the January average is 5.9°C and the July average 17.4°C). The plants do not grow well in direct sunlight, so they are placed either between other larger plants or in a shaded place, as they are in the Fern House. In winter, plants are brought inside and kept in a cool conservatory with a minimum temperature of 10°C.

The compost in which the plants are grown is a peat-based mixture of 60 per cent Einheitserde® ED73, 20 per cent pumice and 20 per cent lava. Einheitserde® ED73 consists of 70 per cent peat and 30 per cent claydust with pH 5.8 and fertiliser with a N:P:K ratio of 14:16:18 plus a slow-release fertiliser with a N:P:K ratio of 20:10:15. Fertiliser is applied every two weeks, increasing to weekly in the height of summer. We use Wuxal® super 8/8/6, consisting of 8 per cent N, 8 per cent K and 6 per cent P at a dilution rate of 0.2 per cent of product in the irrigation water.

Pests and diseases

The most significant problem is the oomycete *Pythium splendens* Braun (identified by E.-C. Oerke and U. Steiner, Institute for Plant Diseases, University of Bonn, pers. comm.), which regularly infects the plants. The fungus is distributed worldwide and is also found in New Caledonia (Huguenin, 1966). The plant at BG Bonn was infected by this fungus for the first time in 2003 during a very hot summer. The fungus thrives in warm temperatures; its optimal temperature is 38°C. In low temperatures it is not dangerous for the plant. The fungus can be controlled by the fungicide Aliette® that contains 746g/kg fosetyl (as Al-salt 800g/kg). Plants are spaced so that they are not touching each other and so that the fungus is not transmitted between plants. To prevent infections after pruning, the cutting areas – especially those of the larger branches – should be rubbed with charcoal powder.

Propagation

Two propagation methods can be used for *Amborella* – cuttings and seeds. Propagation by seed has been successful at several botanic gardens (see Appendix 1). The largest specimen at BG Bonn has now developed fruits, but at the time of writing in May 2011 they have not ripened.

Vegetative propagation is most frequently used at BG Bonn. Both soft tip and semi-ripe cuttings are possible, but it has been found that soft tip cuttings with 2–3 leaf

pairs are most successful. It is important that the cutting material is completely free of disease and the stems of the stock plant from which the cuttings were taken should be disinfected immediately after cutting with charcoal powder to prevent the entry of pathogens to the cuts. Once ready for insertion the cuttings should be treated with a rooting hormone containing 3-indole butyric acid. After this, the cuttings can be inserted into 9cm clay pots, either singly or in groups. The number of cuttings per pot does not have a bearing on subsequent growth. The compost used for rooting cuttings is the same peat-based mix that is used for adult plants. The cuttings should be placed in a humid atmosphere and this is best achieved using a mist unit. The first roots grow in 12–14 weeks, but it takes almost one year for them to develop sufficiently to be removed from the frame and potted on into larger pots.

CONCLUSION

Appendix 1 shows that *Amborella trichopoda* is currently cultivated in at least six botanic gardens. From information obtained from botanic gardens across the world it can be seen that under the right conditions this species can be cultivated in botanic gardens; it flowers regularly and develops fruits. The authors consider this to be a good basis from which to establish *ex situ* conservation collections of the most ancestral angiosperm.

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APPENDIX 1: OVERVIEW OF WORLDWIDE CULTIVATION SUCCESS OF *AMBORELLA*

The authors contacted some large botanic gardens in Europe and USA to find out whether they have cultivated the plant and what their horticultural experiences were. For valuable information we would like to thank Stéphane Buord (Conservatoire botanique national de Brest), Peter Endress (Botanic Garden, University of Zurich), Andreas Franzke (Botanic Garden, University of Heidelberg), William Friedman and Thomas J. Lemieux (Botanic Garden, University of Colorado), Marc Hachadourian (New York Botanic Garden), Dylan P. Hannon (Huntington Botanical Gardens), David Lorence (National Tropical Botanical Garden, Hawaii), Christoph Neinhuis and Barbara Ditsch (Botanic Garden, University of Dresden), Doug Soltis (Botanic Garden, University of Florida), Tim M. Upson (Cambridge University Botanic Garden) and Volker Wissemann (Botanic Garden, University of Gießen). To our knowledge, the following botanic gardens currently cultivate or have cultivated *Amborella*.

EUROPEAN BOTANIC GARDENS

Botanic Gardens, University of Bonn, Germany

Received two cuttings in 2000 from University of California Botanical Garden (Berkeley), California. The material has been propagated and two big plants and a number of small cuttings exist.

Material has been given to:

Botanic Garden, University of Gießen, Germany. Received a rooted cutting on 1 October 2009; a functionally female plant flowered. It is 20cm high and 30cm wide.
Botanic Garden, University of Göttingen, Germany. Received a rooted cutting on 17 December 2010.
Botanic Garden, University of Heidelberg, Germany. Received cuttings in June 2008; during the first three months they rooted and developed well, and plants flowered. Later, however, they all began to die. On 26 October 2010 received a plant.
Botanic Garden, University of Zurich, Switzerland. Received cuttings on 5 October 2006 and 18 November 2008; plants died after a year.
Cambridge University Botanic Garden, UK. Received cuttings; one survived for about six months but no plants remain alive now.
Conservatoire botanique national de Brest, France. Received a plant on 4 October 2010.
Royal Botanic Gardens Kew, UK. Received a plant on 4 October 2010.

Botanic Garden, University of Dresden, Germany

Received seeds from New Caledonia from F. Müller in Dresden Botanic Garden, on 20 September 2003. Three to four germinated and flowered, but no living plants exist today.

Botanic Garden, University of Zurich, Switzerland

Received material from University of California, Santa Cruz, October 1979 and seeds from New Caledonia 1979. Three functionally male plants flowered in 1983 but there are no living plants in the collection today.

Also received cuttings from Botanic Gardens, University of Bonn.

Conservatoire botanique national de Brest, France

Received seeds from the Muséum national d'Histoire naturelle, Paris in 2001. They did not germinate.

Received plants from Botanic Gardens, University of Bonn in 2010.

US BOTANIC GARDENS

Atlanta Botanical Garden, Georgia

Atlanta Botanical Garden successfully cultivates plants.

University of California Botanic Garden (Berkeley), California

Material has been given to:

> Botanic Gardens, University of Bonn, Germany. Received two cuttings in 2000.
> Botanic Garden, University of Florida. Received five plants in 2001 which died in 2005. Received two plants in 2007 which are still alive.
> Huntington Botanical Gardens, California. Received material around 2005. The plant flowered and is a male. It is kept in an intermediate house and grown in a mix of mostly coarse peat, sand and charcoal. It grows well in a shady place.

Botanic Garden, University of Colorado

There are two plants in cultivation but several more have died over the last decade. The material was collected from the wild in New Caledonia.

National Tropical Botanical Garden, Hawaii

Seeds were collected in New Caledonia around 1998. Nearly 50 plants were cultivated in this collection; however, some years ago the plants started to die and in 2010 there were no longer any living plants.

New York Botanic Garden

Material has been introduced twice from New Caledonia. In the first instance plants died soon after introduction. The second occasion, in 2009, used seeds collected in New Caledonia; germination had not yet occurred in 2010.