Parasitic plant cultivation: examples, lessons learned and future directions

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Abstract

Parasitic plants contain some of the most bizarre and fascinating organisms in the plant kingdom. Yet they are notable for their absence from botanic gardens' plant collections and conservation strategies. Besides a handful of species, few are widespread in cultivation; indeed we estimate at least 76 per cent of species are entirely missing from collections today, and most of these have never been grown at all. Here, we place focus on the holoparasites, a group of plants long neglected due to their difficulty in cultivation. We review propagation breakthroughs in temperate and tropical botanic gardens to identify guiding principles for the cultivation of these neglected plants. We document the life cycle of a range of parasitic plants, and assess successful and failed attempts to propagate *Rafflesia* specifically, which has been the focus of decades of research. By uniting isolated case studies from around the world, we identify future directions for the cultivation and possible *ex situ* conservation of these botanical enigmas at a time when this is needed urgently. Finally, we recommend a dedicated global community of purpose as an intentional step forward: this could take the form of a Global Consortium for Conservation for parasitic plants, or a Parasitic Plant Specialist Group under the International Union for Conservation of Nature.

Introduction

Parasitic flowering plants include ecosystem engineers that enhance species richness (Press & Phoenix, 2005; Watson *et al.*, 2011), economically significant pests (Press & Graves, 1995; Joel *et al.*, 2013) and some of the most bizarre and fascinating examples of morphological reduction and reproductive biology in the plant kingdom (Kuijt, 1969; Heide-Jørgensen, 2008; Thorogood, 2020). Yet despite this, many of the c. 4,750 accepted species (Nickrent, 2020) are poorly known to science, and most have never been cultivated. Indeed there is just one book on the cultivation of parasitic flowering plants (Heinricher, 1910; updated 1922). Parasitic flowering plants are reliant on other photosynthetic plants to varying degrees for their nutrition. Green plants are photoautotrophic (or carbon-autotrophic), i.e. they produce their carbohydrates by photosynthesis. In contrast, those that gain

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some or all of their carbohydrates from other organisms are called heterotrophic. Heterotrophic plants can be distinguished by their hosts – as mycoheterotrophs (parasitic on fungi; not a focus of this article) or haustorial parasites (parasitic on other plants). The latter penetrate the vascular tissues of their hosts using specialised organs called haustoria (Kuijt, 1969; Furman & Trappe, 1971; Fay *et al.*, 2010). In this article, we focus on these haustorial parasites.

Haustorial parasites have evolved 12 times independently from their free-living ancestors (Fig. 1), and represent approximately 1.2 per cent of flowering plant species (Nickrent, 2020). A single heterotrophic (parasitic) gymnosperm is known to science – *Parasitaxus usta* (Podocarpaceae), which is native to New Caledonia. Despite repeated attempts at germination and grafting, it has never been cultivated successfully (Sinclair *et al.*, 2002). Traditionally, parasitic flowering plants have been divided into various nutritional groups based on physiological features, in particular those that possess chlorophyll and photosynthesise but obtain some or all water and minerals from their host (hemiparasites; either facultative or obligate) and those that lack chlorophyll and photosynthesis, instead deriving all water, minerals and photo-assimilates from their hosts (holoparasites) (Teixeira-Costa & Davis, 2021). Whilst in reality there exists a spectrum between hemiparasites and holoparasites (sometimes even within a single genus, e.g. in *Cuscuta* or *Striga*), in this article we refer to these groups in broad terms, for simplicity and consistency with other authors. Independent from the distinction made between hemiparasites and holoparasites, parasitic plants can be classified further by their morphology and anatomy, or, more exactly, based on the part

of the host plant they penetrate by their haustorium: root parasites attach to the roots of their host (e.g. broomrapes, *Orobanche*), while stem parasites attach to their hosts' aerial parts (e.g. dodders and all mistletoes except two genera) and endoparasites live entirely within the tissue of their host plants.

Extreme morphological modifications associated with the derived life history of holoparasites long obscured their phylogenetic relatedness to photosynthetic plants; in many cases, they scarcely even resemble plants. Lacking leaves and roots, they bear no similarity to their photosynthetic ancestors. In recent decades, advances in molecular phylogenetic reconstructions have revolutionised our understanding of their evolutionary relatedness (Nickrent, 2020). The most derived of all are the endoparasites (or endophytic holoparasites). These evolved four times independently among flowering plants, and exist for most of their lives embedded within the tissues of their hosts, in a similar way to some fungi (Heinricher, 1917; Thorogood *et al.*, 2021b). One of these four lineages of endoparasitic flowering plants includes the world's largest flowers in the genus *Rafflesia*, a spectacular plant once acclaimed 'the greatest prodigy of the vegetable world' (Nikolov & Davis, 2017).

Despite their intrigue and appeal, many parasitic plants have evaded cultivation efforts (but see early accounts by Heinricher, 1910, 1922). Few non-weedy species are widespread in cultivation or are a focus of botanic gardens' plant collections and conservation strategies. Indeed, many of the vascular plant families noted for being entirely absent from cultivation internationally are parasitic (Mounce *et al.*, 2017). Parasitic plants are also notoriously under-represented in seed bank collections and national *ex situ* conservation programmes

Fig. 1 Representatives of each of the parasitic plant lineages (for details of their existence in cultivation, see Table 1). A. *Cassytha filiformis* (Lauraceae); B. *Hydnora africana* (Aristolochiaceae); C. *Cynomorium coccineum* (Cynomoriaceae); D. *Krameria cristoidea* (Krameriaceae); E. *Rafflesia arnoldii* (Rafflesiaceae); F. *Pilostyles* sp. (Apodanthaceae); G. *Cytinus hypocistis* (Cytinaceae); H. *Balanophora fungosa* (Balanophoraceae); I. *Mitrastemon matudae* (Mitrastemonaceae); J. *Pholisma arenarium* (Lennoaceae); K. *Cuscuta hygrophilae* (Convolvulaceae); L. *Cistanche tubulosa* (Orobanchaceae). Photo D: Nicolas Lavandero; photo F: Danilo Soares Gissi; photo J: David Greenberger; all other photos and illustrations: C.J. Thorogood.

(North *et al.*, 2021). In fact we estimate that at least 76 per cent of parasitic plant species are missing from collections internationally today, based on a sample of >500 species from across the 12 independent lineages (Table 1); furthermore, of those that are missing, few have even been grown historically, according to the isolated accounts in the literature (Table 2). In a climate of high levels of biodiversity loss globally, this places parasitic plants at a particularly high risk of extinction, which is compounded by the added consideration of suitable host availability for their conservation. Here we unite the various isolated case studies and breakthroughs in the propagation and cultivation of parasitic plants with a view to identifying avenues for future work and encouraging botanic garden curators to include these important plants in collection strategies.

Growing and propagating parasitic plants

Parasitic plants' life cycles are coordinated with those of their hosts, and their successful cultivation relies on an understanding of their development. The general life cycle of a parasitic plant can be divided into stages, or developmental checkpoints (Thorogood & Hiscock, 2010a; Teixeira-Costa & Davis, 2021). The life cycle begins with parasite seed germination, often after a period of preconditioning, and host plant localisation (Fig. 2 Top stages 1–2). Following physical attachment to the host by a sucker or appressorium (usually on the roots or stems) (Fig. 2 Top stage 3), haustorium development proceeds, forming a physiological connection which involves initiation followed by intrusive and then conductive phases. Following the establishment of host–parasite vascular connections, the parasite develops further (Fig. 2 Top stage 4), in most cases

externally or, in the case of endoparasites, within host tissues. Here we place specific emphasis on holoparasites and especially the endoparasites, because they are notoriously difficult to establish and propagate in cultivation.

Eventually the parasite flowers and sets seed (Fig. 2 Top stage 5). The length of each of these developmental stages, and in some cases the absence of certain phases altogether, varies according to parasitic plants' various functional characteristics (Teixeira-Costa & Davis, 2021). Moreover, in some cases (e.g. Orobanchaceae), distinct compatibility and incompatibility interactions between host and parasite occur at different developmental checkpoints. In simple terms, multiple layers of incompatibility contribute to host specificity in parasitic plants (Yoshida & Shirasu, 2009; Thorogood & Hiscock, 2010a). In cultivation (as in nature), this can manifest itself in the form of necrotic specimens that die off at various stages (Fig. 3A). For these reasons, selection of the optimal host in cultivation is essential for propagation success. Some parasitic plants show a wide host range, while others only parasitise a single plant genus or, in extreme cases, a single host plant species or even population (Uhlich *et al.*, 1995; Joel *et al.*, 2013). For cultivation purposes, collecting host material from the same population as the parasite is a good rule of thumb. It is also important to note that most parasitic plants cannot establish on seedlings or immature host specimens (if they do, both host and parasite may be killed). Hence the suitable host plant should ideally be well established before inoculating with the parasite.

Here we provide a summary for each of the main developmental stages from across parasitic plant groups, drawing upon research into both weedy and non-weedy parasites.

Table 1 An approximate estimation of the number of threatened parasitic plant species and their relative representation in conservation, based on a sample of 548 species from 12 genera. Genera were selected to cover all independent lineages (Fig. 1) and are ordered here in phylogenetic sequence. For families with multiple genera, those estimated to have the most species of holoparasites (or those best characterised and resolved taxonomically) were prioritised. For threatened species, only accepted species (according to POWO (2022)) were considered; infraspecific taxa, synonyms and duplications were filtered out and geography was not considered. Note that the total 17 per cent is likely to be a gross underestimation given our rudimentary understanding of the taxonomy of most groups and the fact that many taxa are difficult to observe due to their largely subterranean life history. For the number of species for which 'live' ex situ collections are listed worldwide, infraspecific taxa, synonyms and duplications were filtered out (i.e. any species represented across several collections was counted as 1).

Genus (representing all 12 parasitic lineages)	Estimated number of accepted species (POWO, 2022)	Number of threatened species (BGCI, 2022b); percentages are estimates based on estimated total numbers of accepted species	Number of species for which ex situ sites are listed worldwide (BGCI, 2022a)
Cassytha (Lauraceae)	20	3 (15%)	9 (45%)
Hydnora (Aristolochiaceae/Hydnoraceae)	6	0 (0%)	1 (16%)
Cynomorium (Cynomoriaceae)	1	1 (100%)	1 (100%)
Krameria (Krameriaceae)	17	1 (6%)	8 (47%)
Pilostyles (Apodanthaceae)	11	0 (0%)	0 (0%)
Rafflesia (Rafflesiaceae)	40	10 (25%)	1 (3%)
Cytinus (Cytinaceae)	8	1 (13%)	1 (13%)
Balanophora (Santalales: 20 families)	23	6 (26%)	3 (13%)
Mitrastemon (Mitrastemonaceae)	2	1 (50%)	0 (0%)
Pholisma (Lennoaceae/Boraginaceae)	3	1 (33%)	2 (66%)
Cuscuta (Convolvulaceae)	218	32 (16%)	46 (21%)
Orobanche (Orobanchaceae)	199	36 (18%)	57 (29%)
Total no. of species considered	548	92 (17%)	129 (24%)

Table 2 A summary of genera from each of the 12 parasitic plant lineages known to exist widely in cultivation or that are the focus of research programmes, or have been grown historically. This is not an exhaustive list, and is ordered phylogenetically.

Parasitic plant lineage (representatives shown in Fig. 1)	Examples of genera known to exist or have existed in cultivation, or the focus of propagation research (not an exhaustive list)	Unknown in cultivation outside of isolated propagation trials (not an exhaustive list)	First published account of successful cultivation, and/or very detailed reports on cultivation
Lauraceae	Cassytha		Boewig (1904); Heinricher (1922)
Aristolochiaceae (Hydnoraceae)	Hydnora	Prosopanche	Hydnora: Carlquist (1989)
Cynomoriaceae		Cynomorium (seed germination protocols explored)	
Krameriaceae	Krameria		Musselman (1977); Weigend & Dostert (2005)
Rafflesiaceae	Rafflesia	Rhizanthes, Sapria	Rafflesia: Mursidawati (2017)
Apodanthaceae		Apodanthes Pilostyles	
Cytinaceae	Cytinus	Bdallophytum	Cytinus: Heinricher (1917)
Santalales (20 families)	Balanophora; Arceuthobium, Loranthus, Nuytsia, Tristerix, Viscum; Thesium, Osyris	Numerous genera, most absent from cultivation	Balanophora: Heinricher (1907); Loranthaceae: numerous; Tropical species in the greenhouse: Kuijt (1966); Viscaceae: e.g. Heinricher (1910, 1915); Santalaceae: Heinricher (1910); Santalum: Sedgley (1984)
Mitrastemonaceae		Mitrastemon	Planted at Oxford Botanic Garden (no signs of growth to date)
Lennoaceae		Ammobroma Lennoa Pholisma	
Convolvulaceae (Cuscutaceae)	Cuscuta		Many reports
Orobanchaceae	Aeginetia; Cistanche; Lathraea; Orobanche s.l. (Orobanche, Phelipanche, Aphyllon); Phelypaea; Striga gesnerioides; Cistanche (farmed); the hemiparasitic Orobanchaceae are cultivated more widely	Christisonia (grown in Queen Sirikit Botanic Garden, Thailand), Boulardia	Many reports of weedy taxa; fewer of non-weedy holoparasites and hemiparasites: Heinricher (1910); Usage of hemiparasites as ornamental garden plants: Weber et al. (1980); Weber (1981); Seth (2020)

Much of our understanding of root parasite development was brought to bear by weed research scientists growing the plants in Petri dish bioassays called rhizotrons, in which the infection process is observed over the course of the life cycle (Fig. 2 Bottom). In the following five stages, we highlight commonalities that can be important considerations when cultivating these challenging plants.

Stage 1: seed storage and preconditioning

Many parasitic plants produce large numbers of seeds that, like those of nonparasitic plants, remain dormant after dispersal. They are often minute (for a full account of parasitic seed dimensions and characteristics see Baskin & Baskin (2021)). However, some produce fleshy fruits with large oily seeds (Santalaceae) or a fully differentiated embryo inside (mistletoe 'pseudoberries' of Viscaceae and Loranthaceae bar *Nuytsia*) – these seeds are short-lived and cannot be stored (for some limited storage conditions for dried mistletoe fruits, see Baskin & Baskin (2014)). Dispersal mechanisms in nature are varied; in many Orobanchaceae, the minute seeds are wind- or water-dispersed (Thorogood & Rumsey, 2021). In many tropical parasites, dispersal mechanisms are poorly understood; ants and mammals ranging from rodents to elephants have variously been theorised as dispersal agents for the seeds of Rafflesiaceae (Nais, 2001; Pelser *et al.*, 2013).

The seeds of most parasitic plants can be stored in cool, dry conditions, in which they remain in a state of dormancy (exceptions are genera with fleshy seeds or non-dormant embryos). Under conditions of elevated temperature and moisture (typically 1–2 weeks), dormancy is released, sensitising the seeds to the presence of germination stimulants. If exposure to germination stimulants is absent, the seeds can enter a secondary dormancy (Matusova *et al.*, 2004; Bouwmeester *et al.*, 2021). The mechanisms underlying release from dormancy are poorly understood in most parasitic plants, but well known in some. For example gibberellic acid (GA3) and abscisic acid (ABA) appear to be important in some species (Yao *et al.*, 2016; Bao *et al.*, 2017; Bouwmeester *et al.*, 2021), while a cold stratification (vernalisation) is necessary in others (e.g. many temperate species of *Cuscuta*; temperate hemiparasitic Orobanchaceae; Weber, 1981; AF, pers. obs.). Seed scarification helps to trigger germination and increase germination rates in seeds with thick testae and long physiological seed dormancy (e.g. *Cassytha*, some *Cuscuta* species, *Krameria*; AF, pers. obs.). In many endoparasites, the dormancy, viability and preconditioning requirements remain a mystery; prolonged dormancy has been proposed as a possibility for *Rafflesia* (Wicaksono *et al.*, 2020), but further work is required.

Stage 2: germination in response to stimulants

Germination of the seed of root holoparasites usually requires the presence of a host, because the process is triggered by exposure to particular host signal molecules. A body of evidence exists for some weedy root holoparasites (especially Orobanchaceae), for which the plant hormones Strigolactones are the major germination stimulants (Bouwmeester *et al.*, 2021). Detailed studies of *Orobanche* and *Phelipanche* seed and germination biology (including for non-weedy species) were made by Teryokhin (1997); meanwhile, accounts of host ranges of European species (species for which physiological connections have been confirmed) are given by Uhlich *et al.*
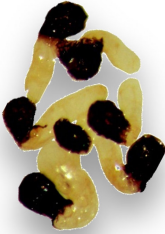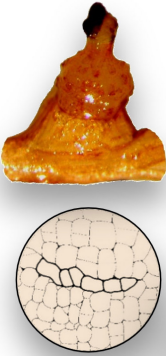
1	2	3	4	5
Seed storage and preconditioning	Germination in response to stimulants	Attachment to a suitable host	Development on a suitable host	Flower and seed production

Fig. 2 Top: The life cycle of a parasitic plant is coordinated with that of its hosts. The main stages summarised are discussed here in relation to propagation (see 'Growing and propagating parasitic plants'). Bottom: A rhizotron bioassay showing the various stages of the life cycle of *Orobanche minor* on its host (*Trifolium pratense*).

(1995) and Pusch (2009). The principles of host stimulant-triggered germination are widespread in root holoparasites across the 12 independent lineages, however data for most non-weedy species – especially endoparasites and stem parasites – are scant. Root holoparasites are often highly host specific, and this can manifest itself even at the point of germination. For example, studies using wild populations of *Orobanche* show variation in germination rates on different hosts (Thorogood & Hiscock, 2010b), suggesting that even at this early stage in the life cycle, optimal host selection is essential for growth success. Accounts of cultivation of other root holoparasites are scant. Author AF planted fruits of *Cynomorium coccineum* on a pot-grown host plant of *Atriplex portulacoides* in 2014, but to date the parasite has shown no sign of growth. Author CT is also working with local ecologists in the Canary Islands to inoculate hosts (*Salsola divariatca*) *in situ* with this species to augment wild populations on sand dunes; again, there are no results to date. We suggest that this parasite may need a substantial host root run, given the size of its underground stem system (like *Hydnora*); therefore pot cultivation may be particularly difficult for this species.

Observations of germination for most endoparasites are absent but, unsurprisingly, it appears that host-derived stimulants are also required for these plants (Wicaksono *et al.*, 2020). Seeds of endoparasites are notoriously difficult to germinate, and even using seeds or flower buds as explants in tissue culture has proved unsuccessful (Abdullah *et al.*, 2020). It is possible that determinants for germination in some species are complex and multi-faceted, potentially involving other organisms or interactions, e.g. mycorrhizas (Thorogood *et al.*, 2021b) or microbial partners (Wicaksono *et al.*, 2020).

For some endoparasites, propagation by seed remains an unviable route to practical cultivation. Despite isolated reports of artificial inoculation of *Rafflesia* by seed (Wicaksono *et al.*, 2020) propagation in this way is generally unsuccessful. In the absence of further research, grafting remains the optimal method for intractable parasites such as *Rafflesia*. It has been suggested that seedlings of *Rafflesia* may enter host tissues through the roots or bark; further research is needed here. The only endoparasitic plant that has been cultivated successfully across multiple botanical gardens is *Cytinus* (Cytinaceae), which produces copious dust-like seeds. Seeds of the unrelated endoparasite *Pilostyles* (Apodanthaceae) (Fig. 1F) are larger and sticky (AF, pers. obs.). It seems likely that the seeds of this genus enter their hosts through the aerial shoots. Fresh fruits of the endoparasite *Pilostyles hamiltonii* were placed on twigs and stems of potted hosts (Australian shrubby Fabaceae) at Munich Botanic Garden (Germany) by AF; however, no germination was observed (possibly due to the wrong choice of host species, as *Daviesia* was unavailable in Munich).

Stage 3: attachment to a suitable host

Host–parasite attachment facilitation is another important consideration when cultivating parasitic plants. For many root parasites, seeds are minute and dust-like, and are wind-dispersed and/or washed into crevices in nature. In cultivation, scattering seeds on the soil surface can be suboptimal because close proximity to host root systems is required. Furthermore, many root holoparasites attach to young or actively growing roots. In most root parasites, the first point of attachment (via a primary

haustorium) occurs on actively growing host roots, rather than on mature roots. Therefore host root architecture and age structure are also important considerations for root parasite cultivation. Two means of facilitating host–parasite attachment are (1) digging seeds into the soil close to host plants' root systems, and (2) potting on hosts with parasite seed mixed into the soil.

Authors AF and CT have employed similar methods for establishing root holoparasites on their hosts, summarised as follows:

(1) The host plant is grown in a nutrient-poor substrate to promote the production of germination stimulants; strigolactones are naturally produced by plants to attract mycorrhizal soil fungi under nutrient-stressed conditions (Akiyama *et al.*, 2005). A pinch of parasite seed is mixed with either fertile soil (as followed by AF; fertile soil may help promote new root growth) or simply loose sand (CT).

(2) A hole close to the host plant is excavated close to the root system, which is filled with the seed-soil/sand mix; the uppermost layer is then covered with the nutrient-poor growing substrate.

(3) Care must be taken not to wash out the seeds from the pot or rhizosphere of the host when watering; for potted hosts, a tray-based system is preferred. The host plant will establish new roots in soil inoculated with parasite. Alternatively, in pot-grown systems, parasite seed can be dusted on the root ball of an established host plant before potting on. We should note that seeds of facultative hemiparasitic Orobanchaceae cannot be sown by this method, as they require light-induced germination, i.e. they must be sown on the soil surface. For the cultivation of hemiparasitic

Orobanchaceae, potted or in the garden (for some with or without host), see Weber (1981), Weber *et al.* (1980) and Seth (2020).

The quantity of parasite seed required depends on the size of the host and the volume of soil in question; a low application rate can reduce the likelihood of successful parasite establishment, whereas a high application rate can reduce the vigour of the host (or eventually even kill it). Whilst it is not possible to list optimal seed doses for all parasitic plants, by way of an example cultivation trials using *Orobanche* grown for weed research purposes show that the parasite reduces the biomass of its host even at low levels of infection (Barker *et al.*, 1996). In this work, as the infection density of *Orobanche* increased, the effects of the parasite also increased to a point beyond which there was no further reduction (10 mg/1,000 seeds dm−3 soil). In the agricultural weed *O. cernua*, as the number of parasite attachments decreased, the size of each parasite increased, suggesting that a finite amount of resource was available to the parasite (Hibberd *et al.*, 1998). Of course, for cultivation purposes in botanic gardens, a significant reduction in host vigour is undesirable, so trial and error may be required when determining seed inoculation rates for a given host–parasite pair. For this reason, in the method described above the seed-soil mix for inoculation can be added to the host plant at a single point. This can be labelled easily, and enables the sustainable growth of both host and parasite.

For stem holoparasites such as *Cassytha* (Fig. 1A), *Cuscuta* (Fig. 1K) and mistletoes, seeds can be germinated in the absence of germination stimulants, as long as they are positioned near (or on) a suitable host early in

their development. At Oxford Botanic Garden (UK), *Cassytha* has been propagated in this way to create a stock plant, from which stem cuttings of the host to which the parasite is attached can be propagated easily (Fig. 3C). This is necessary in the case of perennial parasites such as *Cassytha* if they are grown on an annual host (in this case *Bidens*). At both Oxford Botanic Garden and Munich Botanic Garden, *Cassytha* is propagated by stem cuttings. Similarly, AF has cultivated around 25 species of *Cuscuta*, all germinated from seed but later propagated by cuttings, using *Coleus* s.l. (Lamiaceae) as a surrogate host. *Coleus* has proven an optimal surrogate host for all species of *Cuscuta* cultivated to date, including species with a narrow natural host range (even a single host species, such as *C. epilinum* on *Linum usitatissimum*). Joel McNeal (pers. comm.) also grows his research collection of *Cuscuta* on *Coleus*. *Cuscuta* will quickly kill its host, especially if raised in pots, therefore a sustainable supply of host plants is advisable. Although this paper focuses predominantly on holoparasites, we note that stem hemiparasites are also grown widely in collections; their propagation generally requires simply placing the seeds on growing host tissue. For example *Viscum minimum* (Fig. 4E) is distributed widely along with its host *Euphorbia* spp. by succulent plant enthusiasts as a curiosity worldwide. A detailed account of its propagation is given by Kuijt (1986).

The process of early attachment and development of most endoparasitic plants remains a mystery. Successful cultivation has thus far only been achieved on a wider basis in botanic gardens with *Cytinus* on *Cistus* spp. (Fig. 1G). Following attachment to the host, the epicotyl of the endoparasite seedling appears to die off, after which the endophyte ramifies invasively through host tissues, losing contact with the initial site of penetration

(Wicaksono *et al.*, 2020). A breakthrough in the propagation of *Rafflesia* was the successful grafting of a host *Tetrastigma* vine infected with *R. patma* onto an uninfected *Tetrastigma* rootstock in Bogor Botanic Garden (Indonesia). Veneer grafting and cleft grafting were successful, leading first to bud emergence in two years, then to blooming in three years from veneer-grafted material and in six years from cleft-grafted material (Mursidawati *et al.*, 2015). Propagation efforts outside the native range of *Rafflesia* have been less fruitful to date. Attempts in the United States to propagate host cuttings infected with *R. speciosa* and to germinate *R. speciosa* seeds in vitro using various plant growth regulators have all been unsuccessful (Molina *et al.*, 2017). However, this work does represent the first time that living *Rafflesia* material has been imported and survived outside Asia.

Stage 4: development on a suitable host

Following compatible attachment and haustorium development, the parasite draws nutrients from the host and develops a vegetative body (bar the endoparasites). In the case of root holoparasites like *Orobanche*, this can take the form of an underground tubercle, sometimes with projecting structures that store host-derived starch (Teryokhin, 1997; Thorogood & Rumsey, 2021); these may later develop secondary haustoria and bring about perennation (observed by CT in *O. minor* on *Brachyglottis* and *O. hederae* on *Hedera*). The extraordinary root holoparasite *Hydnora* has been documented to grow on a range of hosts (Kuijt, 1969) and cultivation from seed is possible. *H. africana* was successfully grown for at least 12 years on succulent *Euphorbia caputmedusae* in California in the late 1970s

from wild-collected seed by Carlquist (1989); the host was infected on potted plants which were subsequently planted in a garden. The parasite took five-and-a-half years to flower, and the author was even able to divide and propagate *Hydnora* in his garden, using three additional succulent *Euphorbia* taxa as hosts. The parasite flowered in his garden each year from 1981 to at least 1989 (Carlquist, 1989). The author wrote:

> I would encourage others to attempt cultivation of this and other species of *Hydnora* – lack of host specificity would seem to favour cultivation. Obviously, considerable patience is involved, judging from the interval between sowing seeds and flowering […]. Although seeds may well be capable of dormancy, one is well advised when cultivating any species not hitherto attempted to begin with seeds taken directly from fresh fruits. (Carlquist, 1989, p. 3)

Beside this historic account, *Hydnora* is, to the authors' knowledge, unknown in collections today; *H. africana* occurs naturally in the Little Karoo desert close to the Karoo Desert National Botanical Garden in Worcester, South Africa. CT has attempted cultivation of *H. africana* on pot-grown *Euphorbia tirucalli* (mislabelled as *E. mauritanica*); no flowers emerged in a decade. The trial has been repeated on the correct host (planted in 2019), but has not flowered to date. Stem parasites such as *Cassytha* and *Cuscuta* possess climbing stems that develop numerous haustoria and can spread to new hosts.

The development of endoparasites is more complex. A series of studies on Rafflesiaceae has transformed our understanding of the development of endoparasites within their hosts (Nikolov *et al.*, 2013; Nikolov & Davis, 2017; Wicaksono *et al.*, 2020). As the endoparasite develops, it can trigger substantial alterations to host xylem micromorphology. This is potentially a means of optimising 'hydraulic safety', enabling the parasite to divert significant volumes of water from its host (Thorogood *et al.*, 2021b). There is also evidence in *Rafflesia* of dispersal of the endophyte through the host, for example towards younger host tissues (Heide-Jørgensen, 2008; Wicaksono *et al.*, 2020). For these reasons, selection of mature hosts may be desirable for endoparasites in particular. The authors achieved successful cultivation of *Cytinus hypocistis* using seed and a small, pot-grown two-year-old *Cistus* host about 30 cm high (Fig. 3B). The parasite flowered after two years, for two consecutive years, each year producing just two small inflorescences. Heinricher (1917) observed first flowers in that species in his cultivation trial three years after sowing the seeds. The small stature of the plants raised indicates possible regulation of parasite biomass in relation to that of the host. Woody hosts such as *Cistus* can perform poorly in pot cultivation (in this case the host declined, and the parasite along with it, in the third year). Some hosts require a substantial volume to develop a healthy and sustainable root system. Air-Pots®, plunge planting or, where possible, planting *in situ* may be desirable when cultivating endoparasites on large and slow-growing woody hosts.

Stage 5: flower and seed production

Following a period of successful development on or inside the host, the parasite emerges to flower and set seed. The longevity of parasitic plants is variable and, in some cases,

reported inconsistently in the literature. For example *Orobanche* (s.l.) are usually annuals or monocarpic biennials to monocarpic perennials (by anthesis, the haustorial connection to the host is lost). However some species can persist as perennials on their hosts by division and development of secondary haustoria on perennial hosts, such as *O. hederae* on *Hedera*, or *O. minor* on woody shrubs. Other holoparasitic Orobanchaceae are long-lived, persistent perennials that develop a substantial underground stem system with age, e.g. *Lathraea*. In the authors' experience, *L. clandestina* takes two to four years to flower from seed, while *L. squamaria* appears to grow more slowly, and can take five to ten years (Heinricher, 1910; AF pers. obs.). Both species can be propagated vegetatively by dividing the rootstock in early spring and placing the divisions close to new host roots. In the authors' experience, the tuberous rootstock of tropical/subtropical *Aeginetia indica* is also perennial. The species is shorter-lived but not monocarpic; the plant persisted for years in raised beds under glass at Oxford Botanic Garden and potted on various monocot hosts in the greenhouse and on AF's windowsill (Fig. 4A). Short life cycles can lead to a high turnover of some parasites; in cultivation, repeated sowing at least every two years can prevent parasite populations from dwindling. By contrast, stem parasites such as *Cassytha* and mistletoes can persist for years with minimal intervention providing the host plant is large enough and healthy; vigorous specimens of *Cuscuta*, however, usually kill their host plants.

Our understanding of the longevity of most endoparasites remains obscure. *Cytinus* can reproduce within two years of sowing seed based on trials by CT. In other endoparasites such as *Rafflesia*, due to the prolonged nature of bud development and low flowering incidence, studying the full life cycle is difficult, however investigations suggest a life cycle spanning around three to five years (Hidayati *et al.*, 2000; Susatya, 2007). What triggers the transition from the vegetative stage to the production of a protocorm and flowers is unknown, but again, it may be a variety of factors in combination (Wicaksono *et al.*, 2020). *Rafflesia* shows a notoriously high level of bud mortality which complicates its propagation yet further.

Case studies in the cultivation of parasitic plants

Oxford Botanic Garden

Oxford Botanic Garden is the oldest botanic garden in the UK, founded in 1621. It was established as a physic garden in which medicinal plants were grown for teaching purposes. Today, the garden holds a collection of over 5,000 taxa, some of which have international conservation importance (Thorogood, 2021). A recent collections focus, linked to the garden's programme of research, is parasitic plants. The collection currently contains parasitic plants from five of the twelve families, with global representation. Of notable success is the collection of 11 taxa of wild-sourced *Orobanche*, including species that are locally rare or of conservation concern. For example, local host-specific taxa of *O. minor* (Fig. 3E) and the rare native *O. picridis* (Fig. 3F) have both been cultivated successfully; moreover *O. coerulescens* (Fig. 3G) was grown for the first time in the UK using seed collected on an expedition to Japan. Under glass, *Balanophora tobiracola* has been successfully grown on a pot-grown host of *Pittosporum tobira* (Fig. 3D) for the first time. Many other species have been planted in the collection, but have yet to flower at the time of preparation of this article. Some species of *Balanophora* appear to have a
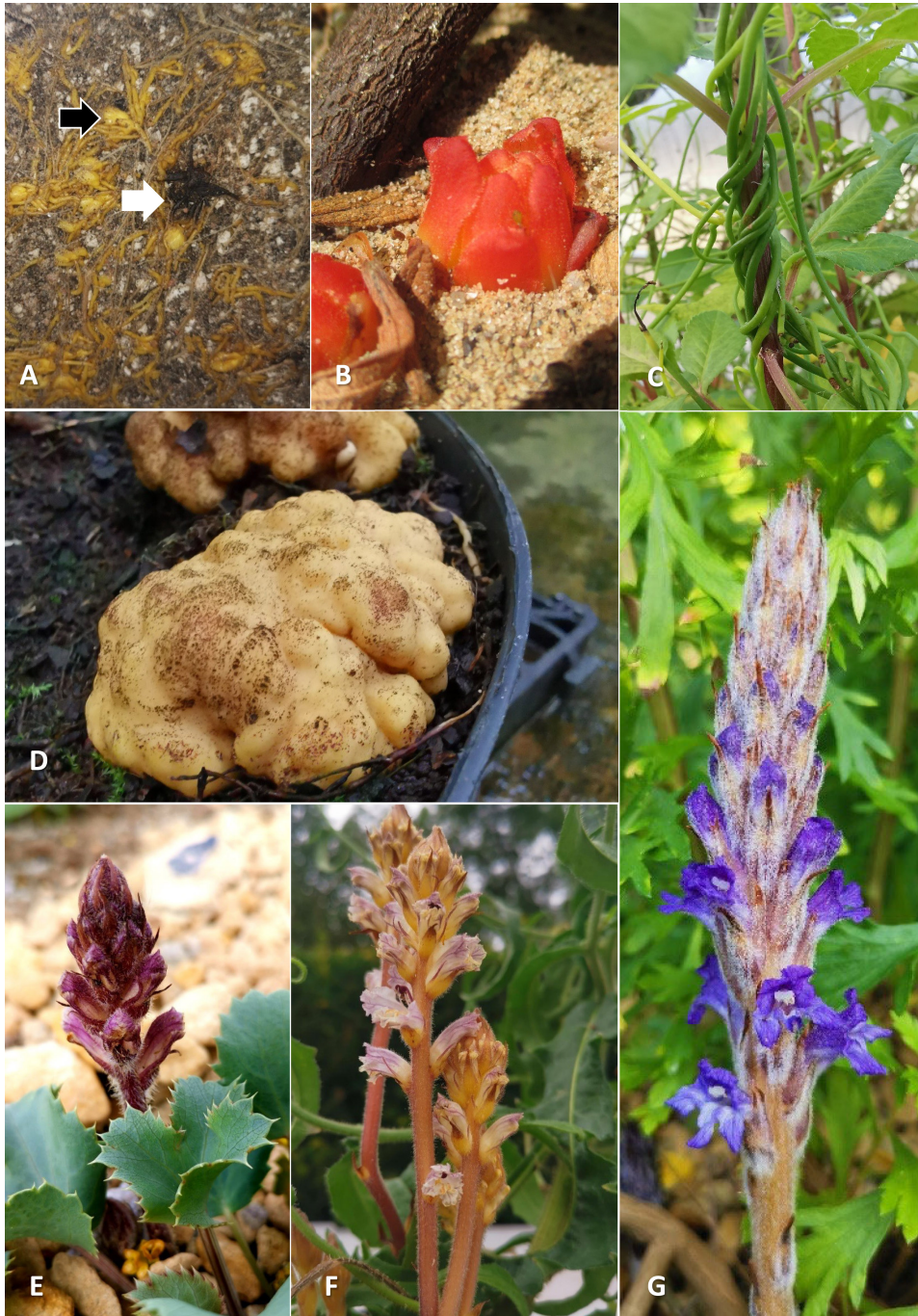
Fig. 3 Examples of parasitic plants in cultivation at Oxford Botanic Garden: A. *Orobanche coerulescens* infecting the rootball of its host *Artemisia japonica*; note the numerous developing tubers (black arrow), one of which is necrotic (white arrow). B. *Cytinus hypocistis* developing on a pot-grown *Cistus monspeliensis*. C. *Cassytha filiformis* growing on *Bidens* sp. D. *Balanophora tobiracola* growing on a pot-grown *Pittosporum tobira* (the tuber of the parasite emerging above the soil surface). E. *Orobanche minor* var. *pseudoamethystea* growing on *Eryngium maritimum* in a raised bed on public display. F. *O. picridis* growing on a pot-grown host of *Picris hieracioides*. G. *O. coerulescens* growing on *Artemisia japonica*, plunge-planted in a raised bed on public display. All photos: C.J. Thorogood.

broad host range, indicated by photographs found online, for example of *B. fungosa* subsp. *fungosa* on a cultivated papaya tree (i.e. a non-native host species) in tropical Queensland, Australia. The first reports on cultivation of *Balanophora* from seed in the tropics was published by Heinricher (1907). Seed of *Mitrastemon yamamotoi* has been sown on potted *Castanopsis* hosts in Oxford (planted 2020), however no flowering shoots have been observed to date.

Other botanic gardens in Europe and private collections

A substantial collection of parasitic plants (especially hemiparasitic Santalales) was grown at Marburg Botanic Garden (Germany), for several decades, in connection with the research of Prof. H.-C. Weber. Unfortunately, this collection vanished with his retirement and the subsequent reorganisation of the botanic garden. AF had the opportunity to see this collection in full bloom, including many tropical mistletoes and sandalwoods. Copenhagen Botanic Garden (Denmark) also holds an extensive collection of parasitic plants (Heide-Jørgensen, 2008). At the beginning of the 20th century, one of the largest collections of cultivated parasitic plants was established at Innsbruck Botanic Garden (Austria), thanks to the research and pioneering cultivation experiments of parasitic plant expert Prof. Emil Heinricher (who was responsible for the first cultivation of many holoparasitic genera, e.g. Heinricher, 1907, 1910, 1915, 1917, 1922). An overview of the most commonly grown species of *Orobanche* and *Phelipanche* in European botanic gardens is given by Uhlich *et al.* (1995, p. 186).

At Munich Botanic Garden, a number of parasitic plants have been grown successfully,

including *Krameria lappacea* on potted cacti (this hemiparasite is a host generalist; see Musselman (1977)); *Cassytha ciliolata* on *Indigofera* (*C. pubescens* was also grown and propagated on *Abutilon* spp. at Munich Botanic Garden at the beginning of the 20th century and distributed as cuttings on host plants to other botanic gardens; see Cartellieri (1928)); *Aeginetia indica* on *Setaria palmifolia*; and various *Orobanche* and *Phelipanche* on their natural hosts outdoors. The striking *Phelypaea coccinea* has repeatedly been raised from seed on *Centaurea* sect. *Psephellus* (Fig. 4C). The first report of successful cultivation of this stunning parasite was by Heinricher (1910); recently *P. boissieri* was also grown near Cambridge (UK) (Cullen, 2010). Seeds of *Rafflesia* were collected in Borneo about 30 years ago by the late Josef Bogner from Munich Botanic Garden, where he tried to inoculate a large *Tetrastigma* vine planted in the greenhouses (J. Bogner, pers. comm.). The parasite failed to establish, possibly due to low temperatures and the incorrect *Tetrastigma* species (see the detailed account of *Rafflesia* cultivation below).

AF has grown parasitic plants in his private garden and greenhouse for over 20 years, including outdoor cultivation of 35 European species of *Orobanche* and *Phelipanche* and 3 North American species of *Aphyllon* (Fig. 4B), as well as *Lathraea squamaria* and *L. clandestina*, and numerous hemiparasitic Orobanchaceae. *Aeginetia indica* has proven to be amenable to pot cultivation under glass and even on the author's windowsill, on a range of hosts including perennial tropical Poaceae and Cyperaceae, as well as on *Liriope* and *Aspidistra*. He also germinated 60-year-old seeds of *Cistanche violacea*, from herbarium material, on potted 6-month-old beetroot

plants in large pots (50 cm in diameter) in an unheated greenhouse. The *Cistanche* developed tubers around 5 cm in diameter, but died when their biannual hosts ceased in the second year. Reports exist for *C. phelypaea* growing on sugar beet plantations in Saudi Arabia (Farah, 1987), including a photograph of three well-developed *Cistanche* tubers (one of them flowering) attached to the roots of a comparatively small specimen of *Beta vulgaris* (Farah, 1987, p. 191). It should be noted that author CT has had limited success to date growing *Cistanche* on pot-grown *Atriplex halimus*. Attempts by AF to grow *Prosopanche* on a potted *Gossypium* plant failed, probably because the fruits sent from Argentina arrived in poor condition.

Cultivation of parasitic plants can allow for a critical evaluation of host range. AF has validated/refuted various hosts reported for a range of *Orobanche* using cultivation experiments. For example *Tussilago* was debated as possible host plant of *O. flava* in the literature (e.g. Pusch, 2009), which potted cultivation with *T. farfara* confirmed (as first observed by Beck, 1890; Fig. 4D). *Petasites paradoxus* and *P. albus* were also confirmed as suitable hosts for *O. flava*; meanwhile *P. hybridus* was refuted as a host for *O. lutea*. *O. elatior* s.str. is often cited to be host-specific on *Centaurea* (Asteraceae; e.g. Pusch, 2009), although older literature also cites unrelated *Thalictrum* (Ranunculaceae) as a host. The latter had been doubted by many authors (Pusch, 2009; Zázvorka, 2010), but this was validated at Munich Botanic Garden; *O. elatior* of unknown origin recurred for years in a bed of *Thalictrum aquilegiifolium*. AF has also grown the species successfully on pot-grown *Centaurea scabiosa*, *T. aquilegiifolium* and *T. minus* in his garden (Fleischmann, 2013). Cultivation experiments can also shed light on phenotypic plasticity induced by the host plant. For example the morphology of three distinct forms of *O. alsatica* in Central Europe appears to be influenced by host rather than genetics (as postulated by H. Uhlich (pers. comm.)). Again, this was confirmed by the author's cultivation experiments on different host species.

Bogor Botanic Garden

Bogor Botanic Garden, founded in 1817, is the oldest botanic garden in Southeast Asia. It has a long and rich history of successful conservation of Indonesian and other tropical plant species from across the world. In particular, the garden has a collections focus on tropical parasitic plants, including *Rafflesia*. This iconic and much celebrated flower featured on a commemorative monument marking the bicentenary of Bogor Botanic Garden in 2017 (Fig. 5A,B) that was signed by the Indonesian President. Bogor has a long history of cultivating this enigmatic parasite. According to Meijer (1997) and Vieldkamp (2007), host vines infected with *Rafflesia patma* and *R. rochussenii* respectively were successfully relocated to Bogor Botanic Garden in 1850, followed by *R. arnoldii* in 1856. More recent attempts to translocate *R. patma* have been challenging, and in many cases unsuccessful (Mursidawati *et al.*, 2014). However to date, Bogor Botanic Garden has successfully translocated six accessions of *R. patma* which are now located in the Plant Reintroduction Nursery, as well as five species of *Tetrastigma* which were collected from the habitats of *R. patma*, *R. tuan-mudae* and *R. arnoldii*. This shows great promise for future research on the genus at Bogor.

The propagation of *Rafflesia* has long been a research focus at Bogor Botanic Garden, especially using *R. patma* on its host vine, *Tetrastigma leucostaphylum* (Fig. 5C–E).

Fig. 4 Parasitic flowering plants grown by A. Fleischmann: A. *Aeginetia indica* on *Setaria palmifolia* (Poaceae) in the tropical greenhouse. B. *Aphyllon californicum* subsp. *californicum* on potted *Grindelia integrifolia* (Asteraceae). C. *Phelypaea coccinea* on *Centaurea simplicicaulis* (Asteraceae) grown at Munich Botanic Garden. D. *Orobanche flava* on *Tussilago farfara* (Asteraceae) in the open garden. E. *Viscum minimum* on *Euphorbia jansenvillensis* grown in the greenhouse. Note the old germinated seedling still adhering to the host plant, and the two desiccated primary haustoria of the seedling, which led to endophytic infection of the host plant. Photo C: Andreas Gröger; all other photos: A. Fleischmann.

Attempts to grow this species have been conducted in the *ex situ* conservation area of the garden since 2004 (Mursidawati, 2017). The first flower of *R. patma* appeared after six years' research trialling two methods of propagation. Of the two methods, grafting (cleft and veneer) on the host plant proved the more successful. Flowering has been observed sixteen times on three different host vines since 2010 (ten female and six male flowers).

This phenomenal cultivation success has been the platform for a multi-pronged programme of research into *Rafflesia* at Bogor Botanic Garden examining various aspects of the plants' biology, using two species: *R. patma* and *R. arnoldii*. One aspect has explored the reproductive ecology, for example the pollination biology of *R. patma* (Kahono *et al.*, 2010), and the morphology of the fruits and seeds of both *R. patma* and *R. arnoldii* (Mursidawati, 2012). Another has focused on the anatomy and physiology of growth and development within the host plant. This line of research has examined the development of *R. patma* inside its host tissues (Mursidawati & Sunaryo, 2012); the dispersal of the parasite within host tissues after grafting (Wicaksono *et al.*, 2017); the development of the endophyte in association with host vascular cambium (Mursidawati *et al.*, 2019); tissue differentiation of the early- and late-stage flower buds (Mursidawati & Wicaksono, 2020); and histology of the epidermis and vascular structures of the mature flower (Mursidawati *et al.*, 2020). Together, this campaign of research represents a step change in our understanding of how to propagate *Rafflesia*. Building on this success, two active lines of research now seek to advance our understanding of the propagation biology and conservation of *Rafflesia* at Bogor:

(1) Grafting techniques

Grafting has proved to be the most successful means of propagation of *Rafflesia patma* at Bogor Botanic Garden (Mursidawati *et al.*, 2014; Wicaksono *et al.*, 2016). A *Tetrastigma leucostaphylum* vine infected with the parasite, sourced from the Pangandaran Nature Reserve, West Java, was grafted onto a locally grown vine in the botanic garden in 2006. Whilst this method proved successful and enabled close examination 'in real time', many aspects underpinning its success still remain a mystery. To date, only 16 out of 216 inoculated individuals of *R. patma* on 3 host vines have completed their life cycle to the advanced stage of flowering. This indicates that high rates of abortion of the parasite may be inherent in this species, even under well-maintained controlled conditions. Indeed, we have observed no difference in flowering behaviour in the botanic garden compared with populations growing *in situ*. For example, new buds emerge throughout the year, but the rate of mortality is always high; furthermore, the unisexual nature of the flowers makes artificial pollination (and therefore seed set) difficult in cultivated and natural stands alike. Multiple flowers arose on three occasions during the cultivation trials at Bogor. On two such occasions, all flowers were female; on the third, a single male and two female flowers were observed. However even with the simultaneous occurrence of both male and female flowers, cross-fertilisation failed for unknown reasons. These results highlight the unpredictability and challenges associated with *Rafflesia* cultivation, even under optimal conditions using multiple accessions, following successful propagation.

(2) In vitro culture

Most attempts at in vitro culture have failed. Successful propagation of *Rafflesia arnoldii*

tissue in vitro is reported by Sukamto & Mujiono (2010). In their study, a young floral bud about 2 cm in diameter was collected from Bengkulu, Sumatra. The authors report successful culture of the bud on Murashige and Skoog basal medium with the addition of 0.1 and 1.0 mg/l of 2,4 D or 0.5–1.0 mg/l Picloram. Three types of callus developed from different treatments. The explant that produced the most profuse and best-quality callus was cultured using the 1.0 mg/l 2,4 D treatment. Some callus cultures produced white strands and inhibited callus growth, however these were absent from specimens grown in Picloram treatments. Further work is needed to extend this research to other species of *Rafflesia*, assess its repeatability and apply the principles of its success to a general propagation protocol.

There have been several attempts at in vitro culture at Bogor Botanic Garden, for example using the seed of *Rafflesia patma* and *R. arnoldii* in various treatments, as described by Matusova *et al.* (2004). Attempts have included the addition of Strigol (a stimulant used widely for parasitic plant seed germination), the co-culture of these two species alongside the tissues of their hosts and *R. meijerii*-infected bud and root explants; all attempts were unsuccessful (Mursidawati & Handini, 2009). Again, these failed attempts highlight the intractability of *Rafflesia* to cultivation protocols known to be successful for other parasitic plants, and the need for further research into the propagation of these elusive plants.

Cistanche *farming in China*

Whilst some Orobanchaceae are pernicious weeds, with research aimed at their eradication, attention has largely shifted towards those that have growing potential in a changing climate. *Cistanche* is now cultivated at scale in China for use in traditional herbal medicine, and shows promise as a possible future crop in arid climates. In the context of a global desertification crisis, and the need to feed a growing human population, there is significant potential to expand *Cistanche* cultivation beyond China. The plant could be grown as an ancillary crop alongside forests planted to halt land degradation. Stabilising 'shelter forests' involves the plantation of drought-tolerant small trees and shrubs such as saxaul (*Haloxylon*; Orlovsky & Birnbaum, 2002) and tamarisk (*Tamarix*) (Ning *et al.*, 2021) both of which are ideal hosts for *Cistanche*. Indeed *Cistanche* is already being grown in this way in China's provinces of Xinjiang, Ningxia, Gansu and Inner Mongolia (Song *et al.*, 2021), and has globally important potential (Xu *et al.*, 2009). To realise this potential, and to monitor trade to control unsustainable harvesting of threatened wild populations, robust taxonomy is needed for the genus; species limits are currently confused across the range of the genus (Thorogood *et al.*, 2021a; Lei *et al.*, 2021). Botanic gardens could play an important role in the cultivation of a range of useful parasitic plants, beyond *Cistanche*, that have potential for commercial scale-up. For example *Cynomorium* is also prized in traditional herbal medicine and wild harvested, yet to our knowledge the plant is absent from both botanic gardens and larger-scale cultivation trials (and see details of the failed attempts at cultivation above).

Outstanding questions and future directions

The case studies we present above highlight inconsistencies in taxonomic representation of the 12 parasitic plant lineages in cultivation. They also highlight opportunities,

Fig. 5 A & B: The bicentenary monument of Bogor Botanic Garden that was signed by the Indonesian President in March 2018 and features *Rafflesia patma*. C–E: *R. patma* in cultivation, following the successful grafting of an infected host *Tetrastigma* vine onto an uninfected *Tetrastigma* rootstock, in Bogor Botanic Garden. Photos A & B: Joko Witono; photos C & D: Deniek G. Sukarya; photo E: Sofi Mursidawati.

for example for a renewed focus on rare or locally endangered parasitic taxa in botanic gardens' collections, and even the potential for commercial cultivation in some cases. In our assessment, we have identified the following three challenges, and associated considerations or solutions during the development of collections strategies.

Biology

The life cycles of parasitic plants are synchronised with those of their hosts, but in many cases they are poorly understood. Correct host choice, vigour and root run are often important considerations. This creates an added layer of complexity and interdependency for parasitic plant cultivation.

- Careful examination of each stage of the parasite's life cycle is beneficial.
- Collecting host material alongside the parasite ensures compatibility.
- A blended approach to propagation (grafting, seed, in vitro) may be desirable for recalcitrant taxa like *Rafflesia*.

Turnover

The longevity of parasitic plants in cultivation is variable; many are relatively short lived or require intensive intervention such as annual or biennial re-sowing of seed, or disturbance; therefore collections are at risk of attrition of institutional knowledge, and accessions, over time.

- Integration of re-sowing into annual maintenance plans is useful for annual/ monocarpic taxa such as *Orobanche*, *Phelipanche* and *Aphyllon.*
- Plunge-planting of pot-grown hosts where appropriate enables control over, and examination of, the root run.

- For fast-growing stem parasites (especially *Cuscuta*), the continuous propagation of suitable hosts for fresh supply should be guaranteed.
- Holoparasitic Orobanchaceae, *Cuscuta* and *Cassytha* have long-lived seeds that can be stored in seed banks for decades (even at room temperature without any additional measures). Hemiparasites, by contrast, usually have short-lived seed that cannot be stored for long periods (days to weeks in the case of the fruits of some mistletoes, 1–2 years only in most hemiparasitic Orobanchaceae; AF pers. obs.).
- Protocols and observations should be documented alongside accessions in databases.

Effort

Botanic gardens have broad remits spanning education, community engagement, conservation and research, often with limited resources and budget; parasitic plants are not 'quick wins' and so may be absent from collections strategies.

- Focus on local species facilitates duplication of natural conditions.
- Collaboration with local partners is beneficial.
- Parasitic plants should be integrated into a broader strategy; they are, for example, highly successful tools for public engagement and education (Thorogood, 2020).

In this article we place particular focus on *Rafflesia*, which has been the object of much research yet in many respects remains a mystery; this highlights lessons applicable to other tropical parasites. Most *Rafflesia* species are rare and severely threatened

by land conversion and harvesting for medicinal purposes (Nais, 2001), and they may be particularly vulnerable because of their high flower mortality and reproductive ecology (Nais, 2001); a stronger grasp of their propagation requirements is therefore needed urgently. Since mature, viable seeds are difficult to obtain, grafting is currently the most effective means of propagating *Rafflesia* (Mursidawati *et al.*, 2015; Wicaksono *et al.*, 2016) as we discuss in detail in this paper. We assert that the next step is much more challenging: propagation of *Rafflesia* at the population level. High flower mortality and low probability of male and female flowers occurring in synchrony make reliable seed production in cultivation virtually impossible. Whilst our experience in propagating *R. patma* by grafting has identified first principles for success, scaling up time- and labour-intensive propagation by grafting to whole population establishment will be ambitious. But while much of the biology of these plants is a mystery, and their natural habitats are disappearing rapidly (Mursidawati & Irawati, 2017), this is an ambition worth pursuing. In light of this urgent need for further work, we suggest the following priorities for research into *Rafflesia* propagation:

(1) Deployment of the successful grafting protocol, piloted for *Rafflesia patma*, to other species of *Rafflesia* at a local level across Southeast Asia to create *ex situ* conservation collections. For example propagation trials in the Philippines – a centre of diversity for the genus – are currently absent.

(2) Further attempts at artificial pollination of *ex situ* grown plants, as well as natural populations, to generate seed for research purposes, and the establishment of new plants at a population level.

(3) Continued exploration of a viable in vitro protocol, with a view to establishing a low-technology means of propagation that is effective across species.

Importantly, we highlight the importance of conservation and research investment in rare and obscure parasitic plants beyond the better-studied examples such as *Rafflesia*. Parasitic plants have been neglected from *ex situ* collections strategies all too often, and their ecological dependencies make them especially vulnerable to habitat loss and extinction. A powerful route to moving them up the priority list may be the creation of a dedicated Global Conservation Consortium. These initiatives, led by Botanic Gardens Conservation International, mobilise coordinated networks of institutions and experts to implement conservation strategies for priority threatened plant groups. We urge that now is the time to extend focus on parasitic plant cultivation and conservation from a small number of isolated botanic gardens to mainstream collections strategies worldwide.

Acknowledgements

Renner and Sidonie Bellot are thanked for providing fresh fruits of *Pilostyles* for germination experiments, as is Klaus Kubitzki for sending fruits of *Prosopanche* from Argentina. Thanks also go to Natalie Cusimano for providing fresh fruits and living material of *Cynomorium* from Sardinia for research.

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