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New knowledge in dragon tree research

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Abstract: Dragon trees, arborescent members of the genus *Dracaena* (Asparagaceae), provide a wide range of ecosystem services and have been ethnobotanically important plants since ancient times. Currently, their relictual distribution is fragmented, populations are isolated and often under threat. We provide a brief overview of scientific studies and the state of knowledge on dragon trees published since 2020, when the last review was published. More than 120 papers dealing with dragon trees have appeared, indicating a significant interest in their research, cultural uses and conservation. The most intensively investigated species are *Dracaena cochinchinensis*, *D. cinnabari*, *D. draco* and *D. cambodiana*. Almost half of the papers deal with the chemical composition of resin and its bioactivity, in addition to studies on ecology, conservation and genetics. Only a few studies are devoted to taxonomy and ethnobotany.

Keywords: anatomy; bioactivity; conservation; dragon tree group; morphology; phylogeny; phylogeography; resin; tree age estimation; threat

Dragon trees, arborescent members of the genus *Dracaena* Vand. ex L. (Asparagaceae), have fascinated scientists for centuries. These aesthetically appealing trees have been widely studied because of their ancient history, their extensive range of ecosystem services, their role as umbrella species, their ethnobotanical uses important for indigenous cultures in different continents around the world, and many other fascinating aspects (Maděra et al. 2020a). The most recent comprehensive review on the scientific aspects of dragon trees (Maděra et al. 2020a) was published in a special issue of MDPI Forests as part of the proceedings of the first World Conference organised by the Dragon Tree Consortium at Mendel University in Brno, Czech Republic, in 2019 (Maděra et al. 2021). Since then, numerous new studies have appeared, covering a broad range of scientific topics (Figure 1). Here, we provide a brief overview of the progress of knowledge in arborescent *Dracaena* since 2020, focusing on some of the important and globally endangered tree species in the genus (Figure 1). The articles for this review have been selected from scientific databases (Web of Science and Scopus) by using the keywords '*Dracaena*' and 'dragon trees'.

Among the recently published articles mentioned herein, a collection of seven papers has been published in 2022–2023 in the special issue 'New Knowledge in Dragon Tree Research' in MDPI Forests. The topical collection results from the 2nd World Conference on Dragon Trees (prepared

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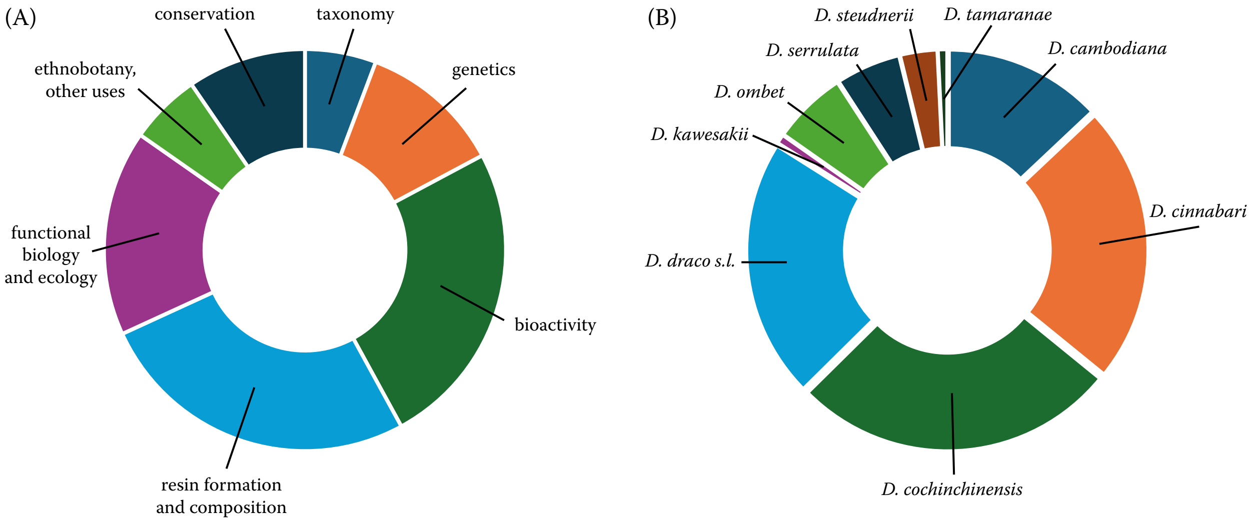

Figure 1. Representation of (A) broad topics, and (B) *Dracaena* species among articles published on dragon trees since 2020

jointly with the 20th Friends of Socotra Conference), hosted by Ghent University Botanical Garden (Belgium) during a most challenging COVID period (September 27, 2021). The conference hosted about 30 attendees from 10 different countries, the majority of whom attended online. These conferences are organised by the Dragon Tree Consortium (www.dragontreeconsortium.com), an informal open consortium which focuses on scientific cooperation in dragon tree research and conservation, originally established by researchers of Mendel University in Brno (Czech Republic), Ghent University (Belgium), La Sapienza University/Rome Botanical Garden (Italy) and Adam Mickiewicz University, Poznań (Poland).

The main aims of this review are to provide an update since Maděra et al. (2020a), including an overview of the progress in dragon tree research, and to formulate potential new directions in research on these fascinating plants, based on identified knowledge gaps.

TAXONOMY, PHYLOGENY AND PHYLOGEOGRAPHY

Since the genus *Sansevieria* Thunb. was sunk into the genus *Dracaena*, a number of nomenclatural changes have been made. Takawira-Nyenya et al. (2021) presented fourteen name changes, including twelve new combinations in *Dracaena* and two rank adjustments, one new synonym, and one lectotypification, aiming at further standardisation of the complex taxonomy of the genus *Dracaena*. In addition, four new names were proposed and many lectotypes were designated in the genus *Dracaena* (Idrees et al. 2022; Zhang et al. 2022). Ferrer-Gallego and Martínez Labarga (2021) even proposed to conserve the name *Asparagus draco* L. as basionym of the widely accepted name *Dracaena draco* L.

Vahalík et al. (2020a) tested a new approach in botanical taxonomy using several dragon trees as an example. They tried to use metrics of growth habit derived from the 3D tree point cloud for *Dracaena* species identification.

Plastid DNA markers have been used in a phylogenetic and biogeographic study of the Macaronesian *Dracaena* taxa and related species of the genus (Durán et al. 2020). In addition, the entire circular chloroplast genome was sequenced for *D. cinnabari* Balf. f. from Socotra Island (Yemen), *D. draco* (Canary Islands) and *D. serrulata* Baker from mainland Yemen (Celiński et al. 2020, 2022; Ahmad et al. 2022). A chromosome-level genome was assembled for the Asian *D. cochinchinensis* (Lour.) S.C. Chen (Xu et al. 2022a). Chen et al. (2024) assembled a haplotype-resolved genome of *D. cambodiana* Pierre ex Gagnep.

According to Zhao et al. (2021), four studied *Dracaena* species, including *D. cambodiana* and *D. cochinchinesis*, show hybridisation signals in the paracentromeric region of a pair of chromosomes, and the chromosome number of all four studied *Dracaena* species is $2n = 40$.

The progress in exploring chloroplast genomes applying NGS (next generation sequencing)

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to *Dracaena* is useful for phylogeny, but it can also be applied to study chloroplast gene functions in these trees in the future (Celiński et al. 2022).

ANATOMY AND MORPHOLOGY AND ITS ECOLOGICAL IMPLICATIONS

Several studies were published which relate to the anatomy and morphology of individual dragon tree organs, predominantly to investigate major adaptations to harsh (arid) environments. An important topic explored by Jura-Morawiec and Marcinkiewicz (2020) is wettability (water absorption and water storage in rosette leaves) of *Dracaena draco*, and leaf features related to capturing water from horizontal precipitation in *D. cinnabari* (Kalivodová et al. 2020). These studies are widely applicable to other dragon tree species and reveal their high importance in local hydrological cycles (in this case, on islands) as a major ecosystem service (Kalivodová et al. 2020). Aerial roots in these trees are significant structures able to absorb water through surface condensation from air humidity (Jura-Morawiec et al. 2021a). Jura-Morawiec et al. (2021b) revisited the anatomy of monocot cambium (responsible for secondary thickening) in arborescent *Dracaena* and the radial growth of the stem. The same radial growth of the stem can be used for direct (Bauerová et al. 2023) or indirect (Maděra et al. 2020b) age estimation of dragon trees. In young stems of *Dracaena draco*, primary xylem has a higher conductive function in comparison to secondary xylem with a higher mechanical function (Tulik et al. 2022). Similarly, the structural characteristics of the different developmental stages of stems of *D. cambodiana* were observed and described in detail using SEM (scanning electron microscope) (Zhang et al. 2023). Finally, Marcinkiewicz and Jura-Morawiec (2024) investigated secondary growth in the roots of *Dracaena draco*. These studies greatly contribute to a better understanding of adaptations and functional morphology of arborescent *Dracaena*.

DRAGON'S BLOOD, ITS FORMATION, CHEMICAL COMPOSITION AND BIOACTIVE PROPERTIES

Dragon trees produce a blood-coloured secretion, called dragon's blood, which is an integral part of the normal development of the leaves and of the tissue protecting the trunk. This resin has a high ethnobotanical significance in several indigenous cultures around the world (Ding et al. 2020; Maděra et al. 2020a; Liu et al. 2021; Mělo 2023; Almaghrebi et al. 2024). Jura-Morawiec et al. (2023) have shown, for the first time, that this resin occurs in parenchyma cells in the form of terpene-filled vesicles, which tend to aggregate. The resin is an anatomical marker of the area where the leaf's abscission zone will be formed. After shedding of the leaf, the leaf scars containing the resin completely cover the trunk. Their study highlights that dragon's blood is secreted not only following wounding caused by external biotic and/or abiotic factors, but also during the undisturbed growth of dragon trees. Local communities of Socotra Island (Yemen) know this well and collect resin of *D. cinnabari* (Figure 2) of the highest quality, which is found just below the leaf rosettes (Al-Okaishi 2020).

Zhu et al. (2020, 2021), Sun et al. (2021) and Gao et al. (2024) clarified the mechanisms forming dragon's blood in *D. cochinchinensis* and *D. cambodiana*, describing gene expression in the flavonoid biosynthesis pathway. Concentration of flavonoids in this resin and gene expression in different tissues of *D. cochinchinensis* were investigated by Wang et al. (2022b). Transcriptomics and metabolomics studies reveal defensive responses and flavonoid biosynthesis by *D. cochinchinensis* under wound stress (Liu et al. 2022) and UV-B radiation (Liang et al. 2023). By combining traditional histochemistry with modern spatial mass spectrometry imaging, Zhang et al. (2024b) elucidated the complexity of wound-induced resin formation in *D. cambodiana*, the spatial distribution of plant defence metabolites in the stem under wound stress. The formation of chalcane-containing dimers, major compounds identified from dragon's blood, was studied in *D. cambodiana* (Liao et al. 2022). Vaníčková et al. (2020) found that terpenoid profiles of the resin in the genus *Dracaena* have a phylogenetic signature (i.e. they are species-specific). Similarly, *D. cambodiana* and *D. cochinchinesis* differ in phenolic compounds of resin, not only between species but in the geographical origin of populations of the same species (Sun et al. 2024). DNA barcoding was successfully used for the identification of the resin of seven *Dracaena* species (Zhang et al. 2021).

The historical use of dragon's blood from *D. draco* was discussed by Herold and Cabral (2023), based

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(A)

(B)

Figure 2. Wounds on the trunk of dragon tree (*Dracaena cinnabari*, Socotra Island): (A) tree possibly used for centuries for the collection of dragon's blood resin; (B) recovering old wound without signs of repeated injury

Source: Photos by PM, Socotra Island (Yemen)

on a forgotten manuscript of apothecary, alchemist, astrologer and healer Leonhard Thurneysser zum Thurn (1531–1596). Among the important groups of ancient dyes recovered were flavylium/anthocyanin reds from *D. draco* in the ancient Mediterranean civilisations (Mělo 2023).

In general, the analysis of the chemical compounds of *Dracaena* resin and their bioactivity (Al-Fatimi 2020; Lang et al. 2020; Niu et al. 2020; Helal et al. 2021; Noshita et al. 2021; Pang et al. 2021; Thu et al. 2021; Kwon et al. 2023; Akbulut et al. 2024; Hoang et al. 2024; Lou et al. 2024; Yen et al. 2024), has become a significant field of study in itself; the highest number of articles has been published on this topic during the evaluated period (Figure 1). Based on ethnopharmacological surveys, such as the study by Al-Fatimi (2023), conducted in recent years, many studies have been published on the bioactive properties of *Dracaena* resin, reviewed recently by Thu et al. (2020), Al-Awthan and Bahattab (2021) and Peres et al. (2023). For example, Irani et al. (2024) studied cytotoxicity, antibacterial, and wound healing activities of *D. cinnabari* resin. Many authors referred the same effects of various chemical constituents of the resin of *D. cochinchinensis*, *D. cambodiana, D. serrulata*, and *D. steudneri* species antioxidant (Kamal et al. 2022; Soingam, Srithaworn 2023; Wu et al. 2023; Guo et al. 2024a; Yang et al. 2024), antimicrobial (Mouzié et al. 2022; Yin et al. 2024), wound healing (He et al. 2021; Vakilian et al. 2021) and anti-inflammatory (Van Anh et al. 2021; Ospondpant et al. 2023, 2024) activities. Similarly, Gohar et al. (2020) showed a cytotoxic effect and induced apoptotic cell death by activation of the intrinsic apoptosis pathway and the mitochondrial pathway of nasopharyngeal carcinoma cells, caused by *D. cinnabari* extract. Several other studies mentioned different kinds of cancer inhibition using extracts of dragon's blood (Chen et al. 2020; Tian et al. 2021, 2023; Nchiozem-Ngnitedem et al. 2022; Rola et al. 2022; Ouyang et al. 2023; Tu, Li 2023). Najafi et al. (2024) examined the effect of the hydroalcoholic extract of *D. cinnabari* on sex hormones and ovarian and uterine tissues of rats. Mothana et al. (2022) identified anti-Hepatitis B virus activity of two chalcone derivatives from *D. cinnabari*, and Guo et al. (2024b) mentioned that Loureirin C extracted from *D. cochinchinensis* prevents rotaviral diarrhoea; Abutaha and Almutairi (2023) explored the therapeutic potential of GC–MS (gas chromatography–mass spectrometry)-separated compounds from *D. cinnabari* against dengue virus. Zhang et al. (2024a) discuss the pharmacological action and biomolecular mechanism of dragon's blood from *D. cochinchinensis* and how it pre-

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vents and protects against cardiovascular diseases. Other effects of dragon's blood were published (Li et al. 2021; Helal et al. 2022; Xu et al. 2022a), for example the compound Loureirin C, extracted from Chinese dragon tree resin, has anti-Alzheimer's disease effect (Xu et al. 2023); dragon blood resin also ameliorated steroid-induced osteonecrosis of the femoral head (Liu et al. 2023), and alleviated acute ulcerative colitis (Lin et al. 2020); *D. cochinchinensis* stemwood extracts promote neuronal cell differentiation (Ospondpant et al. 2022).

Generally speaking, these studies illustrate that we still do not fully comprehend the diversity of beneficial medicinal properties of the dragon tree resin, and the current trend seems to indicate that this field of study (phytochemistry of *Dracaena*) will likely expand further.

SEED GERMINATION

Seed germination is crucial to ensure that both natural and artificial regeneration of dragon trees are viable. Generally, both seed production and germination rates are good in dragon trees and do not limit regeneration. However, not all species have been investigated so far, so there could be some exceptions. The effects of different pre-sowing treatments to break seed dormancy and different seed collection methods, substrate and light conditions on the germination and seedling establishment of *D. steudneri* (Munie et al. 2022) and *D. draco* (Kheloufi et al. 2020) were recently studied and confirm easy germination.

AGE ESTIMATION

Four papers were published recently on the improvement of age estimation techniques of *Dracaena* trees. Bauerová et al. (2023) developed a direct method for the first time to determine the lifespan of *D. cinnabari* based on repeated measurement of the stem diameter of more than 1 000 trees over 10 years on Socotra Island. Maděra et al. (2020b) focused on age estimation of juvenile *D. cinnabari* trees using allometric equations, while Biondi et al. (2024) used radiocarbon dating for the first time in *D. draco* to estimate the age of sampled trees. Lengálová et al. (2020) developed a model of age estimation for *D. ombet* Kotschy & Peyr. and *D. draco* subsp. *caboverdeana* Marrero Rodr. & R.S. Almeida in Ethiopia and Cape Verde Islands, respectively.

The longevity of dragon trees depends on genetic and epigenetic mechanisms (Batalova, Krutovsky 2023); a key trait associated with plant longevity is the enhanced immune defence, which is linked to the expansion of appropriate gene families (Xu et al. 2022b). *Dracaena cochinchinensis* has undergone two whole-genome duplications and two bursts of long terminal repeat insertions (Xu et al. 2022b). The expansion of two gene classes (*cis*-zeatin O-glucosyltransferase and small auxin upregulated RNA) is thought to be correlated with longevity and slow growth (Xu et al. 2022b). In addition, two transcription factors [bHLH (basic helix–loop–helix) and MYB (myeloblastosis)] seem to be the main regulators of the flavonoid biosynthesis pathway, while reactive oxygen species were identified as specific signalling molecules responsible for injury-induced formation of dragon's blood. Finally, Schweiger et al. (2020) suggested dynamic management for long-lived plant species with sporadic recruitment (like *D. cinnabari*) in human-dominated landscapes, which brings us to the next section on conservation and population ecology.

POPULATION ECOLOGY, DISTRIBUTION AND CONSERVATION

Our knowledge of the past and present distribution of dragon trees has significantly improved over the last years, as well as efforts and insights into the ecology and conservation of these species.

New investigation of plant macrofossils from early Miocene deposits of western Turkey (Soma, Manisa) demonstrates the earlier significant expansion of *Dracaena* species (Denk et al. 2022).

In recent years, several studies on the distribution and population structure of dragon trees appeared; in some cases, dragon trees were found in unexpected places. El Mokni and Verloove (2022) mentioned *D. draco* as a non-native alien plant in Tunisia and North Africa and Cerrato et al. (2023) in the Balearic Islands. It seems that also in Gibraltar, *D. draco*, which had 'escaped' from a botanical garden, has been able to spread here (PM, personal observation). Guix (2021) found a probably natural population of *D. draco* on the seaside cliffs of Flores Island (Azores, Portugal; Figure 3).

Al-Okaishi (2021) used phytotoponyms (plant-name derived toponyms) to investigate a potential historical distribution of *D. cinnabari* on Socotra

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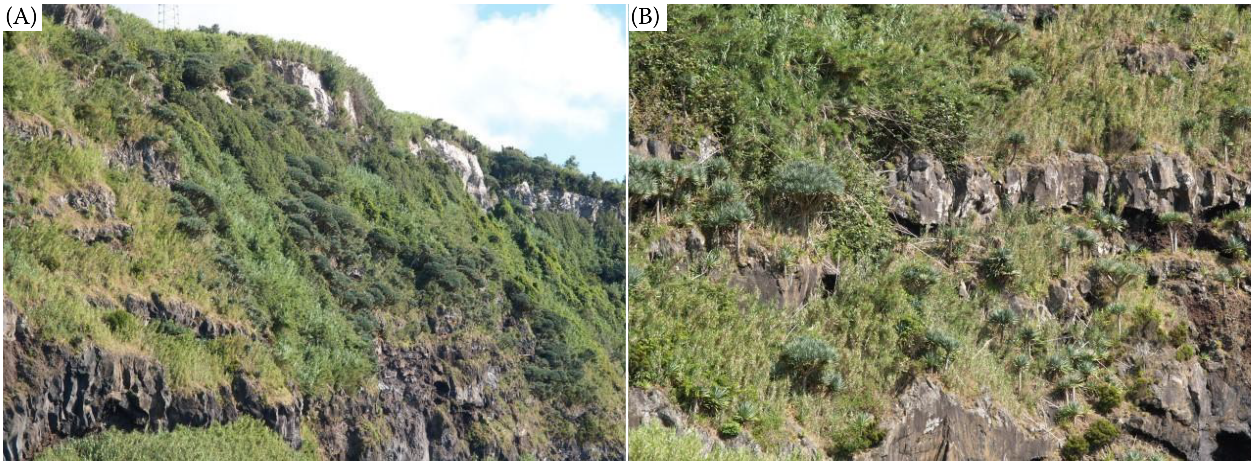

Figure 3. (A) Population of *Dracaena draco* on the cliff near the harbour in Laches, Flores Island, Azores, Portugal; (B) both old and young trees occur (same locality)

Source: Photos by PM, August 2023

Island (Yemen). Wood from *D. draco* in Gran Canaria (Canary Islands) that was used for funerary practices of indigenous populations was identified in archaeobotanical samples, thus proving the natural origin of *D. draco* in this island (Vidal-Matutano et al. 2021). Multiple paleobotanical studies proved the natural origin of *D. draco* subsp. *caboverdeana* on São Nicolau, Cape Verde (Castilla-Belrtrán et al. 2020).

Vegetation surveys of plant communities associated with *D. ombet* in Gebel Elba (Egypt) and *D. serrulata* in Jandaf Mountain (Saudi Arabia) or Dhofar Mountains (Oman) helped to identify the main environmental drivers responsible for their distribution, rich biodiversity and conservation value (Abutaha et al. 2020; Vahalík et al. 2020b; Al-Namazi et al. 2022). Gidey et al. (2024) evaluated the distribution, population and conservation status of the endangered *D. ombet* in dry Afromontane forests in Ethiopia and suggested priority forest conservation strategies using a multi-attribute decision model (Gidey et al. 2023). Andersen et al. (2022) presented updates on a population of *D. ombet* in the Red Sea Hills (Sudan), where this tree has recovered and regenerates at higher altitudes than where it previously occurred. This could be related to global climate change, as a shift of area of distribution has been modelled recently by many authors, for *D. ombet* by Birhane et al. (2023), for *D. draco* subsp. *draco* by Cartereau et al. (2023), for *D. draco* subsp. *caboverdeana* by Varela et al. (2022) and for three African species (*D. afromontana*, *D. camerooniana* and *D. surculosa*) by Bogawski et al. (2019). Such modelling, taking a wide range of available data into account, can be applied to assess the suitability of areas for conservation and determine long-term strategies based on scientific data, e.g. for *D. cinnabari* (Rezende et al. 2022) or for *D. draco* (Cartereau et al. 2025). An additional useful tool in such surveys is the application of UAVs (unmanned aerial vehicles) for high resolution remote sensing, applied by Vahalík et al. (2023) to *D. cinnabari* in order to assess the impacts of recent climate effects (cyclones) on the only remaining dragon tree forest in the world, on Socotra Island (Figure 4).

In addition, dragon trees have a key function as important habitats for other species, particularly in islands with often vulnerable associated endemic fauna and flora. Vasconcelos et al. (2020) showed the importance of *D. cinnabari* as an umbrella species for endemic Socotran reptiles; Al-Jaradi et al. (2020) described new species of fungi (*Phaeosphaeriopsis omaniana* Al-Jaradi, Al-Sadi & Maharachch.) from leaves of *D. serrulata*; Du et al. (2021) described two new wood-rotting fungi in the family Hymenochaetaceae, *Fulvifomes dracaenicola* Z.B. Liu & Y.C. Dai and *Hymenochaete dracaenicola* Z.B. Liu & Y.C. Dai, on *D. cambodiana* from tropical China; and Wang et al. (2022a) first reported finding of *Colletotrichum queenslandicum* Weir & Johnst. causing leaf anthracnose on *D. cambodiana* in China. Calvagna (2022) illustrated the importance of veteran dragon tree (*D. draco*) in Drago Park in Icod, Tenerife (Canary Islands), including major aesthetic, cultural and natural values.

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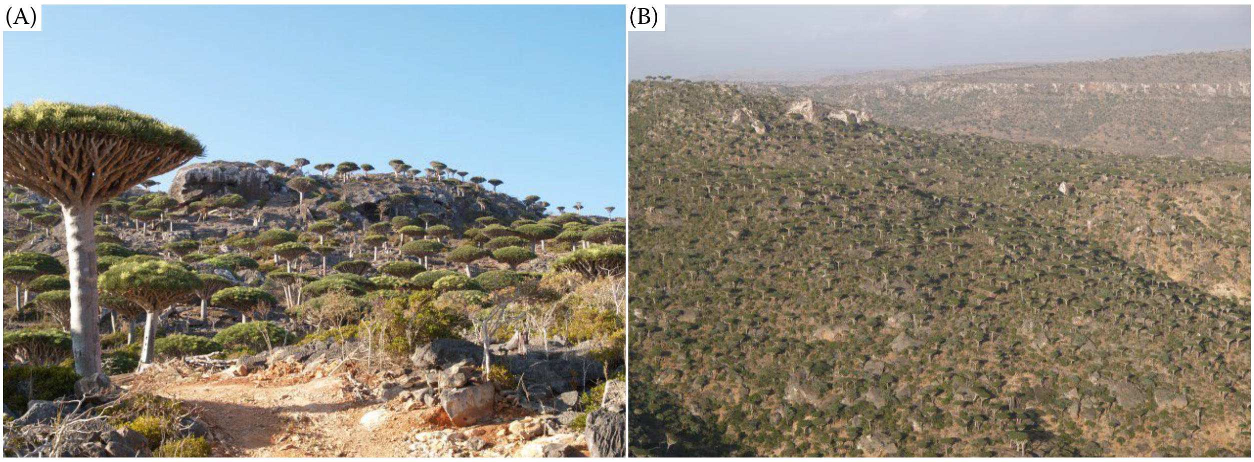

Figure 4. (A, B) Dragon tree forest in Firmihin, Socotra Island
Source: Photos by PM, June 2009

The conservation of dragon trees helps to maintain unique biodiversity elements within special ecosystems, as well as key cultural values that are disappearing all over the world.

ETHNOBOTANY AND OTHER USES

Gebregiorgis et al. (2024) suggested *D. steudneri* as a promising fodder tree species for agroforestry systems (Getachew, Mulatu 2024) in the midland of Ethiopia, improving biomass production.

Dracaena cochinchinensis and *D. kaweesakii* belong to the top three plant species recommended for a low-maintenance green roof in tropical climates, improving drought- and extreme weather tolerance, disease and insect resistance, because of the short spreading roots, succulent leaves with the ability to store water, low water requirements, slow growth rate, easy availability locally and affordability, thriving in low-nutrient conditions, and a high evapotranspiration rate (Kachenchart, Panprayun 2024).

Hadou et al. (2024) investigated the potential of *D. draco* cellulose fibre as a viable option for the development of biodegradable natural composites, with the objective of making a valuable contribution to the field of environmentally sustainable materials for a wide range of industrial applications.

Finally, an *in vitro*-to-*ex vitro* shoot tip-derived protocol was developed for the mass propagation of *D. cambodiana*, allowing for market demand to be met and plants to be produced in sufficient volumes for eco-restoration projects (Zheng et al. 2022).

CONCLUSION

We provided a brief overview herein of the main studies on dragon trees published since 2020, including seven articles which appeared in the second special issue on dragon trees (the Proceedings of the 2nd World Conference on Dragon Trees at Ghent University Botanical Garden, Belgium, organised by the Dragon Tree Consortium and Ghent University). The most investigated species are *Dracaena cochinchinensis*, *D. cinnabari*, *D. draco* and *D. cambodiana*. Almost half of all the papers deal with the chemical composition of resin and its bioactivity. In general, ecology, including functional genetical, anatomical and morphological traits related to the adaptation to harsh environments, as well as conservation, are also subjects of interest. Only a few studies are devoted to taxonomy and ethnobotany. Almost missing is the investigation of physiological processes, as well as up-to-date conservation status assessment of the populations of many individual species. However, research on arborescent *Dracaena* progressed substantially in recent years, illustrating that effective protection on the ground of these fascinating, culturally significant and highly endangered trees is increasingly needed.

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