Assessing the risks of plant invasions arising from collections in tropical botanical gardens

Wayne Dawson · Ahmed S. Mndolwa · David F. R. P. Burslem · Philip E. Hulme

Abstract   Tropical botanical gardens have played an important role in the distribution, naturalisation and spread of non-native plants worldwide. Appropriate guidance relating to risk assessments of established botanical garden collections is often scarce. This paper uses the Amani Botanical Garden (ABG), Tanzania, as a case study to highlight appropriate methods to assess the risks posed by existing and future collections in tropical botanical gardens. Key considerations included field assessments of species status using accepted definitions of naturalisation, spread and invasion, distinguishing between intentionally and unintentionally introduced species, identifying taxonomic patterns in invasion status, assessing patterns in habitats colonised, and determining how knowledge of invasion elsewhere might be useful in forecasting risk. Out of the 214 alien plant species surviving from the original plantings in the early 20th century, 35 had only regenerated, 38 had locally naturalised while 16 had spread widely in the botanical garden. A further 16 species with unclear introduction records in the garden were also found to be naturalised. A greater proportion of introduced species were potentially invasive than might be expected from previous analyses of global floras. Overall, just over half of all naturalised and spreading species were also observed in forest fragments and edges. The proportion of species that had been recorded elsewhere as naturalised/invasive was significantly related to their status in ABG,

W. Dawson (✉) · D. F. R. P. Burslem
School of Biological sciences, University of Aberdeen, Cruickshank Building, Aberdeen AB24 3UU, UK
e-mail: wda@ceh.ac.uk

W. Dawson
Centre for Ecology and Hydrology (Edinburgh), Bush Estate, Penicuik, Midlothian EH26 OQB, UK

A. S. Mndolwa
Tanzanian Forestry Research Institute (TAFORI) Herbarium, P.O. Box 95, Lushoto, Tanzania

P. E. Hulme
National Center for Advanced Bio-Protection Technologies, Lincoln University, P.O. Box 84, Canterbury, New Zealand

with 94% of spreading species and 79% of naturalising species being recorded as natura-
lised or invasive elsewhere, compared to 57% of species that were only regenerating and
49% of species only surviving. Recommendations for further risk assessments of botanical
garden collections are discussed.

Keywords   Alien · Exotic · Horticulture · Invasion · Naturalisation · Risk assessment ·
Weeds · Tanzania

Abbreviation
ABG   Amani Botanical Garden

Introduction

A substantial body of evidence highlights the important role horticulture has played in the
dissemination, naturalisation and invasion of alien plants worldwide (Reichard and White
2001; Weber 2003; Hulme 2005; Mack 2005; Dehnen-Schmutz et al. 2007). The increasing
awareness among industry representatives to tackle this issue (Peters et al. 2006) has
resulted in attempts to establish new codes of conduct within the horticultural trade (Baskin
2002; Reichard 2004). Botanical gardens play a unique role within the horticultural sector
by contributing to the selection and propagation of new plant varieties (Dosman and Del
Tredici 2003; Anderson et al. 2006), the conservation of endangered or economically valu-
able species, public education and recreation (Maunder 1994; Muller 1994; Maunder et al.
2001; Waylen 2006) and in many cases they are of historical as well as cultural signifi-
cance. However, in contrast to the current philosophy of botanical gardens, it was the
importance of trade and commerce as well as competition between colonial powers in the
18 and 19th centuries that drove the establishment of botanical gardens in the tropics (Hey-
wood 1987). As a result, large numbers of tropical and subtropical plant species, including
fruits, spices, legumes, as well as hardwoods and softwoods were transported across the
tropical regions of the globe and ultimately, some became invasive in the subsequent
decades and centuries (Cronk and Fuller 1995).

   Although direct attribution is difficult, there are several cases where tropical botanical
gardens have allegedly played a key role in the establishment of invasive plant species
(Table 1). This risk was highlighted at the 2nd World Botanical Gardens Congress (Lead-
lay 2004) and resulted in a recommendation that all botanical gardens carry out invasive
species risk assessments of their collections and management practices. Yet, appropriate
guidance relating to risk assessments of established collections is scarce (Jefferson et al.
2004). In this paper, we use the Amani Botanical Garden (ABG) in the East Usambara
Mountains, Tanzania, as a case study to highlight key considerations and appropriate meth-
ods to assess the risks posed by existing and future collections in tropical botanical gardens.
Previous surveys of the ABG (Sheil 1994), and surrounding forests in the Usambara Moun-
tains (Iversen 1991), have highlighted the relatively high number of naturalised alien plant
species (48 and 239 respectively). Many of the species listed in both inventories were
intentionally introduced via the botanical garden (Greenway 1934), but survey methods to
construct these lists did not focus specifically on invasion risk from the ABG collections.
The quantitative assessment of the risks posed by ABG presented here include:

(1) Clearly differentiating among regenerating, naturalised and spreading species (*sensu*
    Richardson et al. 2000a; Pyšek et al. 2004);

Table 1 Invasive species that were probably initially introduced into new countries in the tropics via botanic gardens

Botanic garden	Species invading	Date introduced	Reference
Cinchona, Jamaica	*Pittosporum undulatum* Vent.	1883	Binggelli (1998)
			Bellingham et al. (2005)
Bogor, Indonesia	*Piper aduncum* L.	1860	Hartemink (2001)
	Limnocharis flava Buchenau	Late 1800	ISSG (2007)
Pamplemousses, Mauritius	*Psidium cattleianum* Sabine	By 1810	Vaughan and Wiehe (1937)
	Syzygium jambos (L.) Alston	By 1810	Lorence and Sussman (1986)
Peradeniya, Sri Lanka	*Clidemia hirta* D.Don.	1894	Wijesundra (1999)
			Marambe (2001)
	Eichhornea crassipes Solms.	1905	–
	Lantana camara L.	1926	–
	Miconia calvescens DC.	1888	–
	Prosopis juliflora DC.	1880	–
	Tithonia diversifolia A.Gray	1851	–
	Ulex europaeus L.	1888	–
	Limnocharis flava Buchenau	Late 1800	ISSG (2007)
Singapore	*Dioscorea sansibarensis* Pax		Whitmore (1991)
	Thunbergia grandiflora Roxb.		–
Darwin, Australia	*Mimosa pigra* L.		Miller and Lonsdale (1987)
Wahiawa, Hawaii	*Clidemia hirta* D.Don.	By 1941	Binggeli (1998)
Harrison Smith (Papeari), Tahiti	*Miconia calvescens* DC.	1937	Meyer (1998)
Amani, Tanzania	*Clidemia hirta* D.Don.	By 1930	Newmark (2002)
	Lantana camara L.	By 1930	Newmark (2002)
	Maesopsis eminii Engl.	1912	Greenway (1934)
Limbe, Cameroon	*Cecropia peltata* L.	1910	McKey (1988)
			Binggeli (1998)
Eala, Zaire	*Hevea* sp.	1900	Kembelo (1996)
	Psidium guajava L.		
	Cecropia sp.		
	Inga edulis Mart,		
Kisantu, Zaire	*Chromolaena odorata* (L.) R. M. King & H. Rob.	1900	Kembelo (1996)
Ibadan, Nigeria	*Asystasia* sp.		Jayeola (2006)
	Ruellia tuberosa L.		
Mayaguez. Puerto Rico	*Melaleuca quinquenervia* (Cav.) S.T.Blake	1930	
Caracas, Venezuela	*Persicaria capitata* (Buch.-Ham. ex D.Don) H.Gross	1968	Meier (2006)

The introduction date and pathway of *Clidemia hirta* into Hawaii is unknown, but it was grown in the botanic garden mentioned

(2) Distinguishing between opportunistic species unintentionally introduced into the botanical garden from species establishing from the collections (Hulme et al. in press);

(3) Assessing whether colonisation occurs exclusively in disturbed areas or also in neighbouring semi-natural ecosystems (Hulme 2003).

Consistent data collation procedures should assist in identifying whether the risks of invasion from botanical gardens are as low as the 0.1% found in other floristic inventories (Williamson 1996), help recognise taxonomic patterns in invasion risk (Daehler 1998; Pyšek 1998) and assess whether knowledge of invasion from other tropical ecosystems is a useful indicator of potential risk (Daehler et al. 2004).

Methods

Study site

The ABG (5°05′30″ S, 38°38′10″ E) is situated in the lowland and submontane rainforests of the East Usambara Mountains in northeast Tanzania. The ABG was formally established under the German administration in 1902, although a small medicinal garden was present in the late nineteenth century (Greenway 1934; Iversen 1991). After the First World War, the British managed the gardens for agricultural research until the early 1950s, when the research station closed and the herbarium was moved to Nairobi (Iversen 1991). Over 500 species (mostly woody) were planted at ABG over a 30-year period from 1902 to 1930 in a series of trial plantations (Greenway 1934). The majority of species were introduced for potential commercial gain, with economic development of the area being the central goal (Iversen 1991; Cronk and Fuller 1995). The botanical gardens are spread over some 300 ha, and originally consisted of 20 plantation blocks, divided into 141 compartments; these compartments vary in shape and size, from 0.1 to 7 ha, and originally contained almost 2,000 species plots of varying size (Greenway 1934; Sandy et al. 1997). Greenway (1934) and Honess (1963) conducted detailed surveys of the plantations, and recorded plot location and species survival, and in many cases the planting date as well as the numbers of individuals planted. Today, approximately one third of species and plots remain.

Survey protocol

In the 1960s a total of 1,005 plots (amounting to 1,032 species plots, as a number of plots contained more than one species) containing the original species recorded by Greenway (1934) were still in existence (Honess 1963). These surviving plots were resurveyed during 2005. There were 12 compartments (containing a total of 41 plots in 1934) that were omitted from the survey that had either been destroyed, were inaccessible, or originally comprised unplanted areas containing remnant native forest trees. The 2005 resurvey accounted for just over half of those plots originally surveyed by Greenway (1934). Extant plots were found throughout the ABG including both lowland (below 700 m altitude) and submontane forest areas (above 700 m) and while 45% of the original plots from 1934 were no longer present, there was no systematic bias in the loss of plots either in relation to elevation, species or plot size (Table 2). Efforts were taken to make survey methods as systematic as possible, and plots were examined either in their entirety for smaller areas, or by walking a diagonal transect across larger plots. The survival of originally planted individuals, evidence of regeneration and the presence of other unplanted alien species were recorded. Observations of alien plant presence were made in the majority of forest areas adjoining the botanical garden, especially forest edges. In addition, where access to other forest areas was possible, further records were made. For taxa with no clear record of planting effort or location, presence or absence was also recorded in each plot. Alien species status was classified following ecologically sound definitions of naturalisation and invasion (Richardson et al. 2000b; Pyšek et al. 2004) where to be naturalised, a species must have a self-perpetuating population that is persistent independently of human intervention and further introductions, whilst evidence of significant spatial spread is indicative of invasion. Three invasion status categories were identified:

(1) Regenerating: presence of seedlings, saplings, or vegetative propagation, but not necessarily naturalized;

Table 2 Summary of the ABG plantation blocks, including block names and altitude (m), areas of plantation blocks and compartments (ha), and the numbers of original species plots and numbers surveyed per plantation block and compartment

| Plantation (altitude, m)	Plantation area (ha)	Number of compartments (number surveyed)	Compartment area (ha)	Plots per plantation	Percentage of original 1934 plots re-surveyed per plantation (%)	Number of existing (2005) plots per compartment	Percentage of original 1934 plots re surveyed per compartment (%)
Amani (850–920)	2.6	4 (4)	0.3–1	75	23 (31)	2–52	1–16 (25–100)
Amani Chini (830–900)	7	5 (5)	1–2	121	55 (45)	6–59	1–32 (17–54)
Bomole (1000–1150)	14	4 (4)	3–5	74	67 (91)	10–28	10–24 (90–100)
Boma Hill (900–930)	2	8 (8)	0.2–0.5	195	72 (37)	6–41	3–15 (12–100)
Coconut Slope (500–650)	21	4 (4)	3–7	88	62 (70)	4–45	(64–100)
Dodwe (900)	1.2	2 (2)	0.2–1	17	4 (24)	6, 11	1, 3 (16, 27)
Drachensberg East (850–900)	10.7	7 (7)	0.3–3	82	43 (52)	3–25	1–12 (13–80)
Drachensberg North (820–900)	7.3	11 (10)	0.2–2	279	100 (36)	1–94	1–30 (4–100)
Drachensberg West (850)	4.5	7 (7)	0.2–1	88	46 (52)	1–58	1–24 (41–100)
Forest House (900–950)	0.7	2 (2)	0.3–0.4	25	10 (40)	10, 15	4, 6 (40)
Ilsestein (550–650)	6.6	7 (7)	0.2–2	16	15 (94)	1–5	1–4 (80–100)
Kiumba Chini (650–750)	9.2	4 (4)	0.2–6	52	40 (77)	1–29	1–24 (57–100)
Kiumba Juu (700–850)	15.2	12 (9)	0.1–3	168	102 (61)	1–37	1–25 (28–100)
Laboratory (900–930)	2.6	17 (9)	0.1–0.5	153	52 (34)	1–35	0–14 (20–100)
Monga Road (900)	1.3	5 (5)	0.2–0.5	101	71 (70)	4–79	1–58 (16–100)
Maiskopf Kiumba (850–900)	8.4	7 (7)	0.1–2	16	15 (94)	1–4	1–4 (50–100)
Maiskopf Lion Hill (900–930)	2	2 (2)	1	32	10 (31)	5, 27	2, 8 (29, 40)
Maiskopf Main Road (900)	1	1 (1)	1	6	3 (50)	6	3 (50)
Sigi Chini (400–475)	23.3	17 (17)	0.1–4	199	136 (68)	2–28	4–21 (40–100)
Sigi Juu (410–500)	10.9	15 (15)	0.2–2	204	106 (52)	1–37	1–15 (19–100)

Areas were obtained from Sandy et al. (1997)
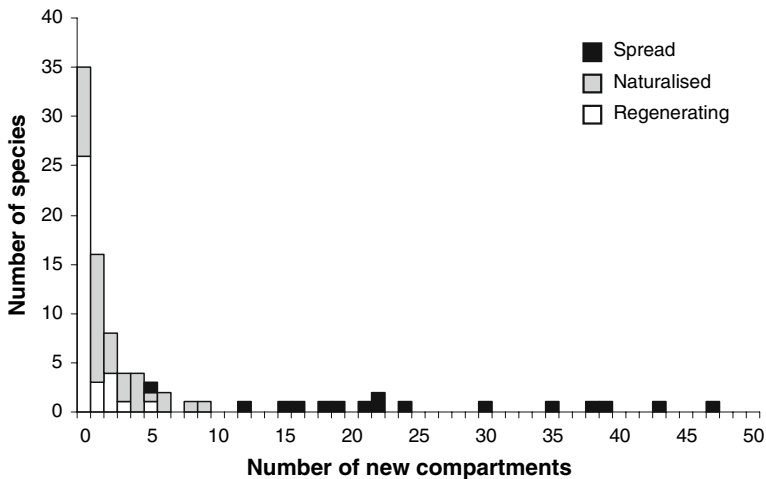
Fig. 1 Frequency distribution of alien plant species found in additional compartments other than those originally planted. Species found in zero new compartments were regenerating or naturalising in original compartments only. The spreading species found in five compartments was *Chimonobambusa quadrangularis* (spreading vegetatively)

(2) Naturalised: regenerating species that have recruited new adults, but have spread to less than 10 compartments where previously unplanted. For specific life-forms this was defined as:

Palmoid species—presence of new adults, stemmed individuals;
Bamboos—presence of at least second generation individuals (for monocarpic species);
Lianas—new stems >5 cm diameter at breast height (dbh), or on trees other than originals;
Shrubs/small trees—new stems > 5 cm dbh;
Trees—new stems >10 cm dbh;

(3) Spreading: a naturalised species that has spread to 10 or more new compartments. The threshold demarcating spreading species reflects a clear separation from the bulk of regenerating and naturalising species (Fig. 1).

The exceptions to this classification were species spreading vegetatively, for example the bamboos *Phyllostachys* spp. and *Chimonobambusa quadrangularis*. These species were either considered to be regenerating (1), naturalised (2), or spreading (3), with spread defined as escaping to more than one new compartment. In all cases, if adults were found outside the originally planted plots, the species was automatically considered naturalised. Existing herbaceous perennials were automatically considered naturalised, as original plants of herbaceous species were assumed to have perished after at least 75 years. All species were checked for records of naturalisation and invasion elsewhere in the tropics, using a range of sources: Cronk and Fuller (1995), Binggeli (1998), Haysom and Murphy (2003), CABI Forestry Compendium (CAB International 2005); the Global Compendium of Weeds online version (Randall 2007) and the Pacific Islands Ecosystems at Risk (PIER) project species list version 5.1 (PIER 2006). Species nomenclature follows the International Plant Names Index, accessed via the Electronic Plant Information Centre (Royal Botanic Gardens, Kew 2002), and the Germplasm Resources Information Network (GRIN) taxonomy for plants (USDA, ARS, National Genetic Resources Program).

Results

Regenerating, naturalising and spreading species

Of the 554 named alien plant species that were originally planted in the early 20th century, 214 species were still extant in 2005. Examination of the data in Honess (1963) revealed that by 1963, the families Asparagaceae, Dipterocarpaceae, Malvaceae, Fabaceae (subfamily Mimosoidae), Poaceae, Rosaceae, Rutaceae, Sapindaceae and Solanaceae were under-represented among the extant taxa, whereas the Araceae, Araucariaceae, Arecaceae, Cupressaceae, Clusiaceae and Myrtaceae were over-represented ($\chi^2 = 74.41$, df = 31, $P < 0.001$, across 32 families). By 2005, the Araucariaceae, Cupressaceae, Clusiaceae, Lauraceae, and Myrtaceae were still over-represented among surviving species ($\chi^2 = 57.33$, df = 31, $P = 0.003$, across 32 families). Survival of species between 1963 and 2005 did not vary significantly among the extant families ($\chi^2 = 25.47$, df = 19, $P = 0.15$, 20 families).

In 2005, out of the 214 surviving alien plant species with detailed records, 35 (16%) were regenerating but not naturalised, 38 (18%) had naturalised and a further 16 (7%) had spread to more than 10 compartments (Tables 3–5). Overall, 16% (89) of the original 554 species planted were at least regenerating, 10% (54) were at least naturalising and 3% (16) were spreading. A further 16 species with unclear introduction records were also observed as at least naturalised (Table 6). Only four species, *Caesalpinia decapetala*, *Clidemia hirta*, *Olyra latifolia* and *Stachyphrynium repens* (Table 6), were not mentioned in Greenway (1934) or Honess (1963). However, only *Clidemia hirta* was likely to be an unintentional introduction as the native distribution of *Olyra latifolia* is unclear (PIER 2006), and *Caesalpinia decapetala* and *Stachyphrynium repens* have probably escaped from nearby gardens (Table 6).

Families well represented by species that were able to regenerate included the Arecaceae, Clusiaceae, Myrtaceae and Fabaceae (subfamily Papilionoidae) (Table 3). Naturalised species failing to spread to 10 or more compartments were well represented within the Araceae and Euphorbiaceae (Table 4). Three species in the Myrtaceae and two species in each of the Arecaceae, Meliaceae and Rhamnaceae were found to have spread to 10 or more compartments (Table 5). The proportions of species that were at least naturalised varied significantly across 13 families with more than five surviving species in 2005 ($\chi^2 = 22.36$, df = 12, $P = 0.03$). Only in the Araceae and Euphorbiaceae were more than half of the species naturalised (4 out of 6 and 4 out of 7 species, respectively). The proportion of species that were naturalising also varied significantly but weakly across 33 families with more than five species originally introduced ($\chi^2 = 47.65$, df = 32, $P = 0.05$). Across all 99 families represented in ABG, there was a significant positive correlation at the family level between the number of species originally planted and the number subsequently naturalised (rho = 0.46, $P < 0.001$). There was also a significant positive correlation between number of surviving species in 2005 and the number of species at least naturalised (rho = 0.47, $P < 0.001$, for 61 families with at least one species surviving).

Colonisation patterns

Of the 56 species at least regenerating in compartments other than where originally planted, 72% were present in fewer than 10 new compartments (Fig. 1). The majority of regenerating species that were not known to have naturalised had propagated only in the compartment in which they had been originally planted (71%), with relatively few species found elsewhere and none found in more than five compartments (Fig. 1). Naturalising species were more widespread with 76% found in at least one other compartment, and a total of 16

Table 3 Regenerating species with known planting history in ABG

Species	Family	Habitat found	Naturalised or invasive elsewhere
Agave angustifolia Haw.	Asparagaceae	P	
Yucca filamentosa L.	Asparagaceae	P	
Chonemorpha macrophylla G.Don.	Apocynaceae	P	
Araucaria cunninghamii Sweet	Araucariaceae	P	6
Phytelephas macrocarpa Ruiz. & Pav.	Arecaceae	A; P	
Ptychosperma macarthurii (H.Wendl. ex H.J.Veitch) H.Wendl. ex Hook.f.	Arecaceae	A; P	3,5,6
Licuala peltata Roxb. ex Buch.-Ham.	Arecaceae	P	
Livistona chinensis (Jacq.) R.Br. ex Mart.	Arecaceae	A; P	5,6
Livistona rotundifolia (Lam.) Mart.	Arecaceae	A; P	6
Aristolochia brasiliensis Mart. & Zucc.	Aristolochiaceae	P	
Buddleja madagascariensis Lam.	Buddlejaceae	P	5,6
Ceiba pentandra (L.) Gaertn.	Bombacaceae	P	2,3,5,6
Peltophorum dasyrachis Kurz ex Baker	Fabaceae (Caesalpinioidae)	A; P	
Calophyllum inophyllum L.	Clusiaceae	P	3,6
Garcinia ferrea Pierre	Clusiaceae	P	
Mammea americana L.	Clusiaceae	P	
Pentadesma butyracea Sabine	Clusiaceae	P	6
Aleurites moluccana (L.) Willd.	Euphorbiaceae	P	2,3,5,6
Croton megalocarpus Hutch. (Native to W Usambaras)	Euphorbiaceae	P	4
Hydnocarpus wightiana Blume	Flacourtiaceae	P	
Michelia champaca L.	Magnoliaceae	A; P; F	
Tetrapleura tetraptera Taub.	Fabaceae (Mimosoidae)	P	
Derris elliptica Benth.	Fabaceae (Papilionoidae)	P	2,5,6
Andira inermis (W.Wright) DC.	Fabaceae (Papilionoidae)	P	
Myroxylon peruiferum L.f.	Fabaceae (Papilionoidae)	P	
Artocarpus altilis (Parkinson) Fosberg.	Moraceae	P	2,3,6
Eugenia uniflora L.	Myrtaceae	A; P	2,5,6
Eugenia capuli Schltdl.	Myrtaceae	A; P	
Syzygium malaccense (L.) Merr. & L.M. Perry	Myrtaceae	A; P	2,3,5,6
Pimenta racemosa (Mill.) O. Berg.	Myrtaceae	P	5,6
Bougainvillea spectabilis Willd.	Nyctaginaceae	A; P	6
Averrhoa carambola L.	Oxalidaceae	P	6
Passiflora quadrangularis L.	Passifloraceae	P	5,6
Bambusa vulgaris Schrad. (vegetative)	Poaceae	P	2,3,4,5,6
Phyllostachys aurea Riviere & C.Riviere. (vegetative)	Poaceae	P	5,6

Location found is indicated—P = found in plantation compartments originally planted only, A = found in additional compartments, F = forest fragment/edge. Naturalisation/invasion elsewhere is indicated, according to 1 = Cronk and Fuller (1995); 2 = Binggeli (1998); 3 = Haysom and Murphy (2003); 4 = CAB International (2005); 5 = PIER species list (PIER 2006); and 6 = Global Compendium of Weeds (Randall, 2007)

species had spread to more than 10 new compartments (except *Chimonobambusa quadrangularis*, which was found in five new compartments but had spread vegetatively, thus it was considered 'spreading'). There was also a significant correlation between compartment area and the number of alien species found that were not planted (rho = 0.46, $P < 0.001$, across 125 compartments with area data available), suggesting that survey efforts were systematic and in proportion with compartment size.

Table 4 Naturalising species with known planting history in ABG

Species	Family	Habitat found	Invasive elsewhere
Thunbergia grandiflora Roxb.	Acanthaceae	A; P; F	1,2,5,6
Acer oblongum Wall. ex DC.	Aceraceae	P	
Ilex paraguariensis St. Hil.	Aquifoliaceae	P	2,5,6
Epipremnum aureum (Linden & Andre) G.S. Bunting	Araceae	A; P; F	5,6
Philodendron sagittifolium Liebm.	Araceae	A; P; F	
Monstera deliciosa Liebm.	Araceae	F	6
Xanthosoma sagittifolium (L.) Schott.	Araceae	P	6
Aiphanes horrida (Jacq.) Burnett	Arecaceae	A; P	6
Areca catechu L.	Arecaceae	A; P	6
Tithonia diversifolia A. Gray	Asteraceae	A; P	5,6
Pyrostegia venusta Miers	Bignoniaceae	A; P; F	5,6
Spathodea campanulata P. Beauv.	Bignoniaceae	A; P; F	2,3,4,5,6
Schizolobium parahyba (Vell.) S.F. Blake	Fabaceae (Caesalpinioidae)	A; P	3,6
Senna multijuga (Rich.) H.S. Irwin & Barneby	Fabaceae (Caesalpinioidae)	A; P	4,5,6
Carludovica palmata Ruiz. & Pav.	Cyclanthaceae	A; P; F	5,6
Cyclanthus bipartitus Poit. ex A.Rich	Cyclanthaceae	A; P; F	
Vernicia fordii (Hemsl.) Airy Shaw	Euphorbiaceae	A; P	2,3,6
Hura crepitans L.	Euphorbiaceae	A; P	5,6
Hevea brasiliensis Müll. Arg.	Euphorbiaceae	A; P	3,6
Manihot glaziovii Müll. Arg.	Euphorbiaceae	A; P	2,5,6
Cinnamomum camphora (L.) J.Presl	Lauraceae	A; P	1,3,5,6
Cinnamomum verum J. Presl	Lauraceae	A; P	1,2,4,5,6
Albizia chinensis (Osbeck.) Merr.	Fabaceae (Mimosoidae)	A; P	2,5,6
Mimosa pudica L.	Fabaceae (Mimosoidae)	Roadsides	5,6
Artocarpus heterophyllus Lam.	Moraceae	A; P; F	3,6
Eugenia sp.	Myrtaceae	A; P	
Piper nigrum L.	Piperaceae	A; P	6
Phyllostachys nigra (Lodd. Ex Lindl.) Munro (vegetative spread)	Poaceae	A; P	5,6
Schizostachyum dullooa (Gamble) R.B. Majumdar	Poaceae	A; P	
Bambusa bambos (L.) Voss	Poaceae	P	2,6
Rubus ellipticus Sm.	Rosaceae	A; P	2,5,6
Cinchona pubescens Vahl	Rubiaceae	P	1,2,3,4,5,6
Coffea canephora Pierre ex A. Froehn.	Rubiaceae	A; P; F	
Brugmansia suaveolens (Willd.) Bercht. & C. Presl	Solanaceae	A; P; F	5,6
Cola nitida A. Chev.	Sterculiaceae	P	
Camellia sinensis Kuntze	Theaceae	A; P; F	6
Duranta erecta L.	Verbenaceae	A; P	5,6
Hemerocallis sp.	Xanthorrhoeaceae	A; P	

Habitat found is indicated—P = found in plantation compartments originally planted only, A = found in additional compartments , F = forest edge/fragment. Naturalisation/invasion elsewhere is indicated, according to 1 = Cronk and Fuller (1995); 2 = Binggeli (1998); 3 = Haysom and Murphy (2003); 4 = CAB International (2005); 5 = PIER species list (PIER 2006); and 6 = Global Compendium of Weeds (Randall, 2007)

Only 32 species were found outside of the plantations in forest fragments and edges. The majority of regenerating species that were not known to have naturalised had propagated only in plantation/botanical garden areas (97%), with only a single sapling of *Michelia champaca* found in a forest area (Table 3). One third of species that had only naturalised were observed in a forest fragment or edge (Table 4). The more widely spread within the plantation area, the greater the likelihood the species would be found in neighbouring

Table 5 Spreading species with known planting history in ABG

Species	Family	Found in forest	Naturalised or Invasive elsewhere
Landolphia owariensis P.Beauv.	Apocynaceae	Yes	
Elaeis guineensis Jacq.	Arecaceae	Yes	3,5,6
Arenga pinnata (Wurmb) Merr.	Arecaceae	Yes	6
Macfadyena unguis-cati (L.) A.H.Gentry	Bignoniaceae	Yes	5,6
Cordia alliodora (Ruiz. & Pav.) Cham.	Boraginaceae	Yes	3,4,5,6
Cedrela odorata L.	Meliaceae	Yes	1,2,3,5,6
Toona ciliata M.Roem.	Meliaceae	Yes	2,3,5,6
Castilla elastica Cerv.	Moraceae	Yes	2,3,5,6
Psidium cattleianum Sabine (spread vegetatively and by seed)	Myrtaceae	Yes	1,2,4,5,6
Psidium guajava L.	Myrtaceae	Yes	1,2,3,4,5,6
Syzygium jambos (L.) Alston	Myrtaceae	Yes	1,2,4,5,6
Piper aduncum L.	Piperaceae	Yes	5,6
Chimonobambusa quadrangularis Makino (vegetative spread)	Poaceae	No	4
Maesopsis eminii Engl.	Rhamnaceae	Yes	1,2,3,6
Hovenia dulcis Thunb.	Rhamnaceae	No	2,6
Rubus rosaefolius Sm.	Rosaceae	Yes	2,5,6

Presence/absence in forest areas is indicated. Naturalisation/invasion elsewhere is indicated, according to 1 = Cronk and Fuller (1995); 2 = Binggeli (1998); 3 = Haysom and Murphy (2003); 4 = CAB International (2005); 5 = PIER species list (PIER 2006); and 6 = Global Compendium of Weeds (Randall 2007)

forest, with all but two of the spreading species occurring in forest (Table 5). Overall, around half of species that were at least naturalised were found in forest areas (Tables 4 and 5). Two species were only found naturalising outside of compartments—*Mimosa pudica* was a common weed on paths and roadsides (Table 4), and the vine *Monstera deliciosa*, was observed growing up trees in a forest fragment (Table 4). A third of species with unclear introduction records were observed both in plantation and forest areas (Table 6).

Invasion elsewhere

The proportion of species recorded as at least naturalised elsewhere was significantly related to invasion status in ABG ($\chi^2 = 19.64$, df = 3, $P < 0.001$). There was a clear association with species status in ABG and records of naturalisation and/or invasion elsewhere in the tropics. Thus, while 49% (61 out of 125) of species only surviving were recorded as naturalised or invasive elsewhere, 57% of regenerating species, 79% of naturalised species and 94% of spreading species were recorded as naturalised or invasive elsewhere (Tables 3–5; surviving only species not shown). Overall, 83% of species at least naturalising in ABG were recorded as naturalised elsewhere (Tables 4 and 5). Two-thirds of species with unclear introduction records that had at least naturalised in ABG were also recorded as naturalising elsewhere (Table 6). Only one species, the Congo Rubber Vine *Landolphia owariensis*, was found to be spreading in ABG but not listed as invasive elsewhere (Table 5).

Discussion

Out of the original 554 species that were introduced intentionally into ABG at the beginning of the 20th century, 39% have survived, 41% of survivors are capable of regeneration,

Table 6 Naturalised alien plant species at Amani that have unclear planting history (planting locations and effort are unknown)

Species	Family	Planting Record	Habitat found	Naturalised/ invasive elsewhere
Montanoa hibiscifolia K.Koch	Asteraceae	Yes	P	5,6
Tecoma capensis Lindl.	Bignoniaceae	Yes	P	6
Caesalpinia decapetala (Roth) Alston	Fabaceae (Caesalpinioidae)	No	P	1,2,4,5,6
Senna occidentalis (L.) Link	Fabaceae (Caesalpinioidae)	Yes	P	5,6
Homalanthus populifolius Graham	Euphorbiaceae	Yes	P; F	5,6
Stachyphrynium repens (Körn) Sulsathan & Borchs.	Marantaceae	No	P	
Clidemia hirta L. D. Don.	Melastomataceae	No	P; F	1,2,5,6
Broussonetia papyrifera Vent.	Moraceae	Yes	P	1,2,3,4,6
Piper betle L.	Piperaceae	Yes	P	6
Olyra latifolia L. (native distribution unclear)	Poaceae	No	P; F	(5,6)
Rubus niveus Thunb.	Rosaceae	Yes	P	2,5,6
Selaginella biformis A.Br. ex Kuhn	Selaginellaceae	Yes	P; F	
Boehmeria nivea (L.) Gaudich.	Urticaceae	Yes	P	6
Clerodendrum chinense (Osb.) Mabb.	Verbenaceae	Yes	P	5,6
Lantana camara L.	Verbenaceae	Yes	P; F	1,2,5,6
Stachytarpheta cayennensis (Rich.) Vahl	Verbenaceae	Yes	P	5,6

All species were recorded in Greenway (1934) or Honess (1963) except *Caesalpinia decapetala*, *Clidemia hirta*, *Olyra latifolia* and *Stachyphrynium repens*. Habitat found is indicated—P = plantation/botanic garden areas, F = forest fragments/edges. Naturalisation/invasion elsewhere is indicated, according to 1 = Cronk and Fuller (1995); 2 = Binggeli (1998); 3 = Haysom and Murphy (2003); 4 = CAB International (2005); 5 = PIER species list (PIER, 2006); and 6 = Global Compendium of Weeds (Randall, 2007)

61% of those regenerating have naturalised, and 30% of naturalised species have spread considerably. These percentages of successful species at each stage of the invasion process clearly violate the 'tens rule', which states that only 10% of species would progress to the subsequent stage of the invasion pathway (Williamson and Fitter 1996). Even though only 16 species originally introduced have spread, the tens rule would predict just one species. The tens rule does not clearly hold for alien plant species introduced into ABG. However, Williamson and Fitter (1996) note a number of exceptions to the rule, and several reasons may explain why ABG and botanical gardens and arboreta in general pose a higher invasion risk than other sources of invasive plant species.

First, the deliberate cultivation of alien species in botanical gardens increases the likelihood of plant survival, by reducing competition from native species and managing the impacts of natural enemies. Such practices, often combined with extensive planting and high propagule pressure, increase the likelihood of escape and establishment in uncultivated areas (Mack 2005). Conversely, the absence of cultivation practice for accidentally introduced species would result in success of only opportunistic and 'weedy' species, which can tolerate a wide range of environmental conditions (Mack 2005). Historical records suggest that ABG was largely well managed until the 1960s (Honess 1963), ensuring survival of many woody species to maturity. The lack of management since the 1960s may have enabled seedlings and saplings to reach maturity, naturalise in other compartments and to spread into neighbouring forest. In contrast, perhaps only one accidentally introduced species has naturalised and spread.

Second, species and cultivars chosen for horticultural use are often selected according to traits that correlate with invasiveness (Anderson et al. 2006). Plant breeders, horticulturalists and foresters often select species on the basis of early age to maturity, fast growth rate, high seed output, and a tolerance of various environmental conditions, which would all lead to rapid domestication (Bellingham et al. 2004; Richardson and Rejmánek 2004; Anderson et al. 2006). These same traits however have been linked to invasion success, at least in disturbed ecosystems (Rejmánek and Richardson 1996; Rejmánek 2000). Given the economic thrust behind the establishment of colonial botanical gardens in the tropics, the same selection strategies may have applied in the past, therefore increasing the subsequent establishment rate of introduced taxa.

Whilst no strong taxonomic patterns were apparent among naturalised and spreading species, the Araceae and the Euphorbiaceae were well represented by naturalising species, and the Arecaceae and Myrtaceae by species in all three invasion categories (Tables 3 and 5). Although frequently naturalising, the Euphorbiaceae were not well represented in the spreading category. This result partly corroborates previous global studies on taxonomic patterns of invasive species that describe both the Euphorbiaceae and Myrtaceae as 'invasive families' (Daehler 1998; Pyšek 1998). However, taxonomic trends can be misleading if the introduction effort varies across families (Daehler 1998; Pyšek 1998). This study found that the number of species surviving and naturalising in a particular family in the 2005 resurvey was a function of the number of species initially planted in the early 20th century. This may account for the over-representation by the Myrtaceae and Arecaceae (the two most speciose families in ABG) and to a lesser extent the Euphorbiaceae and Araceae. Out of 99 families planted at ABG the Myrtaceae was the most numerous (45 species), followed by the Arecaceae (43 species); the Euphorbiaceae was the sixth most numerous family (23 species) whilst the Araceae family was 13th (13 species). However, only 9% (4 out of 45) of species that were originally introduced from the Myrtaceae had naturalised. In contrast, three families had disproportionately high numbers of species naturalising; these were the Bignoniaceae with 43% (3 out of 7 species), Lauraceae with 40% (2 out of 5 species), and Araceae with 30% (4 out of 13 species). Inferring real taxonomic trends in naturalisation rates is difficult, given the relatively low number of species originally introduced for these families. Thus, while some families have disproportionately high numbers of species naturalising, over-representation of some families in absolute terms will also be a consequence of greater family introduction effort.

What does 'invasive' mean? The importance of definitions

For a species to be invasive, Richardson et al. (2000b) suggest somewhat arbitrarily a spread of 100 m distance in under 50 years between original plants and 2nd generation adults for (naturalised) seeded species, and more than 6 m spread over a 3-year-period for vegetative invaders. These measures of spread are probably on the low side for most invasive plants (Pyšek and Hulme 2005). Spread is used in this survey rather than invasion, as colonisation of overgrown plantations and abandoned areas by an introduced species may not constitute invasion (Richardson et al. 2000a). Furthermore, spread at ABG may only be local in compartments adjacent to those originally planted with the species. However, there does appear to be a valid distinction between the majority of species being found in fewer than 10 new compartments, and those that have spread to more than 10 compartments after 75–103 years (Fig. 1).

Many species that have spread in the ABG plantations were also observed at forest edges and in forest fragments (Table 5), suggesting that species spreading in ABG pose the

greatest invasion risk to forest areas. Indeed, some may already be invasive, and the survey efforts presented here would not have detected these potential invasion events in more distant areas of forest. In total, 5% of the 554 species originally introduced to ABG have naturalised in forest areas. All but one species found in forest areas were at least naturalised in plantations, indicating that all species that are able to naturalise could be considered to have an elevated risk of invasion, especially those that have already spread considerably within the compartments. Fine (2002) reviewed instances of alien plant invasion into tropical forests, and concluded that the low number of invasion events observed globally may be attributed to low levels of human disturbance, and a lack of life history traits required for success in forests among introduced alien species, such as shade tolerance. In this study, it is evident that when alien plants are introduced to a site directly juxtaposed to existing forest, spread into forest areas can be achieved by a number of species, at least in more disturbed sites such as forest edges. The pioneer tree *Maesopsis eminii* is the most well known invasive plant in the East Usambaras, and has infiltrated natural forest disturbances such as treefalls, through dispersal by hornbills (Binggeli and Hamilton 1993; Cordeiro et al. 2004). A number of species spreading at ABG are known to exhibit shade tolerance, such as *Syzygium jambos* (CAB International 2005) and *Psidium cattleianum* (Cronk and Fuller 1995). It remains to be seen if such species are capable of invading or have invaded areas of undisturbed, interior forest in the East Usambaras.

Invasion elsewhere: the usual suspects?

A large proportion of naturalising and spreading species found in ABG had records of naturalisation or invasion elsewhere. Several studies have pointed out that "invasion elsewhere" is an important predictor of invasion success (Scott and Panetta 1993; Reichard and Hamilton 1997; Rejmánek 2000; Daehler et al. 2004). Interestingly, 12 of the 23 species listed in Table 1 as naturalised/invasive in other tropical botanical gardens were introduced to ABG (Greenway 1934), of which nine have at least naturalised. Only *Clidemia hirta* was introduced unintentionally. The same economically valuable species planted at Amani would have been introduced to many other new regions during and since the colonial era (Cronk and Fuller 1995), and if these species were planted in great numbers (i.e. they had a high introduction effort), then likelihood of naturalisation and spread would be increased (Lockwood et al. 2005). The colonial networks of botanical gardens would have ensured exchange of plant material and information on optimal planting sites (Heywood 1987; Cronk and Fuller 1995), resulting in early climate matching that would increase the likelihood of establishment. Such exchange of plant material and soil is likely to have contributed to the unintentional introduction of *Clidemia hirta* to areas throughout the tropics. Alternatively, species introduced throughout the tropics may also possess certain traits that predispose them to successful naturalisation and invasion in the introduced range (Rejmánek and Richardson 1996). For example, species planted for their edible fruits may attract new mutualist frugivorous birds and animals in the introduced range that will aid in dispersal and establishment of an escaped population (Richardson et al. 2000a; Hulme 2006). Further, a number of species mentioned here have long been used and cultivated by local people, including *Cedrela odorata* and *Artocarpus heterophyllus* (Jackfruit); their spread in ABG may be partially explained by human factors, with villages, paths and roads located throughout the botanical garden plantations and surrounding forest.

  The result obtained for ABG reinforces the importance of using previous invasion history in botanical garden invasion risk assessments. However, there will be exceptions; one species was spreading at ABG that had not been recorded elsewhere. In contrast, nearly

half of those species only surviving (not regenerating) were also recorded as naturalised/ invasive elsewhere in the tropics. The use of the "invasion elsewhere" criterion is only valuable if the species has been introduced before, and preferably, widely. In circumstances where a species is introduced to a region for the first time or no records of past introductions are kept, then intuitively "invasion elsewhere" is not especially helpful. Further, the absence of a species from other lists may be due to a lack of adequate records where this species is actually a problem. Invasion success of any alien introduced species will be context dependent, to some extent, and relying too heavily on "invasion elsewhere" as a predictive tool could lead to large numbers of low risk species being misidentified as higher risk, whilst novel invasive species may go unnoticed, and become a problem.

Implications for other botanical gardens

There is a growing awareness among botanical gardens and horticultural bodies that the risk of alien plant escape and invasion from cultivation should be formally assessed (Baskin 2002; Mack 2005). Both the Missouri and Chicago Botanical Gardens have devised and implemented protocols to assess invasion risk from established collections (Baskin 2002; Jefferson et al. 2004) but this approach has yet to be applied in the tropics. The Chicago Botanical Garden model presents an integrated approach, incorporating the use of an adapted Weed Risk Assessment scheme, regional invasive plant lists, on-site plant evaluation of collections and information on commercial availability (Jefferson et al. 2004). The case study of ABG presented here highlights that botanical gardens should concentrate risk assessment efforts on plant species introduced intentionally, whilst also aiming to minimise the risk of unintentional introductions, by avoiding transport of plants in soil from elsewhere.

It is widely recognised that plant invasions are likely to occur but that alien plant introductions are on the whole socially, economically and scientifically beneficial (Dosman and Del Tredici 2003; Mack 2005; Anderson et al. 2006). However, it should be possible to meet human needs for introduction of new taxa, whilst simultaneously reducing the likelihood of invasion by the most pernicious alien plant species. Botanical gardens have a potentially unique role to play in preventing and mitigating plant invasions, and would benefit from adopting a methodologically rigorous protocol as presented here, to quantify the risk of invasion from their own collections into surrounding ecosystems that may be of significant conservation value. As such, assessing invasion risk should become an integral part of conservation goals for all botanical gardens, and not just those located in the tropics. The survey and methods used have highlighted some key issues to consider regarding patterns in species survival, naturalisation and spread, invasion terminology, and knowledge of invasion elsewhere.

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