Trees
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Massive aerial roots affect growth and form of *Dracaena draco*

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Abstract
Key message **Large aerial roots grow out from the branches of injured *Dracaena draco* trees. They integrate with the trunk or cause the branches to break off the tree and deform it.**
Abstract *Dracaena draco*, the dragon tree, is an iconic monocot of the Canary Islands with a tree-like growth habit and some distinctive features that are unique in the plant kingdom. We report about the massive aerial roots in this tree. They appear on trees that are injured or under environmental stress and affect growth form and the whole life of the plant. We analysed the growth of these roots and tested our findings in experiments on plants. Clusters of these roots emerge from the bases of the lowest branches and growing down they may reach the soil. Descending along the trunk, they cling tightly to the trunk, integrate with it and contribute to its radial growth. This may explain (1) why the trunk of a mature *D. draco* tree looks fibrous, as if made of many individual strands, and (2) how some trees reach enormous radial dimensions. Alternately, a large, 2–5 m high, multi-segmented branch with aerial roots at its base, may break off the tree and grow on its own, as a mammoth off-cut, perhaps the largest known in the plant kingdom. This detachment would cause a significant reduction in the size of the crown and deform its original, highly organized pattern of branching. In the extreme condition this may result in the destruction of the mother plant.

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Introduction

The dragon tree, *Dracaena draco,* is a rare relic of an ancient, Mio-Pliocene Southern Tethys flora (Marrero et al. 1998). The plant is endemic to North Africa, Canary Islands, Cape Verde and Madeira (Cabrera Pérez 1999). It is a monocot from Asparagaceae (subfamily Nolinoidae, Chase et al. 2009) with secondary growth, a tree-like habit (Halle et al. 1978) and some distinctive features, unique in the plant kingdom and poorly understood.

A distinctive feature of the plant is the regular rhythm of vegetative growth and flowering that occurs at long time intervals varying from 10 to 11 years (Symon 1974), 10–14 years (Byström 1960) or even 15–20 years (Mägdefrau 1975). The growth pattern gives an umbrella-like appearance to the mature tree, leading to a highly organized canopy consisting of several orders of branches (Byström 1960; Symon 1974, 2000; Mägdefrau 1975) which, in terms of fractal geometry (Mandelbrot 1982), are "self-similar units" (Beyhl 1995, 2001). The modus operandi of *D. draco*, called *Dracoid habitus,* is rare in modern plants (Beyhl 1996) and inspires designing "fractal trees" (http://www.YouTube:fractal trees). For such theoretical tree forms, Beyhl (2013 pers. comm.) proposed the name "dractals".

D. draco attains gigantic size. The so-called "Monster of Orotava", the biggest on record, was 21 m high with a trunk diameter of about 8 m when it was destroyed (Humboldt 1850; Gebauer 2009). "Drago Milenario" (or "El Drago") and "Drago Chico" (Dominguez 2008) are two current giants of Tenerife. For a long time, "Drago

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Milenario" was thought to be the oldest plant alive, until Mägdefrau (1975) estimated its age as ca. 400 years. There are also some other sizeable trees like the one in Los Realejos (Tenerife), with 3.5 m diameter trunk (see Gebauer 2009). The gigantic size is regarded as a curious feature of *D. draco* (Mägdefrau 1975; Symon unpubl. res.). However, the antiquity of the species (Mio-Pliocene origin, Marrero et al. 1998), living on insulated islands in favourable climate and soil conditions and in the absence of predators (the Canary Islands do not have any large, native herbivores) make the authors believe that the massive size of *D. draco* is an expression of island gigantism. In this respect, *D. draco* seems to resemble herbs in the Sakhalin Island (Poberezhnaya and Kopanina 2009) and the well-known giant turtles on the Galápagos Islands and some islands of the Indian Ocean.

The aerial roots are an unusual feature of the *D. draco* tree. There are few data on these roots; they vary in growth form and their biological role is uncertain. In humid places of Cape Verde Islands, the trees grow many soft, ciliated aerial roots covering their branches like a beard, while in drier sites these roots are less numerous, larger and growing mostly from the forking points of the old branches (Byström 1960). In Adelaide (Australia), only some trees have them appearing as "conical woody pegs", usually 15–30 cm long and dormant (Symon unpubl. res). Also with *D. cinnabari* from Socotra Island, which is very similar to *D. draco*, there are some specimens bearing aerial roots and others without them (Beyhl and Mies 2007).

This paper reports the massive, aerial roots in plants growing in Canary Islands and Melbourne, Australia. They emerge from the first set of branches, descend the trunk and may affect many aspects of life of the tree.

Materials and methods

This work is based on direct observations of over 100–120 trees during our three trips to Tenerife and La Palma, Canary Islands (Spain) in July–September 2008–2010. We travelled there surveying *D. draco* trees that we found growing on the streets, in public parks and in the private gardens. We also surveyed about ten advanced trees in Melbourne Royal Botanic Garden and Geelong Botanic Gardens, Geelong, VIC, Australia. We also analysed the photographs of about 15 trees growing in Waite Arboretum and on the streets in Adelaide (Australia) courtesy of Dr. D. E. Symon, as well as those given to us by Mr. Peter Warren of Sydney (from his trip to Canary Islands in 2005) and other photographs available online. Together, we viewed a few hundred *D. draco* plants. Among them, we found about a dozen trees with large, aerial roots growing out of the first generation of branches and have reported on six of them.

To test our findings we performed some experiments on young, potted plants that we have been growing in our farm in Hoppers Crossing, Melbourne. We grew them from seeds, some in the ground and some in small pots. Some had their growing tips removed to encourage branching. Anatomical details of a large aerial root and the trunk, both with the secondary thickening were compared. Tissue samples were taken from one of our plants, thin, microscopic sections were made and analysed under the optical Bios M microscope.

All our photographs were taken with Nikon D300 camera.

Results

Case 1: trees in La Laguna, Tenerife

La Laguna, the oldest city in the Canary Islands, is a home of numerous, ageing *D. draco* trees growing in a variety of environments.

The tree, Fig. 1a, grows in an open, commercial area (Calle St. Antonio X Calle Juana Blanca), is about 6 m tall and has three generations (orders) of branches, so it is about 40 years old. Its columnar trunk (2.1 m perimeter at breast, radius 0.34 m up to its first branching point, 2.6 m high) has many scars covered with resin. A striking feature is the clusters of massive aerial roots emerging off the bases of the primary branches and descending the trunk; Fig. 1b, c. When seen first in August 2008 they were about 0.3–0.9 m long, 0.3 m wide, 0.35 m thick and grew off five of the eight branches. Bonding tightly to the trunk they increased the perimeter from 2.1 to 3 m. The bases of the higher branches also have aerial roots, but they are small and hang down or stick out without aligning with the trunk (Fig. 1d). An individual aerial root emerges from the base of the branch without having a clear border with its base (Fig. 1b, c). At this early stage the individual roots, from adjacent branches, can still be recognized, but later they fuse with each other into massive, irregular clumps, which cover the trunk and overhang from it. The growing front of such a clump contains many smaller, thumb-like projections (Fig. 1e).

The roots are woody and firmly attached to the trunk and seem to integrate with the trunk's tissues. We were unable to separate them by hand. This means that these roots are being incorporated into the trunk, contributing to its radial expansion. The presence of 35 cm-thick aerial roots (Fig. 1b, c) along the trunk would increase the radius of the trunk by a massive 35 cm. This also means that the thickening of this trunk of *D. draco* proceeds from the first

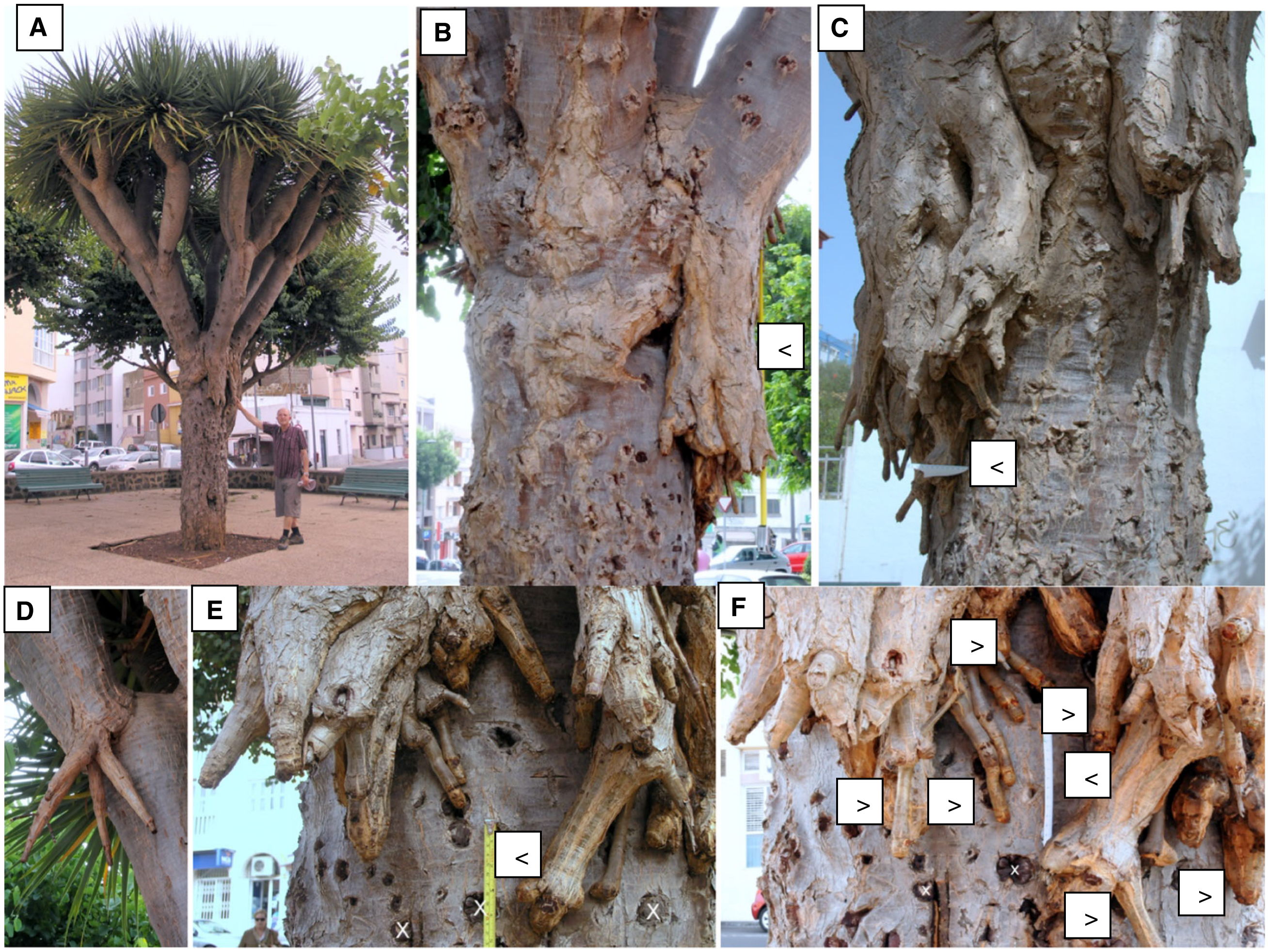

Fig. 1 *D. draco*, La Laguna: Calle St. Antonio x Calle Juana Blanca. **a** Seen from the south side. **b**, **c** *Side views* of the trunk at the branching point with clusters of aerial roots growing off the bases of the first order of branches. **d** Aerial roots growing off the second order of branches. **e** *Front view* of the lowest cluster of aerial roots. *X* shows markings on the bark as reference. **f** The same area 2 years later, with new root growth shown by arrows. *Scale* shown by *left-handed arrows* **b** 1 m, **c** 15 cm, **e** in cm, **f** 12 cm

branching point down, so that the tree in Fig. 1 is at the initial stage of its trunk increment.

To estimate how fast these roots grow, we measured the positions of the tips of three single roots, at the face of one clump in August 2008 and 2010, using marks on the bark as reference points (Fig. 1e, f). They grew down by 5, 7, 8 cm, giving an average of 3.3 cm/year. At this rate, about 75–80 years would be needed for the roots to reach the soil, so it would occur around years 2085–2090.

Two large trees, each about 10 m tall, Fig. 2a, grow in Plaza de la Concepción. They look different, though they seem to have been planted at the same time and grow in similar settings. The crown of one tree (*x* in Fig. 2a) looks like an inverted pyramid. Its six forking points suggest that it is about 70 years old. The crown of the other tree (*y* in Fig. 2b) seems to be falling apart with some of its branches already missing. The trunk of the tree is columnar at the bottom, but much deformed at its branching points (3 m and about 4.5 m high) by the massive clusters of aerial roots (Fig. 2b, c). The upper cluster grows from the bases of five large branches and consists of 1–1.5 m-long roots. At their upper ends, they seem to adhere tightly to the trunk while still sticking out at their growing face, where there are many larger and smaller individual roots (Fig. 2c, d). The lower cluster of aerial roots (Fig. 2b, c) grows down from the two large branches, fully embracing the bases of the branches and clinging tightly to them and to the trunk. The lower part of the clump still shows separated roots. In August 2010 this cluster was 1.9 m long, 60 cm thick (radially) and overlapped almost half of the trunk's perimeter. These two lower branches tilt away from the main trunk and are on the brink of collapse (Fig. 2b). Such collapse (or intentional removal) would cause further destruction of the tree. The two large scars (Fig. 2b) show that some branches have been removed already and, probably, replanted for further growth as individual plants.

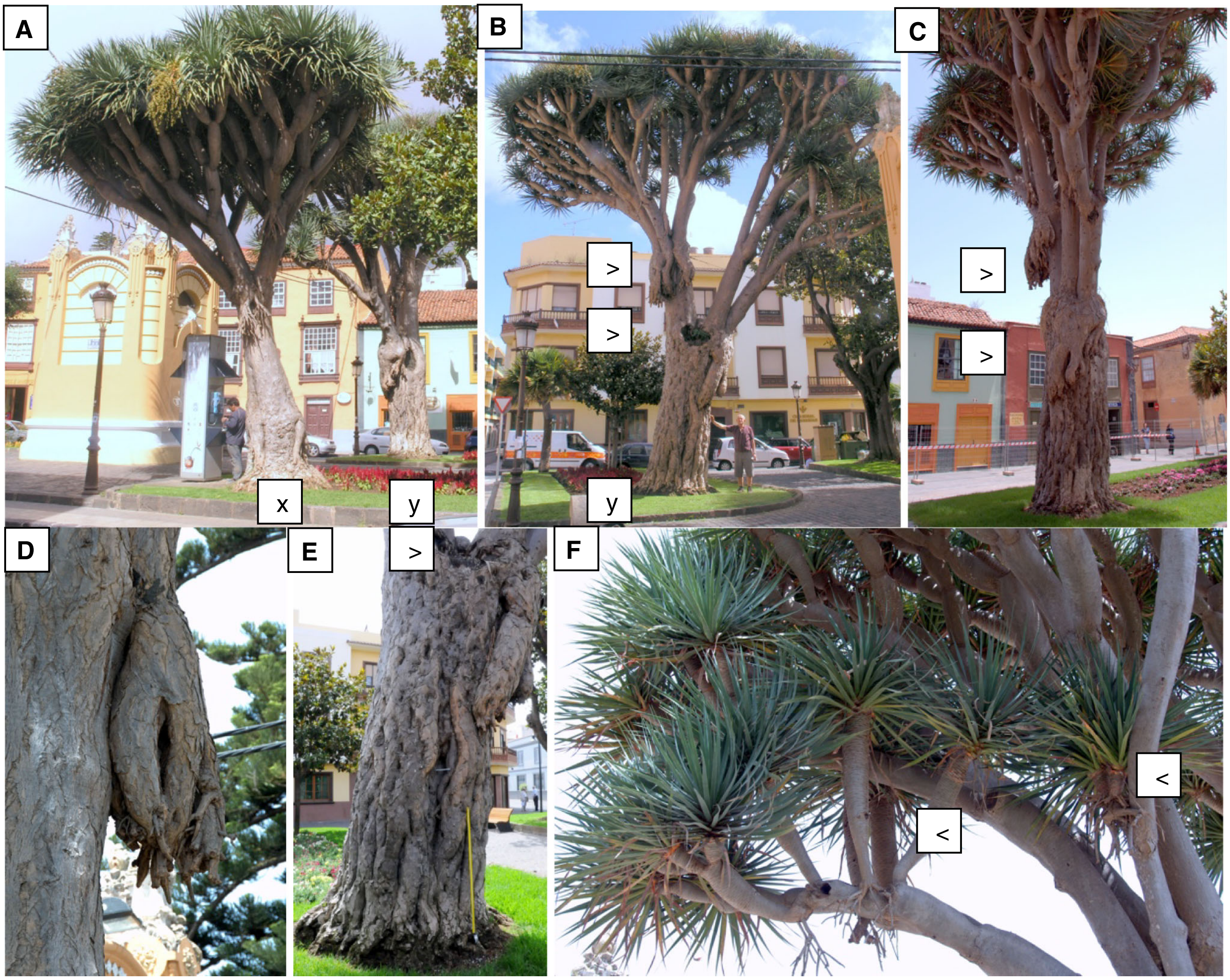

Fig. 2 *D. draco* trees, La Laguna, Plaza de la Concepción. **a** Tree *x* with enlarged trunk base and regular crown; tree *y* with trunk distorted by aerial roots. **b, c** Tree *y* with two groups of branches, each with a clump of aerial roots at its base. **d** The higher clump of aerial roots. **e** The lower cluster of aerial roots, below a large scar (indicated by an *arrow*) left after removal of another branch. **f** Small, vertical branches with aerial root that could partake in vegetative propagation. *Scale* in **e** is 1 m

Many of the air roots growing from the branches, as well as from behind the scar, are imbedded to the trunk's surface. This makes the trunk look fibrous, as if it were made of many longitudinal strands extending to the ground and interwoven with one another (Fig. 2e). Some strands are still separated by long furrows, up to 30 cm deep. The floor of the furrows, as revealed by closer checking, is in fact the surface of the older trunk.

Another striking feature of the tree is a few branches, about 0.3–1 m long, that grow vertically, at odds with the rest of the crown; Fig. 2f. They also have at their bases aerial roots, so that they will be suitable for vegetative propagation after falling to the ground. The branches, though sharing the same genetics, vary in length and in numbers of forking points, to initiate a new generation of offspring that would differ from each other and from their mother plant.

Figure 3a presents the tree in Plaza de la Junta Suprema. It grows close to a tall building, is about 11 m high and its eight to nine branching points implies it is about 80–90 years old. Its striking feature is an asymmetrical crown resembling half of an inverted pyramid with the other half missing. On that "missing" side, at the branching point, there are two large scars. The larger scar (Fig. 3b) is partly covered by a large cluster of aerial roots growing from a nearby branch. It is reasonable to think that the removal of the missing branches may have been associated with the presence of similar large roots on their bases.

The surface of the trunk is fibrous, made of many longitudinal strands that are interwoven with each other or joining each other, still separated by 1–3 cm deep furrows. They originate at the first branching point, below the scars left from the removed branches and descend the trunk.

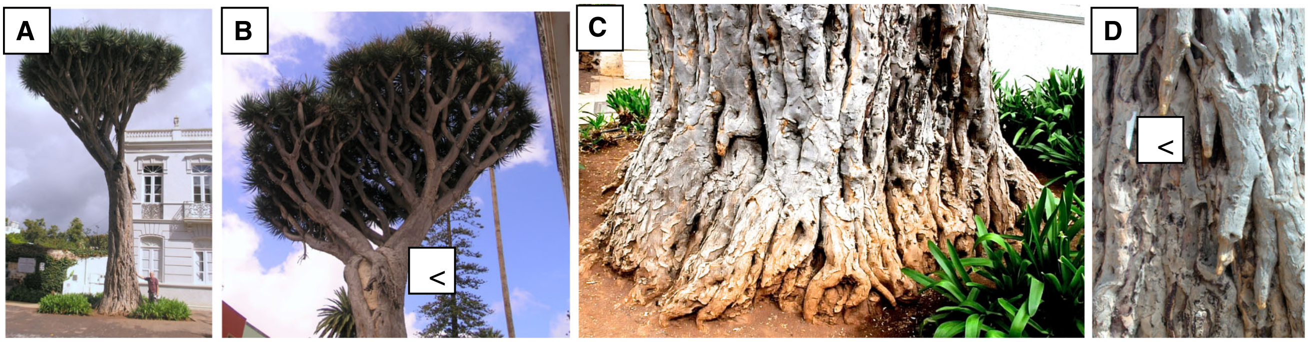

Fig. 3 *D. draco*, La Laguna: Plaza de la Junta Suprema, with half of its crown removed. **a** *Front view*. **b** *Side view* of the crown with a large scar (an *arrow*) partly covered by the aerial roots growing from the branch nearby. **c** The trunk, with aerial roots that have reached the soil. **d** The trunk's surface with longitudinal strands terminating with aerial roots still 0.5 m above the soil. An *arrow* in **d** indicates a 12 cm scale. Photographs were taken in August 2009

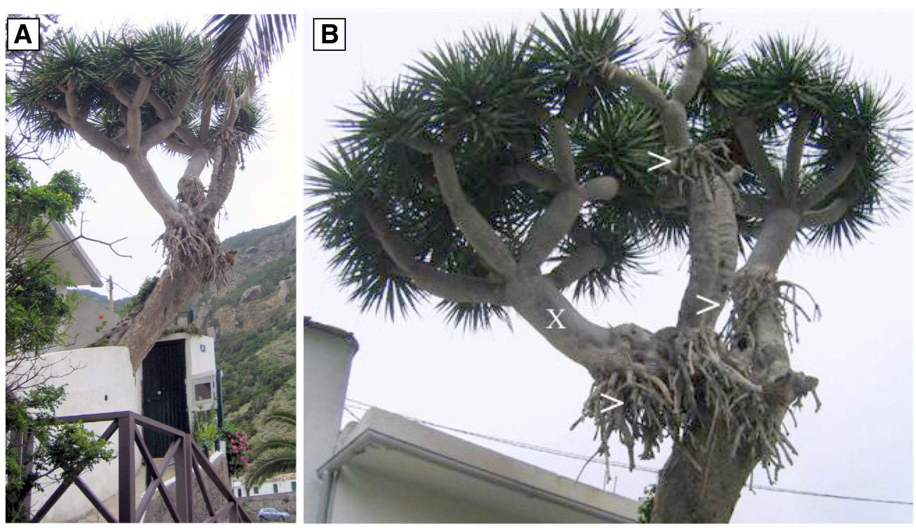

Fig. 4 *D. draco* of Chamorga village, Tenerife. **a** *Side view*. **b** *Front view* of the heavily distorted crown of the tree. *Arrows* indicate aerial roots at the bases of large branches. *X* shows a branch on the brink of collapse. Photographs courtesy P. Warren. Taken in June 2006

Most have reached the ground already (Fig. 3c), while some are still about 0.5 m from it, terminating with the individual roots (Fig. 3d). This may support our belief that they are, in fact, aerial roots that originated from the removed branches and still growing down the trunk.

Case 2: Chamorga village, Tenerife

Figure 4 shows a *D. draco* tree sticking out of a balcony. It has four branching points suggesting its age as about 40–45 years. Its striking feature is the irregular crown with three large branches, each with a mass of aerial roots at the base. One of the branches (*x* in Fig. 4b) appears on the brink of collapse and ultimately will be detached from the trunk by wind, weight, or deliberate removal. On the whole, the crown looks like three massive plantlets attached to the common trunk. Detachment will arise due to the growth and expansion of aerial roots, pushing the branches apart. In this way, the crown of the tree would be completely destroyed.

Case 3: Drago Milenario of Icod De Los Vinos, Tenerife

The legendary tree of Icod is the oldest and largest living *D. draco* tree (Fig. 5a). It has been first mentioned in 1503 (Ommen 2009). It is umbrella shaped, approximately 20–21 m high with a similar spread of the crown. The trunk appears to be made of massive individual strands extending from the branches to the ground (Fig. 5b) with two bulky humps hanging from the branching point (about 13 m high) to the midpoint of the trunk (Fig. 5c). The humps look like enormous clumps of aerial roots. One clump is about 2 m long, 1 m wide (tangentially), 0.6–0.7 m thick (radially) and ends about 4–5 m above the ground. The other clump is similar in radial and tangential directions, while about 0.5 m longer and closer to the ground. The trunk has a few longitudinal cracks going right through the trunk. It widens enormously at the base. The other side of the trunk has a large opening (about 1.65 m high and 0.9 m wide; Fig. 5d), into a mostly

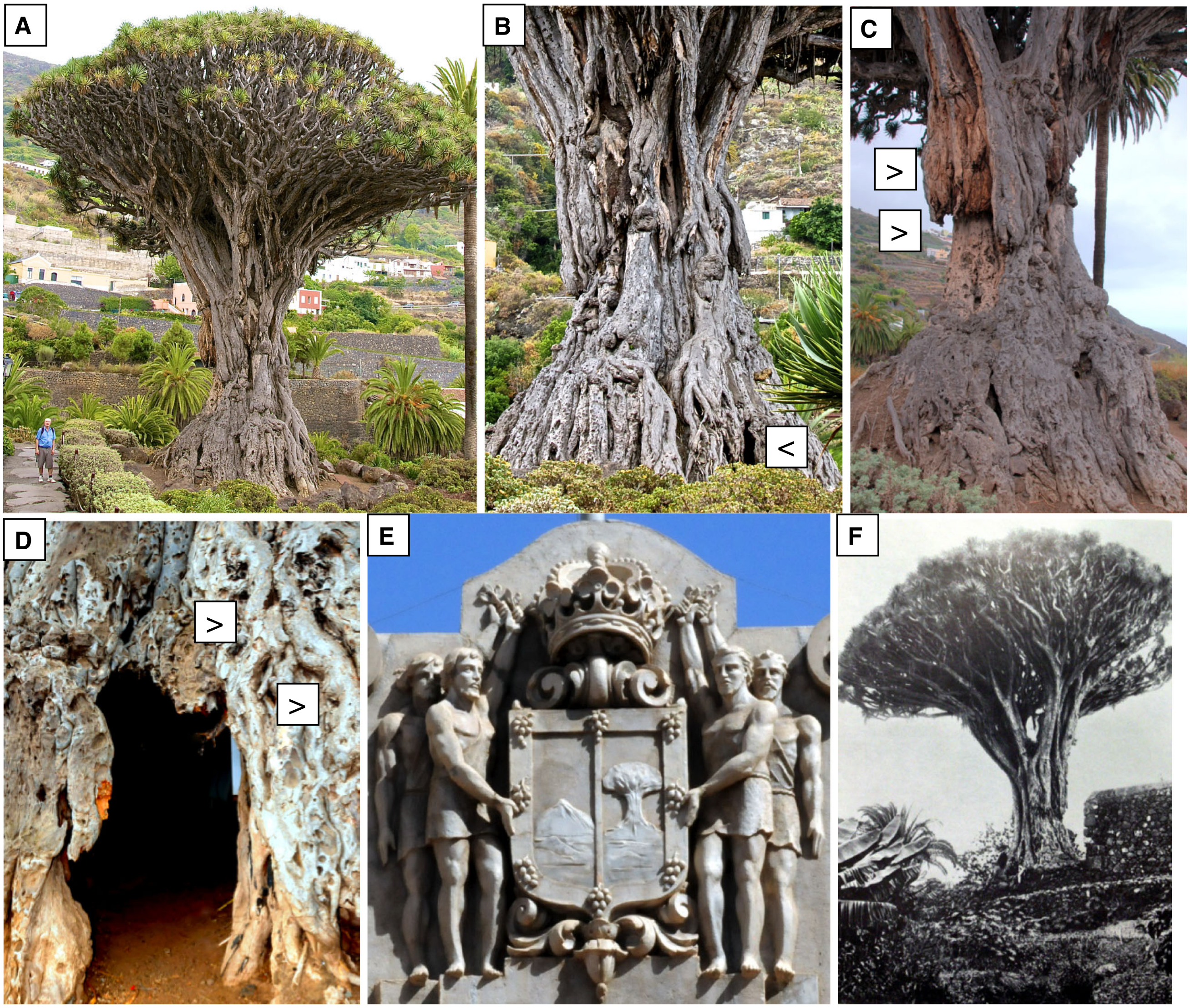

Fig. 5 The "El Drago" of Icod. **a** The trunk with massive aerial roots growing from the branches. **b** Details of the trunk. An *arrow* shows the location of a large opening in the trunk. **c** Two large humps on the trunk (*arrows*) that are massive clusters of aerial roots. **d** Large opening in the trunk surrounded by aerial roots (*arrows*). Some of them have reached the soil. **e** The emblem of Tenerife on the Iglesias San Augustine (built in 1850s) showing the iconic plant. **f** The plant as seen in 1898 (Schenck 1907). Photographs **a**–**e** taken in August 2009

hollow core that is about 4 m in diameter and 4–5 m high. The wall of the trunk, about 30 cm thick, is made mostly of interwoven aerial roots and bark tissues. Most of the aerial roots show connections with the branches higher up and with the soil. The two humps, in 2010, had reached half way towards the tree base.

The question is how long have they been growing? We found an old image of the plant on an emblem of the Canary Islands on the tower of the church Iglesias San Augustine, Icod (built in 1850s). It shows the plant with a smooth trunk (Fig. 5e). This may suggest that the clumps were hardly noticeable in the 1850s. In another photograph of this plant (Fig. 5f) from 1898 by Schenck (1907), there are no bulging humps but smaller and flatter extensions of two large branches. These are, in fact, aerial roots descending the trunk. We also found five photographs of the plant on display at the nearby El Casa del Drago (taken in 1930s, Jose Miranda Diaz, pers. comm.) showing clumps of similar size to those seen today, suggesting negligible growth in the past 80 years.

Case 4: Geelong Botanic Gardens, Victoria, Australia

This tree (Fig. 6a), believed to have been planted in 1869, is the oldest *D. draco* in Australia. It grew in competition

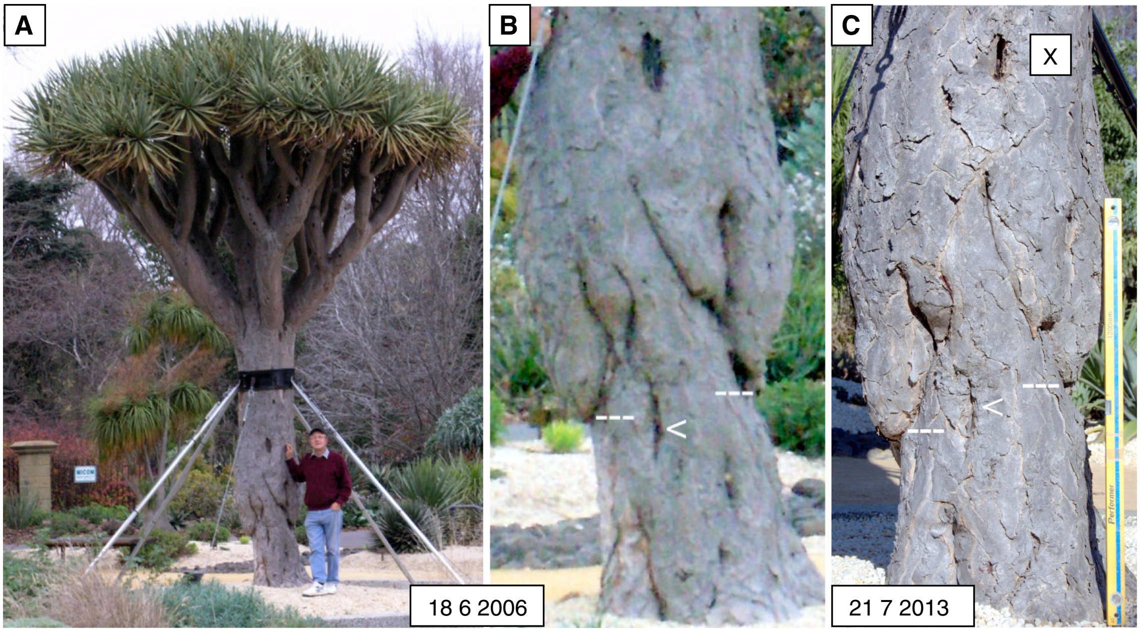

Fig. 6 **a** *D. draco* in Botanic Gardens Geelong, VIC, Australia. On the photograph only four to five branching points can be seen, as the last branches are very short and covered by tufts of leaves. **b** The trunk showing the tips of massive aerial roots. **c** The same trunk 7 years later. *Arrows* in **b** and **c** indicate the fissure in the bark as reference point, dotted lines the position of tips of two aerial roots and *X* in **c** the crevice that is closing. *Scale* in **c** is 1.2 m

with a Phoenix palm (Symon unpubl. res.) until 2000, when it was transplanted in its current location. Its crown forms an inverted pyramid, which may have arisen from seeking light overhead. The trunk swells below its middle, due to the aerial roots growing down. There were four such roots on the south side (Fig. 6b) distant 0.4–0.9 m from the ground level.

Their bases, where they join together, were 0.3–0.4 m wide (tangentially), 0.72–1.04 m long and 0.25 m thick (radially). Table 1 shows some data on the plant when first seen in June 2006.

The aerial roots descend down the trunk, growing separately at their lower ends but joined together at their bases, forming a cylinder that tightly covers the surface of an older, thinner trunk up to the branching point. In some places this cylinder is still being completed. This is seen from a longitudinal crevice (in the middle of the trunk), that, as seen from *x* in Fig. 6c, gets much smaller as it closes in. It is reasonable to conjecture that these roots started growing from the bases of the first set of branches. Looking for signs of growth of these roots, we photographed the same side of the trunk in 2006 and 2013, marking the positions of two root tips in relation to the reference point (a small, longitudinal fissure on the trunk's surface (arrows in Fig. 6b, c). The tips of these roots, in Fig. 6c, are distinctly lower than in photograph 6b, in relation to the reference point. This clearly demonstrates the downwards growth of the aerial roots.

Table 1 Characteristics of *D. draco* in Geelong Botanic Garden (June 2006)

Height	~5.5–6.0 m
1st branching	2.7 m high
Number of 1st order of branches	9
Number of branching points	7–8[a]
Time lapse *b/n* flowering	~20 years
Maximum trunk diameter ~1.2 m above ground	0.83 m
Minimum trunk diameter ~0.27 m above ground	0.59 m

[a] On the photograph in Fig. 6a, only four to five branching points can be seen, as the last branches are very short and covered by tufts of leaves

Case 5: Dracaena Draco Research Farm, Melbourne, Australia

We suspect that large aerial roots might grow in response to environmental stress or physical injury. We tested this conjecture on young plants that we have been growing in Melbourne, Australia. The results are presented in Fig. 7.

A 15-year-old plant grew beside a concrete slab (a). From the side closest to the concrete, a cluster of large aerial roots developed, about 30 cm above the soil. A plant that was kept for 6 years in a small 5 cm pot developed, at its base, many small yet rigid air roots (b). Later, after a deep incision was made in the trunk (b, arrow), it grew similar roots above the scar (c, d). Aerial roots also

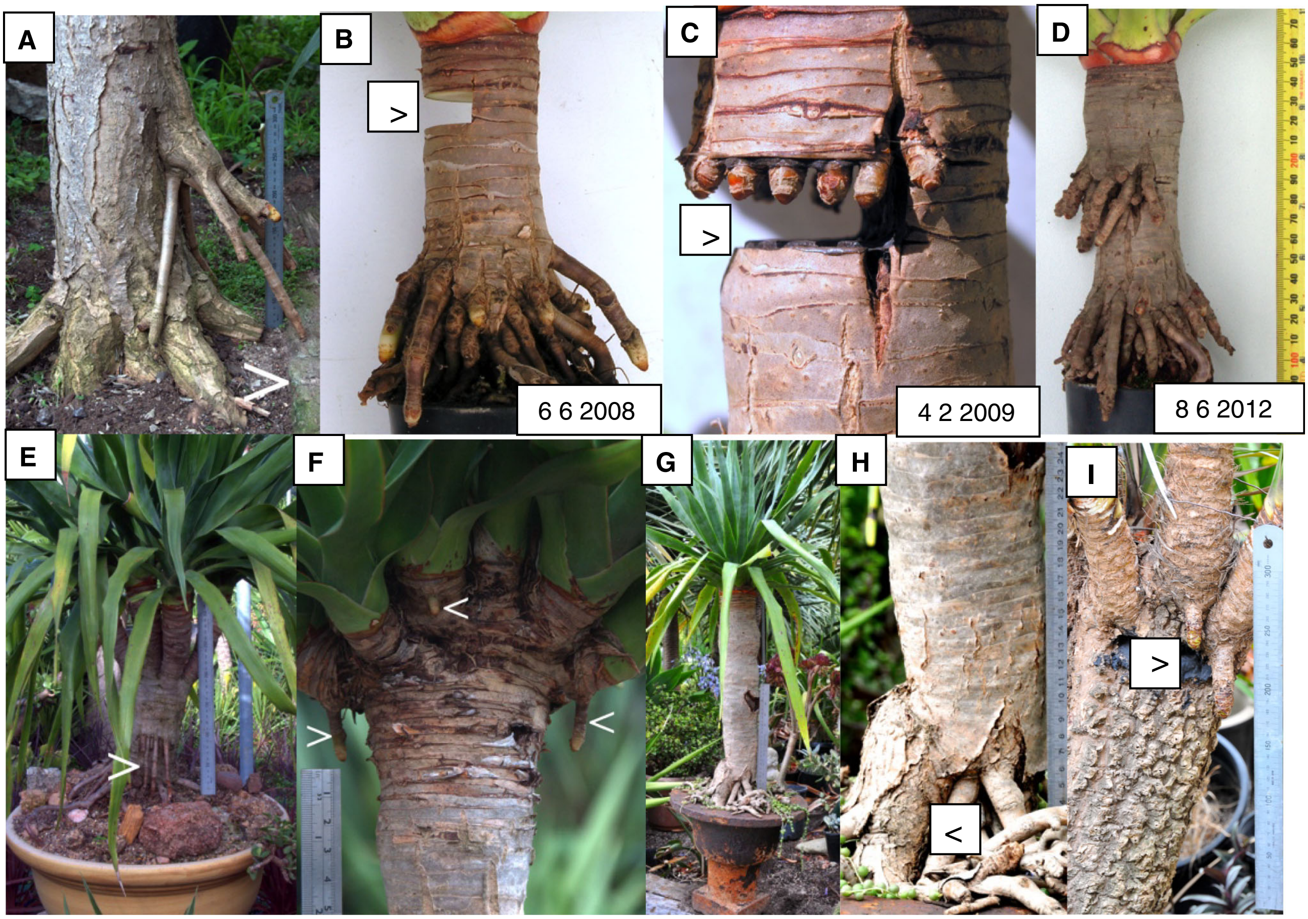

Fig. 7 Growth of aerial roots in traumatic conditions: *D. draco* (**a**–**h**) and *Cordyline australis* (**l**). **a** Large aerial roots growing above the trunk's base from the side close to a concrete slab (an *arrow*). **b**–**d** Aerial roots in a 5-year-old traumatized plant. *Arrows* in **b**, **c** indicate the place from which a half ring of the tissues was removed. Dates when the photos were taken are also shown. **e** Aerial roots (*arrow*) on the trunk of a miniature 7-year-old potted plant. *Scale* 30 cm. **f** Aerial roots on the branches of a 5-year-old plant that was beheaded and forced to branch. **g**, **h** A miniature plant, growing for 16 years in a cast iron vase, with a large root (*arrow*) at the base. **i** *Cordyline australis*: with large aerial roots on the branches after a partial ring barking. *Scale* in cm

appeared in many other plants and only on those that grew in small pots or were damaged. For example, Fig. 6e shows a plant, grown with crowded soil roots that developed aerial roots from its trunk. Figure 7f shows a plant that developed aerial roots at the bases of mini-branches that were induced to grow by beheading. One of our plants that grew without re-potting for 15 years in a small cast iron pot with only about 3 L of soil developed many small aerial roots and one very large one at its base (Fig. 7g, h). All these data indicate that, in response to stress or injury, small *D. draco* plants may grow an abundance of small air roots (Fig. 7b–f), while a full-scale tree can grow large aerial roots (Fig. 7a, g, h).

Similar response to injuries was observed in *Cordyline australis* that like *D. draco* is a monocot with a tree growth habit, although its soil roots are thin (a few mm in diameter) and fibrous. When a deep incision was made and bark tissue below a small branch was removed, extremely large aerial roots appeared from the base of the branches; Fig. 7i. This further supports our view that damage to the trunk in *D. draco* may be a factor in the growth of larger aerial roots.

Discussion

Aerial roots grow off the stems, branches and leaves of many monocots and dicots. They vary in appearance, structure and function (Fahn 1974). In *D. draco* they are rarely reported and little understood. This part will discuss possible factors that are involved in their appearance and their far-reaching effects on the life of this species.

Aerial roots and the ageing of *D. draco* plants

The earliest known plant's image (Clusius 1576; Fig. 8a) does not have any aerial roots, while another old one

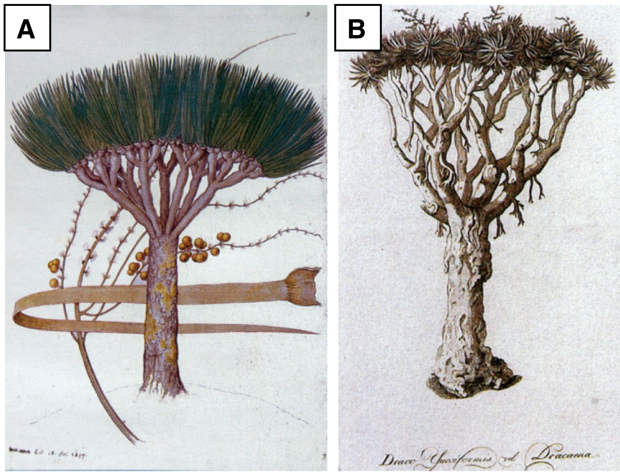

Fig. 8 Early botanical illustrations of *D. draco*. **a** Clusius (1576). Plant with three sets of branches, about 35 to 40 years old. **b** Vandelli (1768). Plant with seven to eight sets of branches, about 80 to 90 years old

(Vandelli 1768; Fig. 8b) shows them in the crown and descending the trunk. The first plant is younger than the second one (3 sets of branches versus 7–8), so it may be alleged that the presence of the roots is related to the plant's age. However, the plant in Fig. 1a is about the age of Clusius' plant and yet has aerial roots like that of Vandelli. Furthermore, in Adelaide, Australia, only some plants of a similar age grow them (Symon unpubl. res.). In Canary Islands, we saw young plants with aerial roots and old ones without them. Clearly then, age is not the only factor in growing these roots in *D. draco*.

Morphing of the aerial roots in response to air humidity

Cape Verdean Dragon trees grow two kinds of aerial roots: small, ciliated and in masses like a beard in humid, foggy places and much larger, hard and less numerous in dry places (Byström 1960). In the dry climate of Adelaide, Australia, aerial roots resemble wooden, peg-like roots, like those in dry places of Cape Verde Islands (Symon unpubl. res.). These data suggest that humid air promotes growing masses of small aerial roots by *D. draco*, like in other species (Meislik 2014).

In the Canaries, the trees we saw had aerial roots, like "wooden pegs". This is puzzling. This Atlantic archipelago would be expected to have humid air and, thus, trees with masses of ciliated, soft roots. It appears, however, that the air here is extremely moist from April to August and very dry from September to March (Marzol et al. 2011). The seasonal growth of these roots is not known, but, if it were limited to dry season, it would bring about growth of wooden peg-like roots.

Byström (1960) noted that older trees grow their successive branches shorter and shorter with fewer and shorter leaves that result in its "desiccated appearance". In such a case, aerial roots would grow in response to a decline in availability of water as according to Lyons (1974), they may absorb moisture from the air.

The role of trauma in the growth of massive aerial roots in *D. draco*

The practice of drawing "Dragon's blood" resin was common in old days and it caused these roots to grow. "The cluster of (…) thick air roots gradually grow downwards and cover the whole trunk, which has been gashed and hacked by the collectors of Dragon's blood" noted Anonymous (1914). The Vandelli plant (Fig. 8b) of those days with the roots descending the trunk may support this view. We have seen massive aerial roots on modern trees (Fig. 1) with evident signs of injury that may have induced the large aerial roots to grow.

Rot of the trunk could be another factor in inducing large aerial roots and "El Drago" is an example of that (Fig. 5a–c). It is believed that its large, internal cavity was carved by the natives of the Canaries, the Guanches (Wikipedia), but rot is a more likely reason. We noted that another giant of Icod, "Drago Chico" (Dominguez 2008), had a trunk with a rotten base and protruding massive aerial roots. Another plant, "the Monster of Orotava", due to "rot disease … had a cavity so big that a chapel was built" in it (L.C. 1940). The presence of large undulations on the surface of its trunk is an indication that this plant had aerial roots in the past. It is notable that the trunk of *D. draco* with a large pith and soft parenchyma (Wossidlo 1868) would be prone to infection and rotting. Berthelot (1827), dividing the life of *D. draco* into the "age of infancy, maturity and decay" noted that in "the age of decay aerial roots appear".

The trees in Figs. 2, 3, 4 and 6 do not show any visible sign of injury but, in our view, have grown under environmental stress. The tree in Fig. 2b, observed on our three visits (2008–2010), seems to grow in soggy soil. Surrounded by annuals, it was watered more than any other dragon tree we have ever seen. If this continued over years, it could have adversely affected its soil roots and the whole tree. Sandy soil and good drainage are vital for this species (http://www.dracaenadraco.com). The tree presented in Fig. 3 could have its soil roots affected by closeness to building foundations (like tree in Fig. 7a) and by dark paving attracting the summer heat. Although the soil roots of *D. draco* are robust and show secondary growth (Fahn 1974), they are shallow (Symon unpubl. res.) and potentially prone to injury by overheating and dehydration.

The tree in Fig. 4 grows with its roots restricted by the building and its crown exposed to winds blowing along the valley and buffeting its branches. These factors may have led to its current, remarkable appearance. The tree in Fig. 6 (Geelong) grew for over a 100 years next to the *Phoenix* sp. palm, seeking sunlight from overhead. This may have resulted in the flat top of its canopy (see Tudge 2006) and, perhaps, inducing the large aerial roots.

Further evidence comes from our six dragon trees growing under environmental stress (Fig. 7). Two of them (Fig. 7a, g, h) grew large aerial roots; the others (Fig. 7b–f) also grew aerial roots but, being miniature trees, they were unable to grow the large ones. It is intriguing that *Cordyline australis,* a monocot with its soil roots small and fibrous and with tree growth habit, responds to trunk injury (Fig. 7i) in a way similar to *D. draco* (Fig. 1).

These data support our view that *D. draco* grows large aerial roots in response to injury and/or environmental stress which is not species specific.

Growth of aerial roots and their contribution to the trunk's radial expansion

The growth of large aerial roots is too slow for its downward progress to be seen directly. However, we can visualize it by comparing the same tree at long time intervals (Fig. 6b, c). Similar insight might be reached by comparing trees from Figs. 1, 8b and 6 that represent three consecutive stages of growth of their aerial roots. This is shown in Table 2, which represents yet another time-lapse record of downward growth of the aerial roots.

We have already estimated the growth rate for the tree in Fig. 1 as about 3.3 cm/year. The tree in Fig. 6 is about 150 years old (in 2014). Assuming that this growth rate is applicable to it, then for its roots to grow down 2.7 m from the branching point, about 70 years would be needed. Hence, they could have started growing around 1940. They will cover the remaining distance, of about 0.6 m, in about 20 years, so that the bottle shape of the trunk would vanish around the year 2030. Our first estimate cannot be verified as the gardens in Geelong have no record on this matter, but the second one may be tested at that time. On the other hand, the downward growth rate of aerial roots seems to vary from tree to tree. For example,

Table 2 *D. draco* trees in order of downward growth of their aerial roots

Plant	No of branching points	Age in years	Downward root progress
Figure 1 La Laguna	3–3.5	~40–45	Start
Figure 8b Vandelli	6–7	~70–80	~1/3
Figure 6 Geelong[a]	7–8	150	~3/4

[a] The pattern of branching of this dated tree shows that it flowered in 20-year cycles. Two other trees are considered as flowering in 10- to 12-year cycles (Symon 1974; Mägdefrau 1975)

the growth rate of the tree in Fig. 1 is high (3.3 cm/year). By contrast, there is no significant growth of the bulging humps in El Drago over the past 100 years (as seen in Fig. 5c compared with the flatter extensions in Fig. 5f). This shows that the downward growth of aerial roots could be individual specific or age dependant.

The trunk of *D. draco* thickens by means of a secondary thickening meristem (STM) or "monocot cambium" that is not homologous with the vascular cambium of dicotyledons (Cheadle 1937; Tomlinson and Zimmermann 1969; Rudall 1991; Carlquist 2012). Its structure and modus operandi are also vastly different from the vascular cambium of forest trees (Krawczyszyn 1977; Krawczyszyn and Romberger 1980; Larson 1994; Karczewska et al. 2009). The STP is well documented in both stems and roots of *Dracaena* (e.g. Tomlinson and Zimmermann 1969), but there is negligible quantitative data on its radial growth.

We observed two young trees in Tenerife that grew quickly with trunk radial growth rate 1.7 cm/year (a 12-year-old tree in Icod) and 1.0 cm/year (40-year-old, La Laguna). However, 120–250 years old trees, as Mägdefrau (1975) recorded, grew only 0.44–0.25 cm/year. This data imply that with further ageing of *D. draco*, the radial growth rate would be even slower. This poses the question, how is it possible for a *D. draco* tree to ever attain its gigantic trunk? Our data clearly suggest that this would be by adding thick aerial roots to its waist. This increase could be enormous indeed. This way of trunk thickening, unique to *D. draco*, seems to operate only under stress, so it is not common and, to our knowledge, it hasn't been reported before.

Large aerial roots inosculation and independency of branches

When dicot trees grow together they often inosculate: their roots, branches and stems fuse, their cambia fuse and vascular joining, as in grafting takes place. This occurs within the same or allied species (Tudge 2006; Abasolo et al. 2009; Post 1987). Its mechanics involves touching of growing parts. Later, after their surfaces are abraded away, their vascular cambia can fuse. The mature tissues of partakers stay apart, so the bond is weak. Yet, frail trees benefit from it by getting mechanical support and a larger share of nutrients (Tudge 2006).

D. draco is a monocot. It is envisaged that in this group neither inosculation nor grafting is possible as the stems (roots) have many separate vascular bundles, which makes matching of two parts impossible (Post 1987). In this respect, it is remarkable that our two *D. draco* trees (from Figs. 1, 2) form strong mechanical bonds between the aerial roots and the trunks and in one tree (Fig. 6, much older than the two previous ones), its large aerial roots are fully integrated, along their lengths, with the trunk.

Moreover, such bonding revitalizes the trees, so their trunks can thicken enormously. All this may suggest that in *D. draco* somehow the large aerial roots and/or trunk fuse as if the plant were inosculated with itself. It is noteworthy that in *Dracaena* "the secondary tissue in the root is identical in structure and origin with that in the stem" (Tomlinson and Zimmermann 1969). Our microscopic analysis of the secondary tissues of the large aerial root (7.5 cm in diameter) and the trunk from the tree in Fig. 7a, indicates that they are also identical. They have similar arrays of secondary vascular bundles that are amphivasal: with phloem (sieve tube elements) enclosed by xylem (tracheids). The bundles are embedded in ground parenchyma cells that are thin walled around the recently formed bundles and thick walled (due to lignification) around the older ones. The aerial root we analysed even had, behind the thick layer of cork, green chloroplasts. This is quite extraordinary and makes these roots more closely related to the trunk than to their soil counterparts. It is accepted that roots of vascular plants lack chloroplasts, except for aerial roots of certain water plants and epiphytes (Fahn 1974).

These anatomical parallels of large aerial roots and the trunks in *D. draco* may speak in favour of their strong union, though its mechanism is difficult to visualize. So, at the moment it cannot be decided if inosculation of the STM (monocot cambia) takes place between stem and aerial roots or, rather STM of both counterparts co-exist and function at least for some time in "self-grafted" *D. draco* tree, before the new STM takes over. The anatomy of this feature can probably be established when more material is available.

Smyth (1858) and Byström (1960) noted that ageing dragon trees have their trunks corrugated, with a "rib" extending from each of the lowest branches to a ground root. Hence the tree "has as many "feet" as primary branches" (Byström (1960). The trunks of El Drago (Figs. 6a, b), "Monster of Orotava" and the tree in Los Realejos (see Gebaue) have trunks like this. Corrugations also cover the trunks in *Ficus religiosa*, where they develop on the trunk itself, as the tree does not grow any aerial roots (Glil 2008). They also cover the bases in many tropical trees as "buttress roots", where they develop as these roots thicken mostly on the upper side (see Fahn 1974).

Our data suggest that the corrugations in *D. draco* are probably associated with the large aerial roots. However, to appear as ribs, the roots need to grow without fusing with other roots growing beside them. How this occurs is not known, but we noted that corrugations are more often found on trees with short trunks and fewer primary branches. Trees with tall trunks (like plant in Fig. 6 and "Draco Chico" of Icod) do not show them.

Byström (1960) noted that as a tree "has as many feet as primary branches" such a branch could have a potential of "independency" from the trunk. This is illustrated by Dragoeiro in Lisboa: Tapada das Necessidades (Bico 2014 photo online) where, around the circumference of a rotted out old trunk, a ring of young plants appears. The phenomenon of independency can also be illustrated by trees in Figs. 2b, f and 4, where massive, mature branches can be detached and grow on their own. These data are also consistent with the concept that in view of fractal geometry, the branches of *D. draco* are self-similar units (Beyhl 1995, 2001).

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References

Abasolo WP, Yoshida M, Yamamoto H, Okuyama T (2009) Stress generation in aerial roots of *Ficus elastica* (Moraceae). IAWA J 30:216–224

Anonymous (1914) Royal Gardens Kew official guide to the North Gallery, 6th edn. His Majesty's Stationary Office, London

Berthelot M (1827) Observations sur le *Dracaena Draco* L. Act. Leop. 13(2):782

Beyhl FE (1995) Two different growth forms of *Dracaena draco* L. (Monocotyledones: Liliales: Agavaceae). Boletim do Museu Municipal do Funchal, Suplemento 4:91–93 (ISSN 0870-3876)

Beyhl FE (1996) The emta tree (*Euphorbia arbuscula* Balf. Fil.), A succulent tree of *Dracoid habitus* from the island of Soqotra (Dicotyledones: Tricoccae: Euphorbiaceae). In: Proceedings of the first international symposium on Soqotra Island: present and future. UN Publication, pp 115–122

Beyhl FE (2001) Dragon trees (*Dracaena draco* L.) with aberrant growth forms (Monocotyledones: Lilliflorae: Agavaceae) Arquipelago. Life Mar Sci Suppl 2(part B):101–103. Ponta Delgada. ISSN 0873-4704

Beyhl FE, Mies BA (2007) Die Wuchsformen des Drachenbaums (*Dracaena cinnabari* Balf. Fil.) auf der Insel Soqotra.—growth forms of the Dragon tree (*Dracaena cinnabari* Balf. Fil.) of Soqotra island. Acta Biol Benrodis 14:55–66

Bico M (2014) Dragoeiros: Lisboa. http://www.panoramio.com. Accessed 5 Feb 2014

Byström K (1960) *Dracaena draco* L. in the Cape Verde Islands. Acta Horti Gotobg 23:179–214

Cabrera Pérez MA (1999) Visit native flora of the Canary Islands. Editorial Everest SA, Spain

Carlquist S (2012) Monocot xylem revisited: new information, new paradigms. Bot Rev 78(87–153). doi:10.1007/s12229-012-9096-1

Chase MW, Reveal JL, Fay MF (2009) A subfamilial classification for the expanded asparagalean families Amaryllidaceae, Asparagaceae and Xanthorrhoeaceae. Bot J Linn Soc 161:132–136. doi:10.1111/j.1095-8339.2009.00999.x

Cheadle VI (1937) Secondary growth by means of a thickening ring in certain monocotyledons. Bot Gaz 98:535–555

Clusius C (1576) Liber Picturatus A 23 Biblioteka Jagiellońska Kraków

Dominguez B (2008) Tenerife, tourist guidebook. Ediciones AM, Tenerife, Spain

Fahn A (1974) Plant anatomy, 2nd edn. Pergamon Press, Oxford

Gebauer A (2009) Alexander von Humboldt. Seine Woche auf Teneriffa 1799. Santa Ursula (Teneriffa) Spain, Zech Verlag

Glil J (2008) *Ficus religiosa* L.—the tree-splitter. Bot J Linnaean Soc 88(3):185–203 (April 1984). doi:10.1111/j.1095-8339.1984.tb01570.x. Accessed 10 June 2013

Halle FR, Oldeman AA, Tomlinson PB (1978) Tropical trees and forests, an architectural analysis. Springer, Berlin

Karczewska D, Karczewski J, Włoch W, Jura-Morawiec J, Kojs P, Iqbal M, Krawczyszyn J (2009) Mathematical modelling of intrusive growth of fusiform initials in relation to radial growth and expanding cambial circumference in *Pinus sylvestris* L. Acta Biotheoretica. doi:10.1007/s10441-009-9068-y

Krawczyszyn J (1977) The transition from nonstoried to storied cambium in *Fraxinus excelsior*. I. The occurrence of radial anticlinal divisions. Can J Bot 55:3034–3041

Krawczyszyn J, Romberger J (1980) Interlocked grain, cambial domains, endogenous rhythms, and time relations, with emphasis on *Nyssa sylvatica*. Am J Bot 67:228–236

Larson PR (1994) The vascular cambium: development and structure. In: Timell TE (ed) Springer series in wood science. Springer, Berlin

L.C. (1940) The Dragon-blood tree. Miss Bot Gard Bull 28:41–42

Lyons G (1974) In search of Dragons. Cactus Succul J (US) 46:267–282

Mägdefrau K (1975) Das Alter der Drachenbäume auf Tenerife. Flora 164:347–357

Mandelbrot B (1982) The fractal geometry of nature. Freeman WH & Co, USA

Marrero A, Almeida RS, Gonzales-Martin M (1998) A new species of the wild dragon tree, *Dracaena* (Dracaenacae) from Gran Canaria and its taxonomic and biogeographic implications. Bot J Linnaean Soc 128:291–314

Marzol MV, Sánchez Megía JL, Yanes A (2011) Meteorological patterns and fog water collection in Morocco and the Canary Islands. Erdkunde 65:291–303. doi:10.3112/erdkunde.2011.03.06, http://www.erdkunde.uni-bonn.de

Meislik J (2014) Banyan, strangler and epiphytic figs. Accessed 5 Feb 2014

Ommen K (2009) [PDF] Carolus: the exotic world of Carolus Clusius (1526–1609). Kleine publicaties van de Leidse Universiteitsbibliotheek Nr.80. https://openaccess.leidenuniv.nl/bitstream/KP%2080%20scherm.pdf

Poberezhnaya TM, Kopanina AV (2009) On causes of gigantism in herbaceous plants. Russ J Ecol 40:241–246

Post RL (1987) Grafting and budding. University of Nevada. Fact Sheet 87-47. Accessed 15 Feb 2013

Rudall P (1991) Lateral meristems and stem thickening growth in monocotyledons. Bot Rev 57:150–163

Schenck H (1907) Beiträge zur Kenntnis der Vegetation der Kanarischen Inseln, Jena

Smyth CP (1858) Report on the Teneriffe astronomical experiment of 1856, London

Symon DE (1974) The growth of *Dracaena draco*—Dragon's blood tree. J Arnold Arbor 55:51–58

Symon DE (2000) Dragon's blood tree. Mediterr Gard Soc 21:30–32

Tomlinson PB, Zimmermann MH (1969) Vascular anatomy of monocotyledons with secondary growth—an introduction. J Arnold Arbor 50:159–179

Tudge C (2006) The secret life of trees. How they live and why they matter. Penguin Books, Clays Ltd, St. Ives plc., England

Vandelli D (1768) Dissertatio de Arbore draconis, sev Dracaena. Scriptores de plantis Hispanicis, Lusitanicis. Brasiliensibus 37-46 Norimbergae (Ed Roemer I.I.) [Originaldruck Olisipone 1768]

von Humboldt FHA (1850) Views of nature, or contemplation on the sublime phenomenon of creation', English edn. Bohn HG, London

Wossidlo P (1868) Ueber Wachstum und Structur der Drachenbäume. Jahresbericht. d. Realschule am Zwinger in Breslau für 1868, 1–32. http://www.dracaenadraco.com. Accessed 5 Feb 2014. http://www.Youtube:Fractal tree. Accessed 5 Feb 2014